**From:** Ben Livneh
**To:** Guinotte, John
**Cc:** Joseph Barsugli - NOAA Affiliate; Aaron Joseph Heldmyer; Andrea Ray - NOAA Federal; Steve Torbit
**Subject:** Re: Wolverine call at 2??
**Date:** Thursday, March 30, 2017 1:16:15 PM

---

Meetings all afternoon today. Perhaps you can fill me in later on.

Sent from my phone. Please forgive the brevity, the typos, and the lack of nuance

On Mar 30, 2017 1:10 PM, "Guinotte, John" <john_guinotte@fws.gov> wrote:

> Hi Andrea,
> I can do 2pm. I'm working on the romo dhsvm / Mckelvey comparison now. Might have those maps ready by 2.
> Best, John
>
> John Guinotte
> Fish and Wildlife Biologist
> Ecological Services
> U.S. Fish and Wildlife Service
> Mountain Prairie Region 6
> 134 Union Blvd., Lakewood, CO 80228
> 303-236-4264
> john_guinotte@fws.gov
>
> On Thu, Mar 30, 2017 at 1:07 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:
>
> > Hi All, we've got a lot of new wolverine work, and I know Ben is out on Friday. Can we catch up today at 2? I'll put an item on the calenda
> >
> > Steve can join us then, but not after 3. However, if you can't make it at 2 let me know and we'll talk just to john at 2.
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> > apologies for the last minute notice -- we discussed this yesterday, but I've got too many balls in the air!
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> > put anything you have to show on the drive -- we won't do a goto meeting. Maps John did yesterday are here: https://drive.google.com/drive/folders/0B6ksrl3lWQI4dW5sYzdfSmVkSzA
> >
> > Thanks, Andrea
> >
> > --
> > --
> > Andrea J. Ray, Ph.D.
> > NOAA Earth System Research Lab, Mailcode R/PSD1
> > 325 Broadway, Boulder, CO 80305-3328
> > (tel) 303-497-6434
> > (fax) 303-497-6449
> > andrea.ray@noaa.gov
> > www.researchgate.net/profile/Andrea_Ray2

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; joseph.barsugli@noaa.gov; aahe1976@colorado.edu; beli1098@colorado.edu; stephen_torbit@fws.gov
**Subject:** Wolverine Meeting via phone
**Attachments:** invite.ics

---

more details » <https://www.google.com/calendar/event?
action=VIEW&eid=dTI5M2plcXMycG1tbmJvdGtjNHUyOW1mOTAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjViMTFjMmQ3Y2Y1NGMzOWZhNDE0NGFhZjJkNGQxNDY3OGE0MjI1NWQ&ctz=America/Denver&hl=en>

Wolverine Meeting via phone

When
Thu Mar 30, 2017 2:15pm – 3:15pm Mountain Time
Where
phone: 1-866-874-0311 Passcode: 7440794# (map <https://maps.google.com/maps?q=phone:+1-866-874-0311+Passcode:+7440794%23&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• joseph.barsugli@noaa.gov
• aahe1976@colorado.edu
• john_guinotte@fws.gov
• beli1098@colorado.edu
• stephen_torbit@fws.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=dTI5M2plcXMycG1tbmJvdGtjNHUyOW1mOTAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjViMTFjMmQ3Y2Y1NGMzOWZhNDE0NGFhZjJkNGQxNDY3OGE0MjI1NWQ&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?
action=RESPOND&eid=dTI5M2plcXMycG1tbmJvdGtjNHUyOW1mOTAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjViMTFjMmQ3Y2Y1NGMzOWZhNDE0NGFhZjJkNGQxNDY3OGE0MjI1NWQ&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?
action=RESPOND&eid=dTI5M2plcXMycG1tbmJvdGtjNHUyOW1mOTAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjViMTFjMmQ3Y2Y1NGMzOWZhNDE0NGFhZjJkNGQxNDY3OGE0MjI1NWQ&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?
action=VIEW&eid=dTI5M2plcXMycG1tbmJvdGtjNHUyOW1mOTAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjViMTFjMmQ3Y2Y1NGMzOWZhNDE0NGFhZjJkNGQxNDY3OGE0MjI1NWQ&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

Attachment 20170330 131624_EM_Wolverine Meeting via phone.ics (1735 Bytes) cannot be converted to PDF format.

**From:** Andrea Ray - NOAA Federal
**To:** Stephen Torbit; Ben Livneh
**Cc:** John Guinotte; Joseph Barsugli; Aaron Joseph Heldmyer
**Subject:** Re: Wolverine call at 2??
**Date:** Thursday, March 30, 2017 1:58:21 PM

---

Ben can't be on, and I think Aaron has classes. Joe will be on at 2:15 so I moved it out, but I'll start up the conference call in 5 min, about 2:05, and we can get started with anything that doesnt need Joe

Ben has confirmed that he's available at the usual time at 3 on Monday. I'll be out at a drought meeting, but may be able to call in.

Andrea

On Thu, Mar 30, 2017 at 1:48 PM, Stephen Torbit <Stephen_Torbit@fws.gov> wrote:

> I can do a 2 pm.
>
> Stephen C. Torbit
>
> Assistant Regional Director
>
> Science Applications
>
> U.S. Fish and Wildlife Service
>
> 134 Union Blvd.
>
> Lakewood, Colorado 80228
>
> 303-236-4602 – Office
>
> 720-626-7504 – Cell
>
> **From:** Guinotte, John [mailto:john_guinotte@fws.gov]
> **Sent:** Thursday, March 30, 2017 1:10 PM
> **To:** Andrea Ray - NOAA Federal
> **Cc:** Steve Torbit; Ben Livneh; Joseph Barsugli; Aaron Joseph Heldmyer
> **Subject:** Re: Wolverine call at 2??
>
> Hi Andrea,
>
> I can do 2pm. I'm working on the romo dhsvm / Mckelvey comparison now. Might have those maps ready by 2.

Best, John

John Guinotte
Fish and Wildlife Biologist

Ecological Services
U.S. Fish and Wildlife Service
Mountain Prairie Region 6

134 Union Blvd., Lakewood, CO 80228

303-236-4264
john_guinotte@fws.gov

On Thu, Mar 30, 2017 at 1:07 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:

Hi All, we've got a lot of new wolverine work, and I know Ben is out on Friday. Can we catch up today at 2? I'll put an item on the calenda

Steve can join us then, but not after 3. However, if you can't make it at 2 let me know and we'll talk just to john at 2.

apologies for the last minute notice -- we discussed this yesterday, but I've got too many balls in the air!

put anything you have to show on the drive -- we won't do a goto meeting. Maps John did yesterday are here: https://drive.google.com/drive/folders/0B6ksrl3lWQI4dW5sYzdfSmVkSzA

Thanks, Andrea

--

--
Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1

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(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

**From:** Bush, Jodi
**To:** Shoemaker, Justin
**Cc:** Betty Grizzle
**Subject:** Re: 2014 wolverine expert meeting
**Date:** Friday, March 31, 2017 8:42:59 AM
**Attachments:** Attendee List_ Wolverine Panel Elicitation.docx
Final_Wolverine_Panel_Report-4-2014.pdf
Final Panelists and contact.xlsx

---

Here is the entire list of folks who attended that meeting -including the experts. Also attached panelist contact information and final report. Who needed this? JB

Jodi L. Bush
Office Supervisor
Montana State Ecological Services Office
585 Shepard Way, Suite 1
Helena, MT 59601
(406) 449-5225, ext.205

On Thu, Mar 30, 2017 at 12:00 PM, Shoemaker, Justin <justin_shoemaker@fws.gov> wrote:

> Jodi,
>
> Do you have a list of the 9 experts on the panel at the Spokane meeting?
>
> Justin Shoemaker
> Acting Branch Chief for Classification and Recovery
> U.S. Fish and Wildlife Service, Region 6
> Phone: 303-236-4217
> Email: justin_shoemaker@fws.gov

ATTACHMENT

Attendee List

**Expertise in wildlife biology/ecology**

1. Dr. Bob Garrott, Montana State Univ. Relevant expertise in mammalian ecology
2. Dr. Steve Buskirk, Univ of Wyoming. Relevant expertise in mammalian (carnivore) ecology.
3. Dr. Dan Pletscher, Prof. University of Montana, Ret. Relevant expertise in mammalian ecology
4. Dr. Eric Lofroth, British Columbia Ministry of Environment, Relevant expertise in wolverine biology.

**Expertise in habitat modeling, remote sensing, biostatistics.**

1. Dr. Oz Garton, Univ of Idaho. Relevant expertise population dynamics, experimental design and analysis
2. Dr. Jason Karl, USDA, New Mexico. Research Ecologist,

**Expertise in climate change as it relates to wildlife impacts, including knowledge on the current and projected trends in snowfall/cover/depth as well as the appropriate uses of climate change models.**

1. Dr. John Abatzoglou, Univ of Idaho. Relevant expertise in climate modeling.
2. Dr. Tim Link, Univ of Idaho. Relevant expertise in snow hydrology, variability in snow measurements.
3. Dr. Sarah Kapnick, Princeton Univ. Relevant expertise in modeling snowpack in complex terrain.

**FACILITATORS/ORGANIZERS (3)**

Steven Morey. USFWS-R1.
Teresa Woods. Retired USFWS-R3
Mike Mitchell. UM, Montana Cooperative Wildlife Research Unit

**OBSERVERS (10)**

- Shawn Sartorius, FWS-Montana
- Hilary Cooley, FWS-Idaho
- Mary Grim, FWS-California
- Bridget Fahey, FWS-Denver
- Justin Shoemaker, FWS-Denver
- Leona Svancara, Idaho Fish and Game
- Jim Unsworth, Program Chief, Idaho Fish and Game
- Bob Lanka, Wyoming Game and Fish
- George Pauley, Idaho Fish and Game & MFWP
- Ken McDonald, Division Administrator-Wildlife, MFWP
- Jodi Bush, Project Leader, Montana
- Noreen Walsh, RD –Mountain Prairie
- Matt Hogan, Deputy RD-Mountain Prairie
- Rich Hannan, Deputy RD-Pacific Region
- Terry Rabot, ARD-Ecological Services, Pacific Region
- Mike Fris, ARD-Ecological Services, California-Nevada

**DECISION MAKERS (6)**

# WOLVERINE SCIENCE PANEL WORKSHOP

Spokane, Washington
3-4 April 2014

Facilitators

Teresa Woods
Steve Morey
Michael Mitchell

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## INTRODUCTION

The wolverine (*Gulo gulo*) is the largest extant terrestrial member of the Mustelidae family. It has a circumboreal distribution, and the subspecies *G. g. luscus* extends into the mountainous regions of the western United States. In 2013, the US Fish and Wildlife Service (FWS) proposed to list the wolverines that occur in the contiguous United States as threatened under the Endangered Species Act[1], in part because of projected reduction in important snow habitat from climate change. Comments on the proposal raised questions about the uncertainties associated with forecasting the specific on-the-ground physical effects of climate change and with the uncertainties these effects may have on the species' persistence. In April 2014, the FWS and partners from wildlife agencies in the states of Idaho, Montana, and Wyoming convened a panel of experts in climate change, wolverines and other mammalian carnivores, habitat modelers, and population ecologists to discuss climate-related habitat issues and possible future population trends for wolverines.

The objective, strategy, and outcomes for the agenda, in the text box below, were developed by a planning committee of State and FWS representatives (Appendix 1). The agenda was carefully crafted to avoid seeking consensus among, or recommendations from, panelists, and therefore avoiding any compliance issues with the Federal Advisory Committee Act[2]. The planning team invited the panelists, and their methods and criteria for selecting panelists are outside the scope of this report.

OBJECTIVE

Better understand the strength of the relationships between climate change, wolverine habitat, and future wolverine population trends through dialogue with an expert panel.

STRATEGY
Conduct the meeting in a setting that allows for uninhibited interactions among panelists and between panelists and FWS decision makers and State partners.

OUTCOME
Expected output from this meeting is a packet of information, which captures essential discussions and results from scoring exercises.

## METHODS

The authors of this report facilitated an expert panel through a structured agenda with exercises and discussions to investigate whether and how climate change might affect wolverines in the US (Appendix 2). Nine people participated in the panel (Appendix 3). Sixteen managers and decision makers from the FWS and State agencies (Appendix 3) participated in open question and answer periods following panel activities.

[1] "Endangered and Threatened Wildlife and Plants; Threatened Status for the Distinct Population Segment of the North American Wolverine Occurring in the Contiguous United States; Establishment of a Nonessential Experimental Population of the North American Wolverine in Colorado, Wyoming, and New Mexico; Proposed Rules," 78 Federal Register 23, February 2013, pp. 7864 – 7890.
[2] Federal Advisory Committee Act (Pub. L. 92–463)

We used Delphi techniques (Charlton 2004), modified for a live panel setting throughout the meeting. It included a first round of discussions followed by group scoring exercises. For preliminary discussions, we projected a matrix with predetermined column headings on a screen at the front of the room, and asked panelists to fill in the columns by offering suggestions out loud. Anonymity was not expected during this phase.

During follow-up scoring exercises, panelists spread 100 points among several choices to represent their uncertainty. Panelists were instructed that allocating 100 points to only one choice would indicate their complete confidence in their selection (e.g., no uncertainty). An even distribution among choices would indicate even chances of each alternative being correct (e.g., complete uncertainty). Uneven distribution of points among choices would weight more and less likely choices.

Panelists used paper score sheets to record their scores. Scores were anonymized and reported back to the group as box plots or line graphs. We then facilitated discussions about the variance in scores to help reduce semantic uncertainty and differences in knowledge about the topics. After the discussion we asked panelists to re-score their score sheets. Unlike more traditional Delphi processes, we did not seek consensus or conformity among panelists because we were more interested in eliciting reasons for the range of variance and uncertainty depicted by the scores. We report only final scores here.

In some exercises we used McKelvey et al. (2011) as a baseline for discussion of snow cover. We picked this document to frame our discussions for several reasons. First, it addresses climate change and wolverine habitat over the area that is the primary focus of this workshop. Second, it provided detailed projections of habitat into the future, unlike other literature on wolverine habitat that do not project into the future ((Copeland et al. (2010); Inman et al. (2012a); Inman et al. (2012 b); McKelvey et al. (2014)). Third, it was cited in the proposed rule and most of the wildlife panelists were familiar with the article. It should be noted, that we did not use McKelvey et al. (2011) because we believed it is right or wrong; it is simply a peer-reviewed, published article that provided a suitable framework for eliciting expert comment on the future of climate change and wolverine habitat.

The agenda was divided into four parts: defining wolverine climate-related habitat, evaluating future snow coverage, evaluating future habitat projections, and future wolverine population trends. The follow section describes the methods in more detail.

## Defining Wolverine Climate-Related Habitat

This session began with a presentation on wolverine natural history by Shawn Sartorius, Ph.D., FWS wildlife biologist (Appendix 4). Then the panelists discussed the ecological relationships between climate and wolverine habitat. We prompted a conversation by asking panelists to complete a matrix with predetermined column headings (Table 1) and took notes of the conversation live onscreen. The panelists had an opportunity to make edits as the conversation progressed. When the discussion among the panelists wore down, the managers and decision makers entered into a brief question and answer period with panelists.

**Table 1. Climate characteristics and ecological relationships important to wolverines.**

| Physical characteristic | Why is it important? (mechanisms/ ecological relationships) | Key references | Notes on confidence |
|---|---|---|---|

| | | | |
|---|---|---|---|
| | | | |
| | | | |

Following the discussion of ecological relationships between climate and habitat, the panelists began an exercise to investigate the strength of the relationship between climate factors and wolverines. This exercise produced quantitative estimates of panelists' beliefs about the strength of the relationship between climate-related habitat features (identified in the earlier discussion) and the landscape's ability to support wolverines. Panelists used a score sheet (Figure 1) to complete two rounds of scoring. The first scoring was used to frame the issue and elicit productive conversation for leveling the knowledge base about habitat relationships and to clear up semantic uncertainty. The second scoring served as a final estimate of the panelists' beliefs about the relationships.

---

On a scale of 1 to 4, spread 100 points among the boxes to express your beliefs about strength of the relationship between the specified climate feature and the landscape's ability to support wolverines.

Definitions for the scale:

1 = no preference or negative preference. Wolverines are or will be found outside of those conditions often and regardless of availability. Female wolverines will establish home ranges and successfully raise young outside of those conditions.

2 = tending toward no preference

3 = tending toward obligate

4 = obligate or essential relationship to areas with those conditions or a close correlate such that it is essentially the same relationship. Wolverines will seldom be found outside of those conditions even in landscapes where those conditions are rare. When they are found outside of those conditions, it will be due to exploratory or dispersal movements and not because they have established home ranges or reproduced.

1st Score

| Feature | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | | | | |

Rescore

| Feature | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | | | | |

**Figure 1. Strength of the relationship score sheet.**

## Evaluating Future Snow Coverage

This portion of the agenda was designed to elicit information about the degree and direction of snow cover as it relates to wolverine habitat. It began with a presentation on

relevant climate change literature by Leona Svancara, Ph.D., Idaho Fish and Game (Appendix 5). The presentation included a summary of the McKelvey et al. (2011) paper on wolverine snow habitat and climate change. At the close of the presentation, panelists participated in an exercise to assess how well they thought the projections in the McKelvey paper represented the future of snow cover (Figure 2). As with the earlier exercise, panelists engaged in discussion first among themselves and then with the other participants before rescoring.

Peering out over the timeline used by McKelvey, are the spring snow cover projections in McKelvey likely to be an underestimate, about the right amount, or an overestimate of snow cover?

Distribute 100 points among the 3 categories to reflect your belief about the spring snow cover projections.

2030 to 2059 (ensemble 2045)
1st Score

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

Rescore

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

2070 to 2099 (ensemble 2085)
1st Score

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

Rescore

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

**Figure 2. Score sheet for exercise to evaluate the snow cover projections in the McKelvey et al. (2011) paper.**

Evaluating Future Habitat Projections

This exercise is an extension of the snow exercise; however, it added other climate-related factors to the discussion relevant to wolverines and changed the perspective from a strictly climate viewpoint to a wolverine habitat perspective. Again, we used a matrix with predetermined columns to elicit ideas from panelists (Table 2). Panelists brainstormed the degree and direction of change of climate features that have been hypothesized to impact wolverines. We took notes on screen and shared the results with panelists before the next scoring exercise about future trends in wolverine habitat.

**Table 2. Degree and direction of change**

| Expected change | Possible Degree and direction of change (can be expressed as a range) | Hypothesized/potential effect on wolverines | Notes (e.g., uncertainty) |
|---|---|---|---|
| | | | |
| | | | |

Using the McKelvey et al. (2011) snow cover projections as a baseline one more time, the group assessed future habitat for wolverines. We asked panelist to complete an exercise with the same scoring options as the climate exercise above (Figure 3); however, this time we asked the panelists to assess how well the snow cover projections in McKelvey et al. (2011) represented wolverine habitat in the future. Panel discussion and a question and answer period with other participants followed a first round of scoring. The experts rescored their score sheets when the discussion concluded. Final results were printed and returned to panelists and other participants before proceeding with a discussion of wolverine population trends.

Peering out over the timeline used by McKelvey, are the spring snow cover projections in McKelvey likely to be an underestimate, about the right amount, or an overestimate of wolverine habitat?

Distribute 100 points among the 3 categories to reflect your belief about the wolverine habitat.

2030 to 2059 (ensemble 2045)
1st Score

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

Rescore

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

2070 to 2099 (ensemble 2085)
1st Score

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

Rescore

| Underestimate | About right | Overestimate |
|---|---|---|
| | | |
| | | |

**Figure 3. Score sheet for habitat change exercise**

### Future Wolverine Population Trends

This session synthesized information from the previous sessions to evaluate future wolverine population trends in the US, given anticipated effects of climate change. It began with a discussion about wolverine life history traits. We again used the matrix format for organizing the discussion about how the wolverine's life history might lead to vulnerability or resiliency to climate change. That discussion led to a conversation among panelists about how anticipated changes in snow might affect wolverines. A panelist suggested that panelists take turns describing their perspective on the future for wolverines. The panelists agreed, and after that round was completed, other participants were brought into the conversation for more discussion.

## RESULTS

In this section we briefly describe the results of the meeting. The discussions among panelists were in depth and complex. We present only a brief summary of the discussions and scoring results. All notes that were taken and edited onscreen, and the complete results of the scoring exercises are presented in Appendices, as indicated below.

### Defining Wolverine Climate-Related Habitat

The panel identified three primary climate related factors that are correlated with wolverines: persistent deep snow, contiguous snow, and temperature. Although, panelists were careful to point out that correlation is not proof of causation. Panelists believed it was helpful to think about deep snow habitat and the ecological relationships with wolverines at three scales, as indicated below. Actual depth was not specified; it was loosely described as meters deep around the den, but could be less deep than that for discussions of contiguous coverage.

Denning area scale → patches of deep snow may be important for refrigeration of food caches and thermal protection for kits; contiguous deep snow may be important as a barrier from other mammalian carnivores.

Home-range scale → contiguous deep snow may be important for refrigeration of food caches, and den safety from other mammalian predators

Species-range scale → deep snow may be important to mediate carnivore community interactions, including prey competition and snow barriers; and for dispersal success

The conversation about temperature focused more on the effect of warming temperatures on snow melt, rather than any direct effect on wolverines. Thermal energetic costs for kits and adults were mentioned as likely to be important; however little is known about temperature thresholds. Summer temperatures were mentioned as a consideration; however, recent dispersal of one male across lowland sagebrush steppe areas has been documented. Refer to Appendix 6 for a complete copy of the onscreen notes taken during this session.

The following section is organized by climate factor at the scales for which they were evaluated. Persistent deep snow was evaluated at all three scales. Contiguous snow and temperature were evaluated at the home-range and range-wide scales only.

Panelists allocated most of their points to an obligate relationship with deep snow at the denning scale, but this pattern was not seen at the larger spatial scales (Figure 4). Within each category at the two larger scales the panelists demonstrate a wide spread of points (see outliers near 100 and scores near 0), indicating that panelists disagreed about the importance of deep snow at scales other than denning. Refer to Appendix 7 for individual scores.

The median score increased progressively toward the more obligate categories for contiguous deep snow at the home-range and species-range scales (Figure 5). Again, there is a wide spread of points within each category, suggesting that panelists disagreed about the importance of the relationship between wolverines and contiguous snow. Refer to Appendix 7 for individual scores.

For temperature, there is a peak in panelist responses on the leaning toward obligate side of the graph (Figure 6). Here each panelist spread his or her points more evenly among categories, thus within category variation appears less than in the other climate factors, which might suggest that individual panelists are more uncertain about the relationship between temperature and wolverine habitat than they were with other climate factors. Refer to Appendix 7 for individual scores.

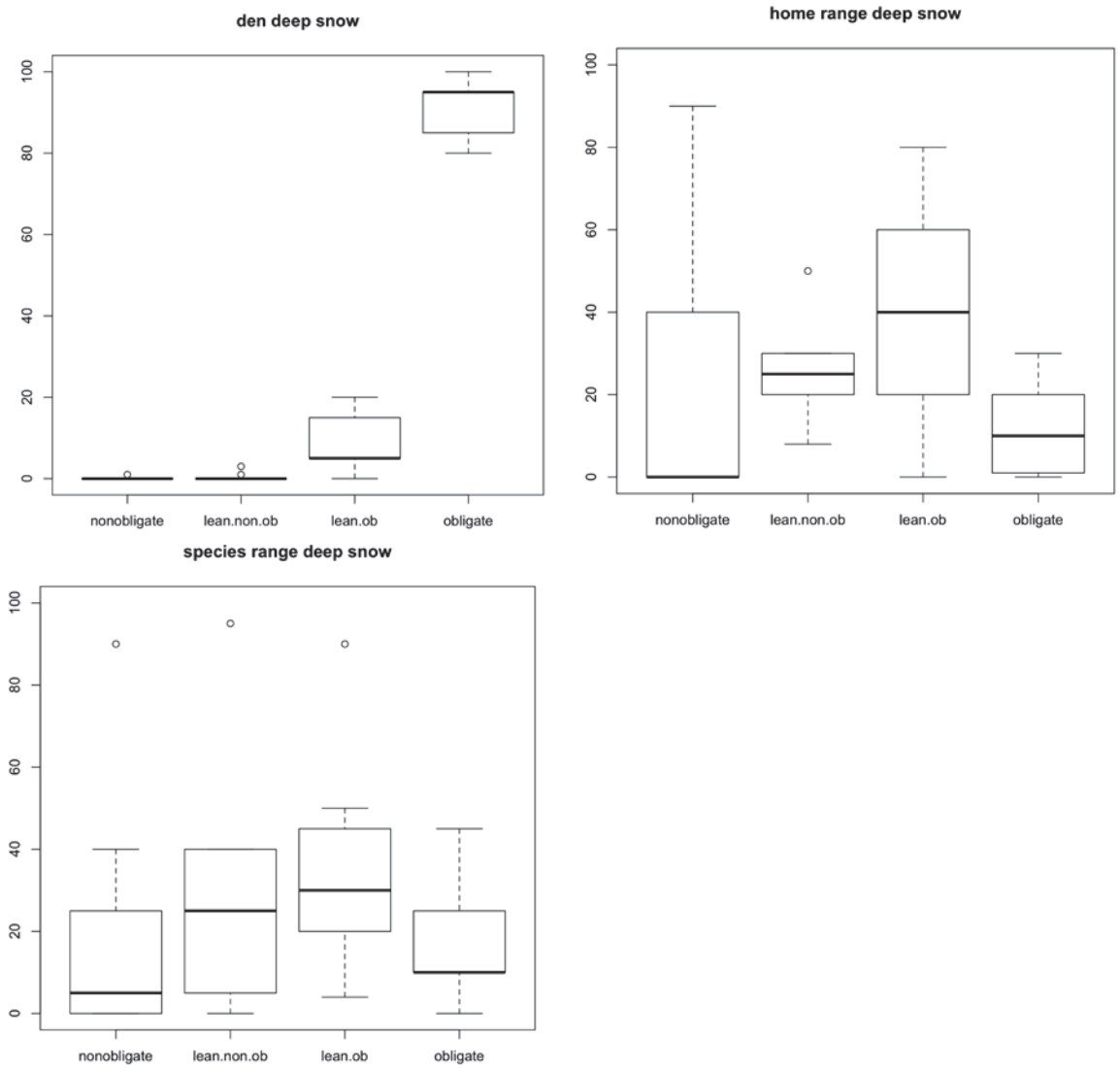


**Figure 4. Results from strength of the range exercise.**

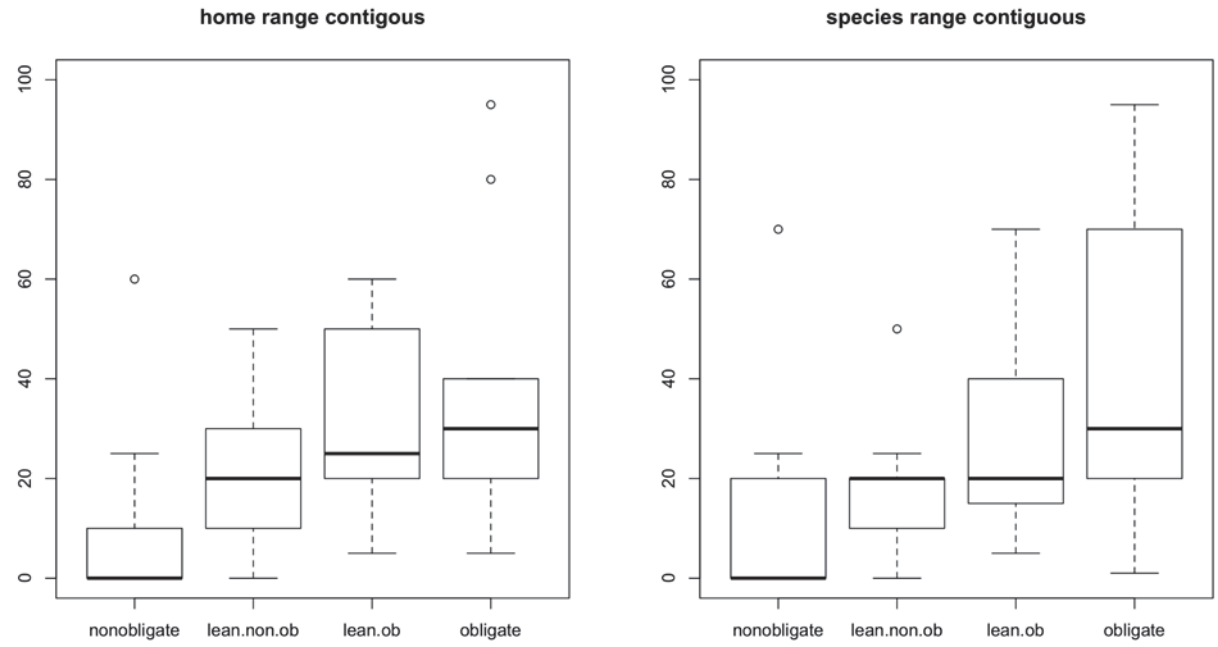


Figure 5. Strength of the relationship between contiguous snow and larger-scale wolverine habitat.

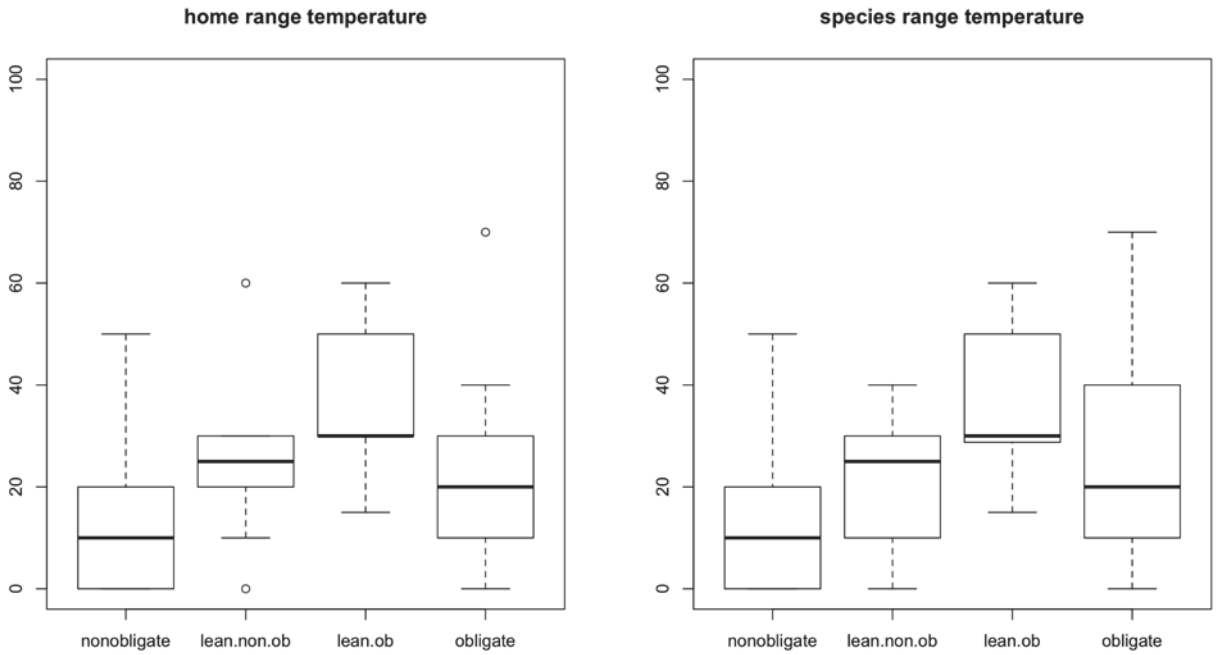


Figure 6. Results of the strength of the relationship exercise between temperature and wolverine habitat.

## Evaluating Future Snow Coverage

We asked panelists to register a score to indicate whether their current information would lead them to believe that the snow cover projections in McKelvey et al. (2011) might be about right or lean toward over- or under-estimates. Points allocated to the "underestimate" bin indicate where McKelvey et al. (2011) may have overestimated the severity of snow

loss. Points allocated to the "overestimate" bin indicate where McKelvey et al. (2011) may have underestimated the severity of snow loss. The results indicated a peak in panelists' belief that McKelvey et al. (2011) was "about right" in the short term. The peak was less pronounced in the long term as support shifted toward the overestimate category (Figure 7). Refer to Appendix 8 for complete scores.

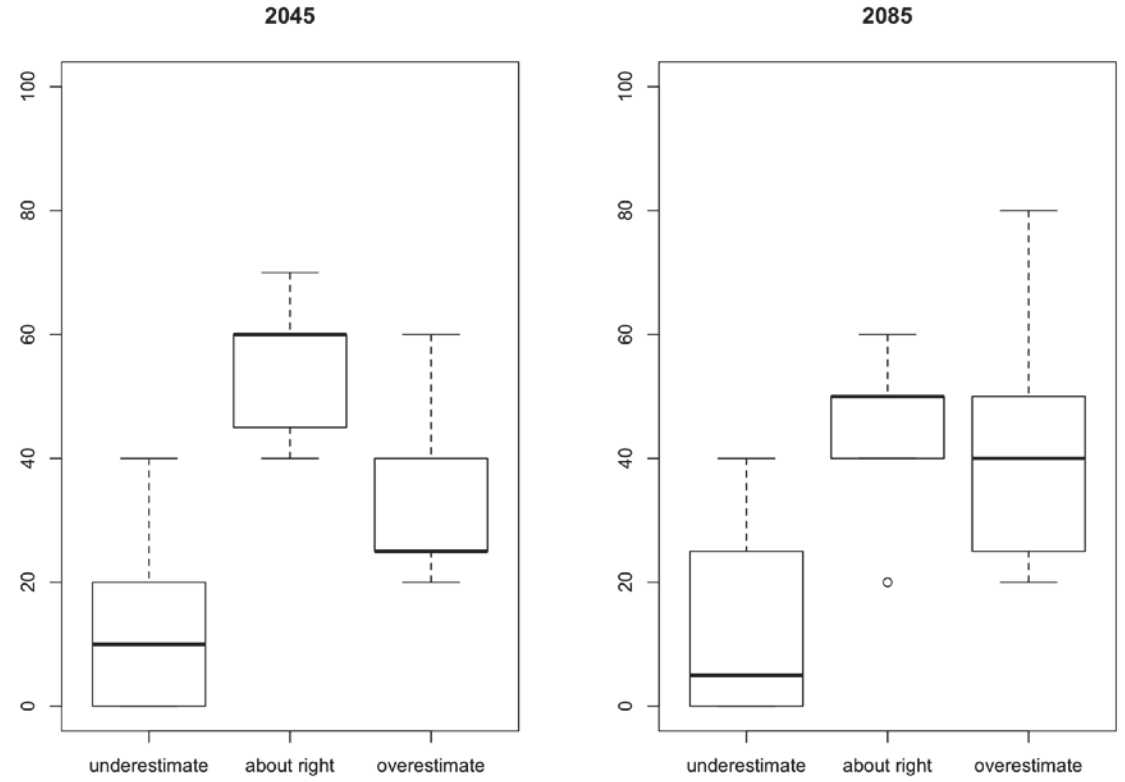


**Figure 7. Results of exercise to evaluate snow coverage.**

## Evaluating Future Habitat Projections

Panelists assessed how well the McKelvey et al. (2011) spring snow cover projections represent wolverine habitat by registering scores to indicate whether the snow cover projections were likely to be just right or an over- or under-estimate of wolverine habitat. Results showed slightly more support in the panelists' belief for the "about right" category than the other two categories in both timeframes (Figure 8). Points allocated to the "underestimate" bin indicate where McKelvey et al. (2011) may have overestimated the severity habitat loss. Points allocated to the "overestimate" bin indicate where McKelvey et al. (2011) may have underestimated the severity habitat loss. That scores do not weight heavily in any one category indicates that the panelists believed that the impacts of climate change on wolverine habitat may be greater than or less than the projections in McKelvey et al. (2011) however, there is no indication that the panelists believed that McKelvey et al. (2011) showed systematic error resulting in a one-sided bias. Refer to Appendix 9 for notes on habitat and complete scores.

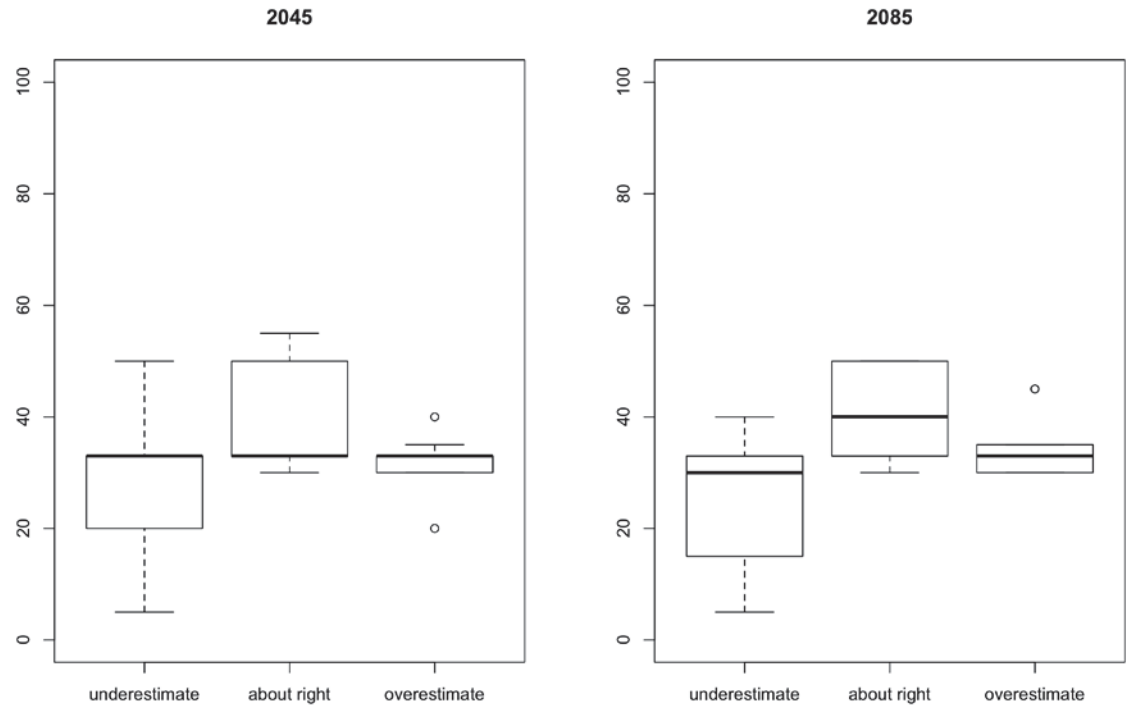


**Figure 8. Results of exercise to evaluate wolverine habitat trends.**

## Future Wolverine Population Trends

Panelists did not use precise demographic or population terms to describe population trends. Instead they referred to optimism or pessimism about wolverine persistence in the US. Panelists expressed cautious optimism for wolverines in the short term, and qualified their optimism with uncertainty about whether wolverines are still expanding into their former range, and whether wolverines had any plasticity to adjust to changing habitats. Although we did not ask for consensus, nine out of nine panelists expressed pessimism for the long-term (roughly end-of-century) future of wolverines in the contiguous US because of the effects of climate change on habitat. The full notes are available in Appendix 10.

References

Charlton, J. (2004). Delphi Technique. In Michael S. Lewis-Beck, A. Bryman, & Tim Futing Liao (Eds.), *The SAGE Encyclopedia of Social Science Research Methods.* (pp. 245-246). Thousand Oaks, CA: Sage Publications, Inc. doi: http://dx.doi.org.ezp1.lib.umn.edu/10.4135/9781412950589.n219

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Inman, R. M., Packila, M. L., Inman, K. H., Mccue, A. J., White, G. C., Persson, J., et al. (2012b). Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management, 76*(4), 778-792. doi:10.1002/jwmg.289

McKelvey, K. S., Copeland, J. P., Schwartz, M. K., Littell, J. S., Aubry, K. B., Squires, J. R., et al. (2011). Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications, 21*(8), 2882-2897.

McKelvey, K. S., Aubry, K. B., Anderson, N. J., Clevenger, A. P., Copeland, J. P., Heinemeyer, K. S., et al. (2014). Recovery of Wolverines in the Western United States: Recent Extirpation and Recolonization or Range Retraction and Expansion? *Journal of Wildlife Management, 78*(2), 325-334. doi:10.1002/jwmg.649

## APPENDIX 1 – PLANNING COMMITTEE MEMBERS

Planning Committee
Bob Lanka, Wyoming Game and Fish
George Pauley, Montana Fish, Wildlife, and Parks
Jodi Bush, FWS Field Office Supervisor, Montana
Leona Svancara, Idaho Fish and Game
Hillary Cooley, FWS-Idaho
Mary Grim, FWS-California
Shawn Sartorius, FWS-Montana

## APPENDIX 2 – ATTENDANCE LIST

ATTENDEE LIST

PANEL
- Dr. Bob Garrott, Montana State University
- Dr. Steve Buskirk, University of Wyoming
- Dr. Dan Pletscher, University of Montana
- Mr. Eric Lofroth, British Columbia Ministry of Environment
- Dr. Oz Garton, University of Idaho
- Dr. Jason Karl, Arid Lands Research Station, USDA, New Mexico
- Dr. John Abatzoglou, University of Idaho
- Dr. Tim Link, University of Idaho
- Dr. Sarah Kapnick, Princeton University
-
- MANAGERS AND DECISION MAKERS
- Bob Lanka, Wyoming Game and Fish
- Bridget Fahey, FWS-Denver
- George Pauley, Montana Fish, Wildlife, and Parks
- Hilary Cooley, FWS-Idaho
- Jim Unsworth, Deputy Director, Idaho Fish and Game
- Jodi Bush, Project Leader, Montana
- Justin Shoemaker, FWS-Denver
- Ken McDonald, Division Administrator-Wildlife, Montana Fish, Wildlife & Parks
- Leona Svancara, Idaho Fish and Game
- Mary Grim, FWS-California
- Matt Hogan, Deputy Regional Director, Mountain Prairie Region
- Mike Fris, Assistant Regional Director, Ecological Services, California-Nevada Region
- Noreen Walsh, Regional Director, Mountain Prairie Region
- Rich Hannan, Deputy Regional Director, Pacific Region
- Shawn Sartorius, FWS-Montana
- Terry Rabot, Assistant Regional Director, Ecological Services, Pacific Region

FACILITATORS/ORGANIZERS
- Steven Morey, USFWS-R1
- Teresa Woods, University of Minnesota
- Mike Mitchell, University of Montana, USGS Cooperative Wildlife Research Unit

## APPENDIX 3 – AGENDA

# Wolverine Science Panel
# Spokane, Washington
# 3 & 4 April 2014

MEETING OBJECTIVE: Better understand the strength of the relationship between climate change, wolverine habitat, and future wolverine population trends through dialogue with an expert panel.

## Agenda — Day 1

**3 April 2014**

INTRODUCTIONS

8:00 Welcome, Introduce Panelists, and Review Agenda

PART 1:
DEFINE CLIMATE-RELATED WOLVERINE HABITAT

What are the climate-related habitat requirements and what is the strength of the relationship between habitat and wolverines?

9:00 Presentation
9:30 Discussion – Identify general climate-related habitat needs
10:15 Break
10:35 Exercise – Strength of the relationship between climate features and the landscape's ability to support wolverines
12:00 Lunch

PART 2:
TRENDS IN SNOW

How is snow likely to change over time?

1:00 Presentation
1:30 Exercise -- Are the spring snow cover projections in McKelvey likely to be an underestimate, about right, or an overestimate of snow cover?
2:30 Break
2:50 Discussion – Degree and direction of change in the other aspects of snow
5:00 Adjourn

DRAFT

# Agenda

Day 2

**4 April 2014**

WELCOME
8:00 Recap and Review Agenda

PART 2 (continued):
TRENDS IN WOLVERINE HABITAT

How is climate-related habitat likely to change over time?

8:30 Discussion – Degree and direction of change of other important climate-related factors
10:00 Break
10:20 Exercise – Are the spring snow cover projections in McKelvey likely to be an underestimate, about right, or an overestimate of wolverine habitat?
11:30 Lunch

PART 3:
WOLVERINE POPULATION TREND

How is the wolverine population likely to change over time considering climate-related drivers?

12:30 Discussion – Follow up items, such as habitat quality and wolverine natural history
1:30 Synthesis: What is the likely future population trend of wolverines given the climate information we talked about during this workshop?
4:00 Adjourn

DRAFT

## APPENDIX 4 - COPY OF PRESENTATION BY SHAWN SARTORIUS

4/18/2014

### Introduction: Wolverine Science Panel

Shawn Sartorius
US Fish and Wildlife Service
Helena, Montana

### Wolverine

- Large, terrestrial Mustelid weighing 8-18 kg
- Large feet that allow easy travel over soft snow
- Uncommon or low densities
  - Large exclusive home ranges:
    - Female 300 – 400 km² (100-150 mi²)
    - Male 800 – 1500 km² (300-600 mi²)
- Scavenger and predator

### Distribution

- Holarctic/circumboreal
- Sea level to over 10,000' elevation
  - Sea level above arctic circle
  - High elevations in southern projections of range, elevations used increase further south
  - Alpine treeline
- Distribution limited to areas where cold, snowy conditions exist for much of the year

### World-wide Distribution

### CONUS Distribution

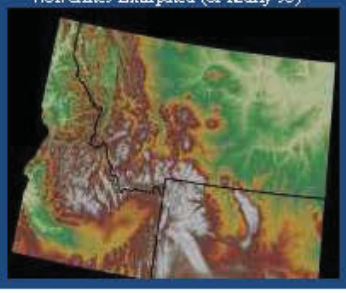
### Currently

- Wolverines occupy most of their historic range in WA, MT, ID, and WY – ca. 250-300 animals
- Wolverines are likely still expanding within northern Rockies, Greater Yellowstone, North Cascades
- Additional expansion is largely dependent on accessing additional portions of historic range
- Colorado has the largest unoccupied area of habitat (~16% of existing habitat)
- Naturally low population density means that there will always be few wolverines

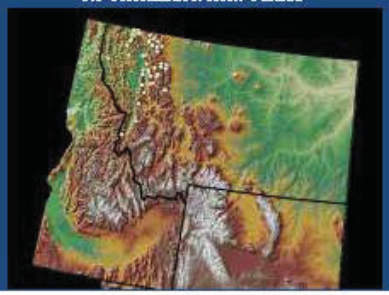
1

4/18/2014

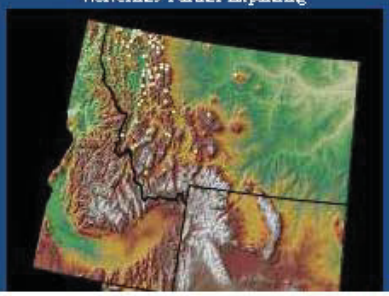
Historic Declines
1920
Wolverines Extirpated (or nearly so)



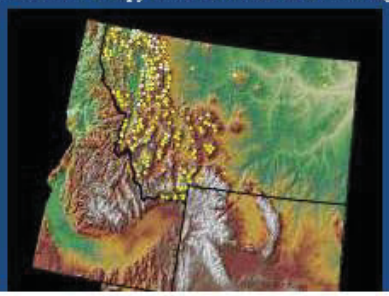
1930 – 1955
Newby & Wright
Re-colonization from Canada



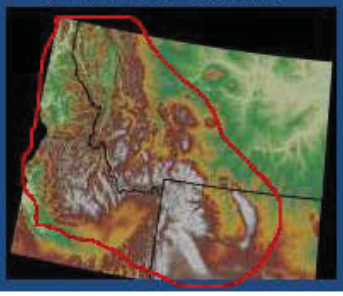
1955 – 1964
Newby & McDougal
Wolverines Further Expanding



1974 – 2000
Wolverines Occupy Much of Historic Montana Range



Estimated Present Wolverine Distribution in the Northern Rockies



## Wolverine Habitat

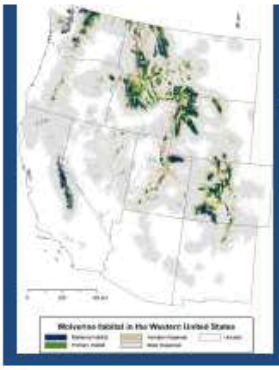
- Two efforts to delineate wolverine habitat in the CONUS:
  - Inman et al. 2013
  - Copeland et al. 2010

2

4/18/2014

## Inman et al. 2013 model

- Used 11 environmental predictors
- Excellent fit to wolverine telemetry data for several study areas in the northern Rockies
- Wolverines selected for:
  - Higher elevation
  - Steeper terrain
  - More snow
  - Fewer roads
  - Less human activity
  - High elevation talus
  - Tree cover
  - April1 snow cover



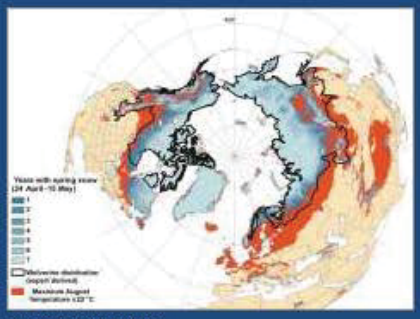
- Inman et al. 2013, Fig. 2

## Copeland et al. 2010

- Obligate snow denning relationship suggested by Magoun and Copeland (1998)
- Aubry et al. (2007) used EASE-Grid probability of snow cover 15-Apr-14 May:
  - Concluded that historical and current wolverine populations occur in areas with persistent spring snow cover
  - But coarse of scale
- Copeland et al. (2010) refined this analysis and applied world-wide

## Copeland et al. 2010

- Used MODIS classified daily snow data (satellite)
  - 500 m spatial resolution
  - Pixels rated as "snow" if 50% or more white
  - Pixel counted as snow if it was 50% or more white in every daily sample from April 24 to May 15 in at least 1 of 7 years of sample
  - Method designed to eliminate ephemeral and shallow snow
  - Pixels that survived this process as "snow" pixels were very snowy places
- Also looked at maximum August temperature as a predictor



Copeland et al., 2010, Fig. 1

3

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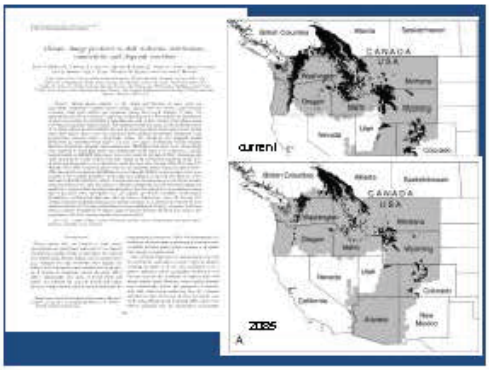
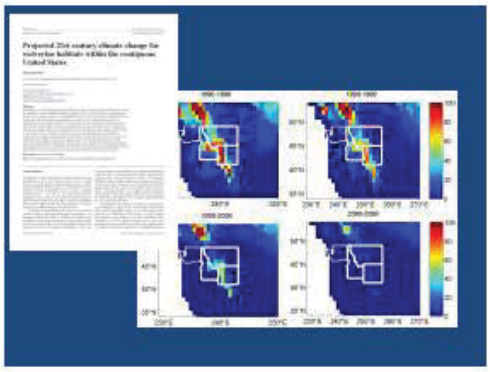
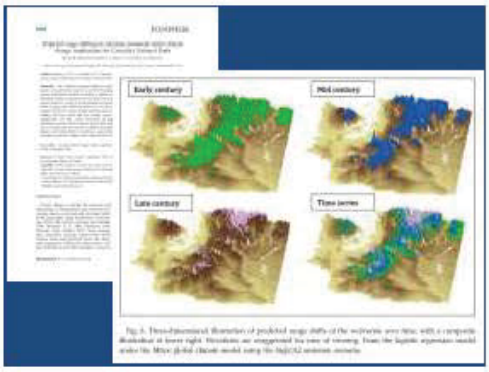
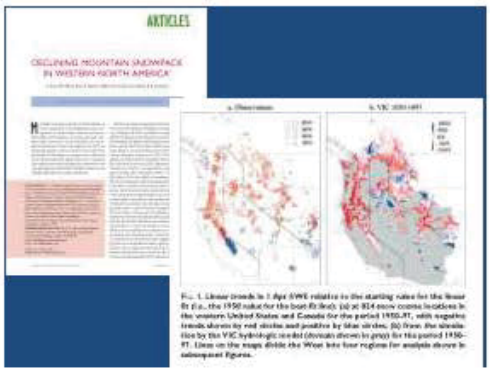
## Climate Change

- USFWS recently proposed wolverines for listing under ESA
- Climate change impacts were the primary threat identified
- There is significant uncertainty regarding the effects of climate change to wolverines and wolverine habitat





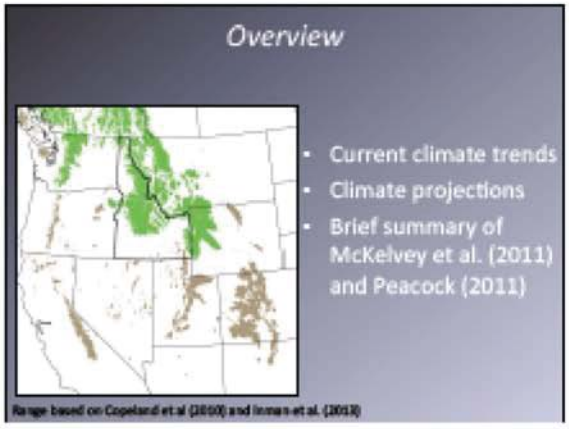



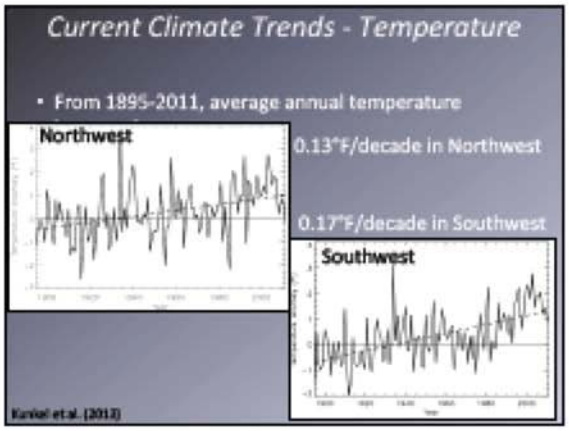

## Our Objective

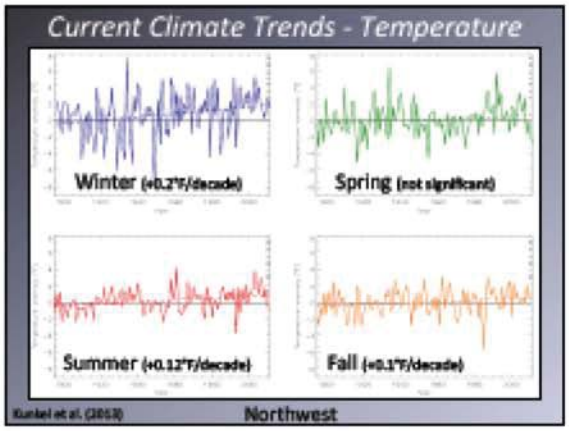
- Through dialogue with the expert panel, to better understand the strength of the relationship between climate change, wolverine habitat and wolverine population trends in the future.

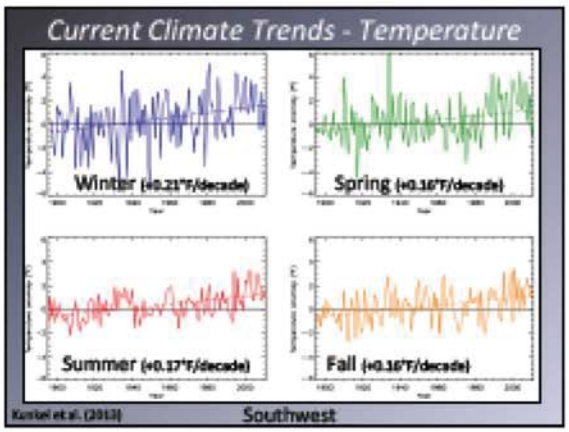
4

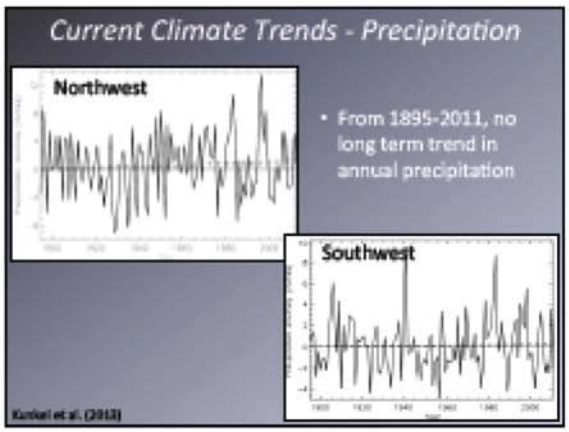
## APPENDIX 5 – PRESENTATION BY LEONA SVANCARA

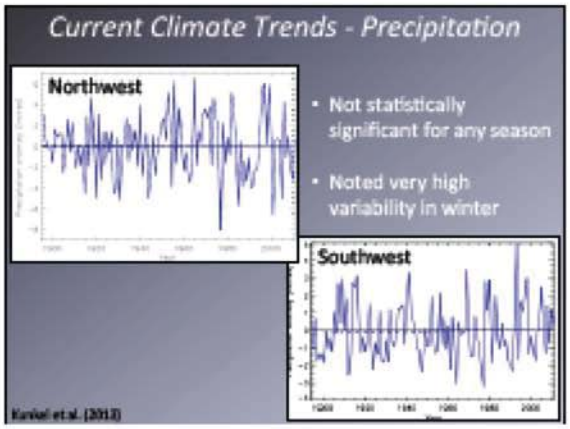


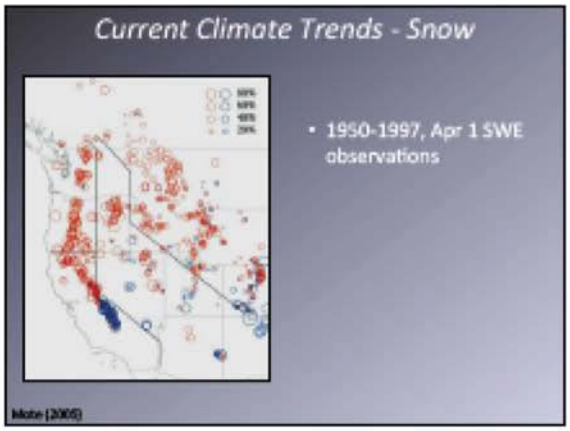



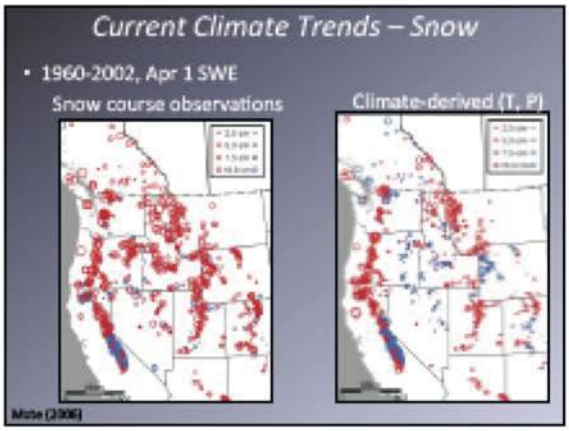



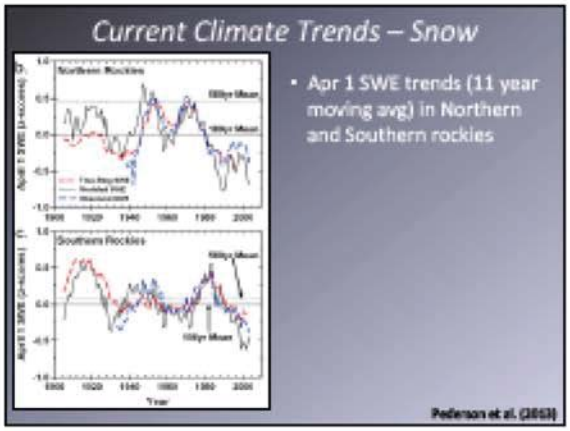



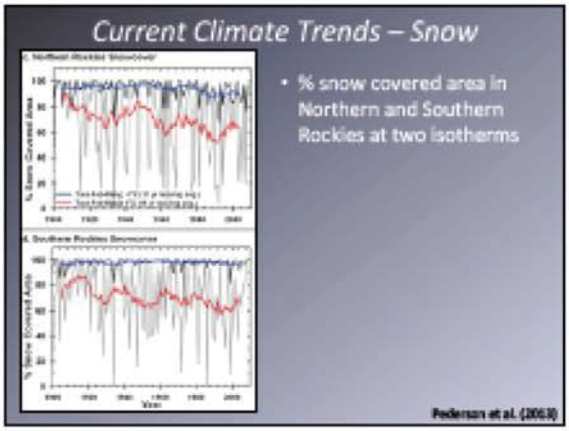

Current Climate Trends - Precipitation
Northwest
Not statistically significant for any season
Noted very high variability in winter
Southwest
Kunkel et al. (2013)

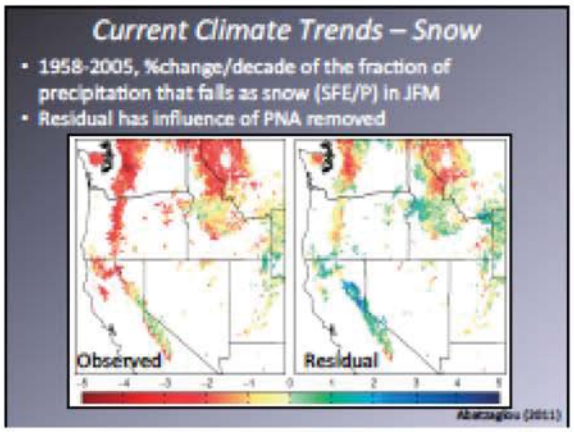
Current Climate Trends - Snow
Several different papers address changes in snow…
By measure (SWE, snowfall, snowpack, snow cover, etc)
By month (April 1, JFM, DJF, etc)
By time periods (1950-1997, 1960-2002, etc)

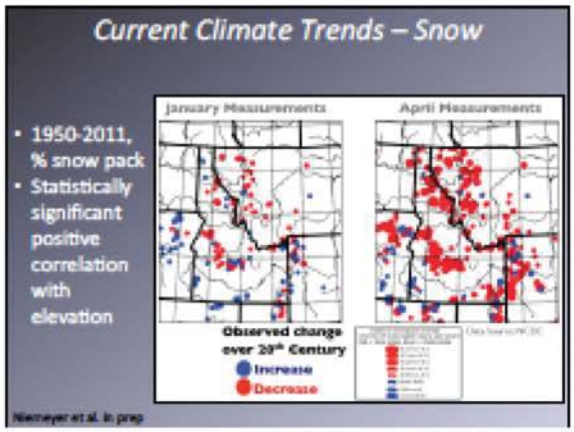

Current Climate Trends - Snow
1950-1997, Apr 1 SWE observations
Mote (2005)

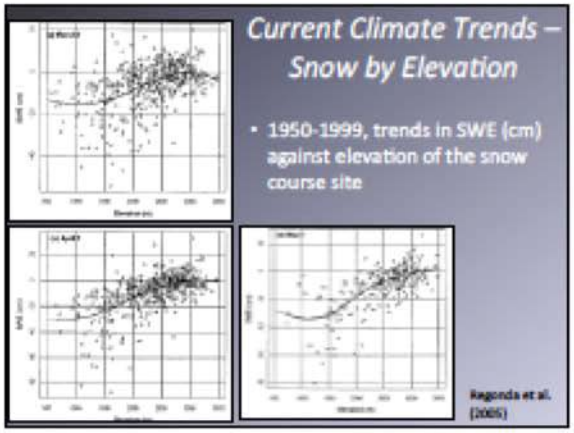

Current Climate Trends – Snow
1960-2002, Apr 1 SWE
Snow course observations
Climate-derived (T, P)
Mote (2008)

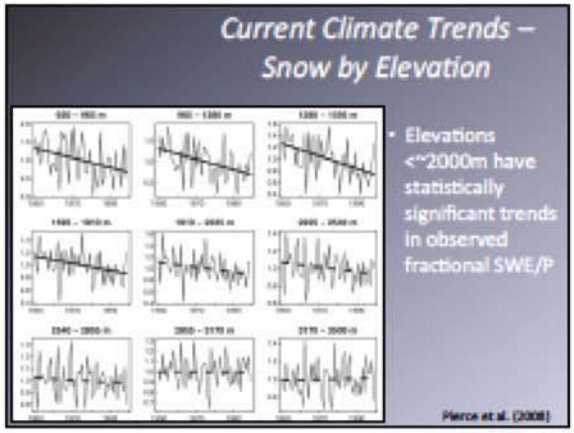

Current Climate Trends – Snow
Apr 1 SWE trends (11 year moving avg) in Northern and Southern rockies
Pederson et al. (2013)

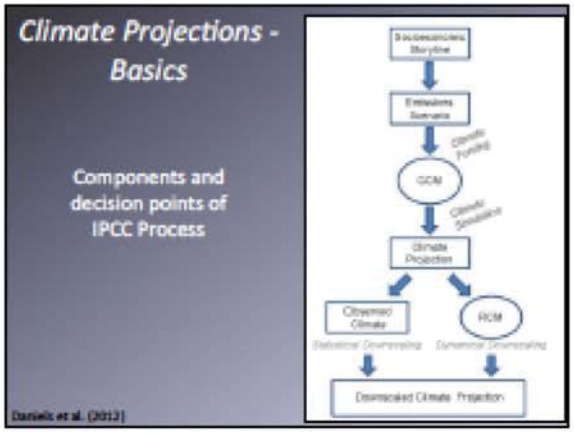

Current Climate Trends – Snow
% snow covered area in Northern and Southern Rockies at two isotherms
Pederson et al. (2013)

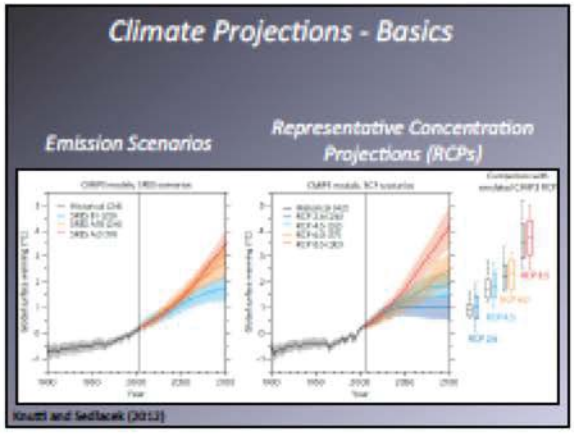

Current Climate Trends – Snow
• 1958-2005, %change/decade of the fraction of precipitation that falls as snow (SFE/P) in JFM
• Residual has influence of PNA removed
Observed
Residual
-5 -4 -3 -2 -1 0 1 2 3 4 5
Abatzoglou (2011)

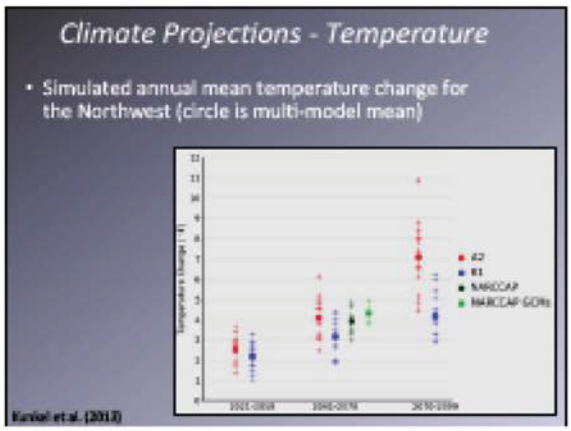

Current Climate Trends – Snow
• 1950-2011, % snow pack
• Statistically significant positive correlation with elevation
January Measurements
April Measurements
Observed change over 20th Century
Increase
Decrease

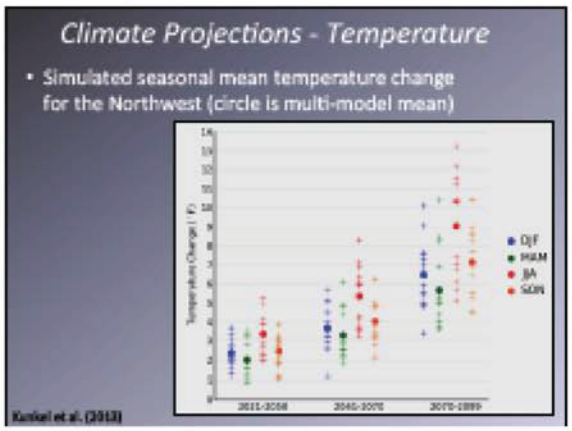

Current Climate Trends – Snow by Elevation
• 1950-1999, trends in SWE (cm) against elevation of the snow course site
Regonda et al. (2005)

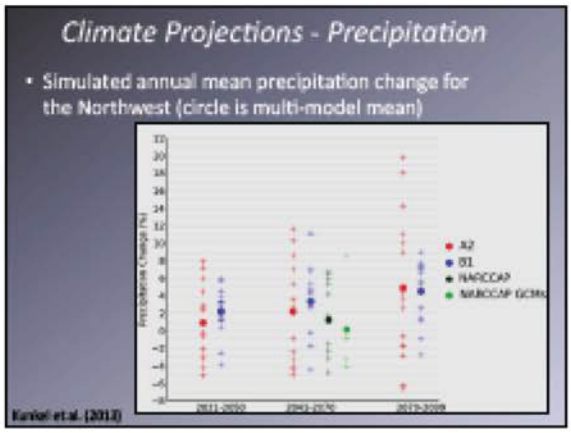

Current Climate Trends – Snow by Elevation
• Elevations <~2000m have statistically significant trends in observed fractional SWE/P
Pierce et al. (2008)

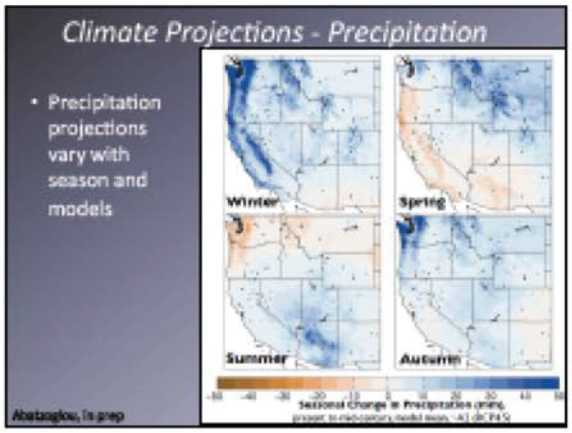

Climate Projections - Basics
Components and decision points of IPCC Process
GCM
RCM
Downscaled Climate Projection
Daniels et al. (2012)

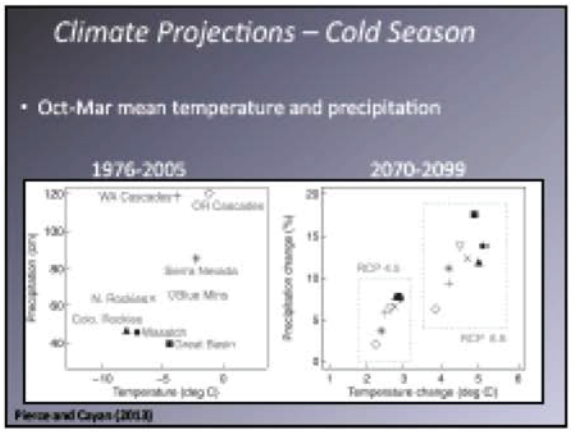

Climate Projections - Basics
Emission Scenarios
Representative Concentration Projections (RCPs)
Knutti and Sedlacek (2012)

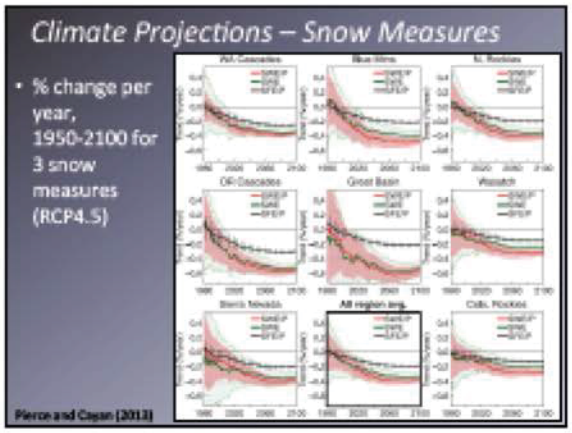

Climate Projections - Temperature
• Simulated annual mean temperature change for the Northwest (circle is multi-model mean)
A2
B1
NARCCAP
NARCCAP GCMs
Kunkel et al. (2013)

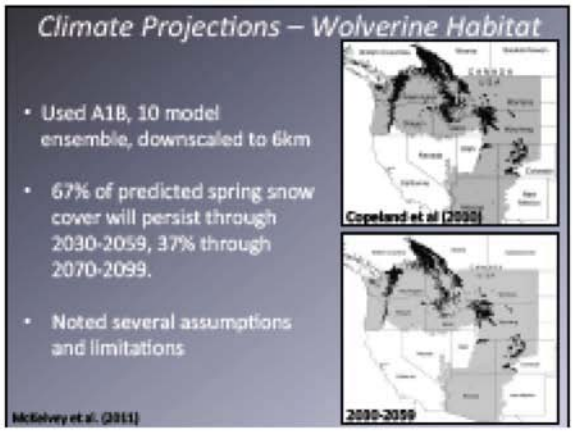

Climate Projections - Temperature
• Simulated seasonal mean temperature change for the Northwest (circle is multi-model mean)
DJF
MAM
JJA
SON
Kunkel et al. (2013)

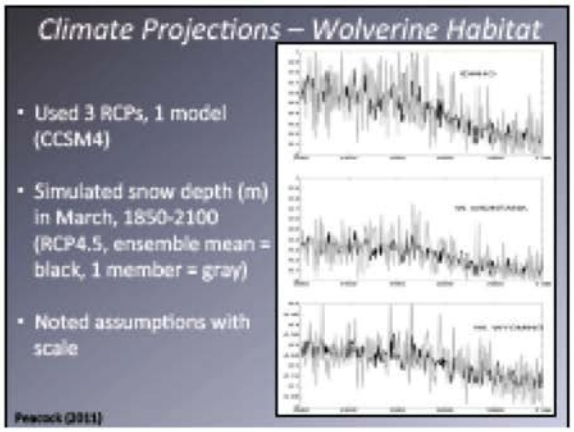

Climate Projections - Precipitation
• Simulated annual mean precipitation change for the Northwest (circle is multi-model mean)
A2
B1
NARCCAP
NARCCAP GCMs
Kunkel et al. (2013)


Climate Projections - Precipitation
• Precipitation projections vary with season and models
Winter
Spring
Summer
Autumn
Abatzoglou, in prep


Climate Projections – Cold Season
• Oct-Mar mean temperature and precipitation
1976-2005
2070-2099
WA Cascades
OR Cascades
Sierra Nevada
N. Rockies
Blue Mtns
Colo. Rockies
Wasatch
Great Basin
RCP 4.5
RCP 8.5
Temperature (deg C)
Temperature change (deg C)
Precipitation (cm)
Precipitation change (%)
Pierce and Cayan (2013)


Climate Projections – Snow Measures
• % change per year, 1950-2100 for 3 snow measures (RCP4.5)
Pierce and Cayan (2013)


Climate Projections – Wolverine Habitat
• Used A1B, 10 model ensemble, downscaled to 6km
• 67% of predicted spring snow cover will persist through 2030-2059, 37% through 2070-2099.
• Noted several assumptions and limitations
Copeland et al (2009)
2030-2059
McKelvey et al. (2011)


Climate Projections – Wolverine Habitat
• Used 3 RCPs, 1 model (CCSM4)
• Simulated snow depth (m) in March, 1850-2100 (RCP4.5, ensemble mean = black, 1 member = gray)
• Noted assumptions with scale
Peacock (2011)

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## APPENDIX 6 – NOTES FROM DISCUSSION ON HABITAT DEFINITION

These are the actual notes that were taken contemporaneously with the meeting and shown onscreen. They have not been edited after the fact and may contain spelling and punctuation errors.

| Physical characteristic | Why is it important? (mechanisms/ ecological relationships) | Key references | Notes on confidence |
|---|---|---|---|
| Deep snow late into denning season | Thermal constraints for kits; may not be just thermal constraints, but also limit predation risk associated with complex denning structures<br><br>Kit survival | Magoun & Copeland<br>Copeland 2010 referencing other papers world wide | All known dens are in snow<br>Lateness in spring varies depending on location.<br>Different denning periods as you go north.<br>Denning periods across the range may vary by prey availability.<br>In lower 48 – late February to early March<br>Copeland 2010 – begins early Feb to late march, weaning in early may |
| Snow den physical, structural characteristic | Avoid predators<br>Thermal considerations for kit survival | Magoun (AK) | Most dens are not typically higher montaine environments, associated with large debris or large avalanche, large talus, large drifts (Magoun in AK), meters of snow; females move to areas where there are fewer carnivores; will move from valley bottoms to den to feed in a single day; more predators farther south; almost all females are pregnant, but only about 5o% produce kits (inman) |
| Snow for thermal properties | To preserve food caches | Copeland et al<br>? | Hypothesis – giving birth at time when food is probably limited |
| Warm season temperature limitation | Thermal regulation | | Hornockers wolverines move up in elevation as temperature warm in lower 48, but don't necessarily do that in more northern areas |

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|---|---|---|---|
| Scale of the habitat relationship between wolverines and snow; | All modeling is at large scales-but if threats are at small scale we might be misdiagnosing the mechanisms<br><br>Big landscapes and big areas of snow – keeps predators out<br><br>Small scale – caching of food and den sites | | Broad scale ecological relationship; literature hypothesizes fine scale relationship that has not been tested (except at den sites); scale for den sites vs whole range; no specific mechanisms, just remember to consider various scales<br><br>Mechanisms are theoretical |
| Deep Snow | Competitive advantage over other carnivores | | Morphological advantage with large broad feet, community interaction question |
| spatial continuity of snow and pathways | Dispersing male and other adult mortality; connectivity between routes; | | Multiple scale considerations; wolverines can travel 100s of miles; patchy distribution of snow allowing denning vs large-scale contiguous snow for distribution; known to pass through sagebrush but risky for long-term stays and movement back and forth may have different success levels (Winds to Rocky Mountain National Park – about 2 months in summer). Physical capacity to make large scale movements is limited – many are unsuccessful because of physical capacity limitations selection index for dens is strong with 6 or 7 years with snow (Copeland); but we don't know the reproductive success among the sites with fewer years snow and more years snow; |

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|---|---|---|---|
| Inter-annual climate variability | Perhaps denning reproduction success – however, there may be other deep snow areas within range<br><br>Annually consistent large snow areas to keep out predators may have population effects | | Copeland has graph showing selection for persistent in most years for many reasons, e.g.,<br><br>Speculative, but effects may manifest in many ways<br><br>First reproduction at 3 and breed to age 7; kit production every other year with average 1.5 kits per year |
| Heterogeneity of snow is greatest in spring | | | |
| Temporal distribution of snow | | | Copeland studied at den abandonment period not den occupation – however, if snow is there when den is abandoned it is probably there when it was occupied; modus indicates deep pack |
| snow | Affect on prey availability | | |
| Summer and year-round temperature | Refrigeration and thermal neutrality<br><br>Early in denning snow provides insulation; late in denning season it could provide cooling properties<br><br>May be an issue for kits and adults | | Mostly hypothetical<br>Loss of snowpack in spring results in faster temperature increase than summer increases<br>They go to cooler sites and does that relate to fitness – comfort translates to energetic costs that could have broader implications<br>Temperature is an easier climate variable to measure and project with certainty. Downscaling temperature is easier than downscaling snow. Temperature is more tenuous/hypothetical as far as our understanding of wolverines |
| | | | |

Deep snow at den sites: In lower 48 almost/all dens sites are in deep snow; in other areas (Northern Europe) there are non-snow dens (information suggests that the dens are snow dens, but not in the snow layer used by Copeland); probably only 1 known non-snow den

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Question is has the modeling been done at a scale that matches the scale of den sites
North facing microsites may be persistent, but modeling may not be specific (properly reflect changes) to those areas
GCMs allow a broad understanding of broad implications, data has to be downscaled to get projections at the right scale. Still, info in the GCMs is useful.
What is the patch size for deep snow for denning? Danger in using a broad-scale model for fine-scale issues may underestimate the available habitat. Models may be biased on the low end with underestimates of snow.

SCALE:

- Denning area (refrigeration, den success, thermal)
- Home range (refrigeration, denning relative to other predators)
- Landscape (carnivore community interactions, dispersal success)

Range of dates: in the lower 48 – easy to do from primary sources. Aubrey offered to make data from Okanagan plateau available. When sites are abandoned may also be important to get end date.

Strong correlations about mechanisms, not absolute proof

Wolverines den on steep north facing slopes – snow melts last, is the annual cycle tied to temperature or day light changes. North aspect seems to matter more the farther south one goes; therefore. seems to be tied to deep longer lasting snow.

Winter recreation use may increase as snow becomes less available because of climate change. Actual effects depend on type of use—temporal vs. development

Food abundance and availability not included as a physical characteristic.

Do we understand enough to know that climate variables drive wolverine populations – we don't know anything from experiments, just from observation data about where they live. Experimental evidence from
Sweden that suggested that reproduction was food limited (with supplemental feeding litter sizes, age of first reproduction, and other things increased).

Hypothesis: Decadal and multi-decadal – does current expansion suggest that food is not limited but that larger-scale climate issues may come into play?

Wolverines are currently rebounding from excessive harvest and poisoning where much suitable habitat was left vacant

Can't conclude ongoing climate effects based on past 30 years because of annual variability

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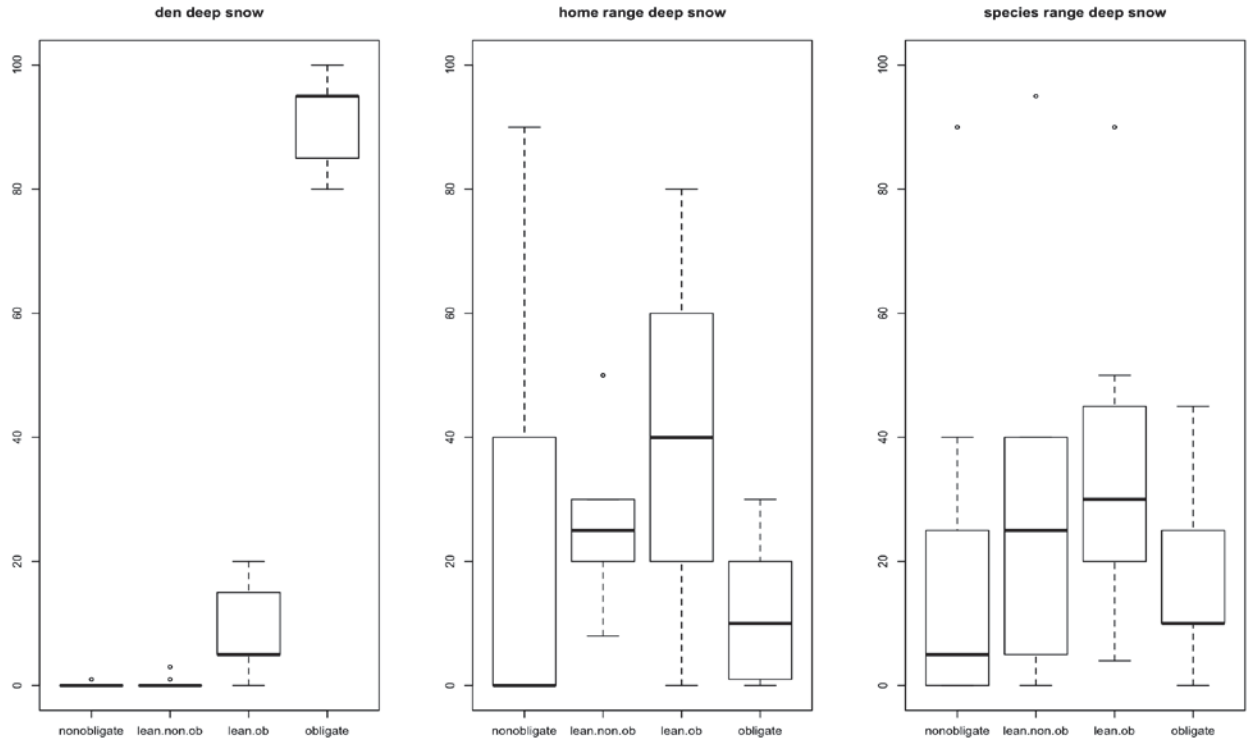
## APPENDIX 7 – RESULTS FROM STRENGTH OF THE RELATIONSHIP BETWEEN CLIMATE FEATURES AND THE LANDSCAPE'S ABILITY TO SUPPORT WOLVERINES

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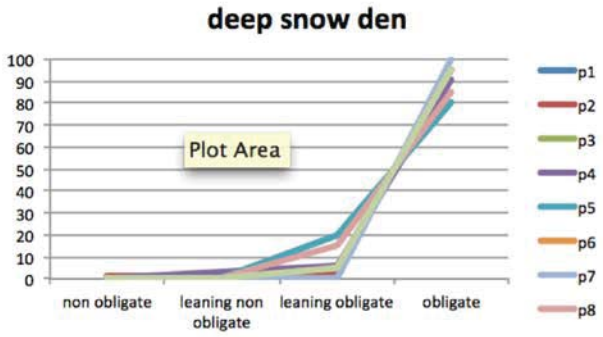
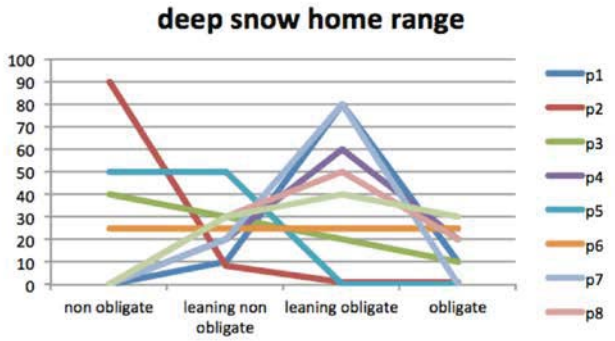
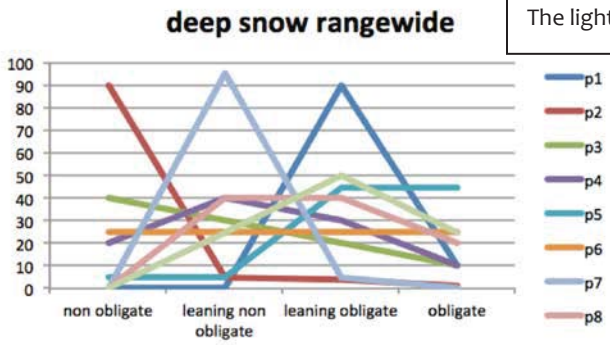
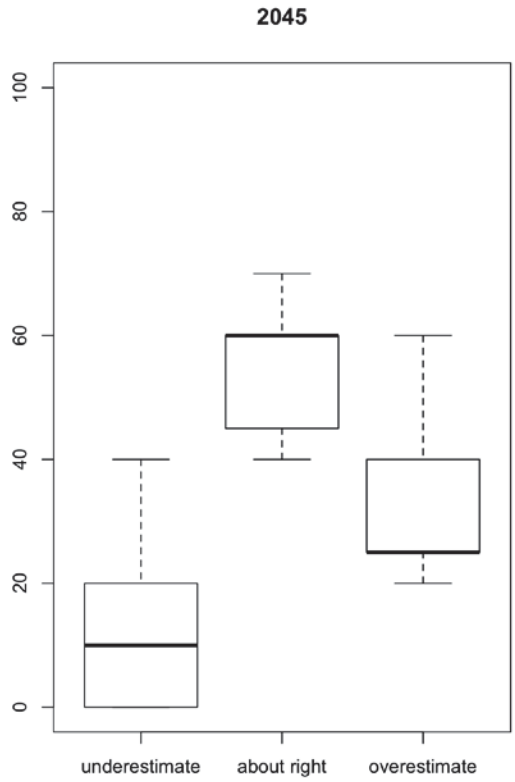
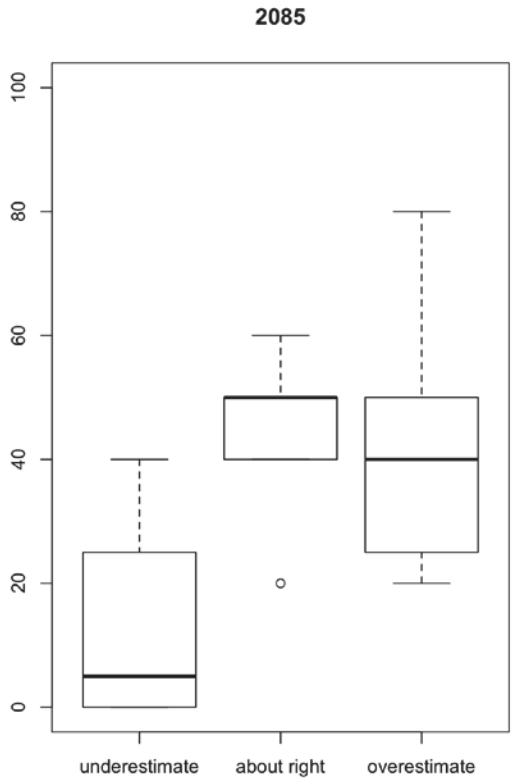


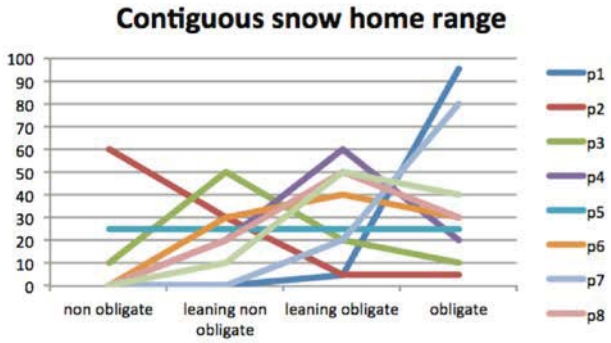




*There were actually 9 responses. The lightest green is number 9.

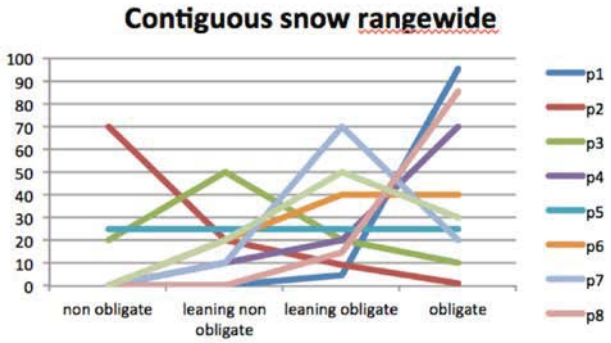


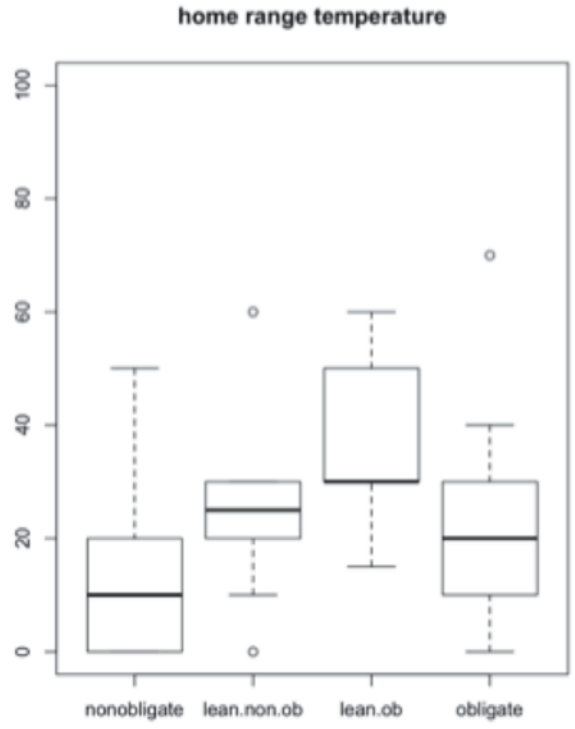


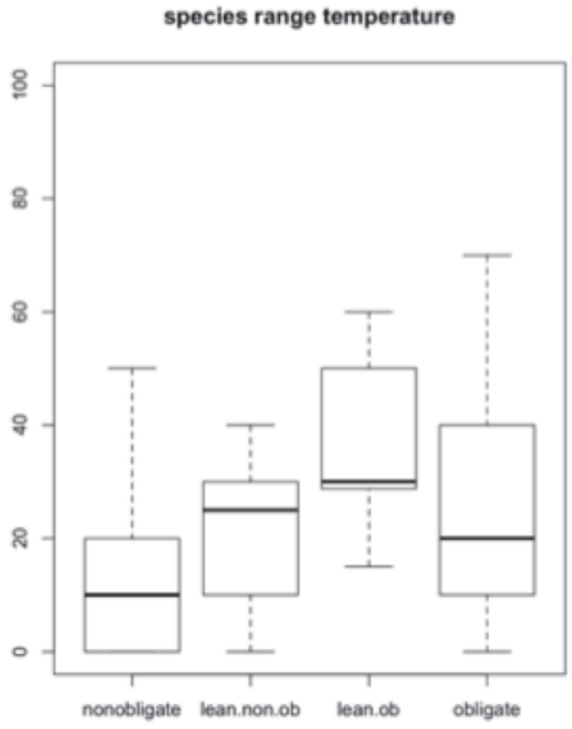

| | | | | |
|---|---|---|---|---|
| mean | 11 | 21 | 31 | 37 |
| median | 0 | 20 | 25 | 30 |

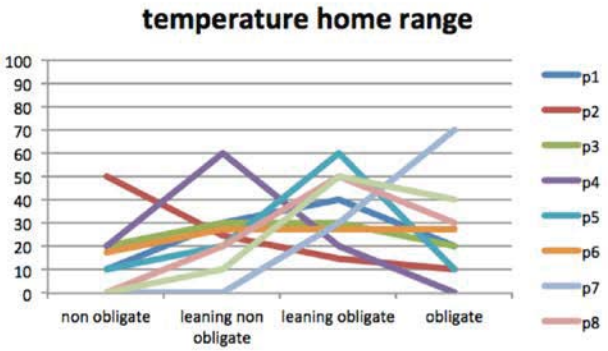


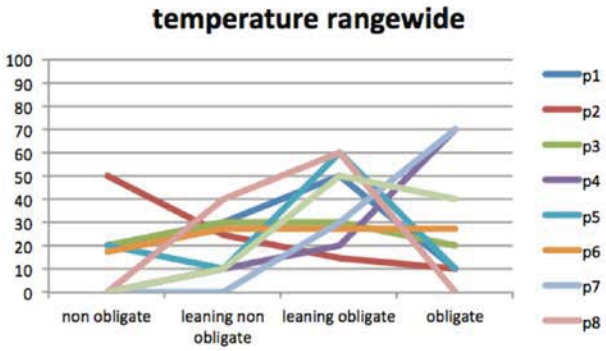

| | | | | |
|---|---|---|---|---|
| mean | 13 | 17 | 28 | 42 |
| median | 0 | 20 | 20 | 30 |

*There were actually 9 responses.
The lightest green is number 9.






| | | | | |
|---|---|---|---|---|
| mean | 14 | 25 | 36 | 25 |
| median | 10 | 25 | 30 | 20 |

| | | | | |
|---|---|---|---|---|
| mean | 14 | 20 | 38 | 29 |
| median | 18 | 25 | 30 | 20 |

*There were actually 9 responses.
The lightest green is number 9.

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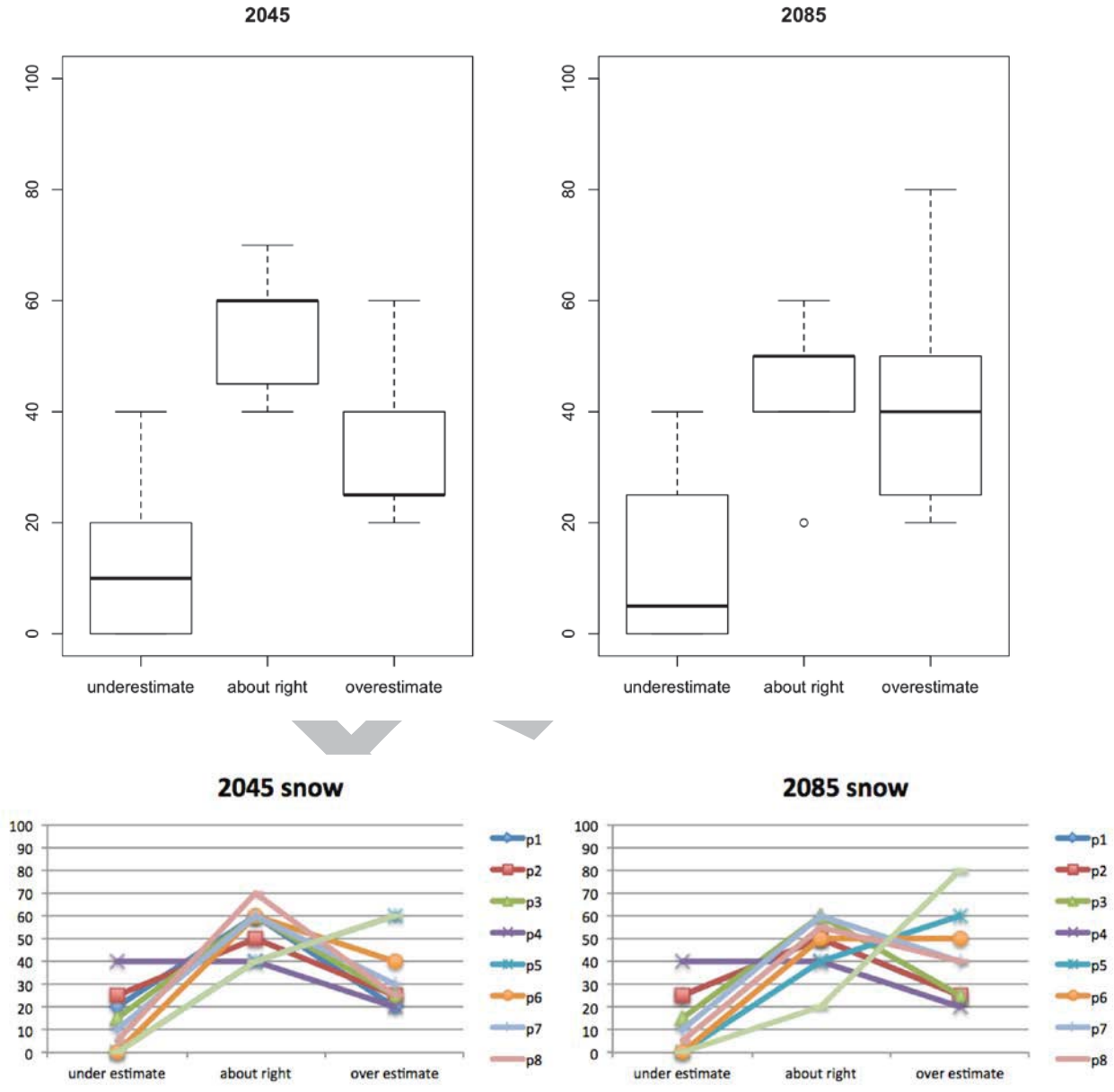
## APPENDIX 8 – RESULTS FROM SNOW COVER PROJECTIONS EXERCISE

Are spring snow cover projections of Mckelvey likely to be an underestimate, about right, or an over estimate of snow cover.




*There were actually 9 responses.
The lightest green is number 9.

## APPENDIX 9 – NOTES AND SCORES ON HABITAT CHANGE

These are the actual notes that were taken contemporaneously with the meeting and shown onscreen. They have not been edited after the fact and may contain spelling and punctuation errors.

Change in Climate Related Habitat Features

| Expected change | Possible Degree and direction of change (can be expressed as a range) | Hypothesized/potential effect on wolverines | Notes (e.g., uncertainty) |
|---|---|---|---|
| Snow depth at den | Decline<br><br>Heterogeneity across the landscape may mean there are many sites for denning per home range<br><br>Denning period might shift to earlier in the season<br><br>Warming spring temperatures and effect on function and thermal properties resulting in fewer den site options per home range.<br><br>Complexes in deep snow on top of desirable substrate for complexity of den. So we might not just be looking at a straight decline in snow, but looking at less snow on a layer of desirable substrate. | Deep snow obligate for denning.<br><br>Wolverines used multiple den sites per year, therefore they might be moving den sites more frequently, which increases risk and energetic demands<br><br>We don't know how plastic the species is in terms of adapting to change?<br><br>The effect on wolverines might affect ability to dig down (unlikely effect) to but more likely could allow other predators to cross snow. Upside, is that ice layers in icepack can keep snow from permeating. | Let's say there are 150 potential microsites for an individual female. Theoretically, if these were reduced by half, there would still be 75 potential den sites.<br><br>More water in the snowpack. Less sites that have deep snow would have greater percentage on rain on snow.<br><br>Inman fig 2 summarizes data.<br><br>Snow is an essential feature of denning habitat, but with the state of knowledge we have uncertainty about what the effects of decreased snow cover has on a wolverine's ability to find and a den site (e.g., there may |

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|---|---|---|---|
| | Snow crust from thaws in midwinter – increasing frequency in crusts<br><br>Den site initiation / abandonment (hard to find initiation because dens are found after occupation begins)<br><br>Could earlier snow melt increase prey availability during denning because prey look to be emerging earlier?<br><br>What is the relationship between food abundance and availability at the den-site level? | | still be sites availability). The effects might be very localized, so the effect on wolverines might occur at a larger scale.<br><br>Nothing in the literature says den sites are limited, however, they may be food limited<br><br>We can't say when the decline in den sites will hit a threshold where there aren't enough<br><br>As snow conditions change, there will still be pockets of deep persistent snow. Presumably, wolverines will find them. Within Copeland et al., wolverines pick the snowiest or the snowy places. They might be able to den in patchy areas, but they seem not to select for them now (according to Copeland)<br><br>Are we running the experiment now? Below persistent |

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|---|---|---|---|
| | | | spring snow (1 in 7) do we not have pockets of deep snow now that wolverines could den in, but aren't now. This goes to the adaptation argument.<br><br>Tree size analogy with martin—they always choose the biggest tree wherever they are and that diameter varies across the range of martin.<br><br>Could wolverines be successfully in landscape with fewer pockets? Maybe experiment is going on now—who know?<br><br>Wolverines are already constrained because they are going to north slopes.<br><br>We know what they like, but we don't know what they need. Probably a collection of attributes.<br><br>How close are we to carrying to capacity? |

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| | | | Will carrying capacity go up or down because of climate change? Montana might be close to carrying capacity, but probably not other areas south<br><br>How does den site selection affect survival? Thermal properties, prey availability, and other stuff.<br><br>Wolverines may move from natal to maternal dens – but is variable among dens – pretty common across carnivores. Don't know why, predator avoidance, ect. maybe |

Temperature is increasing – across the board the onset of snow melt is happening 2 to 3 days earlier per decade

Probably greater than two week shift over 100 years (by the end of the century)

Emission scenario – how right?
Climate simulation – very consistent with reality; generations are from previous IPCC – looks pretty similar to latest IPCC; average change from 10 models—perturbed observed years with projected change; greater confidence in temperature and precipitation than in sequencing; changes in jet stream etc are not noted in the McKelvey model; recent info from IPCC roughly matches McKelvey; current emissions are above the projections used; tends to accelerate the effect over time

Snow melt simulation -

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Snow in general – snow station data – projections vs observations, which show strong trends toward less snow at April 1. GCM also shows this trend. Extrapolations in GCM match and show increasing acceleration over time.

Seasonality – Mckelvey snow hasn't been changing as much in the early season,. . . big decline (rapid change) in the month of March –

Snow is decreasing generally and most rapidly in March. 0 degree Celsius is a threshold – average temp is -5 to 5. Expectation is that if we rise another 3 to 4 degrees there will be rapid melting in March, and we are moving toward that in the next 50 to 60 yrs. We are beginning to see cross this threshold in April, and will see the threshold in March within the century.

Will climate change have an elevational migration - i.e., will conditions move upslope. This might work for temperature, but not for precipitation.

Wolverines in southern clines on northerly aspects – snow persists longer and is deeper. If wolverine really goes for those slopes—you might see wolverines might go for northern clines going for north slopes. Does the tendency to go to northern aspects buffer the wolverine from climate change. Climate change is happening on all aspects. Warming is the same on both sides. Shift from snow to rain is also occurring – small scale pockets and refugia. Still melting on the north slopes, but it is also melting faster. How does the differential in solar radiation –is the melt rate different on both sides? South slope shortwave. North slope longwave. Northern slopes are also in the rain shadow; therefore North slopes already get less snow. Although there might be a watershed scale effect that increases deposition. Bottom line . . . lots of uncertainty in the north/south differential. Precipitation is declining, even if there is an increase in precipitation early in the year.

How about annual variability – interannual variability there is a latitudinal gradient.

Are the spring snow cover projections in McKelvey likely to be an underestimate, about right, or overestimate of wolverine habitat?

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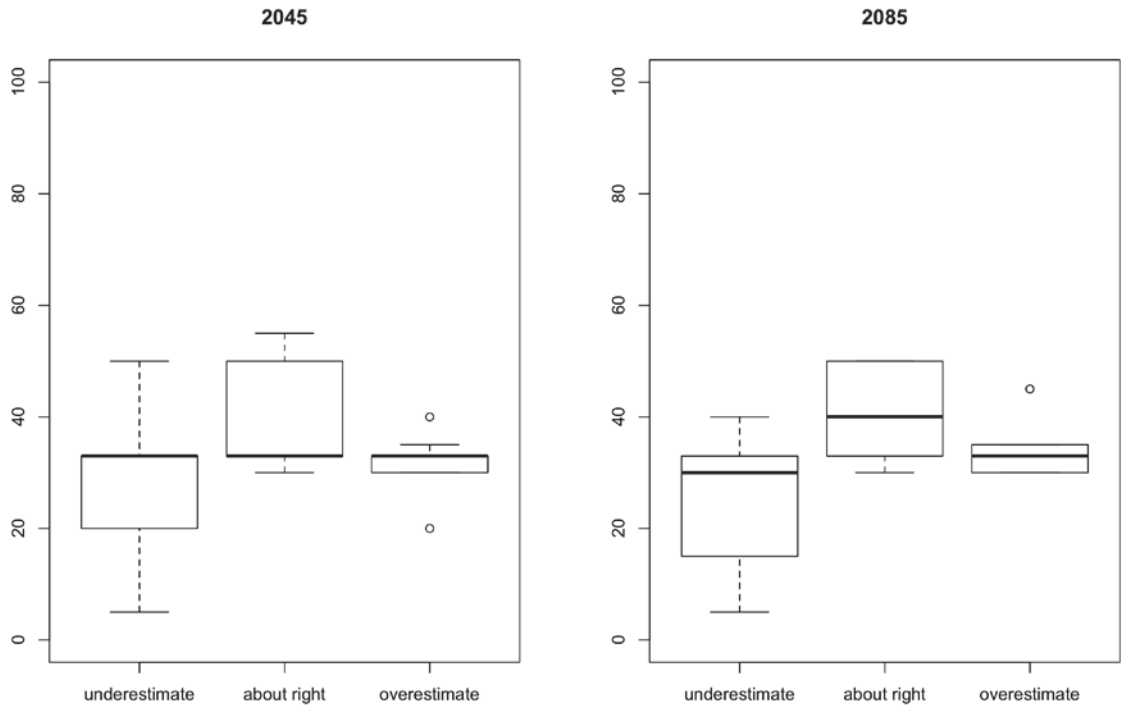
2045
2085
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80
60
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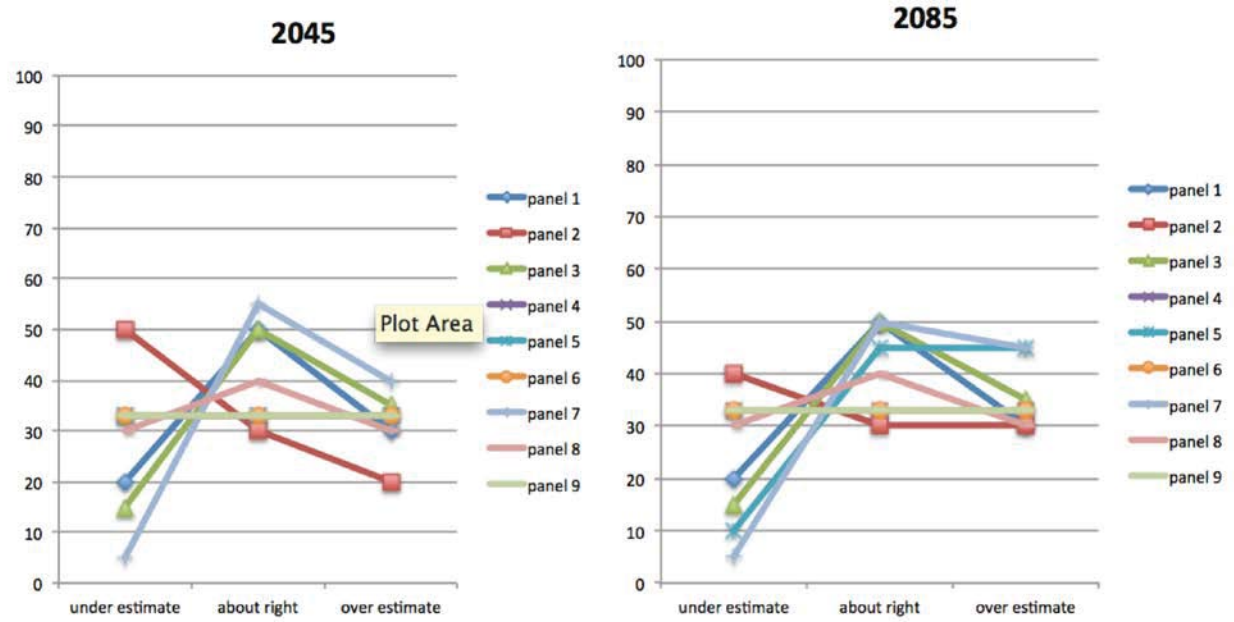
underestimate
about right
overestimate


2045
2085
100
90
80
70
60
50
40
30
20
10
0
under estimate
about right
over estimate
Plot Area
panel 1
panel 2
panel 3
panel 4
panel 5
panel 6
panel 7
panel 8
panel 9

## APPENDIX 10 – NOTES ON WOLVERINE POPULATION TREND

These are the actual notes that were taken contemporaneously with the meeting and shown onscreen. They have not been edited except to fix some spelling and punctuation errors.

Synthesis

Should we expect a linear relationship between habitat loss and population loss?

If you lose 10% of habitat, it is probably the most marginal now, so you will probably lose a somewhat lesser amount of wolverines.

You can absorb a large amount of disturbance until you hit a threshold and have disproportionately large amount of animals (eg., lose more habitat at first compared to animals, then hit a threshold where you lose more animals than habitat). 10% loss in habitat might be distributed differently – in some areas it could result in 10% population decline. In other areas not.

If you lose the marginal habitat first, but the habitat quality within the original area might also be changing for the worse.

Consider seasonality – if you lose 10% of den space you might lose a greater proportion of other habitat

Carrying capacity – is a function of a snow but also a function of food and changes in mortality associated with interspecific competition and territorial behavior.

When we talk about habitat loss – and base it on McKelvey – there is a lot more complexity than just snow.

Forest carnivores. Is the loss of habitat linearly related to decline. Does 10% decline in habitat result in 10% decline in population

No. Not linear. Depends on the mechanism that is lost.

What mechanisms do we expect to change given climate change?

- occupancy might change which affects dispersal, persistence of small populations, and role that dispersal might play in genetics
- natality and mortality and saturation of habitat may change
- whether they go up or down becomes more and more uncertainty the more we speculate on biological response

Example of nonlinearity – small isolated pop of wolverine losing 10% habitat, could result in step function and allee effects might kick in and result in extinction vortex.

Management tactic for uncertainty is to avoid losing habitat

DRAFT

The climate will be different and therefore the wolverine's habitat will be different.

Metapopulation structure of wolverines has enormous implications for persistence. We know almost nothing about demographic rates, but in general, metapopulation structure makes a species like wolverines, more likely to be resilient to occasional disturbances that only occur in portions of the range. How independent are the perturbations throughout the range – will there be different occurrences/rates or bad snow years throughout the range or will they be broad scale? Overall increase in temperature everywhere. Snow variability will also occur, but there is still the overall temperature effect resulting in an earlier and earlier spring onset. North (cascades and northern Rockies)/south (sierras and southern Rockies) differences—when it is wet north, it is often dry in the south. But, there is also a hollowing out of snow in the middle. Source/sink phenomenon.

Interannual variability in northern Rockies has been noted. Precip following snow. North slope of northern Rockies act the same from year to year. Yellowstone has shown more variability. Temperature is the big unifier. We don't know with confidence how changes in the jet stream will affect things. In general, snow tends to be declining. El Niño complex. If you have a El Niño it test to be wetter and dryer in the northwest. If you have a big snow year in the northwest it tends to be dry in the Wasatch. A La Niña will be just the opposite.

How will climate change affect the heart of the range (defined by circumpolar latitude): There is less deep snow in the more northerly parts of the range. There will be more deep snow in the far north, which is not temperature limited in any part of the year. Need to remember food changes as well as snow changes.

If metapopulation dynamics for wolverines are important, will that become a liability when habitat patches get smaller and connectivity becomes stretched. If a population loses the dispersal capability, especially the ability for females to disperse, it is of greater consequences on the probability of persistence.

There are species with metapopulations with lambda less than 1, but losing those areas can still have negative consequences on the populations.

Dispersal success is variable depending on dispersal habitat type and quality.

So what for wolverines, up, down, or stay the same

In lower 48, wolverines have been increasing

- Climate is warming
- Evidence that not all habitat is not currently occupied and not at capacity, especially in southern portions
- No evidence that pop increase will cease
- Probably won't be able to detect a trend for at least the next decade
- Beyond 1o years, future of wolverines in the future is uncertain

- Climate is warming and will continue to warm and accelerate

DRAFT

- Snow is declining
- Wolverines depend on deep snow for denning
- Climate may suppress the population. We don't know whether it will flatten the increase, cause a decline, or something else.

No evidence that the population will continue to increase or decrease. If the desire is a number, climate change will likely decrease available habitat in the long term, but we don't know whether or what the effects on populations will be until the habitat boundaries and climate change bump into each other.

Number or years that are not suitable will likely increase because of declines in snow fall. It would be a stressor on the population. Whether the wolverine can adapt its phenology to address dissynchrony in day length/climate. Could lead to more isolation and smaller populations

Near future, wolverine will probably be fine (with uncertainty). Longer term may be different. Nearer term is not as big of a concern because habitat might not currently be filled. Longer term, it might be limited depending on the ability to adapt.

What are the uncertainties that lead to inconclusive conclusions:

- we don't know how years of variable snow depth affects productivity
- early spring melt affects competition
- changes in snow timing and snow coverage in food availability
- don't know how good persistent snow cover is as an index of wolverine habitat

in the long term (~100 years) we expect negative consequences, but we don't know how severe

Population is increasing and will likely increase based on projected increasing availability of large mammal food resources. Metapopulation structure makes the species resilient to perturbations. If the population goes above carrying capacity it might return to below maximum population levels. It is not at all straight forward that there will be short term negative consequences, but if the snow zone disappears from the mountains it will result in declines.

In shorter term, there is more reason for optimism. Increase of food/predator. More habitat in the short term but getting toward the late 2000's things get more grim

Deep snow dens – places with really deep snow are special and declining
It is hard since the 50 year increase is a rebound from persecution—in 20 years climate variability can be as great as climate change
Sample size of wolverines is so small that it will be difficult –how much time would be needed to know the population response to change?
Heat stress – main population is in northern area and is already high in elevation and there is less space for them to move up the mountain ranges than there are in southerly areas – perhaps where habitat is the least resilient already

Because of snow and climate—if they really need cold temperatures and cold temperatures will decline, there could be a dramatic decline.

Long term – pessimistic

DRAFT

Near term – we will see stasis or imperceptible changes

0 degree isotherm – Tim Link has student working % of snow versus rain across mid to late century. Justine Minder – changes in snowline. Pierce and Cayan: paper about detectability of snow variables through time.

What are the time frames around near and long term -- short term is about mid century; long is late century; short 2 or three decades, long 100 years or so. Short time to see response in management action. Long more than that.

All definitive statements are precluded on emissions forcing scenarios? Change over 100 years is based on emissions scenarios. Near term change is dependent on existing effects. Even if we stop all emissions now, we will keep warming over the next 100 years. We are on the mid-century trajectory now—the question is whether we accelerate a lot or a little depending on the actual emissions. More uncertainty the farther out you go. Snow will decline over the century regardless of actual emissions. Emissions in the models are more conservative than reality.

Concurrence around the table that there isn't a lot of optimism in the long term. In the short term there is a mix of optimism and pessimism tied to whether we are at carrying capacity and whether the species can adapt to occupy to change and to occupy the kinds of environments that they haven't historically occupy.

Can't resolve the future for the southern sierras and southern Rockies – some inversion effect. Might get more snow in those pockets in the near term. Snow enhancement patterns in these areas – haven't reached the 0 isotherm yet because of elevation. More snow in the early season when the average temp is cold. In spring, less accumulation and more melt. Jet stream affects the point at which you transition to dryer or wetter. Detectable snow signal not an overall precipitation signal at the lower elevations.

Why aren't wolverines living in places outside the snow layer now? They are showing us their range of ecological tolerance now. They aren't the most specialized, nor the most generalized carnivore in north America now.

We see some animals 1 in 7 year modus model, there are some in suboptimal but they aren't very common.

They were extirpated from trapping and use of poison. What they will go through in the future is very different. So we should not project their response to climate change to match their response to trapping and poisoning.

Wolverines have not had systematic surveys for wolverines. Most of our observations are incidental to road kill, cameras, trapping records, etc.

Record of occupancy outside snow zone is limited.

DRAFT

We have locations outside of snow layer in Idaho; it is limited. Animals of all kinds show up in places where they have no capacity to make a living. We find them outside, but we don't have evidence that they are thriving.

Magoun has a thesis showing a reproductive den outside Copeland's snow layer.

There might not be as much certainty as the McKelvey paper suggests.

DRAFT

# WOLVERINE EXPERT PANEL ELICITATION- Final List of Panelists (3-20-14)

| | MEMBERS OF PANEL DEVELOPMENT TEAM | Contacted | Responded | | April 3-4 | Paperwork completed |
|---|---|---|---|---|---|---|
| | **POTENTIAL PANELISTS** | | | | | |
| **Wildlife Ecology and Biology** | Dr. Bob Garrott | X | X | 406-994-2270: rgarrott@montana.edu | Yes. Has guest speaker on 4/3 should be fine. | YES |
| | Dr. Steve Buskirk | X | X | 307-766-5626: marten@uwyo.edu | Yes | YES |
| | Dr. Dan Pletscher | X | X | 406-396-4326: dan.pletscher@umontana.edu | YES | |
| | Dr. Eric Lofroth | X | X | 250-387-9798: Eric.Lofroth@gov.bc.ca | YES | YES |
| **Habitat Modeling, Remote Sensing** | Dr. Oz Garton | X | X | 208-885-7426; ogarton@uidaho.edu | YES | |
| | Dr. Jason Karl | X | X | 575-646-1301; 575.386.9125-cell jason.karl@ars.usda.gov | YES | YES |
| **Climate Change and Wildlife, Climate modeling** | Dr. John Abatzoglou | X | X | 208-885-6239; jabatzoglou@uidaho.edu | YES | |
| | Dr. Tim Link | X | X | 208-885-9465; tlink@uidaho.edu | YES | YES |
| | Dr. Sarah Kapnick | X | X | 609.452.6548: skapnick@princeton.edu | YES | YES |

| | |
|---|---|
| | Committed but paperwork not complete. |
| | |

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; imtiaz.rangwala@noaa.gov; coury.ditch@noaa.gov; aahe1976@colorado.edu; stephen_torbit@fws.gov; don.murray@noaa.gov; jest6889@colorado.edu; joseph.barsugli@noaa.gov; beli1098@colorado.edu
**Subject:** Confirmed FWS Wolverine project meeting
**Start:** Monday, April 3, 2017 3:00:00 PM
**End:** Monday, April 3, 2017 4:00:00 PM
**Location:** 1D708
**Attachments:** invite.ics

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action=VIEW&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MDNUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjM3Nzg2MDhlMGQwNzNjMjM5ZDEwZTA4NGI3NGZkOTY5NDI3OGZjNTU&ctz=America/Denver&hl=en>

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Changed: this go-to meeting was set up for us by Don Murray for our Monday meetings

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You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Mon Apr 3, 2017 3pm – 4pm Mountain Time
Where
Changed: 1D708 (map <https://maps.google.com/maps?q=1D708&hl=en> )
Calendar
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Who
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- organizer
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• candida.dewes@noaa.gov
• coury.ditch@noaa.gov
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**Subject:** Confirmed FWS Wolverine project meeting
**Attachments:** invite.ics

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Confirmed FWS Wolverine project meeting

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I'll be at th US Drought Monitor Forum but will be seeing email intermittently, or you can reach me by cell

this go-to meeting was set up for us by Don Murray for our Monday meetings

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You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Mon Apr 3, 2017 3pm – 4pm Mountain Time
Where
1D708 (map <https://maps.google.com/maps?q=1D708&hl=en> )
Calendar
john_guinotte@fws.gov
Who
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- organizer
• beli1098@colorado.edu
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• aahe1976@colorado.edu
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• jest6889@colorado.edu
• candida.dewes@noaa.gov
• coury.ditch@noaa.gov
• imtiaz.rangwala@noaa.gov

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action=RESPOND&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MDNUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjM3Nzg2MDhlMGQwNzNjMjM5ZDEwZTA4NGI3NGZkOTY5NDI3OGZjNTU&ctz=America/Denver&hl=en>
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| | |
|---|---|
| **From:** | Ben Livneh |
| **To:** | Andrea Ray - NOAA Federal |
| **Cc:** | aahe1976@colorado.edu; coury.ditch@noaa.gov; imtiaz.rangwala@noaa.gov; joseph.barsugli@noaa.gov; don.murray@noaa.gov; stephen_torbit@fws.gov; jest6889@colorado.edu; john_guinotte@fws.gov |
| **Subject:** | Re: Updated Invitation: Confirmed FWS Wolverine project meeting @ Mon Apr 3, 2017 3pm - 4pm (beli1098@colorado.edu) |
| **Date:** | Monday, April 3, 2017 3:01:02 PM |

Running 5-10 minutes behind!

Sent from my phone. Please forgive the brevity, the typos, and the lack of nuance

On Apr 2, 2017 6:46 PM, <andrea.ray@noaa.gov> wrote:

> **This event has been changed.**
>
> ## Confirmed FWS Wolverine project meeting
>
> **more details »**
>
> **Changed:** Joe will be starting the go-to meeting b/c I'll be calling in from a meeting off-site. Imtiaz and Candida, you may not be needed for all of this meeting, but please join for the first part in case there are things you need to coordinate on.
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>
> https://global.gotomeeting.com/join/925942125
> You can also dial in using your phone.
> United States +1 (408) 650-3123
> Access Code: 925-942-125
>
> When Mon Apr 3, 2017 3pm – 4pm Mountain Time
>
> Where 1D708 (map)
>
> Calendar beli1098@colorado.edu
>
> Who
> - andrea.ray@noaa.gov - organizer
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> - john_guinotte@fws.gov
> - don.murray@noaa.gov
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> - stephen_torbit@fws.gov
> - coury.ditch@noaa.gov
>
> Going? **Yes** - **Maybe** - **No** more options »

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**Subject:** Confirmed FWS Wolverine project meeting
**Start:** Monday, April 10, 2017 3:00:00 PM
**End:** Monday, April 10, 2017 4:00:00 PM
**Attachments:** invite.ics

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Changed: Confirmed FWS Wolverine project meeting

Changed: We'll discuss anything left on the report before sending it to Steve and John on April 12th, AND get organized for our presentation to the APA team on Thursday April 13th at 1p

Our APA presentation will follow the organization of the presentation at FWS, but we will have the new results from ROMO to include, and the comparison with McKelvey

this go-to meeting was set up for us by Don Murray for our Monday meetings through December

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Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

tachment 20170404 141818_EM_Confirmed FWS Wolverine project meeting.ics (3596 Bytes) cannot be converted to PDF form

| | |
|---|---|
| **From:** | Joe Barsugli |
| **To:** | Andrea Ray; Imtiaz Rangwala; Stephen Torbit; Guinotte, John; Candida Dewes |
| **Subject:** | Proposed "neutral" Scenario Names for Wolverine |
| **Date:** | Wednesday, April 5, 2017 7:25:57 PM |
| **Attachments:** | Fig_S1_ensemble34_scatter_ROMO (1).png<br>Fig_S2_ensemble34_scatter_GLAC.png |

---

Proposed "neutral" Scenario Names for Wolverine. Imtiaz's scatterplots of the scenarios are attached for reference.

Propose to delineate the temperature scenarios by rounding to the nearest whole number. So T1 means a change somewhere between 0.5 and 1.5 C, T2 means 1.5-2.5C change, etc. D means 0-10% drier, W means 0-10% wetter, and WW means approx. 20% wetter. I have given textual names that we could use instead, or in addition , as in T2W (Central Scenario), or T1W (Warm/Wet Scenario).

One other alternative is to note the percent change in precipitation as W7 for 7%wetter, and D5 for 5 % drier.

For GLAC:

# Proposed abbreviation, proposed textual name, alternate abbreviation

1 T2W Central Moderate Snow Change T2W7
2 T3WW Hot/Very Wet
T3W20
3 T4W Hot/Wet Greatest Snow Change T4W10
4 T1W Warm/Wet Least Snow Change T1W10
5 T2D Warm/Dry T2D5

for ROMO:

1 T2W Central Moderate Snow Change T2W5
2 T3D Hot/Dry Greatest Snow Change T3D5
3 T4WW Hot/Very
Wet T4W17
4 T1W Warm/Wet Least Snow Change T1W6
5 T1D Warm/Dry T1D5

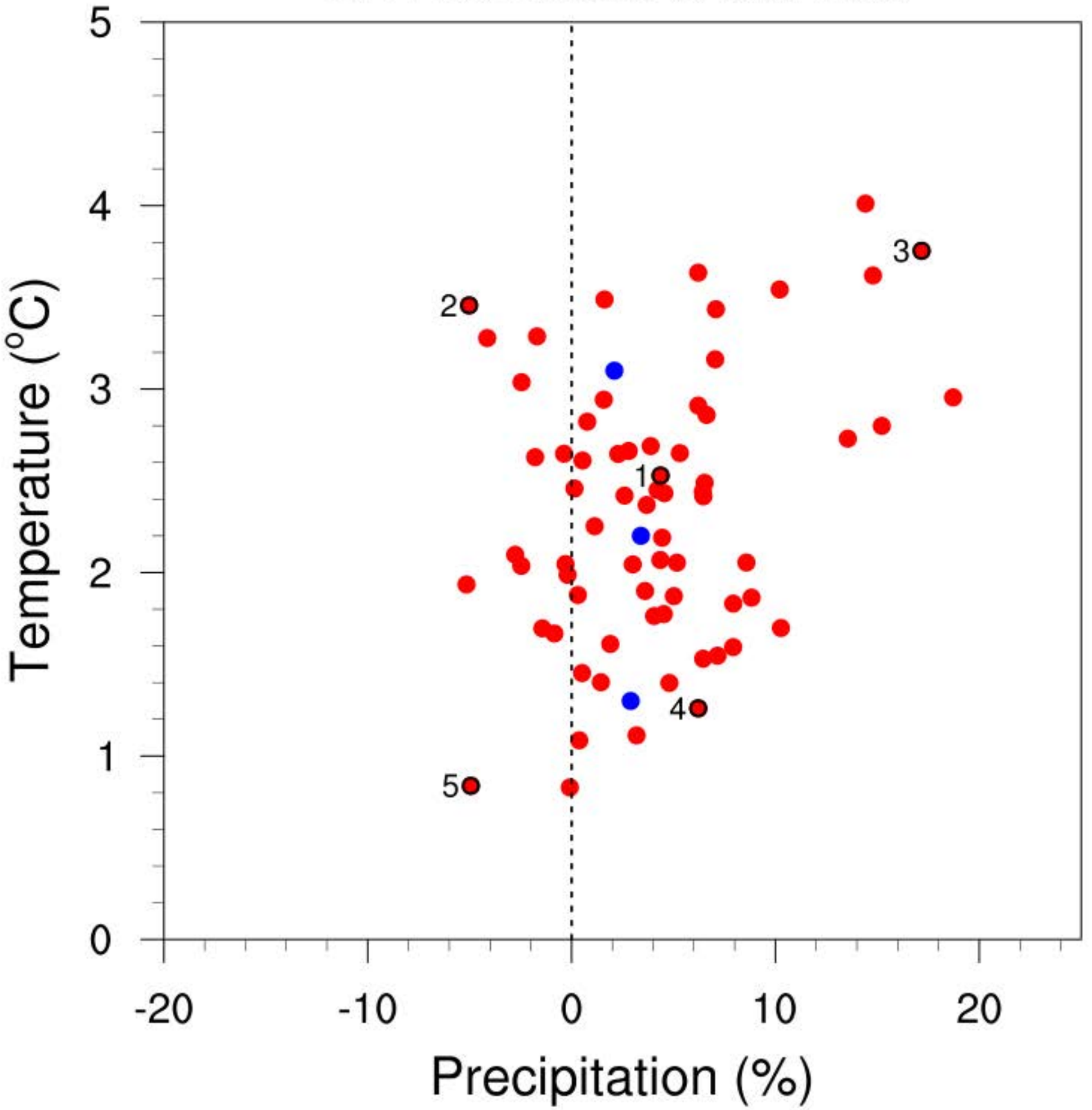
Please give feedback soon so I can get these to our graphics person to label the figures.

Joe

--
Joseph Barsugli
Research Scientist III
CIRES, UCB 216
University of Colorado at Boulder
cell:720-244-5922

# Rocky Mountain NP (38-42N,105-108W): 2055 (Oct-May)

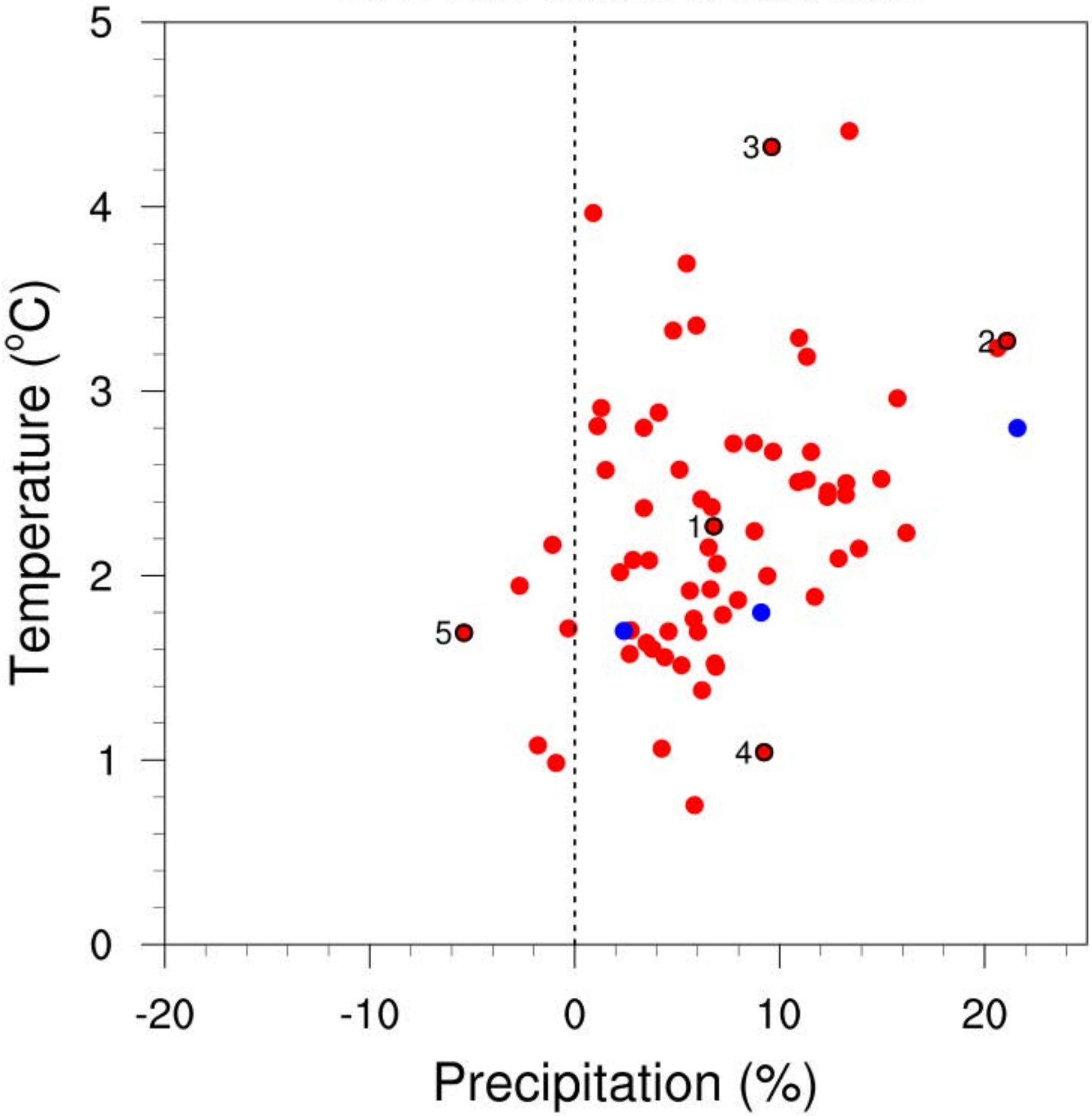
2041-2070 relative to 1986-2015




| | | | | | |
|---|---|---|---|---|---|
| 1 | CNRM-CM5.1.rcp85 | 3 | MIROC-ESM.1.rcp85 | 5 | FIO-ESM.1.rcp45 |
| 2 | HadGEM2-ES.1.rcp85 | 4 | GISS-E2-R.1.rcp45 | | |

# Glacier NP (47-49.4N,115.17-112.33W): 2055 (Oct-May)

2041-2070 relative to 1986-2015




| | | | | | |
|---|---|---|---|---|---|
| 1 | CNRM-CM5.1.rcp85 | 3 | MIROC-ESM.1.rcp85 | 5 | FIO-ESM.1.rcp85 |
| 2 | CanESM2.1.rcp85 | 4 | GISS-E2-R.1.rcp45 | | |

**From:** Imtiaz Rangwala
**To:** Andrea Ray - NOAA Federal; Joe Barsugli
**Cc:** Stephen Torbit; Guinotte, John; Candida Dewes
**Subject:** Re: Proposed "neutral" Scenario Names for Wolverine
**Date:** Thursday, April 6, 2017 9:48:00 AM

---

Yes, me too. Thanks Joe. This has come well. I like what you have put as proposed -- its pretty objective without being too specific. Also like the textual names, just a little bit concerned about the "central" scenario --- studies can focus too strongly on that one scenario with that kind of naming.

Imtiaz

Imtiaz Rangwala, Ph.D.
Research Scientist
Physical Sciences Division, NOAA ESRL
CIRES/Western Water Assessment, University of Colorado
325 Broadway, R/PSD NOAA ESRL
Boulder, CO 80305
Phone: (303)497-6544
http://wwa.colorado.edu/about/rangwala

CIRES APA Team Lead

Climate Team PI, North Central Climate Science Center
http://nccsc.colostate.edu/climate-drivers/team

On 4/6/17 9:11 AM, Andrea Ray - NOAA Federal wrote:

> Hi all, I think these work. FYI, Joe let me know that Barb is out today, but he wants to get these to her so she can work on them tomorrow.
>
> I'm just getting back from the USDM forum, and will be in later this morning -- a part on my braces broke yesterday, and I'm going in to the orthodontist this morning before heading in.
>
> Andrea
>
> On Wed, Apr 5, 2017 at 7:25 PM, Joe Barsugli <joseph.barsugli@noaa.gov> wrote:
>
> > Proposed "neutral" Scenario Names for Wolverine. Imtiaz's scatterplots of the scenarios are attached for reference.
> >
> > Propose to delineate the temperature scenarios by rounding to the nearest whole number. So T1 means a change somewhere between 0.5 and 1.5 C, T2 means 1.5-2.5C change, etc. D means 0-10% drier, W means 0-10% wetter, and WW means approx. 20% wetter. I have given textual names that we could use instead, or in addition , as in T2W (Central Scenario), or T1W (Warm/Wet Scenario).
> >
> > One other alternative is to note the percent change in precipitation as W7 for 7%wetter, and D5 for 5 % drier.

For GLAC:

# Proposed abbreviation, proposed textual name, alternate abbreviation

1 T2W Central Moderate Snow Change T2W7
2 T3WW Hot/Very Wet T3W20
3 T4W Hot/Wet Greatest Snow Change T4W10
4 T1W Warm/Wet Least Snow Change T1W10
5 T2D Warm/Dry T2D5

for ROMO:

1 T2W Central Moderate Snow Change T2W5
2 T3D Hot/Dry Greatest Snow Change T3D5
3 T4WW Hot/Very Wet T4W17
4 T1W Warm/Wet Least Snow Change T1W6
5 T1D Warm/Dry T1D5

Please give feedback soon so I can get these to our graphics person to label the figures.

Joe

--
Joseph Barsugli
Research Scientist III
CIRES, UCB 216
University of Colorado at Boulder
cell:720-244-5922

--
--
Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

**From:** Guinotte, John
**To:** Erich Peitzsch
**Subject:** Re: avalanche info for wolverine
**Date:** Thursday, April 6, 2017 11:35:38 AM

---

Hi Erich, Is it ok if I call you at 9:30 instead of 9 tomorrow?
Thanks John

John Guinotte
Fish and Wildlife Biologist
Ecological Services
U.S. Fish and Wildlife Service
Mountain Prairie Region 6
134 Union Blvd., Lakewood, CO 80228
303-236-4264
john_guinotte@fws.gov

On Wed, Apr 5, 2017 at 11:26 AM, Erich Peitzsch <epeitzsch@usgs.gov> wrote:

> Hi John,
>
> Friday works for me. The morning is better. Give a call 406.599.9970.
>
> Cheers
> Erich
>
> Erich Peitzsch
> Physical Scientist
> USGS Northern Rocky Mountain Science Center
> 215 Mather Dr.
> West Glacier, MT 59936
>
> ---
>
> On: 05 April 2017 10:57, "Guinotte, John" <john_guinotte@fws.gov> wrote:
> Dear Erich,
>
> I spoke to Karl Birkeland yesterday and he gave me your name. I'm wondering if you have some time to chat with me on the phone this week or next? We are working on a species status assessment for the wolverine in the lower 48. NOAA and CU are doing some work for us on predicting future snowpack in Glacier and Rocky Mountain National Parks currently. I've found some interesting relationships re the location of wolverine den sites in Glacier and slope. Many of the den sites are located in potential avalanche run-outs. I can show you some slides to illustrate this. I have a few questions for you regarding this and identification of potential avalanche run-outs.
>
> Thanks John
>
> John Guinotte, PhD
> Fish and Wildlife Biologist
> Ecological Services
> U.S. Fish and Wildlife Service
> Mountain Prairie Region 6
> 134 Union Blvd., Lakewood, CO 80228
> 303-236-4264

john_guinotte@fws.gov

**From:** Guinotte, John
**To:** Peitzsch, Erich
**Subject:** Re: avalanche info for wolverine
**Date:** Thursday, April 6, 2017 4:51:42 PM

---

Sounds good Erich.
I'll call you then.

Best, John

On Thu, Apr 6, 2017 at 3:01 PM, Peitzsch, Erich <epeitzsch@usgs.gov> wrote:

> Hi John,
>
> Yeah, Monday isn't good, but let's shoot for Tuesday at 1:00 pm.
>
> Cheers
> Erich
>
> _____
> Erich Peitzsch
> USGS Northern Rocky Mountain Science Center
> 215 Mather Drive
> West Glacier, MT 59936
> (mobile) 406.599.9970
> (office) 406.888.7925
> https://www.usgs.gov/norock/ccme
>
> On Thu, Apr 6, 2017 at 12:10 PM, Guinotte, John <john_guinotte@fws.gov> wrote:
>
> > Sorry for the emails Erich. Is it possible to reschedule our call tomorrow to sometime early next week? I've had something come up here that is going to take most of the morning tomorrow. If next week doesn't work, I could talk anytime 1-4pm tomorrow. Thanks John
> >
> > John Guinotte
> > Fish and Wildlife Biologist
> > Ecological Services
> > U.S. Fish and Wildlife Service
> > Mountain Prairie Region 6
> > 134 Union Blvd., Lakewood, CO 80228
> > 303-236-4264
> > john_guinotte@fws.gov
> >
> > On Wed, Apr 5, 2017 at 11:26 AM, Erich Peitzsch <epeitzsch@usgs.gov> wrote:
> >
> > > Hi John,
> > >
> > > Friday works for me. The morning is better. Give a call 406.599.9970.
> > >
> > > Cheers
> > > Erich
> > >
> > > Erich Peitzsch

Physical Scientist
USGS Northern Rocky Mountain Science Center
215 Mather Dr.
West Glacier, MT 59936

---

On: 05 April 2017 10:57, "Guinotte, John" <john_guinotte@fws.gov> wrote:

Dear Erich,

I spoke to Karl Birkeland yesterday and he gave me your name. I'm wondering if you have some time to chat with me on the phone this week or next? We are working on a species status assessment for the wolverine in the lower 48. NOAA and CU are doing some work for us on predicting future snowpack in Glacier and Rocky Mountain National Parks currently. I've found some interesting relationships re the location of wolverine den sites in Glacier and slope. Many of the den sites are located in potential avalanche run-outs. I can show you some slides to illustrate this. I have a few questions for you regarding this and identification of potential avalanche run-outs.

Thanks John

John Guinotte, PhD
Fish and Wildlife Biologist
Ecological Services
U.S. Fish and Wildlife Service
Mountain Prairie Region 6
134 Union Blvd., Lakewood, CO 80228
303-236-4264
john_guinotte@fws.gov

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; stephen_torbit@fws.gov; don.murray@noaa.gov; joseph.barsugli@noaa.gov; coury.ditch@noaa.gov; aahe1976@colorado.edu; jest6889@colorado.edu; imtiaz.rangwala@noaa.gov
**Subject:** Cancelled FWS Wolverine project meeting
**Start:** Monday, April 10, 2017 3:00:00 PM
**End:** Monday, April 10, 2017 4:00:00 PM
**Attachments:** invite.ics

---

This event has been changed.

more details » <https://www.google.com/calendar/event?
action=VIEW&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MTBUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmZlYTgzZjlmYjk2OTI3NDRkZTJlZjAzNTRmZWY0Y2RjMGYxODY5MGQ&ctz=America/Denver&hl=en>

Changed: Cancelled FWS Wolverine project meeting

Changed: CANCELLED -- to be rescheduled either Tues am or Wed -- stand by!
We'll discuss anything left on the report before sending it to Steve and John on April 12th, AND get organized for our presentation to the APA team on Thursday April 13th at 1p

Our APA presentation will follow the organization of the presentation at FWS, but we will have the new results from ROMO to include, and the comparison with McKelvey

this go-to meeting was set up for us by Don Murray for our Monday meetings through December

https://global.gotomeeting.com/join/925942125 <https://www.google.com/url?q=https%3A%2F%2Fglobal.gotomeeting.com%2Fjoin%2F925942125&sa=D&ust=1491853891651000&usg=AFQjCNGK4JQO1rhGyg4AeV7fGQTIdjb_hg>
You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Mon Apr 10, 2017 3pm – 4pm Mountain Time
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• stephen_torbit@fws.gov
• don.murray@noaa.gov
• joseph.barsugli@noaa.gov
• beli1098@colorado.edu
• coury.ditch@noaa.gov
• aahe1976@colorado.edu
• jest6889@colorado.edu
• john_guinotte@fws.gov
• imtiaz.rangwala@noaa.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MTBUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmZlYTgzZjlmYjk2OTI3NDRkZTJlZjAzNTRmZWY0Y2RjMGYxODY5MGQ&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?
action=RESPOND&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MTBUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmZlYTgzZjlmYjk2OTI3NDRkZTJlZjAzNTRmZWY0Y2RjMGYxODY5MGQ&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?
action=RESPOND&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MTBUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmZlYTgzZjlmYjk2OTI3NDRkZTJlZjAzNTRmZWY0Y2RjMGYxODY5MGQ&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?
action=VIEW&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MTBUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmZlYTgzZjlmYjk2OTI3NDRkZTJlZjAzNTRmZWY0Y2RjMGYxODY5MGQ&ctz=America/Denver&hl=en>

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tachment 20170410 115152_EM_Cancelled FWS Wolverine project meeting.ics (3508 Bytes) cannot be converted to PDF form

**From:** Andrea Ray - NOAA Federal
**To:** Guinotte, John
**Subject:** Re: sizes of areas? Re: Accepted: Confirmed FWS Wolverine project meeting @ Mon Apr 10, 2017 15:00 - 16:00 (andrea.ray@noaa.gov)
**Date:** Monday, April 10, 2017 1:56:04 PM

---

Thanks!

On Mon, Apr 10, 2017 at 1:48 PM, Guinotte, John <john_guinotte@fws.gov> wrote:

> GLAC = 2901 km2
> ROMO = 1597 km2
>
> On Mon, Apr 10, 2017 at 1:10 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:
>
> > John -- have you sent the calculations of the sized of the two areas? you put in a comment, "I'll have to calculate the areas in GIS and get back to you" thanks!
> >
> > On Mon, Apr 10, 2017 at 12:20 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:
> >
> > > sounds good, I'll be here for a while....
> > >
> > > On Mon, Apr 10, 2017 at 12:16 PM, Guinotte, John <john_guinotte@fws.gov> wrote:
> > >
> > > > Hi Andrea, Tomorrow am works for me. I can give you a ring later this afternoon re the charts. I'm working on some last minute analysis for boreal toad now. Best, John
> > > >
> > > > On Mon, Apr 10, 2017 at 11:21 AM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:
> > > >
> > > > > John -- turns out neither Joe or Ben are available for this -- would tomorrow morning work? I'm about to cancel it, I'm looking for another time for the group to discuss anything left on the report before sending it to Steve and John on April 12th, AND get organized for our presentation to the APA team on Thursday April 13th at 1p.
> > > > >
> > > > > I'm in the office all day & available to talk to you -- in particular, I'd like to talk to you about the bar charts joe sent for ROMO-- they're pretty dramatic and a different story than GLAC, suggesting a different story for the biology too.
> > > > >
> > > > > Andrea
> > > > >
> > > > > On Mon, Apr 10, 2017 at 10:18 AM, <john_guinotte@fws.gov> wrote:
> > > > >
> > > > > > **john_guinotte@fws.gov has accepted this invitation.**
> > > > > >
> > > > > > **Confirmed FWS Wolverine project meeting**
> > > > > >
> > > > > > We'll discuss anything left on the report before sending it to Steve and John on April 12th, AND get organized for our presentation to the APA team on Thursday April 13th at 1p

Our APA presentation will follow the organization of the presentation at FWS, but we will have the new results from ROMO to include, and the comparison with McKelvey

this go-to meeting was set up for us by Don Murray for our Monday meetings through December

https://global.gotomeeting.com/join/925942125
You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When Mon Apr 10, 2017 15:00 – 16:00 Mountain Time

Calendar andrea.ray@noaa.gov

Who
- andrea.ray@noaa.gov - organizer
- john_guinotte@fws.gov
- beli1098@colorado.edu
- joseph.barsugli@noaa.gov
- jest6889@colorado.edu
- candida.dewes@noaa.gov
- stephen_torbit@fws.gov
- don.murray@noaa.gov
- aahe1976@colorado.edu
- coury.ditch@noaa.gov
- imtiaz.rangwala@noaa.gov

Invitation from Google Calendar

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To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More.

--
--
Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov

> > > www.researchgate.net/profile/Andrea_Ray2
>
> --
> --
> Andrea J. Ray, Ph.D.
> NOAA Earth System Research Lab, Mailcode R/PSD1
> 325 Broadway, Boulder, CO 80305-3328
> (tel) 303-497-6434
> (fax) 303-497-6449
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> www.researchgate.net/profile/Andrea_Ray2

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(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; theo.stein@noaa.gov; barb.deluisi@noaa.gov; imtiaz.rangwala@noaa.gov; Kathleen Human; stephen_torbit@fws.gov; aahe1976@colorado.edu; candida.dewes@noaa.gov; joseph.barsugli@noaa.gov; beli1098@colorado.edu
**Subject:** Wolverine presentation to APA Team science mtg
**Start:** Thursday, April 13, 2017 1:00:00 PM
**End:** Thursday, April 13, 2017 2:30:00 PM
**Location:** 1D708 & go-to meeting
**Attachments:** invite.ics

---

This event has been changed.

more details » <https://www.google.com/calendar/event?action=VIEW&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>

Wolverine presentation to APA Team science mtg

Changed: "Wolverine Climate Change and Snow Refugia: An Assessment for the US Fish and Wildlife Service"

this go-to meeting was set up for us by Don Murray for our Monday meetings through December

https://global.gotomeeting.com/join/925942125 <https://www.google.com/url?q=https%3A%2F%2Fglobal.gotomeeting.com%2Fjoin%2F925942125&sa=D&ust=1491864278792000&usg=AFQjCNEz9RuvH0cmCUi6-KWmOM5hENcEkQ>
You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Thu Apr 13, 2017 1pm – 2:30pm Mountain Time
Where
1D708 & go-to meeting (map <https://maps.google.com/maps?q=1D708+%26+go-to+meeting&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• theo.stein@noaa.gov
• barb.deluisi@noaa.gov
• imtiaz.rangwala@noaa.gov
• Kathleen Human
• stephen_torbit@fws.gov
• aahe1976@colorado.edu
• candida.dewes@noaa.gov
• joseph.barsugli@noaa.gov
• john_guinotte@fws.gov
• beli1098@colorado.edu

Going?
Yes <https://www.google.com/calendar/event?action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?action=VIEW&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for updated invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

nment 20170410 144459_EM_Wolverine presentation to APA Team science mt.ics (2857 Bytes) cannot be converted to PDF fo

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; joseph.barsugli@noaa.gov; candida.dewes@noaa.gov; beli1098@colorado.edu; imtiaz.rangwala@noaa.gov; stephen_torbit@fws.gov
**Subject:** Wolverine project call with John and Steve
**Start:** Tuesday, April 11, 2017 9:30:00 AM
**End:** Tuesday, April 11, 2017 10:30:00 AM
**Location:** we"ll use the usual go-to meeting screen and audio & in person in, DSRC - 1D708
**Attachments:** invite.ics

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more details » <https://www.google.com/calendar/event?
action=VIEW&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>

Wolverine project call with John and Steve

Discuss final details on wolverine report and also the map that John sent that I emailed to you

Ben -- would be great if you could be on; IR and CD, not necessary; Joe I know is available, as are Steve and John

When
Tue Apr 11, 2017 9:30am – 10:30am Mountain Time
Where
conf line TBA (map <https://maps.google.com/maps?q=conf+line+TBA&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• john_guinotte@fws.gov
• joseph.barsugli@noaa.gov
• candida.dewes@noaa.gov
• beli1098@colorado.edu
• imtiaz.rangwala@noaa.gov
• stephen_torbit@fws.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?
action=RESPOND&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?
action=RESPOND&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?
action=VIEW&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

achment 20170410 155539_EM_ Wolverine project  call with John and Steve.ics (2108 Bytes) cannot be converted to PDF form

**From:** Andrea Ray - NOAA Federal
**To:** Guinotte, John
**Subject:** Re: Invitation: Wolverine project call with John and Steve @ Tue Apr 11, 2017 9:30am - 10:30am (john_guinotte@fws.gov)
**Date:** Monday, April 10, 2017 4:19:48 PM

---

yes, I just checked, she can,

On Mon, Apr 10, 2017 at 4:06 PM, Guinotte, John <john_guinotte@fws.gov> wrote:

> Hi Andrea, hope Candida can join as we have a couple of questions for her. best, John
>
> John Guinotte
> Fish and Wildlife Biologist
> Ecological Services
> U.S. Fish and Wildlife Service
> Mountain Prairie Region 6
> 134 Union Blvd., Lakewood, CO 80228
> 303-236-4264
> john_guinotte@fws.gov
>
> On Mon, Apr 10, 2017 at 3:55 PM, <andrea.ray@noaa.gov> wrote:
>
> **Wolverine project call with John and Steve** **more details »**
>
> Discuss final details on wolverine report and also the map that John sent that I emailed to you
>
> Ben -- would be great if you could be on; IR and CD, not necessary; Joe I know is available, as are Steve and John
>
> When Tue Apr 11, 2017 9:30am – 10:30am Mountain Time
>
> Where conf line TBA (map)
>
> Calendar john_guinotte@fws.gov
>
> Who
> - andrea.ray@noaa.gov - organizer
> - john_guinotte@fws.gov
> - joseph.barsugli@noaa.gov
> - candida.dewes@noaa.gov
> - beli1098@colorado.edu
> - imtiaz.rangwala@noaa.gov
> - stephen_torbit@fws.gov
>
> Going? **Yes** - **Maybe** - **No** more options »
>
> Invitation from Google Calendar
>
> You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for invitations on calendar john_guinotte@fws.gov.
>
> To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.
>
> Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More.

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Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; imtiaz.rangwala@noaa.gov; beli1098@colorado.edu; joseph.barsugli@noaa.gov; stephen_torbit@fws.gov; candida.dewes@noaa.gov
**Subject:** Wolverine project call with John and Steve
**Start:** Tuesday, April 11, 2017 9:30:00 AM
**End:** Tuesday, April 11, 2017 10:30:00 AM
**Location:** we"ll use the usual go-to meeting screen and audio & in person in, DSRC - 1D708
**Attachments:** invite.ics

---

This event has been changed.

more details » <https://www.google.com/calendar/event?
action=VIEW&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>

Wolverine project call with John and Steve

Changed: Discuss final details on wolverine report and also the map that John sent that I emailed to you, Ben -- would be great if you could be on; IR and CD, not necessary; Joe I know is available, as are Steve and John and we'll start talking about the presentation for Thursday

https://global.gotomeeting.com/join/925942125 <https://www.google.com/url?q=https%3A%2F%2Fglobal.gotomeeting.com%2Fjoin%2F925942125&sa=D&ust=1491873355555000&usg=AFQjCNGf97gsWqp-IJP50KUiLP35iKEYlQ>
You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Tue Apr 11, 2017 9:30am – 10:30am Mountain Time
Where
Changed: we'll use the usual go-to meeting screen and audio & in person in, DSRC - 1D708 (map <https://maps.google.com/maps?q=we%27ll+use+the+usual+go-to+meeting+screen+and+audio+%26+in+person+in,+DSRC+-+1D708&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• imtiaz.rangwala@noaa.gov
• john_guinotte@fws.gov
• beli1098@colorado.edu
• joseph.barsugli@noaa.gov
• stephen_torbit@fws.gov
• candida.dewes@noaa.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?
action=RESPOND&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?
action=RESPOND&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?
action=VIEW&eid=czl2bGgwczlzYWFibzQ2cGs3YTBpa2p2OWcgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmE0NTRiM2NmYWUxYjI5NDRmMzc2ZTFmMmMzOWU5MzcxNWM2OTU5NGU&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for updated invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

achment 20170410 171612_EM_ Wolverine project  call with John and Steve.ics (2574 Bytes) cannot be converted to PDF form

**From:** Andrea Ray - NOAA Federal
**To:** Guinotte, John
**Subject:** Re: Invitation: Wolverine project call with John and Steve @ Tue Apr 11, 2017 9:30am - 10:30am (john_guinotte@fws.gov)
**Date:** Monday, April 10, 2017 5:16:29 PM

---

never mind -- we'll use our go-to meeting

On Mon, Apr 10, 2017 at 5:09 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:

> Also -- could we use your conference line? I haven't heard back about whether ours is available. thanks!
>
> On Mon, Apr 10, 2017 at 4:19 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:
>
> > yes, I just checked, she can,
> >
> > On Mon, Apr 10, 2017 at 4:06 PM, Guinotte, John <john_guinotte@fws.gov> wrote:
> >
> > > Hi Andrea, hope Candida can join as we have a couple of questions for her. best, John
> > >
> > > John Guinotte
> > > Fish and Wildlife Biologist
> > > Ecological Services
> > > U.S. Fish and Wildlife Service
> > > Mountain Prairie Region 6
> > > 134 Union Blvd., Lakewood, CO 80228
> > > 303-236-4264
> > > john_guinotte@fws.gov
> > >
> > > On Mon, Apr 10, 2017 at 3:55 PM, <andrea.ray@noaa.gov> wrote:
> > >
> > > > **Wolverine project call with John and Steve** **more details »**
> > > >
> > > > Discuss final details on wolverine report and also the map that John sent that I emailed to you
> > > >
> > > > Ben -- would be great if you could be on; IR and CD, not necessary; Joe I know is available, as are Steve and John
> > > >
> > > > When Tue Apr 11, 2017 9:30am – 10:30am Mountain Time
> > > > Where conf line TBA (map)
> > > > Calendar john_guinotte@fws.gov
> > > > Who
> > > > - andrea.ray@noaa.gov - organizer
> > > > - john_guinotte@fws.gov
> > > > - joseph.barsugli@noaa.gov
> > > > - candida.dewes@noaa.gov
> > > > - beli1098@colorado.edu
> > > > - imtiaz.rangwala@noaa.gov
> > > > - stephen_torbit@fws.gov
> > > >
> > > > Going? **Yes** - **Maybe** - **No** more options »
```
```

Invitation from Google Calendar

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More.

--
--
Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

--
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Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

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325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

**From:** Andrea Ray - NOAA Federal
**To:** Ben Livneh; John Guinotte; Steve Torbit; Candida Dewes - NOAA Affiliate
**Subject:** Fwd: Wolverine Graphics Instructions -- Both Study Areas
**Date:** Tuesday, April 11, 2017 9:57:14 AM
**Attachments:** histROMOSWE(51507).png.trimmed.png
histROMOSWE(51511).png.trimmed.png
histROMOSWE(51512).png.trimmed.png
histROMOSWE(51502).png.trimmed.png

---

---------- Forwarded message ----------
From: **Joe Barsugli** <joseph.barsugli@noaa.gov>
Date: Mon, Apr 10, 2017 at 11:36 AM
Subject: Re: Wolverine Graphics Instructions -- Both Study Areas
To: Andrea Ray - NOAA Federal <andrea.ray@noaa.gov>
Cc: Barb Deluisi - NOAA Federal <barb.deluisi@noaa.gov>

I am attaching the missing historical ROMO trimmed graphics. I have also uploaded them to the Drive. And now that I checked -- the pixellation is real -- you are seeing the 250 meter grid of the model.

Joe

On 4/10/17 10:33 AM, Andrea Ray - NOAA Federal wrote:

> thanks, Joe -- and Barb, feel free to give me a call if you have questions. Andrea
>
> On Mon, Apr 10, 2017 at 11:25 AM, Joe Barsugli <joseph.barsugli@noaa.gov> wrote:
>
> > 1. hmmm let me check on the historical files
> >
> > 2. yes, the same base verbiage
> >
> > 3. other e-mail -- nothing we can do note trhat the area is smalleer so pixelation of the 250 meter gridbixes might be visible -- that is OK.
> >
> > On 4/10/17 10:03 AM, Barb Deluisi - NOAA Federal wrote:

Hi Joe and Andrea,

I've made progress on the figures. A couple things that have come up...

- There are no 'historical' files for the ROMO figures in the google folder.
- Did you want to use the same 'base verbiage' for the captions that we used on the test figure? It was: "Historical and projected May 15th Snow Water Equivalent (meters). Historical simulation year 2011 (top left), and for three future scenarios applied to 2011, lowest change (top right), moderate change (bottom left), and greatest change (bottom right). Scenarios are listed in Figure 5-7." Perhaps Andrea could stop by if needed?

Thanks,
Barb

---
Barb DeLuisi
Communication Specialist
NOAA Earth System Research Laboratory
Physical Sciences Division
Email: Barb.DeLuisi@noaa.gov
Phone: 303-497-4233

On Fri, Apr 7, 2017 at 2:35 PM, Joe Barsugli <joseph.barsugli@noaa.gov> wrote:

> attached instructions. The files are on the Google Drive in the folder I shared.
>
> Joe
>
> --
> Joseph Barsugli
> Research Scientist III
> CIRES, UCB 216
> University of Colorado at Boulder
> cell:720-244-5922

--

Joseph Barsugli
Research Scientist III
CIRES, UCB 216
University of Colorado at Boulder
cell:720-244-5922

--
--
Andrea J. Ray, Ph.D.
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andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

--
Joseph Barsugli
Research Scientist III
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University of Colorado at Boulder
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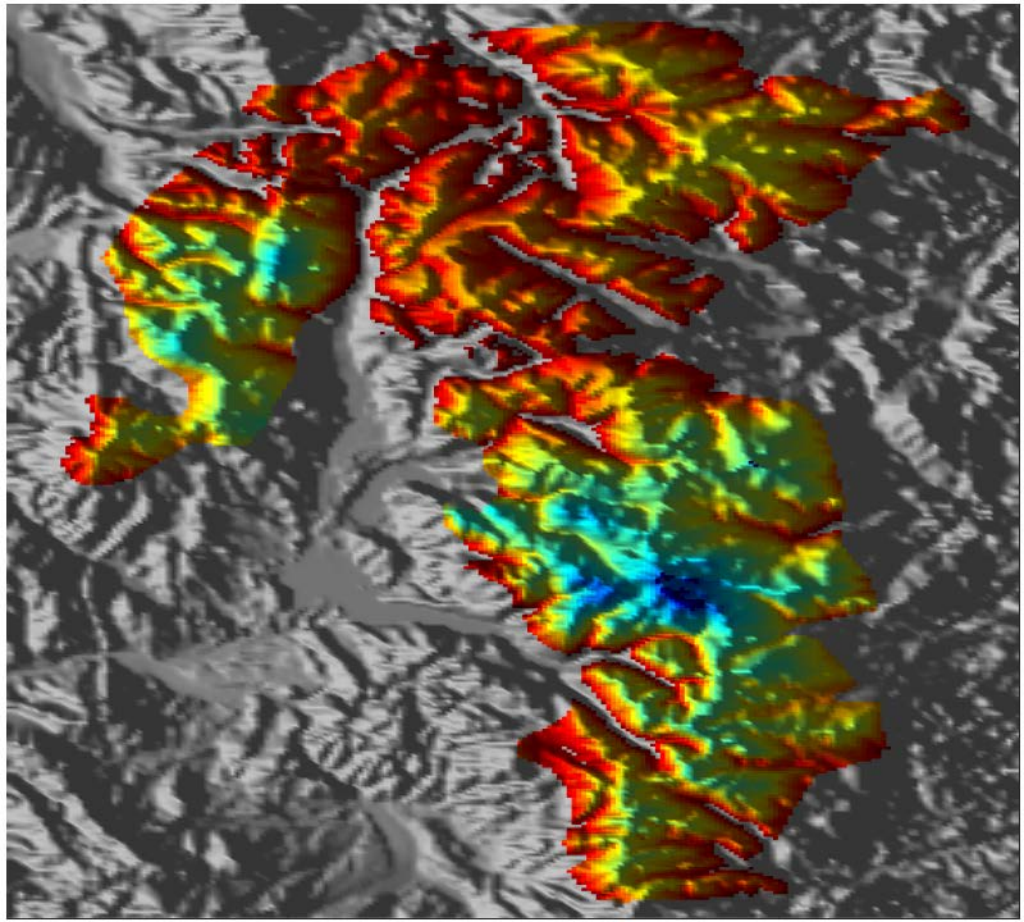
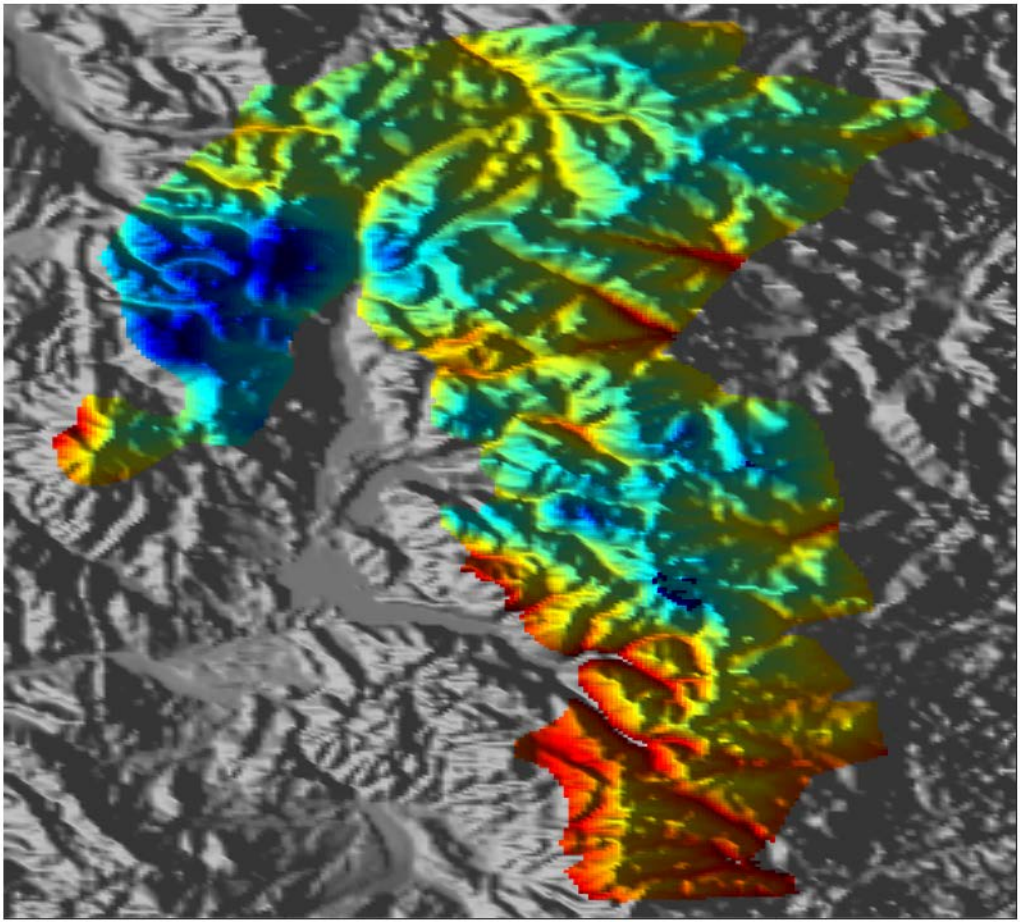
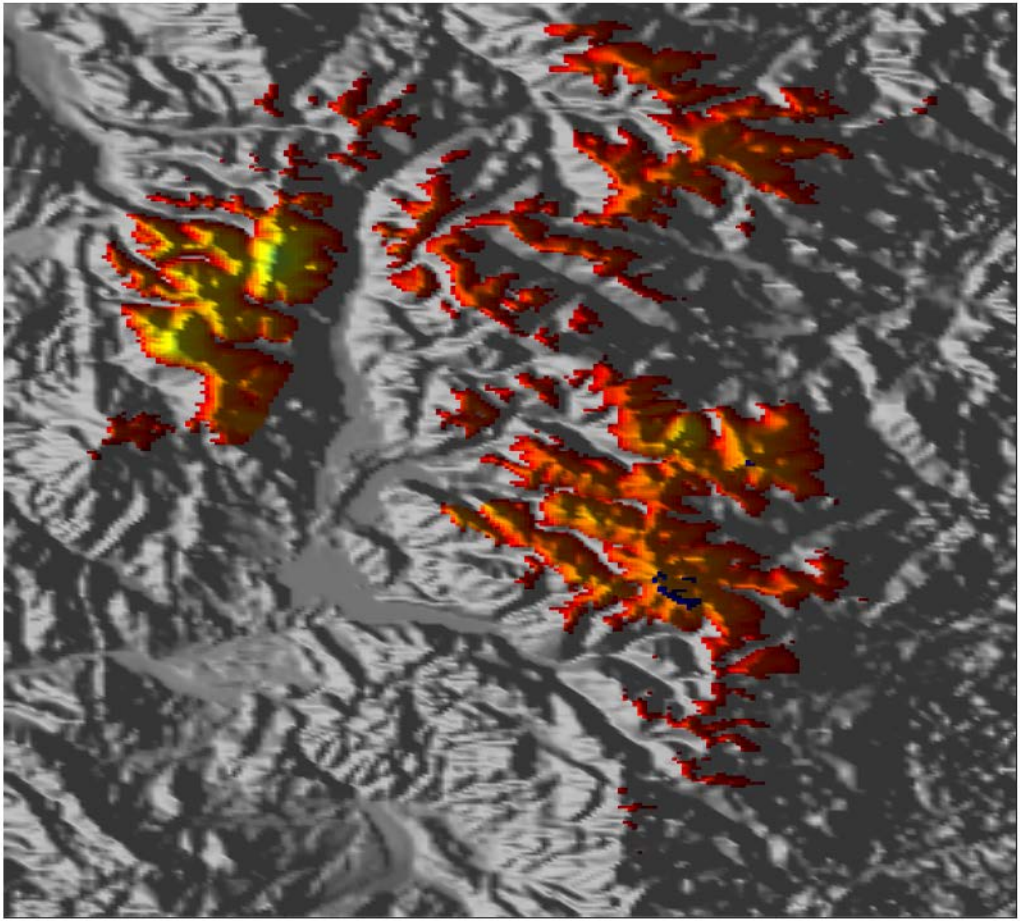
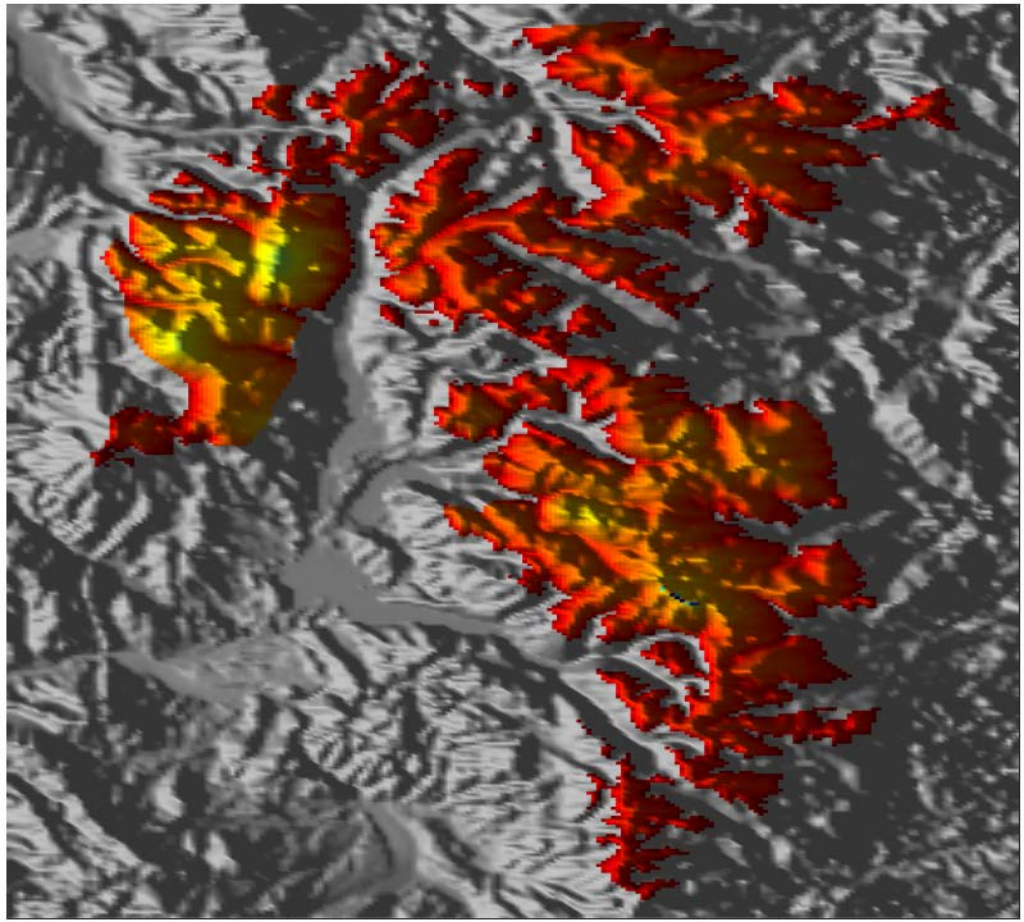
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2









**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; joseph.barsugli@noaa.gov; beli1098@colorado.edu; candida.dewes@noaa.gov; kevin_doherty@fws.gov; aahe1976@colorado.edu; imtiaz.rangwala@noaa.gov; barb.deluisi@noaa.gov; Kathleen Human; kave5703@colorado.edu; theo.stein@noaa.gov; stephen_torbit@fws.gov
**Subject:** Wolverine presentation to PSD/APA Team science mtg
**Start:** Thursday, April 13, 2017 1:00:00 PM
**End:** Thursday, April 13, 2017 2:30:00 PM
**Location:** 1D708 & go-to meeting
**Attachments:** invite.ics

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This event has been changed.

more details » <https://www.google.com/calendar/event?action=VIEW&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>

Changed: Wolverine presentation to PSD/APA Team science mtg

"Wolverine Climate Change and Snow Refugia: An Assessment for the US Fish and Wildlife Service"

this go-to meeting was set up for us by Don Murray for our Monday meetings through December

https://global.gotomeeting.com/join/925942125 <https://www.google.com/url?q=https%3A%2F%2Fglobal.gotomeeting.com%2Fjoin%2F925942125&sa=D&ust=1491942518714000&usg=AFQjCNHgmzQoYh-_a_Fz_64FVOTcJ5EK4w>
You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Thu Apr 13, 2017 1pm – 2:30pm Mountain Time
Where
1D708 & go-to meeting (map <https://maps.google.com/maps?q=1D708+%26+go-to+meeting&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• joseph.barsugli@noaa.gov
• beli1098@colorado.edu
• john_guinotte@fws.gov
• candida.dewes@noaa.gov
• kevin_doherty@fws.gov
• aahe1976@colorado.edu
• imtiaz.rangwala@noaa.gov
• barb.deluisi@noaa.gov
• Kathleen Human
• kave5703@colorado.edu
• theo.stein@noaa.gov
• stephen_torbit@fws.gov

Going?
Yes <https://www.google.com/calendar/event?action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?action=VIEW&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for updated invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

ment 20170411 123008_EM_Wolverine presentation to PSD_APA Team scienc.ics (3159 Bytes) cannot be converted to PDF f

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; joseph.barsugli@noaa.gov; stephen_torbit@fws.gov
**Subject:** Wolverine snow refugia call
**Start:** Wednesday, April 12, 2017 4:00:00 PM
**End:** Wednesday, April 12, 2017 4:50:00 PM
**Location:** 877-953-4978 Code 88468159#
**Attachments:** invite.ics

---

more details » <https://www.google.com/calendar/event?
action=VIEW&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>

Wolverine snow refugia call

When
Wed Apr 12, 2017 4pm – 4:50pm Mountain Time
Where
877-953-4978 Code 88468159# (map <https://maps.google.com/maps?q=877-953-4978+Code+88468159%23&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• joseph.barsugli@noaa.gov
• stephen_torbit@fws.gov
• john_guinotte@fws.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>
-
Maybe <https://www.google.com/calendar/event?
action=RESPOND&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=3&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>
-
No <https://www.google.com/calendar/event?
action=RESPOND&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?
action=VIEW&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>

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Attachment 20170412 143659_EM_Wolverine snow refugia call.ics (1405 Bytes) cannot be converted to PDF format.

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; stephen_torbit@fws.gov; joseph.barsugli@noaa.gov
**Subject:** Wolverine snow refugia call
**Attachments:** invite.ics

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This event has been changed.

more details » <https://www.google.com/calendar/event?
action=VIEW&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>

Wolverine snow refugia call

Changed: Meeting Date: 04/12/2017
Meeting Time: 3:55 PM MOUNTAIN TIME

Instant Net Conference Details:
---
Meeting Number: 741740188
Meeting Passcode: guinotte
Meeting Host: ECOLOGICAL SERV FWS

When
Wed Apr 12, 2017 4pm – 4:50pm Mountain Time
Where
Changed: webex see below (map <https://maps.google.com/maps?q=webex+see+below&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• stephen_torbit@fws.gov
• joseph.barsugli@noaa.gov
• john_guinotte@fws.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>
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-
No <https://www.google.com/calendar/event?
action=RESPOND&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?
action=VIEW&eid=Z2pvOG9vZGhuamk2cTliZmMzaThkZ3V0cXMgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmRhOTE3ODg2YjU2OWU1Mjk4ZmE2MjZlNmRmZGJmNDVmYTdlM2M2NTM&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

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Attachment 20170412 155943_EM_Wolverine snow refugia call.ics (1649 Bytes) cannot be converted to PDF format.

**From:** Andrea Ray - NOAA Federal
**To:** Stephen Torbit
**Cc:** John Guinotte; Joseph Barsugli
**Subject:** Re: latest maps incl ROMO Re: talking this afternoon, use your conference line? and title of report
**Date:** Wednesday, April 12, 2017 4:09:26 PM
**Attachments:** wolverine-graphics-041217.pdf

---

On Wed, Apr 12, 2017 at 2:51 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:

> Here are the re-labelled maps of SWE change, GLAC and ROMO. Talk to you soon on Steve's conf line, below and in the calendar
>
> On Wed, Apr 12, 2017 at 2:35 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:
>
> > thanks, will put it in a calendar event
> >
> > On Wed, Apr 12, 2017 at 2:33 PM, Stephen Torbit <Stephen_Torbit@fws.gov> wrote:
> >
> > > Me too
> > >
> > > We can use 877-953-4978
> > >
> > > Code 88468159#
> > >
> > > Stephen C. Torbit
> > >
> > > Assistant Regional Director
> > >
> > > Science Applications
> > >
> > > U.S. Fish and Wildlife Service
> > >
> > > 134 Union Blvd.
> > >
> > > Lakewood, Colorado 80228
> > >
> > > 303-236-4602 – Office
> > >
> > > 720-626-7504 – Cell
> > >
> > > **From:** Guinotte, John [mailto:john_guinotte@fws.gov]
> > > **Sent:** Wednesday, April 12, 2017 2:18 PM
> > > **To:** Andrea Ray - NOAA Federal
> > > **Cc:** Steve Torbit; Joseph Barsugli

**Subject:** Re: talking this afternoon, use your conference line? and title of report

Hi, I can talk at 4pm.

Best, John

John Guinotte
Fish and Wildlife Biologist

Ecological Services
U.S. Fish and Wildlife Service
Mountain Prairie Region 6

134 Union Blvd., Lakewood, CO 80228

303-236-4264
john_guinotte@fws.gov

On Wed, Apr 12, 2017 at 2:15 PM, Andrea Ray - NOAA Federal <andrea.ray@noaa.gov> wrote:

Hi John and Steve,

Joe's available to talk at 3:30 or after. let us know what time -- and can we use your conference line??

Here's my current tentative title, following on our conversations yesterday and with John before "Wolverine Snow Refugia Study: An analysis of future climate risks"

Andrea

--

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Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328

> > (tel) 303-497-6434
> > (fax) 303-497-6449
> > andrea.ray@noaa.gov
> >
> > www.researchgate.net/profile/Andrea_Ray2
> >
> >
> >
> > --
> > --
> > Andrea J. Ray, Ph.D.
> > NOAA Earth System Research Lab, Mailcode R/PSD1
> > 325 Broadway, Boulder, CO 80305-3328
> > (tel) 303-497-6434
> > (fax) 303-497-6449
> > andrea.ray@noaa.gov
> > www.researchgate.net/profile/Andrea_Ray2
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> --
> --
> Andrea J. Ray, Ph.D.
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> 325 Broadway, Boulder, CO 80305-3328
> (tel) 303-497-6434
> (fax) 303-497-6449
> andrea.ray@noaa.gov
> www.researchgate.net/profile/Andrea_Ray2

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Andrea J. Ray, Ph.D.
NOAA Earth System Research Lab, Mailcode R/PSD1
325 Broadway, Boulder, CO 80305-3328
(tel) 303-497-6434
(fax) 303-497-6449
andrea.ray@noaa.gov
www.researchgate.net/profile/Andrea_Ray2

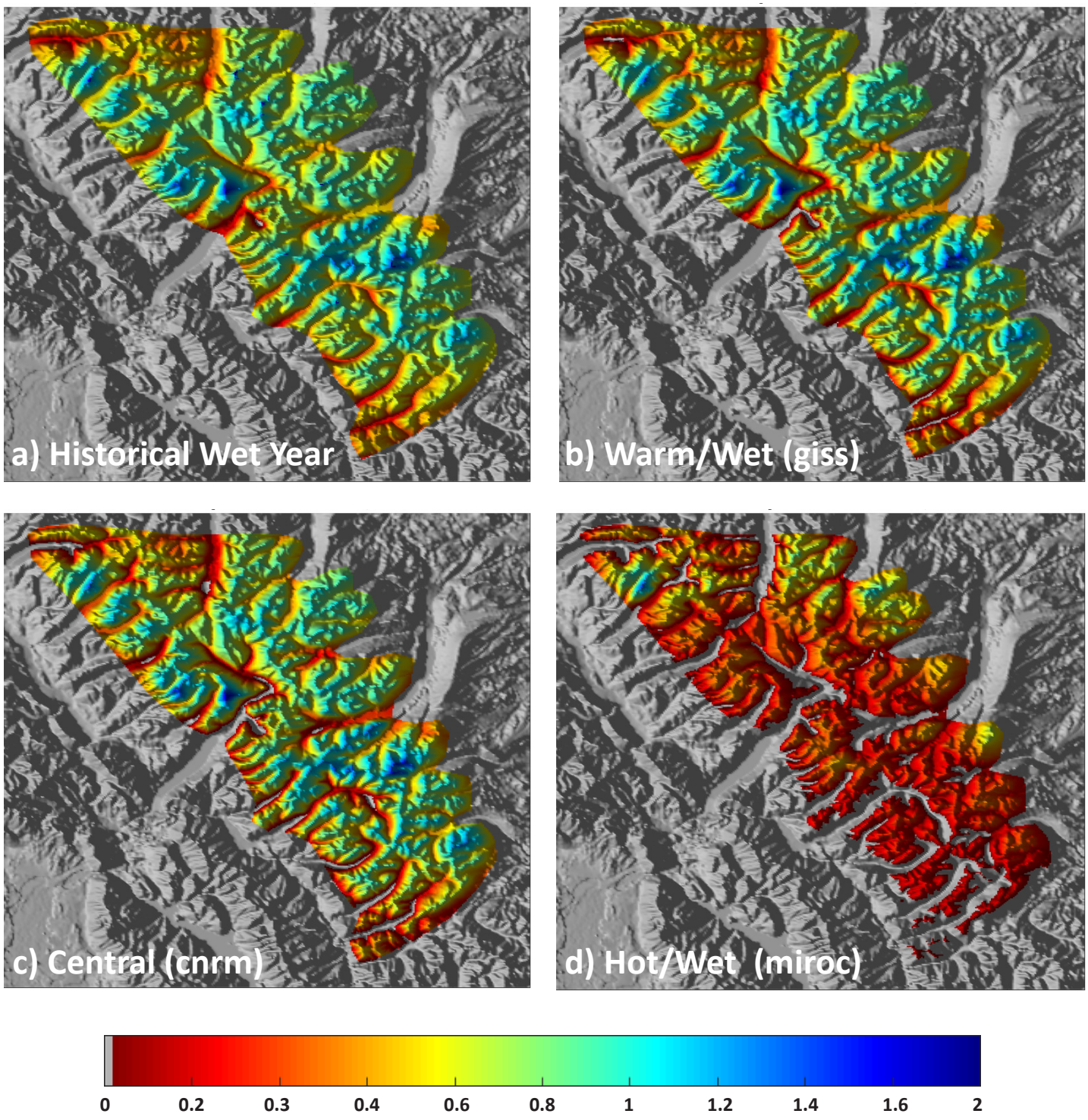


**Figure 5-8. Historical and projected May 15th Snow Water Equivalent (meters) for a Representative Wet Year in GLAC.** Historical simulation year 2011 (wet year, top left), and for three future scenarios applied to 2011: b) the warm/wet (giss) scenario results in the lowest change in SWE (top right), c) the central scenario (cnrm) results in a moderate change in SWE (bottom left), and the, d) hot/wet model results in the greatest change in SWE (bottom right). Scenarios are listed in Table 5-3 and shown in Figure 5-7, maps for additional scenarios are provided in the Supplementary Material.

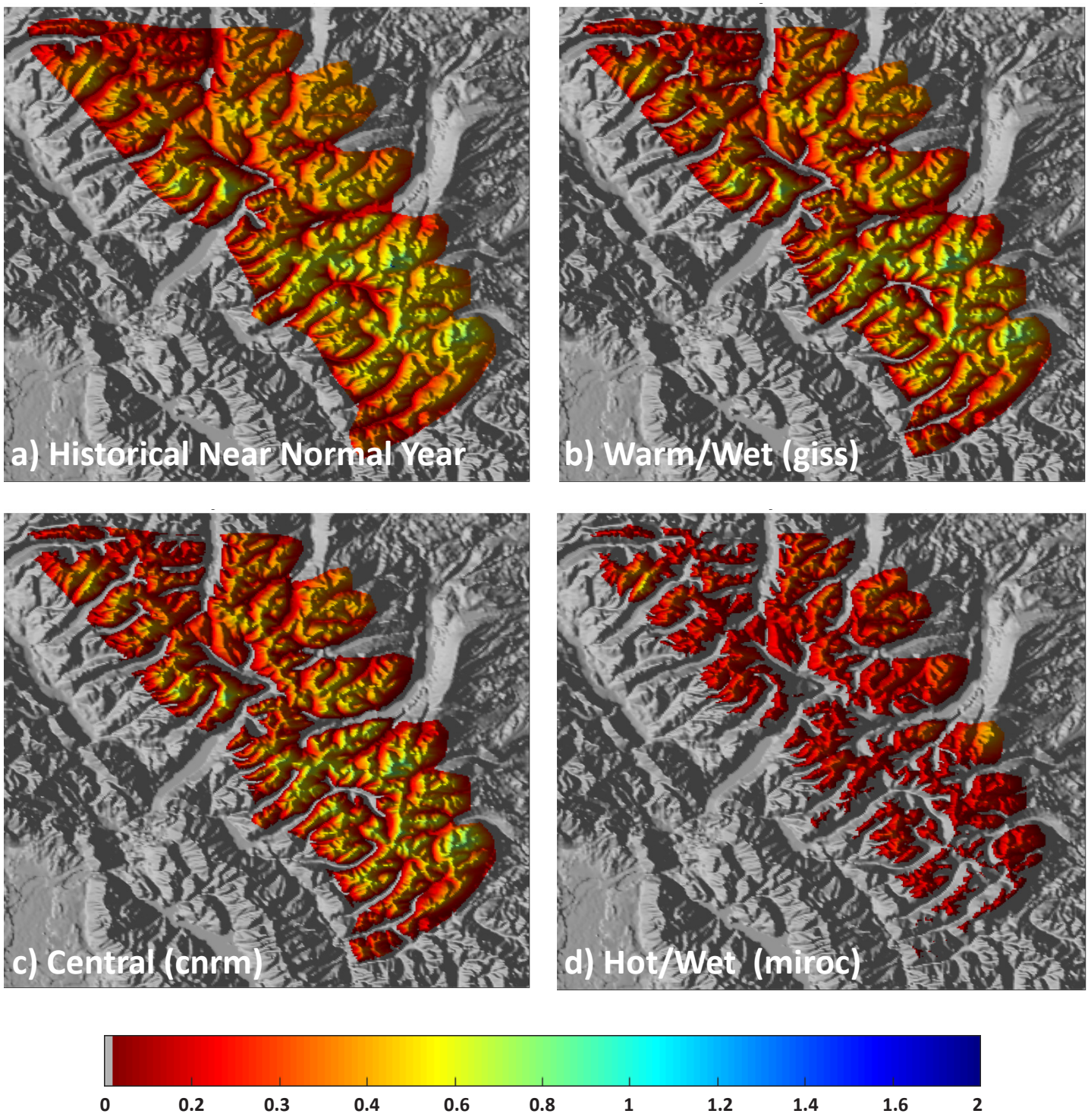


**Figure 5-9. Historical and projected May 15th Snow Water Equivalent (meters) for a Representative Near Normal Year in GLAC.** Historical simulation year 2009 (near normal year, top left), and for three future scenarios applied to 2009: b) the warm/wet (giss) scenario results in the least change in SWE (top right), c) the central scenario (cnrm) results in a moderate change in SWE (bottom left), and, d) the hot/wet model results in the greatest change in SWE (bottom right). Scenarios are listed in Table 5-3 and shown in Figure 5-7, maps for additional scenarios are provided in the Supplementary Material.

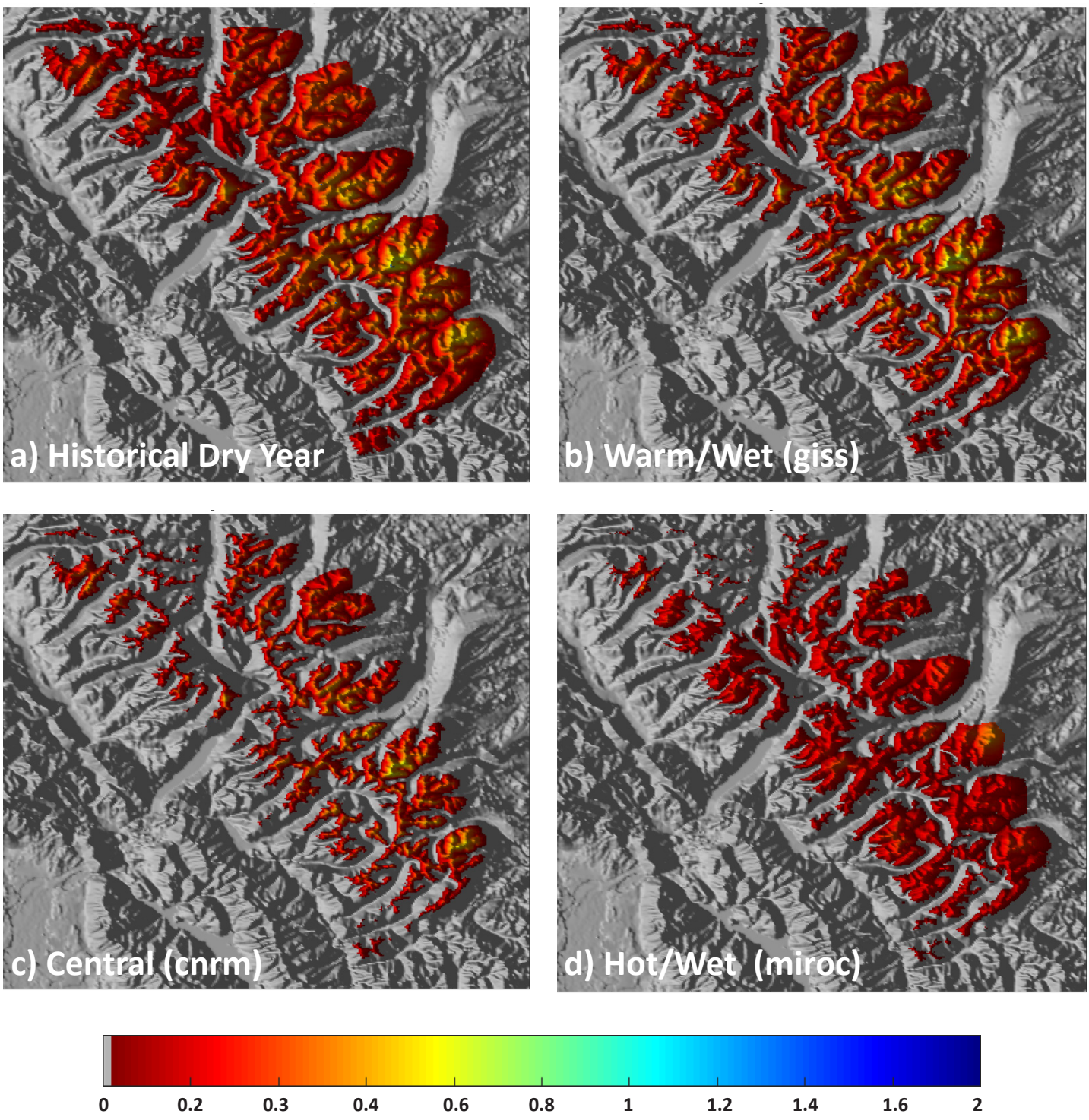


**Figure 5-10. Historical and projected May 15th Snow Water Equivalent (meters) for a Representative Dry Year in GLAC.** Historical simulation year 2005 (dry year, top left), and for three future scenarios applied to 2005: b) the warm/wet (giss) scenario results in the least change in SWE (top right), c) the central scenario (cnrm) results in a moderate change in SWE (bottom left), and, d) the hot/wet model results in the greatest change in SWE (bottom right). Scenarios are listed in Table 5-3 and shown in Figure 5-7, maps for additional scenarios are provided in the Supplementary Material.

# ROMO Representative Wet Year – May 15th SWE

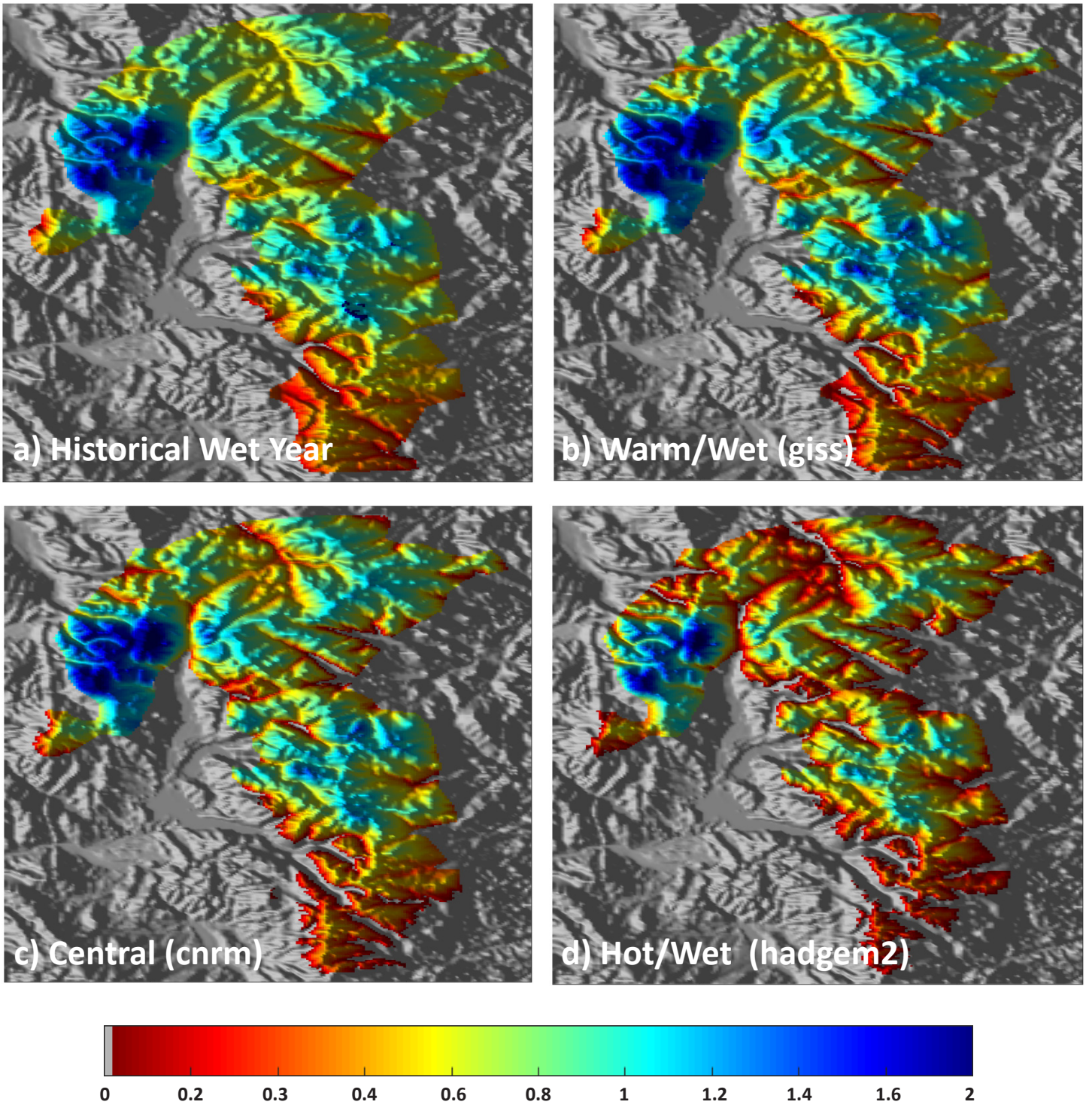


**Figure 5-15. Historical and projected May 15th Snow Water Equivalent (meters) for a Representative Wet Year in ROMO.** Historical simulation year 2011 (wet year, top left), and for three future scenarios applied to 2011: b) the warm/wet (giss) scenario results in the lowest change in SWE (top right), c) the central scenario (cnrm) results in a moderate change in SWE (bottom left), and, d) the hot/wet model results in the greatest change in SWE (bottom right). Note that while the representative wet year is the same in GLAC and ROMO, the representative near normal and dry years used are different, based on climatology (see section 3-3). Scenarios are listed in Table 5-3 and shown in Figure 5-7, maps for additional scenarios are provided in the Supplementary Material.

# ROMO Representative Near Normal Year – May 15th SWE

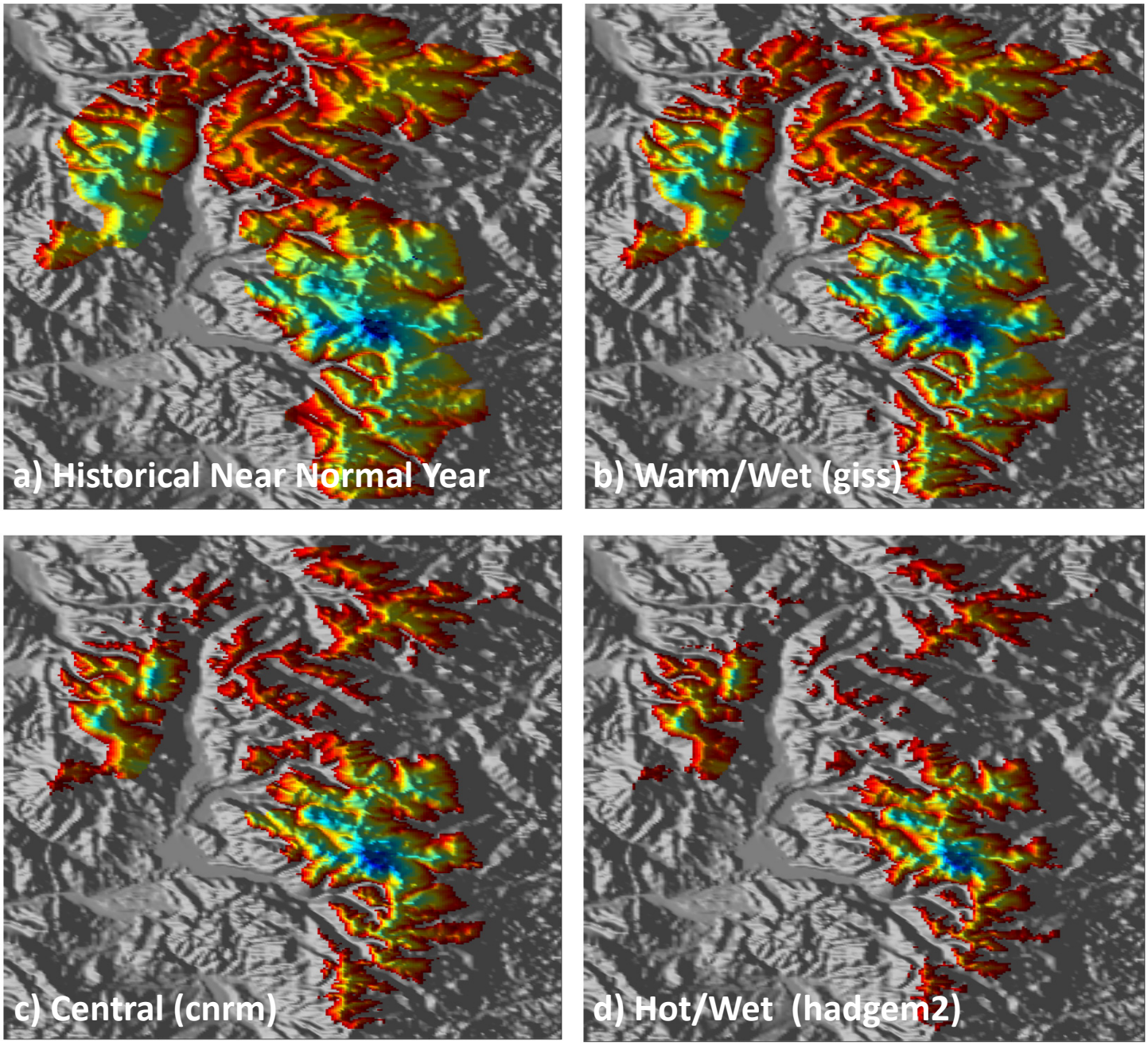


**Figure 5-16. Historical and projected May 15th Snow Water Equivalent (meters) for a Representative Near Normal Year in ROMO.** Historical simulation year 2007 (near normal year, top left), and for three future scenarios applied to 2007: b) the warm/wet (giss) scenario results in the least change in SWE (top right), c) the central scenario (cnrm) results in a moderate change in SWE (bottom left), and, d) the hot/wet model results in the greatest change in SWE (bottom right). Scenarios are listed in Table 5-3 and shown in Figure 5-7, maps for additional scenarios are provided in the Supplementary Material.

# ROMO Representative Dry Year – May 15th SWE

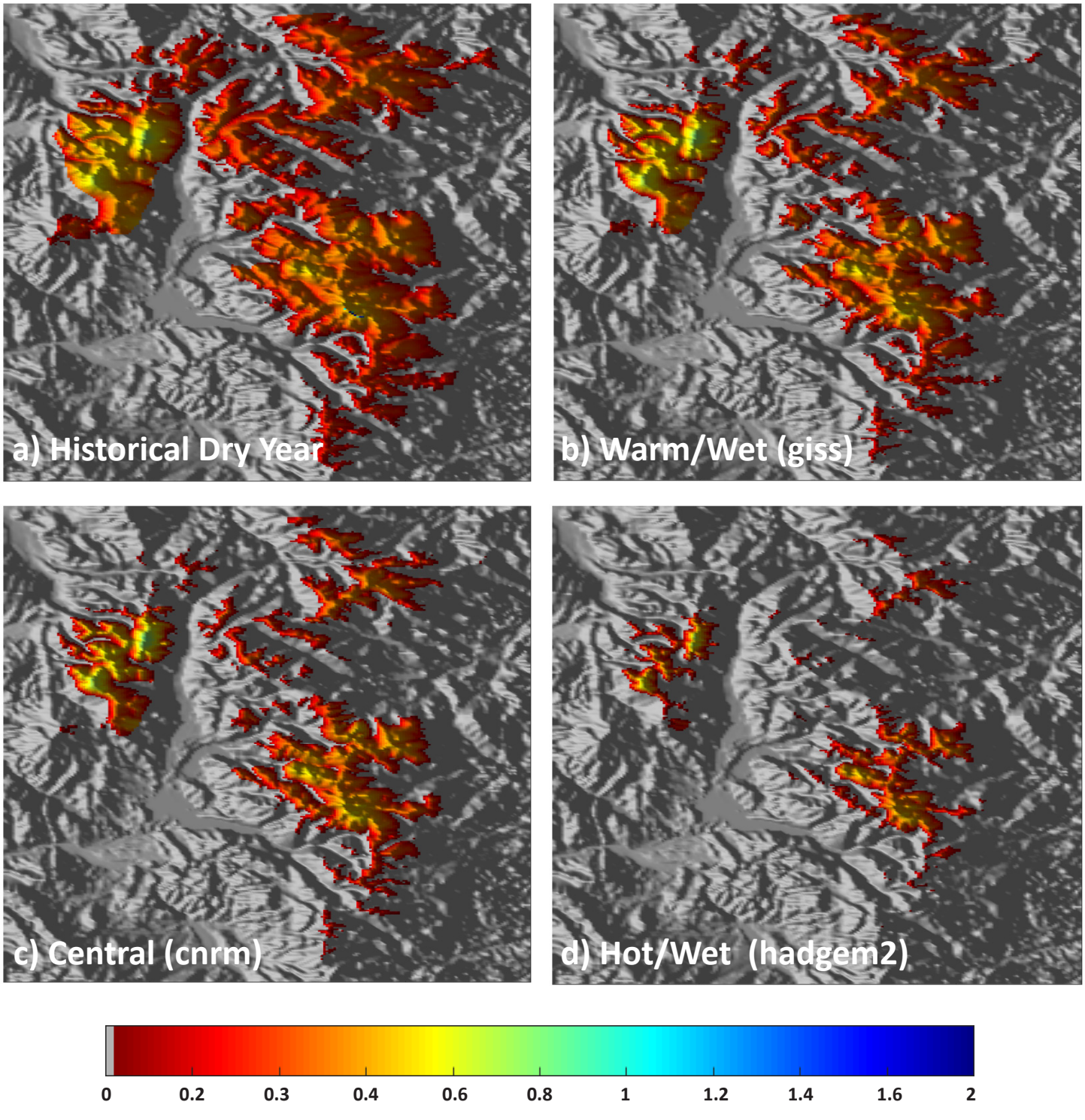


**Figure 5-17. Historical and projected May 15th Snow Water Equivalent (meters) for a Representative Dry Year in ROMO.** Historical simulation year 2002 (dry year, top left), and for three future scenarios applied to 2002: b) the warm/wet (giss) scenario results in the lowest change in SWE (top right), c) the central scenario (cnrm) results in a moderate change in SWE (bottom left), and, d) the hot/wet model results in the greatest change in SWE (bottom right). Scenarios are listed in Table 5-3 and shown in Figure 5-7, maps for additional scenarios are provided in the Supplementary Material.

**From:** Google Calendar on behalf of andrea.ray@noaa.gov
**To:** john_guinotte@fws.gov; beli1098@colorado.edu; stephen_torbit@fws.gov; barb.deluisi@noaa.gov; imtiaz.rangwala@noaa.gov; kave5703@colorado.edu; candida.dewes@noaa.gov; joseph.barsugli@noaa.gov; kevin_doherty@fws.gov; aahe1976@colorado.edu; Kathleen Human
**Subject:** POSTPONED: Wolverine presentation to PSD/APA Team science mtg
**Attachments:** invite.ics

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This event has been changed.

more details » <https://www.google.com/calendar/event?
action=VIEW&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>

Changed: POSTPONED: Wolverine presentation to PSD/APA Team science mtg

Changed: Hi all, with apologies for the last minute change, Joe and I decided to postpone the presentation on the Wolverine project b/c we're still finishing the final details of the report to send to FWS, and that's higher priority right now. We'll get back to you in a few days on when the presentation will be, and we'll be sharing the "final draft" text and figures in Word in the next day or two. Thanks, Andrea

"Wolverine Climate Change and Snow Refugia: An Assessment for the US Fish and Wildlife Service"

this go-to meeting was set up for us by Don Murray for our Monday meetings through December

https://global.gotomeeting.com/join/925942125 <https://www.google.com/url?q=https%3A%2F%2Fglobal.gotomeeting.com%2Fjoin%2F925942125&sa=D&ust=1492058896726000&usg=AFQjCNEuP0JGD9YZphJ5bS7xhQiBPCz_2g>
You can also dial in using your phone.
United States +1 (408) 650-3123
Access Code: 925-942-125

When
Thu Apr 13, 2017 1pm – 2:30pm Mountain Time
Where
1D708 & go-to meeting (map <https://maps.google.com/maps?q=1D708+%26+go-to+meeting&hl=en> )
Calendar
john_guinotte@fws.gov
Who
• andrea.ray@noaa.gov
- organizer
• beli1098@colorado.edu
• theo.stein@noaa.gov
• stephen_torbit@fws.gov
• barb.deluisi@noaa.gov
• imtiaz.rangwala@noaa.gov
• kave5703@colorado.edu
• candida.dewes@noaa.gov
• joseph.barsugli@noaa.gov
• kevin_doherty@fws.gov
• aahe1976@colorado.edu
• Kathleen Human
• john_guinotte@fws.gov

Going?
Yes <https://www.google.com/calendar/event?
action=RESPOND&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&rst=1&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>
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more options » <https://www.google.com/calendar/event?
action=VIEW&eid=ZDdvN3I4MDVmM2pzcnY4b2k3dWhnZGgxODAgam9obl9ndWlub3R0ZUBmd3MuZ292&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdjdkYTgzZjhiYjAxZjhiOWY0ZTVlYzYwN2U0ODdmNWUxMmM1ZTNlMjg&ctz=America/Denver&hl=en>

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ent 20170412 204831_EM_POSTPONED_ Wolverine presentation to PSD_APA .ics (3709 Bytes) cannot be converted to PDF

**From:** Grizzle, Betty
**To:** Hansen, Craig
**Cc:** Stephen Torbit; John Guinotte; Justin Shoemaker
**Subject:** Re: Wolverine Genetics
**Date:** Thursday, April 13, 2017 8:26:43 AM

---

Clarification - the document to which this masters thesis is appended to *is* in the admin record, but it's in the literature considered (so not used as a reference and not cited).

The primary document is: Magoun AJ, P Valkenburg, RE Lowell, CD Long, and J Long 2010. Associations and Movement Patterns of Reproductive Female Wolverines (*Gulo gulo luscus*) on the Southeast Alaska Mainland. Final report February 2010.

It's a very large pdf (30 MB) but I can try to extract the pages if you're interested in reading this.

On Wed, Apr 12, 2017 at 7:47 PM, Hansen, Craig <craig_hansen@fws.gov> wrote:

> Copy. Thank you for the update. Let me know how I can be of assistance.
>
> Craig.
>
> 2017-04-10_Email_Signature_3.jpg
>
> On Wed, Apr 12, 2017 at 12:06 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
>
> > Thanks Steve.
> >
> > After much digging, today I *finally* found a copy of this genetic study buried in another document (I don't think this study was not cited in our previous rules; it is not in the Admin Records I received):
> >
> > Frances J. 2008. Spatial genetic structure and demographic history of wolverine in North America with an emphasis on peripheral populations. MSc Thesis. University of New Mexico, United States. 51 pp.
> >
> > On Wed, Apr 12, 2017 at 9:52 AM, Stephen Torbit <Stephen_Torbit@fws.gov> wrote:
> >
> > > I am finally able to report that Mike Schwartz has connected with me about wolverine genetics. We are going back and forth about status of samples, number of samples, whether they are prepared and ready to run, etc. I will provide an update tomorrow regarding the status of the discussions. In a very rough guess, it looks like to me that we will need about $20k, just as the states estimated, to run a complete nuclear and mitochondrial DNA panel. They will both inform us regarding individuals and the haplotypes for consideration of DPS issues. I hope to get info on the time frame by tomorrow, regardless, I will update everyone before COB tomorrow.

> > Steve
> >
> > Stephen C. Torbit
> > Assistant Regional Director
> > Science Applications
> > U.S. Fish and Wildlife Service
> > 134 Union Blvd.
> > Lakewood, Colorado 80228
> > 303-236-4602 – Office
> > 720-626-7504 – Cell
>
> --
>
> Betty J. Grizzle, D.Env.
> Fish and Wildlife Biologist
> U.S. Fish and Wildlife Service
> Carlsbad Fish and Wildlife Office
> 2177 Salk Ave, Suite 250
> Carlsbad, CA 92008
> 760-431-9440, ext. 215
> 760-431-5901 fax

--

Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

| | |
|---|---|
| **From:** | Imtiaz Rangwala |
| **To:** | joseph.barsugli@noaa.gov; Andrea Ray; Guinotte, John; Stephen Torbit; Candida Dewes; Aaron Joseph Heldmyer; Ben Livneh |
| **Subject:** | Re: FINAL DRAFT of the Wolverine Report |
| **Date:** | Friday, April 14, 2017 9:59:11 PM |

---

Thanks Joe. Looks pretty impressive. Imtiaz

On 4/14/17 9:45 PM, Joe Barsugli wrote:
> All
>
> Andrea and I came pretty darn close to making all the requested
> revisions/comments, adding the text for ROMO, and the elevational
> analysis, as well as a qualitative assessment of the differences with
> McKelvey, and relabeling most of the figures. I have put a version
> of the Wolverine Report on the Google Drive that I am -- perhaps
> presumptuously -- calling FINAL DRAFT 14 APR 2017. It really is a
> quantum leap from the previous draft. As before the figures and
> text are in separate files. I am also attaching the text as it is
> small. There are PDF versions on the drive as well. The requested
> revisions have taken more effort than we anticipated, and there are
> still some small issues to deal with -- particularly a couple of
> figures that still need to be redone. These are not terribly
> substantive changes, but will need to be done. The Supplementary
> Material is not ready for wider distribution yet. At this point I am
> not comfortable going with the latest runs from Aaron (the MIROC
> 2080's McKelvey delta runs) until we understand them better. We can
> discuss later as to how far we want to go on the McKelvey comparison
> in this Report.
>
> Happy Weekend, and I hope Steve has a quick recovery!
>
> Yours,
>
> Joe
>
>
>
>
>

**From:** Andrea Ray - NOAA Federal
**To:** Imtiaz Rangwala
**Cc:** joseph.barsugli@noaa.gov; Guinotte, John; Stephen Torbit; Candida Dewes; Aaron Joseph Heldmyer; Ben Livneh
**Subject:** Re: FINAL DRAFT of the Wolverine Report
**Date:** Friday, April 14, 2017 11:12:52 PM

---

Thanks Joe, it does look great! Andrea

Sent from my iPhone

> On Apr 14, 2017, at 21:59, Imtiaz Rangwala <imtiaz.rangwala@noaa.gov> wrote:
>
> Thanks Joe. Looks pretty impressive. Imtiaz
>
>
>> On 4/14/17 9:45 PM, Joe Barsugli wrote:
>> All
>>
>> Andrea and I came pretty darn close to making all the requested revisions/comments, adding the text for ROMO, and the elevational analysis, as well as a qualitative assessment of the differences with McKelvey, and relabeling most of the figures. I have put a version of the Wolverine Report on the Google Drive that I am -- perhaps presumptuously -- calling FINAL DRAFT 14 APR 2017. It really is a quantum leap from the previous draft. As before the figures and text are in separate files. I am also attaching the text as it is small. There are PDF versions on the drive as well. The requested revisions have taken more effort than we anticipated, and there are still some small issues to deal with -- particularly a couple of figures that still need to be redone. These are not terribly substantive changes, but will need to be done. The Supplementary Material is not ready for wider distribution yet. At this point I am not comfortable going with the latest runs from Aaron (the MIROC 2080's McKelvey delta runs) until we understand them better. We can discuss later as to how far we want to go on the McKelvey comparison in this Report.
>>
>> Happy Weekend, and I hope Steve has a quick recovery!
>>
>> Yours,
>>
>> Joe
>>
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>>
>

**From:** Grizzle, Betty
**To:** Holt, Bryon; John Guinotte; Shoemaker, Justin
**Subject:** Re: wolverine
**Date:** Monday, April 17, 2017 9:13:01 AM

---

Hi Bryon - Yes, I saw it. John and I are looking at latitude, elevation, temp, snow info for this area. I have also sent this story to contact in MT. I expect the researchers in Scandinavia are also digesting this information. Thanks for sending.

On Mon, Apr 17, 2017 at 8:09 AM, Holt, Bryon <bryon_holt@fws.gov> wrote:

> Hi Betty,
>
> I saw this article and thought I would forward it to you (see below). Have you seen or are aware of it? Do you know or can we find out if the wolverine sighting is outside of the range in the sense that it's outside of the known "range" but within predicted habitat, or is this in area that does not provide the expected habitat conditions (e.g., adequate persistent snow).
>
> Bryon
>
> **Wolverine cub born outside normal habitat range**
>
> *Published: Monday, April 17, 2017*
>
> A female wolverine cub born in Belgium is providing hope for the entire species.
>
> Wolverines, which once proliferated across Europe, are now generally found in colder areas like Scandinavia and parts of Russia. Their habitat has been restricted due to steadily warming temperatures, which has pushed conservationists to worry about the species' future.
>
> Recently, however, a female cub was born outside the wolverine's known habitat range — in the Domain of the Caves of Han park, south of Brussels. The cub ventured out of its den just last week. Park officials intend to transfer the yet-to-be-named cub to a zoo after two years, when she's more mature.
>
> The cub is one of 1,300 wolverines in Europe, including 116 that live in either a zoo or a wildlife park (Farah Salhi, **Reuters**, April 14). **— KB**
>
> --
> **********
> **********
> Bryon Holt
> U.S. Fish and Wildlife Service
> Northern Idaho Field Office, Spokane, WA
> Telephone: (509) 893-8014
> Fax: (509) 891-6748
> email: bryon_holt@fws.gov
>
> **********
> **********

--

Betty J. Grizzle, D.Env.
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Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

| | |
|---|---|
| **From:** | Guinotte, John |
| **To:** | Kevin Doherty |
| **Subject:** | Fwd: FINAL DRAFT of the Wolverine Report |
| **Date:** | Monday, April 17, 2017 8:37:10 AM |
| **Attachments:** | Wolverine Report Text FINAL DRAFT 14Apr2017 .docx<br>Wolverine Report Text FINAL DRAFT 14Apr2017.pdf |

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Hey Kevin,

This was in my inbox this am. I'm planning to read it today sometime and start editing over the next couple of days.

Best, J

---------- Forwarded message ----------
From: **Joe Barsugli** <joseph.barsugli@noaa.gov>
Date: Fri, Apr 14, 2017 at 9:45 PM
Subject: FINAL DRAFT of the Wolverine Report
To: Andrea Ray <Andrea.Ray@noaa.gov>, "Guinotte, John" <john_guinotte@fws.gov>, Stephen Torbit <Stephen_Torbit@fws.gov>, Imtiaz Rangwala <Imtiaz.Rangwala@noaa.gov>, Candida Dewes <Candida.Dewes@noaa.gov>, Aaron Joseph Heldmyer <Aaron.Heldmyer@colorado.edu>, Ben Livneh <ben.livneh@colorado.edu>

All

Andrea and I came pretty darn close to making all the requested revisions/comments, adding the text for ROMO, and the elevational analysis, as well as a qualitative assessment of the differences with McKelvey, and relabeling most of the figures. I have put a version of the Wolverine Report on the Google Drive that I am -- perhaps presumptuously -- calling FINAL DRAFT 14 APR 2017. It really is a quantum leap from the previous draft. As before the figures and text are in separate files. I am also attaching the text as it is small. There are PDF versions on the drive as well. The requested revisions have taken more effort than we anticipated, and there are still some small issues to deal with -- particularly a couple of figures that still need to be redone. These are not terribly substantive changes, but will need to be done. The Supplementary Material is not ready for wider distribution yet. At this point I am not comfortable going with the latest runs from Aaron (the MIROC 2080's McKelvey delta runs) until we understand them better. We can discuss later as to how far we want to go on the McKelvey comparison in this Report.

Happy Weekend, and I hope Steve has a quick recovery!

Yours,

Joe

--
Joseph Barsugli, Research Scientist III
CIRES, UCB216
University of Colorado Boulder
Boulder CO 80309
303-497-6042
PSD Science Board and
Attribution and Predictability Assessments Team Member

# Wolverine Snow Refugia Study: An analysis of future climate risks

## A Report to the U.S. Fish and Wildlife Service Region 6

Andrea J. Ray[1], Joseph J. Barsugli[2], Ben Livneh[3] Candida F. Dewes[2], Imtiaz Rangwala[2], Aaron Heldmyer[3], Jenna Stewart[3]

[1]NOAA/ESRL/Physical Sciences Division
Boulder, CO
[2]CU/Cooperative Institute for Research in Environmental Sciences (CIRES)
[3]CU Civil, Environmental & Architectural Engineering

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Andrea
303-497-6434
andrea.ray@noaa.gov

Final Draft 14Apr17

# 1 Introduction

## 1.1 Motivation

This report responds to the United States Fish and Wildlife Service (FWS) need for information on potential climate impacts to snow persistence. The North American wolverine (*Gulo gulo luscus*) is currently being evaluated for listing as a threatened or endangered species under the Endangered Species Act (ESA) and climate change effects on snow persistence was identified as an important factor for the future viability of the wolverine. The species was considered for listing in 2014, but FWS concluded that it did not warrant listing. They further concluded that there is significant uncertainty about how the effects of climate change will affect wolverines and their habitat in the foreseeable future, and that this uncertainty includes information on how fine-scale changes in snow cover and persistence might affect denning site selection.

The U.S. District Court rejected the Service's determination that climate change, small population size (only ~300 wolverines in the northern Rockies and north Cascades), and genetic isolation do not threaten the wolverine's survival in the lower 48 states. The FWS is currently collating the most up to date scientific information to inform the court-ordered re-evaluation of that decision, due in April 2017. This report describes a snow modeling analysis intended to provide FWS with a finer scale assessment of snow extent and depth for future wolverine habitat that extends previous work to finer scales and includes additional snow processes that we believe are critical to future wolverine habitat. Other uncertainties identified by the Service are beyond the scope of this study and report, i.e., whether future snow extent and depth would limit the suitability of habitat within the home range of an individual wolverine, and whether those factors would limit wolverine populations in the foreseeable future.

Funding was provided by the U.S. Fish and Wildlife Service, Region 6 and the NOAA/Earth System Research Lab/Physical Sciences Division. This effort builds on work underway by the project team at NOAA/ESRL/PSD, the NOAA-University of Colorado (CU) Cooperative Institute for Research in Environmental Sciences (CIRES), and CU Department of Civil, Environmental & Architectural Engineering.

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## 1.2 Project Objectives

Persistent spring snowpack has been described as an important factor in determining suitable habitat for the wolverine, including Northern boreal forests and subarctic and alpine tundra (Aubry et al, 2007, Peacock et al, 2011). This relationship was the basis for the analysis done by Copeland et al. (2010) and McKelvey et al. (2011) used in the previous FWS decision. In both studies, climate change projections of snowpack were used to characterize potential future wolverine habitat.

Our primary objective is to advance scientific understanding of the current spatial extent of spring snow retention on the landscape, and the future temporal and spatial extent of snow retention through a thirty-year period, 2041-2070, centered on the year 2055. The goal of this effort is to identify the persistence of snow as potential refugia for wolverine denning. Climate

refugia have been identified as possible targets for conservation in several studies (see Morelli et al. 2016 for a review). We aim to advance snow analysis and modeling to better support assessment of snow-related species, in the following ways:

- Explicitly model the effects of slope and aspect, using fine-scale spatial models to analyze topographic effects on snow
- Better represent of the range of plausible future changes (climate scenarios)
- Analyze extremes: wet and dry years from the historic record and how these might change in the future

Our strategy was to build on previous methods where possible to be comparable to work by McKelvey et al. (2011) and Copeland et al. (2010), and depart from their methods where necessary to take advantage of analysis techniques not feasible at the large scales used in the studies done by those authors. Furthermore, we utilize new scientific data and tools that are now available, including the latest global climate model runs, and conduct Distributed Hydrology Soil Vegetation Model (DHSVM, Wigmosta et al.1994) high resolution hydrologic simulations modeling at highly resolved (250m) spatial scale, as well as analysis of historic snowpack variability to investigate these influences of topography on snowpack, along with the projected physical drivers of snowpack.

First we analyzed historic snow variability from satellite remote sensing of snow extent from the year 2000 to present to determine areas of greater and lesser sensitivity to climate drivers (temperature and precipitation), and identify possible snow refugia. We then did an intercomparison of the satellite observations of snow with that from the DHSVM hydrologic modeling study that includes a representation of slope and aspect (the compass direction that the slope faces) of the terrain and shading on the snowpack. Prior studies also show a relationship between terrain (slope and aspect) and persistence of snow (e.g. Lundquist and Flint, 2006) and the potential importance of this factor under a changed climate. Finally, the DSHVM hydrologic model was forced with five future scenarios of climate change for each of the two study regions. These future climate scenarios were derived from the latest Coupled Model Inter-comparison Project Phase-5 runs (CMIP5, Taylor et al., 2012) which informed the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC AR5, 2013).

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# 2 Project Overview

## 2.1 Study Areas

High-resolution hydrologic modeling was needed to provide fine scale analysis of snow. However, given time, funding and computational constraints, it was necessary to limit the study domain to two areas of about 1500-3000km$^2$ for high-resolution analysis. Two study areas representing core and peripheral habitat regions in the northern and central Rocky Mountains were identified in consultation with FWS Region 6 personnel (Figures 2-1 and 2-2). The highest priority area is in the "Crown of the Continent" region in the high mountain terrain from the Canadian border south to approx. Helena MT, including Glacier National Park, and adjacent areas. An area within Glacier National Park (GLAC) was chosen (Figure 2-1) area at elevations

higher than about 250 m below tree line. Because we were restricted to smaller areas for analysis, these areas were chosen to bracket a range of habitat conditions for wolverine, from a lower elevation domain in Glacier National Park where wolverines have been observed repeatedly, and a very high elevation domain in ROMO, recently occupied by a male wolverine.

The analysis for the GLAC and ROMO study areas is presented in separate sections, repeating descriptions to make the material self-contained for the reader who may read about only one area; similarly, complete captions are given for each area.

### 2.2 Comparison between our analysis and that of Copeland and McKelvey

This project builds on the analyses done by Copeland et al. (2010) and McKelvey et al. (2011) that was used in the previous FWS decision. Copeland et al. (2010) (hereafter, simply Copeland or the Copeland study) calculated the number of years with snowcover on May 15th as detected by MODIS satellite, postulated as a correlate of wolverine habitat (check cite). They found that most (45 of 75) North American den sites were in areas that snow cover persisted with 6 or 7 out of 7 years on May 15th. We also investigated the of number of years of snow persistence for our study areas, however, the new MODIS product has two advantages over that available at the time of their study, 1) improved snow detection (snow covered area, SCA), and 2) 17 years of MODIS data is now available vs the 7 available to Copeland and McKelvey. Furthermore, we investigated the relationships between snow cover persistence and both elevation and aspect (the compass direction of the slope face). A comparison between our work and the studies used previously is summarized in Table 2-1.

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**Table 2-1: Modeling Methods Compared to McKelvey**

| | McKelvey (Littell) | This Study |
|---|---|---|
| Spatial Resolution (modeling) | VIC model – 1/16 degree (~5km x 7 km, ~37km$^2$ cell) | DHSVM model - 250m x 250m UTM grid (~0.0625 km$^2$ cell) |
| Spatial Extent | Westwide except California and Great Basin | ROMO and GLAC study areas, near and above treeline |
| Process differences | ”Flat” pixels, implicit elevation bands. | Slope, aspect, shading, explicit fine scale elevation effects. |
| Validation | None specific to snow | Comparison to SNOTEL (ground stations) and MODIS (satellite) |
| Future Scenarios | Delta Method; “2045”;”2085”; from 3 GCMs selected to span westwide temperature changes. | Delta Method: ”2055” from 5 GCMs spanning regional changes in temperature and precipitation |

| | | |
|---|---|---|
| Analysis | Changes in long-term mean snowpack only | Means and variability, including wet, near normal and dry years. |
| Snow representation | Binary snow/no snow at 13 cm snow depth | Analyzed snow depth at two thresholds: 13mm of SWE ('light snow') and 0.5m depth ('significant snow') |

McKelvey et al. (2011) (hereafter, simply McKelvey or the McKelvey study) used May 1st snow depth simulated by the Variable Infiltration Capacity hydrologic (VIC) hydrology model (1/16 degree, ~5km x 7 km), "flat" gridboxes, or cells, with no slope aspect dependence). The VIC model runs were documented in Littell et al. (2011) and were based on meteorological inputs from Elsner et al. (2010). The present study uses the DHSVM model, which was developed by the same group at the University of Washington for fine-scale simulations, and shares many model components. McKelvey used the "delta method" (described later in Section 5) for the projected changes in climate compared to present day. This study also uses the "delta method." The McKelvey study used a range of temperature change to select GCMs representing the range or spread of future scenarios. As shown below in Section 5.10 and Figure 5.7, their chosen future scenarios reflect a range of precipitation in GLAC, but in ROMO, the three scenarios have similar precipitation changes. This project selected a larger number of future scenarios selected based on changes in both temperature and precipitation.

The McKelvey study calculated a metric for a historic period (1915-2005 average) and two futures, 30-year averages around "2045" and" 2085." This study focused on a 30-year period around mid-century, "2055" to focus on FWS' time horizons for the wolverine and due to time and computational constraints given the project budget. We also reproduce a single future scenario using one of the Littell (2011) "2080's scenarios for direct comparison. Calculations for a later period using the CMIP5 climate models (e.g. ~2100) could easily be made, but were beyond the scope of this project. We provide analysis for two thresholds of snow amount, a "light" snow cover (13mm of snow water equivalent), and significant, or "heavy" snow cover (equivalent to 0.5 m of snow depth). Because McKelvey only had access to May 1st snow depth simulation, they chose to use a 13 cm snow depth on May1st as a proxy for snow disappearance by May 15th. We instead chose to use a much lighter threshold of snow on May 15th itself. Note that SWE is a measure of the water content in the snowpack; to estimate depth, a density of the snow must be assumed, i.e. an approximation of whether the snow is heavy or light. Our threshold of 13mm SWE was originally chosen to be comparable to McKelvey's snow depth. Our assumptions are discussed further in Sec. 5.6.

An important difference between this study and prior work by Copeland et al. (2010) and McKelvey et al. (2011) is the spatial scale of results. McKelvey and Copeland both presented results on a regular 1/16 degree latitude-longitude grid, in which each cell, or gridbox is ~5-7 km on a side. These cells were assumed to be flat in the model-- that is they do not incorporate slope or aspect information in their surface energy balance. The result of this is north-facing slopes are treated identically to south-facing slopes. Our study uses the DHSVM (originally developed by

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Wigmosta et al, 1994, see also http://www.hydro.washington.edu/Lettenmaier/Models/DHSVM/documentation.shtml) for snow at 250m x 250m resolution that incorporates other physical drivers of snowpack (a complete energy balance at the surface, a 2-layer snow model, and a 2-layer vegetation canopy model) and allows analysis of snow at different slopes and aspects (slope directions). The VIC modeling did include the option for elevational snow bands within the VIC grid (Jeremy Littell, pers. comm.) but the snow band information was not explicitly used. Fine-scale elevational effects are implicit in the VIC model whereas it is explicitly modeled in DHSVM. A visual comparison of the gridbox (Fig 2-3).

It should be noted there are tradeoffs between our strategies and the methods of Copeland and McKelvey. The finer scale analysis presented in this report integrates slope and aspect with respect to snow accumulation and retention that are thought to be important for maintaining snow refugia for denning sites (see Fig 2 in McKelvey et al 2011). The disadvantage of this improvement in spatial resolution is we were only able to analyze two study areas due to time and computational constraints. The Copeland and McKelvey projects analyzed a much larger domain, including a significant portion of the wolverine range in the continental US, but does not provide detailed analysis of any habitat area.

### 2.3 A note on description of modeling resolution

The VIC modeling that was the basis for McKelvey was performed on a regular grid in latitude and longitude, with a grid size of 1/16 degree on a side. The distance between degrees of longitude varies due to the curvature of the Earth, and the east-west dimension of a gridbox is smaller than the north-south distance by a factor of the cosine of latitude. At 40°N latitude, the southern extent of Rocky Mountain National Park, the gridbox is ~5km by 7 km (~37km$^2$). Grid boxes at Glacier National Park (~48°N) are slightly smaller. When referring to the McKelvey study we will use the "1/16 degree" notation. The DHSVM modeling used in this study was performed on a uniform grid in the Universal Transverse Mercator (UTM) map projection, which allows a near-uniform grid size of 250m by 250m (0.0625 km$^2$) in both of the study areas.

### 2.4 The Westwide context of future climate

Global climate models (GCMs) are the primary tools used by climate science to examine the nature of climate change during the 21st century. There are currently about 20 modeling centers worldwide that provide output from their best model or models to be considered in the Coupled Model Inter-comparison Project Phase-5 (CMIP5, Taylor et al., 2012) which informed the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC AR5, 2013). When we quantify regional changes in climate variables such as temperature and precipitation by a particular time horizon in the 21st century, we find a large spread in the extent of warming and changes in precipitation, including both increases and decreases in precipitation, as shown in regional maps (Figure 2-4) and described later in Section 5. For temperature change, much of this spread (or uncertainty) is a result of the difference among the formulations of the GCMs (e.g., their climate sensitivities), whereas for precipitation it is both the differences among GCMs and internal climate variability. Some difference also comes out of the choice of future greenhouse gases (GHG) emission scenario. However, the differences among greenhouse gas

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emissions scenarios is less at mid-21st century compared to later in the century, and is much smaller than other sources of uncertainty at the regional scale (IPCC,2013).

Figure 2-4 shows projected annual and seasonal temperature and precipitation changes by 2050 (2035–2064) over the western U.S., including the northern and central Rocky Mountains, from an ensemble of the 34 climate models used for this study under the RCP 8.5, a high-end emissions scenario. The large maps show the average change for all of the models (n=34) for that season, and the small maps show the average changes of the highest 20% and lowest 20% of the models, based on the statewide change for Colorado in temperature or precipitation. For much of the central and northern Rockies, all models show a substantial warming (of +2.5°F to +5.5°F). While fewer models agree about the direction of precipitation change westwide, even the lower (drier) models show an increase in winter precipitation for the area around Glacier National Park, although there is less agreement for the central Rockies area including Rocky Mountain National Park. The GCM output is discussed further in Section 5.

# 3 Observed Climate and Variability

Key Points:

- Both study areas show upward trends in both temperature and freezing level.
- Surface Air Temperature and Atmospheric freezing level are related, with a stronger relationship in ROMO (that is, a greater change in freezing level for a given surface air temperature change)
- Representative years chosen for GLAC: 2011 (cool wet), 2005 (warm dry), 2009 (near normal).
- Representative years chosen for ROMO: 2011 (cool wet), 2002 (warm dry), 2007 (near normal).

## 3.1 Introduction

This section presents a historical analysis of the winter and spring climate variability for the two study regions, GLAC and ROMO. This section presents the following:

- Trends in temperature and freezing level
- Historical variability in cool season (October – May) temperature and precipitation for the study areas.
- Choice of representative years during the simulation period for cool/wet, warm/dry, and near normal conditions for the two areas based on the entire cold season averages
- A ranking of the representative years in a longer climate record to provide context.

A complete description of regional climate is beyond the scope of this project, but may be found in e.g. McWethy et al (2010), Garfin et al (2014), Lukas et al (2014), Shafer et al (2014), and cites therein.

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## 3.2 Trends in Surface Temperature and Freezing Level

Temperature strongly influences hydrologic processes such as evapotranspiration, snowpack accumulation, and timing of snowmelt. Both the Glacier and Rocky Mountain areas show a trend of increasing surface air temperature in the winter season (October-May, Figure 3-1), consistent with trends that have been observed west-wide (Garfin et al 2014; Lukas et al 2014; Shafer et al 2014). While winter season temperatures vary inter-annually, linear regression of these data (not shown) indicates about a 1.4ºC increase in temperature from 1948-2015 for an area around Glacier, and about a 1.2ºC increase around Rocky Mountain National Park. This report analyzes data by "water year," or Oct 1st-Sept 30th, rather than calendar year, in order to capture precipitation over the contiguous winter months.

Atmospheric freezing level height (FLH) represents the altitude in the free atmosphere (that is, away from the surface and its immediate influence) where the temperature is 0 °C. Above this level, the temperature of the air is typically below freezing. Freezing in the free atmosphere is indicative of the level above which precipitation falls as snow rather than rain. Freezing level height can have a strong influence on freeze-thaw processes in high-elevation regions (Bradley et al 2009). As with winter season temperatures, freezing level varies over time (Figures 3-2, 3-3), but linear regression (not shown) indicates about a 160m increase in the freezing level for Glacier (Fig 3-2), and about a 170 m increase in the freezing level for Rocky Mountain (Fig 3-3).

Figure 3-4 illustrates a strong relationship between freezing levels and surface air temperature change for both regions in October-May with explained variance $R^2$ close to 0.8. For GLAC (3-1, left), a 1ºC anomaly in temperature equates to about a 115 m increase in the freezing level, over the period. For ROMO, for 1ºC increase in temperature there has been about a 180 m increase in the freezing level (3-1, right).

## 3.3 Choice of Representative Years for Detailed Analysis

The modeling presented later in the report uses all years from 2000-2013 as "base years." While 1998-1999 are modeled, they are not used for most analyses to be consistent with the availability of satellite data. In addition, the first years of a model simulation are often not analyzed because the soil water content is adjusting to the weather forcing, though that is of less concern for this snow-centric analysis). Climate-model derived change factors (the "delta method") were applied to all these years to generate future simulations of snowpack.

McKelvey et al (2011) studied only the effect of climate change on the *average* snowpack. One of the primary study goals is to extend the analysis to include the effects of climate change on extreme years – both for high- and low- spring snowpack. To drive our choice of years modeled, we investigated historical temperature and precipitation anomalies and MODIS-based snow covered area (shown in the next sub-section). Years were chosen within that range to represent a "Cool/Wet" year, a "Near Normal" year, and a "Warm/Dry" year (Table 3-1). When brevity is required these are later called "Wet", "Near Normal", and "Dry." We put special emphasis on these "representative case study" years in the analysis shown in Sections 4 and 5.

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**Table 3-1: Choice of Representative Years**

| Year Type | GLAC | ROMO |
|---|---|---|
| COOL WET (WET) | 2011 | 2011 |
| WARM DRY (DRY) | 2005 | 2002 |
| Near Normal | 2009 | 2007 |

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### 3.4 Historical Year-to-Year variability in Temperature and Precipitation

Year-to-year variations in average cold season (October – May) and melt season (April – June) temperature and precipitation guide the choice of representative years for closer study and also provide the context of these years in the longer climate record. Figure 3-5 shows scatterplots of the anomalous precipitation (as % of average) and temperature (degrees Celsius) for each year of the primary study period (2000-2013) for the two study areas. The larger context of these climate anomalies is indicated by the unlabeled dots that show the data for 1950-1999. For both study areas, the 2011 winter stands out as a particularly large anomaly. The Livneh dataset was chosen because it is the one that is used for the meteorological inputs to the DHSVM model. Other sources with later data indicate that 2015 and 2016 were near average in precipitation, but anomalously warm, with correspondingly low spring snowpack. These years were not included in the DHSVM modeling study.

Examination of the time series of Snow Covered Area (SCA) derived from the MODIS satellite product (Figure 3-6ab) shows the impact of these climate anomalies in terms of springtime snowpack. Because of the high-elevations, the study areas melt late in the Spring. In wet and near normal years, nearly the entire domains are snow-covered. To verify our choices of representative years, we show the SCA as a function of elevation within the study areas (Figure 3-6cd). These time series show that the near-normal years selected closely follow the median profile.

### 3.5 Historical Context

How often did the study years occur in the longer climatological record? The percentiles of October – May precipitation and temperature averaged over the study areas are shown for the representative wet, near normal and dry in Table 3-2 for both study areas. The percentiles are calculated based on the 63 total years in the 1951-2013 period of the Livneh (2014) dataset. For GLAC, October – May 2011 was at the 98$^{th}$ percentile of precipitation and the 6$^{th}$ percentile of temperature, while 2005 was at the 6$^{th}$ percentile of precipitation and 83$^{rd}$ percentile of temperature. For ROMO, 2011 was in the 96$^{th}$ percentile of October – May precipitation, but

only the 36th percentile of temperature, and while anomalously cold was not extreme in temperature. 2002 was in the 4th percentile of precipitation, but only near the median in temperature.

Tables 3-3 (GLAC) and 3-4 (ROMO) show the percentiles of precipitation and temperature for all the years that were simulated using the DHSVM model (see section 5) as well as the percentiels for the April – June melt season. Note that the year 2012 was also considered as a "representative dry year" for ROMO, but difficulty in accurately modeling the spatial pattern of that year's snowpack using DHSVM led us to use 2002 instead. Even though the precipitation was as extreme in 2002 as in 2012, the temperature was not. This is reflected in the MODIS spring snowcover (Figure 3-6), where 2002 was low, but not as nearly extreme as in 2012.

Percentiles were calculated by ranking the data and using the following formula: percentile = (rank – 0.5)/(total number of years). It should be noted that the exact rankings and percentiles would differ based on the underlying dataset and interpolation methods used, as the study areas have relatively few observing stations. Rankings and "representativeness" have been checked against the PRISM dataset and provide qualitatively similar results.

**Table 3-2: Historical Percentiles of precipitation and temperature for the representative dry, near normal, and wet years for GLAC and ROMO study areas.**

| | Year Type | Year | Oct. - May Precipitation Percentile | Oct. - May Temperature Percentile |
|---|---|---|---|---|
| GLAC | Dry | 2002 | 4 | 45 |
| | Near Normal | 2007 | 56 | 69 |
| | Wet | 2011 | 96 | 36 |
| ROMO | Dry | 2005 | 6 | 83 |
| | Near Normal | 2009 | 45 | 42 |
| | Wet | 2011 | 98 | 6 |

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**Table 3-3: Percentile of temperature and precipitation anomalies for GLAC study area based on the 1951-2013 period.** Percentiles are shown for both the October – May cold season and for the April – June melt season.

| GLAC | Percentile 1951-2013 | | | |
|---|---|---|---|---|
| | Oct. - May Precipitation | Oct. - May Temperature | Apr. - June Precipitation | Apr. - June Temperature |
| 2000 | 31 | 96 | 7 | 66 |
| 2001 | 2 | 37 | 47 | 58 |
| 2002 | 61 | 31 | 91 | 12 |
| 2003 | 33 | 87 | 13 | 69 |
| 2004 | 13 | 63 | 33 | 61 |
| 2005 | 6 | 83 | 80 | 47 |
| 2006 | 37 | 82 | 53 | 93 |
| 2007 | 21 | 72 | 6 | 75 |
| 2008 | 39 | 47 | 60 | 17 |
| 2009 | 45 | 42 | 12 | 34 |
| 2010 | 12 | 55 | 85 | 13 |
| 2011 | 98 | 6 | 87 | 4 |
| 2012 | 40 | 74 | 72 | 53 |
| 2013 | 60 | 66 | 56 | 29 |

**Table 3-4: Percentile of temperature and precipitation anomalies for ROMO study area based on the 1951-2013 period.** Percentiles are shown for both the October – May cold season and for the April – June melt season.

| ROMO | Percentile 1951-2013 | | | |
|---|---|---|---|---|
| | Oct. - May Precipitation | Oct. - May Temperature | Apr. - June Precipitation | Apr. - June Temperature |
| 2000 | 45 | 98 | 40 | 98 |
| 2001 | 29 | 33 | 23 | 91 |
| 2002 | 4 | 45 | 2 | 96 |
| 2003 | 75 | 80 | 77 | 64 |
| 2004 | 21 | 91 | 75 | 77 |
| 2005 | 50 | 82 | 82 | 53 |
| 2006 | 28 | 74 | 4 | 94 |
| 2007 | 56 | 69 | 6 | 75 |
| 2008 | 80 | 12 | 45 | 13 |
| 2009 | 77 | 93 | 88 | 44 |
| 2010 | 48 | 13 | 87 | 37 |
| 2011 | 96 | 36 | 93 | 25 |
| 2012 | 10 | 94 | 7 | 99 |
| 2013 | 64 | 26 | 79 | 42 |

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# 4 MODIS Observed Historic Snowpack Variability Analysis

Key points

- In GLAC, even in dry years, NE-facing slopes tend to hold more snow and melt later in the season. Complete snow cover (over 80%) is around 2000 m of elevation on May 1during dry years, and down to 1200 m during wet years. Snow conditions on June 1during wet years resemble those for May 1 during near-normal years.
- In ROMO, NW-facing slopes tend to hold more snow even during dry years. In very dry years, snow cover peaks at intermediate elevations, suggesting that the high-altitude snowpack may be particularly vulnerable in this region under warm/dry conditions.

## 4.1 Introduction

In this chapter we perform an analysis of the variability of snow cover in the historical period 2000-2016 using gridded snow cover data acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Terra satellite. The analysis for the GLAC and ROMO study areas is presented in separate sections, repeating descriptions to make the material self-contained for the reader who may read about only one area. Each section consists of analysis of the following: a) total snow covered area (SCA), b) SCA fractional area as a function of eight compass directions of slope aspect (octants), and d) elevation dependence. MODIS snow cover data serves two purposes in this study – first for the analysis of historical variability in the study areas, and second to serve as a basis for the spatial evaluation of the hydrologic model simulations.

## 4.2 Methods

### 4.2.1 Data subsetting and re-projection

We downloaded selected MODIS/Terra daily snow cover data on a 500m grid from the recently released version 6 (MOD10A1.006) (Hall and Riggs, 2016). All data from geographic tiles h09v04 (ROMO) and h10v04 (GLAC) were downloaded for days between March 1 and July 1 for all years from 2000 to 2016.

The data are available in daily files, one for each tile, and georeferenced to an equal-area sinusoidal projection. Each tile covers 10° x 10° at the equator or approximately 1200 km by 1200 km, with a nominal pixel resolution of 500 m (actual resolution 463.313 m). To bring the data to the same grid as used in the hydrologic modeling necessitated re-projection of the data onto a Universal Transverse Mercator Grid. We used the MODIS Reprojection Tool (https://lpdaac.usgs.gov/tools/modis_reprojection_tool) to subset the daily tiles to the areas of interest and reproject the subsetted areas to UTM grids with a pixel resolution of 250 m using nearest-neighbor resampling. The ROMO study area perimeter falls at the corner of tile h09v04, and extends slightly beyond the tile boundaries at its southern tip. We excluded this extension of the study from our analysis. Parameters for the MODIS data reprojection are provided in Table S4-1.

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### 4.2.2 Normalized Difference Snow Index

In the MODIS product, snow cover is identified using the Normalized Difference Snow Index (NDSI). Snow covered land typically has very high reflectance in visible bands and very low reflectance in the shortwave infrared, and the magnitude of this difference is quantified by the NDSI. A series of screens is also implemented to alleviate errors and flag uncertain snow cover detections. NDSI is reported as a ratio, with values ranging from 0 to 1 (scaled and reported as 0 to 100 in the data files). In the dataset, certain values over 200 are used to classify grid points as "missing data", "night", "inland water", "cloud", etc. The NDSI Snow Cover variable is comparable to the Fractional Snow Cover (FSC) variable used in previous collections of this data. A user could calculate FSC by applying the following linear relationship: FSC = (-0.01 + (1.45 * NDSI))*100.0 for $0.0 \leq NDSI \leq 1.0$.

The prior work by McKelvey and Copeland both used Collection 4 of the MODIS data which provided them with a binary snow cover classification. These data are only available for the years 2000-2007, necessitating the use of the more recent MODIS products. However, collection 6 does not include a binary snow cover product for the daily data. For the purposes of determining binary snow cover, we applied a threshold of NDSI > 0.1. This choice of threshold is the same as that used in the MODIS 8-day composite product.

### 4.2.3 Snow disappearance date and snow cover on a given date

We defined the Snow Disappearance Date (SDD) as the first day after March 1 in which NDSI/100 was less or equal to 0.1. The SDD is denoted by the Day of Year value, in which January 1 is 1, February 1 is 32, March 1 is 60 (or 61 in leap years), etc. Once SDD was defined at each grid point for each year (resulting in 17 annual maps of SDD for the period of record), we were able to derive snow cover maps for any given date. For example, snow cover on May 1 was inferred by marking grid points as "snow-covered" if their SDD was equal or greater than 121 (or 122 for leap years). We repeated the process to infer snow cover maps for May 15 and June 1. This indirect method to infer snow cover allowed us to circumvent the reality of several missing data points due to cloud cover, and offered a conservative estimate of snow disappearance.

### 4.2.4 Snow cover by elevation and aspect

Using a digital elevation model resampled to a 250m resolution grid, we obtained grids for elevation and aspect octants in both study regions. We reclassified the elevation values into 200 m bins. The elevation bins range from 1000 to 3000 m in GLAC and 2600 to 4200 m in ROMO. Both the slope magnitude and the aspect of the slope (that is the compass direction that the slope faces) were analyzed using functionality in the open source Quantum GIS software. We reclassified the aspect grids into eight 45°-wide directional bins (hereafter, octants) centered on the points of the compass. In both types of analyses (elevation and aspect), we computed snow covered area (SCA) on May1, May15, and June1, in terms of the total area in square kilometers and also in terms of the percentage of snow covered area in several elevation bands and aspect octants.

## 4.3 MODIS analysis for GLAC

MODIS snow cover data was analyzed for March1 – July1 for the years 2000-2016. Data for all years was analyzed. We present here some summary statistics of snow cover, including total

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snow covered area, and number of years during the period of study with snow cover on a given date. For more in depth analysis including aspect and elevation-based analyses the report focuses on the representative years defined in Section 3: 2011 ("wet"), 2009 ("near normal"), and 2005 ("dry").

### 4.3.1 Total Snow Covered Area

Total snow covered area was the primary metric that was analyzed in McKelvey et al (2011) and provides an overall summary of availability of snow. Figure 4-1 presents maps of May 15 snow cover for the GLAC study area and vicinity from MODIS. These maps clearly depict the regional character of the year-to-year variations in snowcover. Figure 4-2 shows the total snow covered area within the study area polygon, which is depicted in red on the previous figure. The year-to-year variations are shown for snowcover on three different dates during the melt season. The behavior in individual year varies considerably, including "wet" years such as 2011 with very persistent snow, years with strong melt in early May, such as 2012, or in late May (2009, 2001), and "dry" years (2004, 2005). Though it is beyond the period of the modeling study, it is worth noting that the last two years of the record, 2015 and 2016 show low snowcover. Both these years had near-normal precipitation, but had anomalously warm temperatures.

To summarize all 17 years of the record, Figure 4-3 presents maps of the number of years with snow cover on May 1, May 15, and June 1. These are similar to the analysis done by the Copeland and McKelvey studies. The primary difference is in the use of the newer MODIS products and the extension of the analysis from seven to seventeen years.

Figure 4-4 quantifies the maps in Figure 4-3, showing the area within the GLAC study area polygon with different numbers of years of snow cover. The three colored bars designate different days of the year. Because the study areas were chosen to be in the vicinity of tree line, it is no surprise that in the present climate there are large areas that see snow every year on May 1$^{st}$.

### 4.3.2 Aspect Dependence of Snowpack: Total Area

One of the primary goals of this study is to investigate topographic factors that influence the persistence of snow during the melt season. One such factor is the "slope aspect" or simply "aspect" – the compass direction that the slope faces. Figure 4-5 presents the dependence of total snow covered area (km$^2$) on aspect for each of the 17 years in the MODIS dataset, for May 1, May 15, and June 1. The shape of the curves for individual years is strongly determined by the topography of the region, with more land area available in the northwest and southeast octants. Upon closer inspection, other features become apparent. Comparing the SW and NE octants we see that there is greater year-to-year variability in the SW, indicating a greater sensitivity of SW-facing slopes to variations in the historical climate.

In Figure 4-6 we examine two of the representative years, 2011 and 2005, to see how the total snow covered area progresses from May 1 to June 1. The dry year, 2005, shows that snow cover declines faster on S, SW, and W slopes, as one would expect; this analysis quantifies the magnitude of this effect.

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### 4.3.3 Aspect Dependence of Snowpack: Fractional area

The total land area within each aspect octant varies due to the orientation of ridges and valleys in the study area. As a result, the analysis of total snow covered area is dominated by the topography itself. To focus on the *relative* importance of the snow processes related to aspect, we calculated the fraction of the total land area within each octant that is snow covered for each of the 17 years in the historical record, while in Figure 4-8 we focus on the representative wet and dry years. For example, in Figure 4-7, the asymmetric shape clearly shows that in GLAC, the NE directions ranging from E to N have much larger fractional area covered by snow. Even in dry years, over 60 % of the NE facing slopes are snow-covered on May 15th.

### 4.3.4 Elevation Dependence

Figure 4-9 shows the elevation dependence of MODIS snow cover for the wet, near-normal and dry years, with the median of all years as reference. The results are shown as a percentage of the total area within each 200-meter elevation band within the study area boundaries.

## 4.4 MODIS analysis for ROMO

MODIS snow cover data was analyzed for March1 – July 1 for the years 2000-2016. Data for all years was analyzed. We present here some summary statistics of snow cover, including total snow covered area, and number of years during the period of study with snow cover on a given date. For more in depth analysis including aspect and elevation-based analyses the report focuses on the representative years defined in Section 3: 2011 ("wet"), 2007 ("near normal"), and 2012 ("dry").

The analysis is presented in separate sections for the GLAC and ROMO study areas repeating descriptions as needed to make each section as independent of the other. Each section consists of analysis of the following: a) total snow covered area (SCA), b) SCA as a function of aspect, c) snow covered fractional area as a function of aspect, and d) elevation dependence.

### 4.4.1 Total Snow Covered Area

Total snow covered area was the primary metric that was analyzed in McKelvey et al (2011) and provides an overall summary of availability of snow. Figure 4-10 presents maps of May 15 snow cover for the ROMO study area and vicinity from MODIS. These maps clearly depict the regional character of the year-to-year variations in snowcover. Figure 4-11 shows the total snow covered area within the study area polygon, which is depicted in red on the previous figure. The year-to-year variations are shown for snowcover on three different dates during the melt season. The behavior in individual year varies considerably, including "wet" years such as 2011 with very persistent snow, years with strong melt in early May, such as 2004, or in late May (2001, 2013), and "dry" years (2002, 2012).

To summarize all 17 years of the record, Figure 4-12 presents maps of the number of years with snow cover on May 1, May 15, and June 1. These are similar to the analysis done by Copeland and McKelvey studies. The primary difference is in the use of the newer MODIS products and the extension of the analysis from seven to seventeen years.

Figure 4-13 quantifies the maps shown in Figure 4-12, showing the area within the GLAC study area polygon with different numbers of years of snow cover. The three colored bars designate

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different days of the year. Because the study areas were chosen to be in the vicinity of tree line, it is no surprise that in the present climate there are large areas that see snow every year on May 1.

### 4.4.2 Slope Aspect Dependence of Snowpack: Total Area

One of the primary goals of this study is to investigate topographic factors the influence the persistence of snow during the melt season. One such factor is the "slope aspect" or simply "aspect" – the compass direction that the slope faces. Figure 4-14 presents the dependence of total snow covered area ($km^2$) on aspect for each of the 17 years in the MODIS dataset for May 1, May 15, and June 1. The shape of the curves for individual years is strongly determined by the topography of the region, with less land area available in the NW octant, and more in the NE. Compared to GLAC, the ROMO study area shows more year-to-year variation in the shape of the curves, likely indicating stronger meteorological controls on the directionality of the snowpack compared to the topographic control seen in GLAC.Comparing the SW and NE octants we see that there is greater year-to-year variability in the SW, indicating a greater sensitivity of SW-facing slopes to variations in the historical climate.

In Figure 4-15 we examine two of the representative years, 2011 and 2012, for how the snow cover progresses from May 1 to June 1. The dry year, 2012, shows that snow cover starts out lower on May1 and declines faster on SE, S and SW slopes.

### 4.4.3 Slope Aspect Dependence of Snowpack: Fractional Area

The total land area within each aspect octant varies due to the orientation of ridges and valleys in the study area. As a result, the analysis of total snow covered area is dominated by the topography itself. To focus on the *relative* importance of the snow processes related to aspect, Figure 4-16 presents an analysis of the fraction of the total land area within each directional "bin" that is snow covered. The asymmetric shape shows that the NW-facing slopes have larger fractional area covered by snow. With the exception of 2012, even in dry years over 60 % of the NW facing slopes are snow-covered on May 15th. Figure 4-17 indicates that for the dry year 2012, snow cover was retained preferentially on NW-facing slopes.

### 4.4.4 Elevation Dependence

Figure 4-18 shows the elevation dependence of MODIS snow cover for the wet, near-normal and dry years, with the median of all years as reference. The results are shown as a percentage of the total elevation within each 200-meter elevation band within the study area boundaries. The ROMO area shows that the dry year, 2002 (as well as the other very dry year during the period, 2012), was significantly different from the other two, with a fractional area declining with altitude above 3400m. This may indicate that the meteorology in this region interacts differently with the topography in extremely dry years than in wetter years. The high-altitude snowpack may be particularly vulnerable in this region if conditions like those in 2002 recur.

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# 5 Future Snowpack Projections: DHSVM Modeling

Key Points - Methods

- The Distributed Hydrology Soil Vegetation (DHSVM) model was run for the historic period 1998-2013 and validated against available SNOTEL observing stations. The spatial patterns of snow were validated against MODIS satellite remotely sensed snow cover.
- Five scenarios of the future – a thirty year period centered on 2055 -- were selected from CMIP5 global climate model (GCM) projections based on a moderate (RCP 4.5) and high (RCP 8.5) emissions scenarios. These were chosen to represent a large fraction of the range of the CMIP5 ensemble projections in each study area in terms of precipitation and temperature changes. The scenarios differ somewhat between the two study areas to better represent the range of climate projections in each area.
- The selected GCM projections were downscaled using the "delta method" which applies change factors from the climate models to the historic temperature and precipitation that are used as inputs to the DHSVM model.
- Analysis is presented for light snow cover (Snow Water Equivalent > 13mm) for comparison with MODIS and McKelvey, and for 0.5 m of snow depth.
- To capture climate variability, Wet, Near Normal, and Dry representative case study years are shown for the historical simulations and how each of these years plays out under these five future scenarios.

Key Points – GLAC study area.

- Snow Covered Area in GLAC and area with snow depth greater than 0.5 meters on May 15 declines on average in all scenarios on average and for almost all years.
- On average, projections for the May 15 snowpack in the GLAC study area show a 12-42 percent decline in snow covered area, and a 15-68 percent decline in area with snow depth > 0.5 meters for the scenarios considered.
- All projections show declines in the number of years with significant snow. The areas with frequent (14-16 years) availability of significant snow become concentrated in smaller high elevation areas.
- For wet years, the high elevations of the study areas result in little loss of snowpack in the under most scenarios of change.
- For GLAC the Warm/Wet scenario shows the least change compared to the historic snow cover in terms of the area of significant (0.5 meter) snowpack, comparable to only a small shift in time. Under the Hot/Wet scenario, the May 1st significant snowpack has been diminished below the level of the historic June 1 snowpack – greater than a month shift.

Key Points – ROMO study area.

- Snow Covered Area in ROMO (13mm threshold on May 15) declines on average in all scenarios on average and for almost all years.

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- On average, projections for the May 15 snowpack in the ROMO study area show a 12-52 percent decline in snow covered area, and a 7-64 percent decline in area with snow depth > 0.5 meters for the scenarios considered.
- Snow Covered Area in ROMO (0.5 m threshold on May 15) generally declines in wet years, but may increase in dry years in those scenarios with increased precipitation.
- Scenarios with increased precipitation may show increases in May 15 snowpack at the higher elevations in both study areas, but decreases in snowpack at lower elevations. This can lead to an increase in the area of significant snow for dry years.
- The beneficial effect of increased precipitation on snowpack is more prominent earlier in the Spring. In the Warm/Wet scenario, the area of significant snow on May1 increases on average, though it decreases on May 15.
- For wet years, the high elevations of the study areas result in only modest loss of snow cover in the under all scenarios of change. However even in wet years, the area of significant snowpack can decline by almost 50% for the Hot/Dry climate change scenario.

## 5.1 Introduction

In this section we describe the hydrologic model along with various modeling assumptions, validation of the model, the choice of risk-spanning future climate scenarios, and present results of historical and projected snowpack for the two study areas.

To determine the projected effects of a changing climate on snowpack we ran a physically-based hydrology model. The physical basis of the model – using a full energy and water balance of the snowpack rather than a simple temperature-index model -- is critical to evaluate change in a non-stationary climate. While ambient temperature is a critical factor in whether precipitation falls as rain or snow, the subsequent evolution of the snowpack, and in particular the melt season, is driven primarily by the energy balance at the surface. The energy balance is the result of several processes, including solar and longwave radiation, sensible and latent heat fluxes, and heat flux into the ground, as well as storage of heat in the snowpack. Therefore, including a realistic energy balance helps to understand how the perturbations to climate will affect the snowpack.

## 5.2 Model Description

The Distributed Hydrology Soil Vegetation Model (DHSVM) provides a physically-based simulation of land surface hydrology, including snowpack. The physical processes include a full surface water and energy balance model, a 2-layer canopy model, a multi-layer soil model, a 2-layer snowpack model (Wigmosta et al. 1994). It has been used in many studies that have provided realistic hydrologic simulations in topographically complex areas (e.g. Livneh et al. 2015). The model has explicit treatment of topographic slope, and aspect (the compass direction that the slope faces).

The model was selected for developing snowpack projections because it can be run at a fine spatial scale (250 m x 250m pixels) yet is able to be run over extensive domains. There are both

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finer-scale snow models, for which it would have been impractical to simulate such a large domain, and coarser-scale models, such as the 1/16 degree grid of the VIC model that the McKelvey study used (see section 2.3). Coarser-scale models do not explicitly model the effects of slope and aspect, which is one of the primary goals of this study. Both DHSVM and VIC were primarily developed at the University of Washington, and are available as open-source community models. The two models share many components in common, including similar snow and canopy models. As such it supports the project goal of building on McKelvey study by modelling at a finer scale and treating slope and aspect explicitly.

The model was set up for both study domains on a 250m grid in Universal Transverse Mercator (UTM) coordinates within the modeling domain defined within the polygons shown in Section 2. Soil properties and vegetation type as well as a digital elevation model (DEM) were adapted to the model grid. A soil hydraulic routing network was also determined from the DEM, though in this project we do not investigate the runoff. The effect of slope and aspect on incoming solar radiation is implemented through a computation of the degree of shading for each 250-m pixel that was variable throughout the day and differed from month to month based on the solar angle in the sky and from the DEM.

The model requires inputs of time-varying meteorological fields on sub-daily time scales. Snow water equivalent was output on May 1, May 15, and June 1 for every year of the simulation. As noted below, snow depth was estimated using a typical snowpack density for late Spring.

More details of the model will be included in the Chapter 5 Supplementary Material.

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## 5.3 Meteorological Inputs

The DHSVM model inputs were derived in a multi-step process. First, values of daily minimum temperature, daily maximum temperature, and precipitation were extracted from the Livneh (2015) dataset, which has a grid resolution of 1/16$^{th}$ degree in latitude and longitude. These daily values were disaggregated in time. Other forcing variables needed by the model, solar radiation, downwelling longwave radiation, specific humidity were derived from empirical relationships using the MTCLIM algorithms which were evaluated by Livneh et al. (2014) finding small overall biases. The Livneh et al (2015) data was then interpolated to the 250m DHSVM grid using an inverse-distance weighting algorithm along with assumed lapse rates (elevation dependence) in temperature and in precipitation. More details of the Livneh 2015 dataset will be included in the Chapter 5 Supplementary Material.

## 5.4 DHSVM Historical Validation

For the purpose of assessing the effects of climate change it is necessary to have reasonably accurate simulations of the present climate; it is not essential that these be perfect. For the purposes of interpreting the modeled snowpack changes, the future model biases are assumed to be similar to the historical biases. The goal of the model evaluation is to assess the magnitude,

temporal, and spatial aspects of the modeled snowpack in the Spring. To do this we compared to point observations at the available SNOTEL sites, and the spatial patterns obtained from the MODIS analysis.

### 5.4.1 Comparison to SNOTEL

The DHSVM historical simulation was compared against the snow data from nine SNOTEL sites in the ROMO study area that were in operation during the full time-period of interest, and the 3 SNOTEL sites in and adjacent to the GLAC study area (Table 5-1). Validation against SNOTEL snow data was performed by running the DHSVM model in "point" mode so that it simulated the conditions at the SNOTEL locations only. Because the SNOTEL stations are deliberately sited in clearings, the canopy was assumed to be open for the validation runs, while the actual 250m grid canopy values were used for the production runs. Two metrics were chosen: the meltout day of year (defined as the date when SWE fell to less than 1mm), and the duration of snow cover (total number of days during the water year (October-September) when SWE > 10cm). Figure 5-1a shows the modeled and observed meltout dates for the GLAC and ROMO SNOTEL sites, and Figure 5-1b shows the duration of snowpack. One does not expect exact reproduction of the snowpack at the SNOTEL sites, but rather a scatter about the 1-to-1 line, which is seen. The Copeland Lake, and to some extent the Many Glacier SNOTEL sites are outliers, with the model retaining snowpack significantly longer than in observations. Both these sites are at relatively low elevations, and are quite sensitive to potential temperature biases in the input data. The Livneh (2015) dataset is known to have a cool bias relative to other datasets, which may influence these sites disproportionately.

**Table 5-1 SNOTEL Sites at Study Areas**

| | SNOTEL SITE NAME (Site Number, Abbreviation) |
|---|---|
| Glacier Study Area | Flattop Mountain (482, flat), Many Glacier (613, many), Pike Creek (693, pike) |
| Rocky Mountain Study Area (used for Validation) | Bear Lake (322, bear), Copeland Lake (412, cope), Joe Wright (551, joew), Lake Eldora (564, eldo), Lake Irene (565, iren), Niwot (663, niwo), Phantom Valley (688, phan), University Camp (838, univ), Willow Park (870, will) |
| Rocky Mountain Study Area (installed after 1997, not used) | Never Summer (1031), Wild Basin (1042), Hourglass Lake (1122), Long Draw Reservoir (1123), High Lonesome (1187), Sawtooth (1251) |

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The year-to-year variations of peak snowpack at the GLAC SNOTEL sites are well captured, as illustrated in Figure 5-2 that shows simulated and observed time series of SWE at these stations. Figure 5-3 shows selected SNOTEL sites in the ROMO area. As can be seen in Figure 5-2, the Copeland Lake site is less well simulated than other sites. We attribute this to being located at a lower elevation than other sites, and hence susceptible to small biases in temperature in the meteorological inputs. Other sites in ROMO are well simulated.

Based on this evaluation of DHSVM performance, the standard set of model parameters was adopted for the GLAC domain without modification.

The question arises of the independence of the SNOTEL data from the Livneh (2015) forcing data. The primary observing station data that were used for interpolation by Livneh (2015) did not include SNOTEL. However, a monthly adjustment factor was applied to the interpolated precipitation to reproduce the 1981-2000 climatology of PRISM. The temperature data in Livneh et al (2015) were entirely independent of SNOTEL data. Therefore, we expect that the errors revealed at the SNOTEL sites should be representative of errors at other, unobserved sites in the domain.

### 5.4.2 Comparison to MODIS Snow Cover

The spatial distribution of snow cover was assessed by comparison with MODIS data. Some care must be taken to compare observed NDSI, which indicated fractional snow cover, with modeled SWE, which does not account for fractional snow cover within a pixel. For this evaluation, a threshold to determine "snow covered ground" was chosen for both the MODIS NDSI (0.1) and for the DHSVM SWE. Figures 5-4 and 5-5 snow spatial overlays of the DHSVM simulated snow cover and the MODIS observed snow cover for the representative "dry" years in ROMO and GLAC. In terms of snow cover, dry years were more difficult to simulate than wet years, and the spatial agreement is good for these two examples.

However, initial attempts to model ROMO indicated biases in the spatial patterns of snow cover compared to MODIS. To overcome model errors at ROMO, an adjustment of two DHSVM snow parameters was conducted. The representative values of the physical quantities of these parameters can span a fairly large range, and hence an experiment was conducted to evaluate the appropriate settings of the model for ROMO based on minimizing differences between simulated and MODIS SCA for the historical period, as well as reducing biases with SNOTEL SWE.

The first parameter modified was the snow-surface roughness (SR), which affects the amount of turbulent heat fluxes that occur between the snow and the atmosphere, whereby a small number corresponds to a smoother snowpack that has less heat exchange with the overlying air, while the opposite is true for a large value. The second parameter was the liquid water capacity (LWC) that describes the volume of water that the snowpack can hold before water will leach out of the snowpack. This parameter is important, since it is common for snow to melt during the day and then for liquid water to refreeze at night.

Adjustments were made to SR and LWC within reasonable physical ranges and the DHSVM simulated SCA was compared with MODIS via a threat score. The threat score used, referred to as the Critical Success Index (CSI) by Zappa (2010), is defined as:

$$CSI = \frac{a}{a + b + c}$$

Where $a$ indicates a snow-covered pixel in both the simulation and observed data, $b$ indicates a snow-covered pixel in the simulation but a bare pixel in the observed ("false positive"), and $c$ is a bare pixel for the simulation and a snow-covered pixel shown by the observed data ("false negative"). The objective was to maximize the threat score. Approximately ten unique parameter settings were tested. Additionally, for each parameter setting the mean bias in meltout day and duration of snow cover between DHSVM simulated and SNOTEL SWE was calculated with the

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objective being a minimization of the bias between the two (bias = simulated – observed). The final DHSVM settings for ROMO were identified by the parameter values that corresponded with a combination of a high threat score and a low bias. The table and figure showing the parameter settings and ensuing objective values are included in the supplementary material (Figure S5.X).

## 5.5 Determination of Snow Depth from DHSVM model output

DHSVM does not compute snow depth as a separate quantity, but instead returns snow water equivalent (SWE). To estimate the snow depth from SWE, a bulk density of the snowpack must be assumed. We adopt a density of 0.4 (or equivalently, at 2.5-to-1 ratio of snow depth to SWE) appropriate for the May snowpack in the study areas. Several lines of evidence point to the reasonableness of this assumption. First, SNOTEL stations where both depth and SWE are measured show similar ratios for the two study areas. Second, we investigated the ratio of density from the SNODAS (Snow Data Assimilation System) product from the NOAA National Operational Hydrologic Remote Sensing Center, which points to a very narrow range around 2.6-2.7 for the ratio. Finally, for comparison with the McKelvey et al (2011) work we compared the May 1 Snow Depth and SWE products from the Littell et al (2011) hydrologic model runs (obtained separately from https://cig.uw.edu/datasets/wus/). These all point to an approximate value consistent with a density between 0.35 and 0.4. The results of this study do not depend on a precise value for snow density. Further discussion can be found in the Chapter 5 Supplementary Material.

## 5.6 Choice of thresholds for analysis

While the the McKelvey study analysis was for the presence or absence of snowcover, this modeling effort produces results in terms of SWE. This allows greater flexibility in evaluation of the depth of the snowpack, but presents a problem in comparison. To compare the model-generated SWE with both the McKelvey study results and our own MODIS historical snow cover analysis we investigated several threshold values of SWE: 1mm, 5mm, 13mm. For the purposes of this chapter we use the 13mm SWE threshold. We also were concerned with analyzing the presence of "significant snow" which we defined as 0.5 m of snow depth, or 0.2 m of snow water equivalent using our assumed May snow density. The value of 0.5 m was arrived at by an analysis of the modeled snow depth at known wolverine denning sites in Glacier National Park (Table 5-2). With the exception of one site that had melted out by May 15$^{th}$, the other sites all have snowpack between 0.4 and 1.4 m.

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**Table 5-2: Modeled Snow Depth on May 15 at reported den sites in the Glacier Study Area** (source: John Guinotte, FWS)

| Den site | Date observed | Meltout Date (MODIS) | May 15 snow depth dhsvm (m) | Notes |
|---|---|---|---|---|
| **1** | Apr-03 | 5/25/2003 | 1.036 | |
| **2** | May-03 | 5/25/2003 | 1.045 | |
| **3** | Apr-04 | 6/4/2004 | 0.407 | |
| **4** | Apr-04 | 6/29/2004 | 0.539 | |
| **5** | May-04 | 6/29/2004 | 0.653 | |
| **6** | Mar-05 | 6/11/2005 | 0.531 | |
| **7** | Apr-05 | 6/11/2005 | 0.531 | |
| **8** | May-05 | 6/11/2005 | 0.468 | |
| **9** | Mar-06 | 5/25/2006 | 1.435 | |
| **10** | Apr-06 | 5/14/2006 | 0 | meltout occurred before may 15 |
| **11** | Apr-06 | 6/7/2006 | 1.233 | |
| **12** | May-06 | 5/31/2006 | 0.611 | |
| **13** | May-06 | 5/31/2006 | 0.611 | duplicate |

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## 5.7 Delta Method for Future Scenarios

Following McKelvey (2011), we use the "delta method" to downscale the climate model data to the 250m modeling grid.

The steps in this method are as follows:

- Start with historical daily meteorological forcings (inputs to the DSHVM model) for the historical baseline period (1998-2013)
- Run DHSVM with the historical forcings to produce the simulated historical snow and hydrology.
- From climate model output, compute the change in 30-year average temperature for each calendar month over the time frame of interest. Do the same for the percent change in precipitation
- Apply these change factors to the historical daily meteorological inputs to DHSVM to generate future scenarios of meteorological inputs.
- Run DHSVM with these new inputs to generate the projected snow and hydrology.
- Compare the projected snow to the historic DHSVM model simulations to infer changes in snowpack.
- Repeat for a set of change factors from different climate models that adequately sample the uncertainty in climate projections.

**The result of the delta method is a continuous-in-time simulation of the historical period (1998-2013), and an equal length simulation of how this sequence of years would play out in**

**the future under five different scenarios of climate change.** Figure 5-6 illustrates typical DHSVM model output using the delta method. Figure 5-6a shows a map of May 15, 2011 Snow Water Equivalent for the Glacier Study Area from the historical simulation, while Figure 5-6b shows a single projected future for what that year's SWE would look like under a particular scenario of climate change. The future scenario represents a year similar to 2011, that is, a relatively wet and cool year in the sequence, however the temperature and precipitation have been adjusted to be consistent with the 2041-2070 projected climate from the MIROC climate model.

The advantages and disadvantages of the delta method have been discussed extensively in the literature (e.g. Sofaer et al, 2016, for a recent review). The primary advantages of this method are its long history of use, its simplicity, and its use of the historical observed weather as the baseline. The simplicity allowed for the study to be completed in a short time-frame, while still reaching our primary objectives of finer spatial scale and a more complete exploration of future climate scenarios. The use of the historical baseline allows us to explore how wet, near normal, and dry "representative years" would play out under the different climate futures. However, it is important to keep in mind that we are "parameterizing the future variability in terms of the historical variability." This treatment of daily variability also leads to the primary disadvantage of the delta method: the assumptions that the changes in extremes follow the changes in the means, and that the pattern of daily weather is simply shifted without changing the sequences of weather. This aspect is less of a concern for this study, as snow accumulation and ablation are cumulative processes, so that the daily sequences of storms is less critical to simulate than the monthly and seasonal totals. Another assumption of the delta method is that the large-scale changes in temperature and precipitation apply uniformly to the study area. Equivalently we assume that change factors in ambient (free-air) temperature and precipitation will not depend on the small scale spatial detail. Because we explicitly compute the surface energy balance, we are able to simulate surface temperature differences that depend on fine-scale terrain, mitigating to some extent this limitation of the delta method.

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## 5.8 GCM Uncertainty and Scenario Planning Approach

As noted in Section 2, global climate models (GCMs) are our primary tools to examine the nature of climate change during the 21st century. There are currently about 20 modeling centers worldwide which provided output from their best model(s) to be considered in the Coupled Model Inter-comparison Project Phase-5 (CMIP5, Taylor et al., 2012) which informed the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC AR5). Here we quantify changes in temperature and precipitation for the two study areas for the 2014-2070 time frame. We find a large spread in the extent of warming and changes in precipitation, including both increases and decreases in precipitation, as shown in Figures 5-6. For temperature, much of this spread (or uncertainty) is a result of the difference between GCMs (e.g., their climate sensitivities), whereas for precipitation it is both the difference between GCMs and internal climate variability. Some difference also comes from the choice of future greenhouse gases (GHG) emission scenario. However, these differences among mid-21st century climate responses are limited compared to later in the century (see a discussion in Ray et al., 2010).

For more robust planning and climate adaptation, experts recommend incorporation of these

uncertainties into the assessment of impacts and developing adaptation strategies. The scenario planning approach has been one method that has been recommend and promoted by different entities and experts (National Park Service, 2013; Rowland et al., 2014; Maier et al., 2016; Murphy et al. 2016; Star et al., 2016, Fisicelli et al, 2016 a,b,).

## 5.9 Climate Projections Evaluation and Scenarios Selection

We compiled output for temperature and precipitation projections for 34 CMIP5 GCMs from the Reclamation (2013; http://gdo-dcp.ucllnl.org/) archive of 1-degree Regridded GCM dataset for Representative Concentration Pathways (RCP) 4.5 and 8.5, which are respectively the moderate and high GHG emissions scenarios --- therefore, a total of 68 GCM projections described in Supplementary Material. These data were then analyzed to quantify broad-scale projections for the two study regions by 2055 (i.e. a mid-point centered on the 2041-2070 period) – primarily changes in the cold season (Oct-May) temperature and precipitation by 2055 relative to the 1986-2015 period. Figures 5-7 show these changes for Rocky Mountain and Glacier National Parks, respectively, which are bounded by rectangular latitude/longitude values. As mentioned earlier, we found a large range in temperature increases (1-4 ºC) and changes in precipitation (-5% to +20%) for these regions by 2055. Table 5-3 shows GCM names, numbers and colors coded in later figures, and relative changes in temperature and precipitation. To incorporate the large range in climate projections, we worked with the ensemble of 68 CMIP5 temperature & precipitation projections, described by the red filled-circles in Figure 5-7, to select five future climate scenarios (black circles) that span the different parts of this projection space. This strategy of selecting multiple divergent future scenarios challenging to the system of interest follows that in Fisichelli et al (2016 a, b). Five GCMs representing these scenarios were identified for both RMNP and GNP. For each of these GCMs, we calculated changes in temperature and precipitation by 2055 for each month of the year, which we call the "monthly delta". These monthly deltas were used to perturb the hydrological models to simulate snow response in RMNP and GNP by 2055.

**Table 5-3. The six future scenarios used** (five for each area) with changes in temperature and precipitation relative to other scenarios (See also Fig 5-7 for an alternate visualization of these changes), and the GCM used as the basis for the deltas for this scenario. More details on the GCMs are in the Glossary.

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| Future Scenario Name and # | Scenario Change in GLAC relative to other scenarios | Scenario Change in ROMO relative to other scenarios | Code and color for GCM used for this scenario |
|---|---|---|---|
| **Central** (#1) | +~2.2 °C increase in temperature (close to the ensemble mean) and +~5% increase in precipitation | +~2.5 °C increase in temperature (close to the ensemble mean) and +~8% increase in precipitation | cnrm, red |
| GLAC: **Hot/ Very Wet** (#2) | relatively higher increase in temperature (+~3.2 C) and the highest increase in precipitation (+20%) for the GLAC scenarios | N/A | canesm, green |
| ROMO: **Hot/Dry** (#2) | N/A | relatively higher temperature increase (+~ 3.5 °C) and -~5% decrease in precipitation. This scenario results in the greatest change (reduction) in snow pack and snowcover. | hadgem, green |
| **Hot/ Wet** (#3) | the highest temperature increase of the GLAC scenarios (+~4.2 °C) and +~10% increase in precipitation | the highest temperature increase of the ROMO scenarios (+~3.7 °C) and the highest increase in precipitation (+~18%). | miroc, purple |
| **Warm/ Wet** (#4) | relatively lower temperature increase (+~1 °C) and +~10% increase in precipitation | relatively lower temperature increase (+~1.3 °C) and +~7% increase in precipitation that appears to partially offset the impacts of the temperature increase. This scenario results in the least change in snow pack and snowcover. | giss, aqua |
| **Warm/ Dry** (#5) | relatively lower temperature increase (+~1.6 °C) and -~5% decrease in precipitation | relatively lower temperature increase (+~0.8 °C) and -~5% decrease in precipitation | fio, orange |

## 5.10 Modeling Caveats

Some processes which may be of relevance not represented in the model include wind and avalanche re-distribution of snowpack. Snow depth is not explicitly modeled, and must be inferred (see below). The meteorological forcing does not take into account cold air pooling or how this may change in the future. While Curtis et al (2014) identify this as a potential process, they do not physically model Cold Air Pooling, but merely include it in their present-day

climatology as a simple "offset" from their unadjusted data. Nonetheless their work provides a complementary approach to the identification of potential snow refugia.

## 5.11 GLAC Study Area Results

### 5.11.1 SWE and Snow Covered Area for representative years

Figures 5-8 shows DHSVM model simulated snow water equivalent (SWE) on May 15 for the wet (2011) representative year. Maps of snow cover derived from SWE by applying a threshold of 13 mm are available in the Supplementary material. Results for thresholds of 1 mm and 5 mm of SWE were also investigated and show similar patterns. Snow covered area with a "light snow cover" threshold was computed primarily for comparison with both the MODIS results from Section 4, and with McKelvey. In Figure 5-8, the historical simulation is shown along with three of the five future scenarios, chosen to represent the central scenario (cnrm), the greatest change in snowpack on average (Hot/Wet (miroc) scenario) and the least change (Warm/Wet (giss) scenario). The projected snow maps answer the question "what would the snowpack in a wet year like 2011 look like in the 2040's through 2070's under these scenarios of climate change."

Figures 5-9 and 5-10 show SWE for the Near Normal (2009) and Dry (2005) representative years. The historical simulation and future scenarios are as in Figure 5-8. Figure 5-11 summarizes the results for snow covered area in terms of the total snow covered area ($km^2$) within the study area polygon. The numerical values of snow covered area for all years in the simulation, as well as percent changes for these quantities are shown in Table 5-4. Table 5-4 indicates that the snowcovered area decreases for all scenarios. **On average, the GLAC study area exhibits a 12-42 percent decline in snow covered area on May 15 for the scenarios considered.**

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Comparing the Wet and Dry representative years we see that dry years are more vulnerable to climate change in terms of percent loss of snow covered area. For the Wet year, the high elevations of the study area result in little loss of snowpack in the study areas under most scenarios of change.

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| GLAC Area (km^2) | Snow Covered Area (13mm SWE threshold) Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | historical | 2552 | 2793 | 2655 | 2802 | 2890 | 2753 | 2533 | 2408 | 2636 | 2491 | 2883 | 2901 | 2524 | 2901 | 2758 | 2851 | 2708 | 2756 |
| | Central (cnrm) | 1768 | 2329 | 2030 | 2459 | 2816 | 2326 | 1812 | 1509 | 1959 | 1816 | 2742 | 2880 | 1886 | 2885 | 2179 | 2561 | 2247 | 2253 |
| | Hot/Very Wet (canesm) | 1394 | 1956 | 1707 | 1955 | 2595 | 1858 | 1303 | 1171 | 1510 | 1174 | 2436 | 2764 | 1293 | 2817 | 1723 | 2127 | 1862 | 1790 |
| | Hot/Wet (miroc) | 1573 | 1686 | 1604 | 1637 | 1518 | 2122 | 998 | 2275 | 1527 | 1517 | 2608 | 2037 | 1618 | 2481 | 1157 | 2165 | 1780 | 1627 |
| | Warm/Wet (gfdl) | 2197 | 2583 | 2388 | 2599 | 2856 | 2486 | 2191 | 2017 | 2312 | 2109 | 2842 | 2895 | 2170 | 2901 | 2485 | 2705 | 2484 | 2486 |
| | Warm/Dry (had) | 2112 | 2440 | 2184 | 2586 | 2830 | 2555 | 2089 | 1776 | 2231 | 2070 | 2806 | 2891 | 2127 | 2900 | 2486 | 2659 | 2421 | 2461 |
| 15-May | historical | 1452 | 2718 | 2433 | 2552 | 2873 | 2636 | 2287 | 2087 | 2373 | 1741 | 2807 | 2825 | 2393 | 2900 | 2557 | 2548 | 2436 | 2490 |
| | Central (cnrm) | 636 | 2114 | 1703 | 1780 | 2661 | 2068 | 1409 | 1104 | 1555 | 963 | 2367 | 2479 | 1664 | 2817 | 1763 | 1733 | 1801 | 1748 |
| | Hot/Very Wet (canesm) | 650 | 1835 | 1447 | 1419 | 2449 | 1652 | 1083 | 887 | 1255 | 657 | 2174 | 2218 | 1118 | 2697 | 1473 | 1584 | 1537 | 1460 |
| | Hot/Wet (miroc) | 1079 | 1440 | 977 | 1051 | 1750 | 1958 | 784 | 1451 | 1152 | 1026 | 2307 | 1677 | 1499 | 2305 | 879 | 1760 | 1411 | 1335 |
| | Warm/Wet (gfdl) | 1079 | 2483 | 2098 | 2062 | 2800 | 2332 | 1963 | 1667 | 1981 | 1299 | 2638 | 2672 | 2034 | 2882 | 2203 | 2247 | 2152 | 2151 |
| | Warm/Dry (had) | 883 | 2224 | 1913 | 1910 | 2712 | 2372 | 1722 | 1397 | 1851 | 1138 | 2515 | 2600 | 1918 | 2864 | 2125 | 1943 | 2009 | 1931 |
| 1-Jun | historical | 863 | 2360 | 1759 | 1114 | 2599 | 1932 | 1864 | 1375 | 1446 | 1061 | 1923 | 2205 | 1907 | 2863 | 2171 | 2035 | 1842 | 1915 |
| | Central (cnrm) | 250 | 1512 | 948 | 628 | 2049 | 1099 | 897 | 560 | 663 | 417 | 1005 | 1397 | 1025 | 2600 | 1281 | 1114 | 1090 | 1015 |
| | Hot/Very Wet (canesm) | 328 | 1393 | 909 | 590 | 1923 | 966 | 742 | 514 | 689 | 347 | 1172 | 1414 | 794 | 2455 | 1118 | 1134 | 1030 | 937 |
| | Hot/Wet (miroc) | 496 | 813 | 359 | 282 | 682 | 1109 | 417 | 552 | 267 | 511 | 1008 | 682 | 831 | 1862 | 527 | 786 | 699 | 617 |
| | Warm/Wet (gfdl) | 613 | 2046 | 1392 | 883 | 2401 | 1507 | 1473 | 1046 | 1063 | 759 | 1574 | 1893 | 1580 | 2789 | 1763 | 1747 | 1533 | 1581 |
| | Warm/Dry (had) | 401 | 1723 | 1137 | 623 | 2217 | 1410 | 1196 | 735 | 810 | 527 | 1222 | 1606 | 1178 | 2691 | 1611 | 1291 | 1274 | 1209 |

| % change | Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | Central (cnrm) | -31 | -17 | -24 | -12 | -3 | -16 | -28 | -37 | -26 | -27 | -5 | -1 | -25 | -1 | -21 | -10 | -17 | -18 |
| | Hot/Very Wet (canesm) | -45 | -30 | -36 | -30 | -10 | -33 | -49 | -51 | -43 | -53 | -15 | -5 | -49 | -3 | -38 | -25 | -31 | -35 |
| | Hot/Wet (miroc) | -38 | -41 | -40 | -42 | -47 | -23 | -61 | -6 | -42 | -39 | -10 | -30 | -36 | -15 | -58 | -24 | -34 | -41 |
| | Warm/Wet (gfdl) | -14 | -8 | -10 | -7 | -1 | -10 | -13 | -16 | -12 | -15 | -1 | 0 | -14 | 0 | -10 | -5 | -8 | -10 |
| | Warm/Dry (had) | -17 | -13 | -18 | -8 | -2 | -7 | -18 | -26 | -15 | -17 | -3 | 0 | -16 | 0 | -10 | -7 | -11 | -11 |
| 15-May | Central (cnrm) | -56 | -22 | -30 | -24 | -7 | -22 | -38 | -47 | -34 | -45 | -16 | -12 | -30 | -3 | -31 | -32 | -26 | -30 |
| | Hot/Very Wet (canesm) | -55 | -32 | -41 | -40 | -15 | -37 | -53 | -58 | -47 | -62 | -23 | -22 | -53 | -7 | -42 | -38 | -37 | -41 |
| | Hot/Wet (miroc) | -26 | -47 | -60 | -55 | -57 | -26 | -66 | -30 | -51 | -41 | -18 | -41 | -37 | -21 | -66 | -31 | -42 | -46 |
| | Warm/Wet (gfdl) | -26 | -9 | -14 | -12 | -3 | -12 | -14 | -20 | -17 | -25 | -6 | -5 | -15 | -1 | -14 | -12 | -12 | -14 |
| | Warm/Dry (had) | -39 | -16 | -21 | -19 | -6 | -10 | -25 | -33 | -22 | -35 | -10 | -8 | -20 | -1 | -17 | -24 | -18 | -22 |
| 1-Jun | Central (cnrm) | -71 | -36 | -46 | -44 | -21 | -43 | -52 | -59 | -54 | -61 | -48 | -37 | -46 | -9 | -41 | -45 | -41 | -47 |
| | Hot/Very Wet (canesm) | -62 | -41 | -48 | -47 | -26 | -50 | -60 | -63 | -52 | -67 | -39 | -36 | -58 | -14 | -49 | -44 | -44 | -51 |
| | Hot/Wet (miroc) | -42 | -66 | -80 | -75 | -74 | -43 | -78 | -60 | -82 | -52 | -48 | -69 | -56 | -35 | -76 | -61 | -62 | -68 |
| | Warm/Wet (gfdl) | -29 | -13 | -21 | -21 | -8 | -22 | -21 | -24 | -27 | -28 | -18 | -14 | -17 | -3 | -19 | -14 | -17 | -20 |
| | Warm/Dry (had) | -54 | -27 | -35 | -44 | -15 | -27 | -36 | -47 | -44 | -50 | -36 | -27 | -38 | -6 | -26 | -37 | -31 | -37 |

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**Table 5-4: GLAC Snow Covered Area (13mm SWE threshold)** Top: Area ($km^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

However, in Figures 5-10 and 5-11 we notice an anomaly – for the dry year, the Hot/Wet scenario does not have the greatest loss of snow covered area. The increase in precipitation in this scenario has somewhat compensated for the loss of snowpack due to warming.

### 5.11.2 Area and Number of years with 0.5 m Snow Depth

Because of interest in wolverine denning sites, we analyze snow depth > 0.5 m, which we will refer to as "significant snow." Figure 5-12 shows the area with snow depth > 0.5 m within the study area for the dry. Near normal, and wet years. Because of the more stringent threshold for snow, the effects are somewhat larger than for the light snow threshold. This is particularly evident in the dry year, which has a 50% decline on May 15 for four of the future scenarios. The numerical values of snow covered area at the > 0.5 m threshold are shown in Table 5-5 for all years, as well as percent changes for these quantities. **On average, the GLAC study area exhibits a 15 – 68 percent decline in the area of snow depth > 0.5 meters for the scenarios considered.**

Figure 5-13 shows a map of the number of years (out of 16 possible) where each model pixel had at least 0.5 m of snow depth on May 15. This number-of-years statistic is analogous to that used by the Copeland study, except that there are more years of data, and these maps use a much higher threshold of snow. The projections show declines in the number of years with significant snow. The areas with frequent (14-16 years) availability of significant snow become concentrated in smaller high elevation areas.

The effects of climate change on snow melt have been presented as analogous to a "time shifting" of the melt season earlier in the year. For example, McKelvey used the May 31 vs. May 15 snow covered area as a proxy for a 2-week shift in the melt season. Figure 5-14 contrasts the evolution of the snowpack from May 1 to June 1 in the historical simulations (Top Row) with the Warm/Wet scenario (Middle Row) and Hot/Wet (Bottom Row) scenarios. We see that the Warm/Wet scenario, shows the least change compared to the historic snow cover in terms of the availability of significant snow. In contrast, under the Hot/Wet scenario, the May 1st significant snowpack has been diminished below the level of the historic June 1 snowpack – greater than a month shift.

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Snow Covered Area (0.5 m depth threshold)

| Area (km^2) | Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | historical | 1594 | 2545 | 2204 | 2326 | 2844 | 2392 | 2032 | 1800 | 2124 | 1571 | 2613 | 2731 | 1692 | 2901 | 2453 | 2625 | 2278 | 2359 |
| | Central (canesm) | 770 | 1826 | 1477 | 1912 | 2530 | 1766 | 1137 | 912 | 1283 | 951 | 2160 | 2383 | 965 | 2847 | 1630 | 1893 | 1653 | 1698 |
| 1-May | Hot/Very Wet (canesm) | 733 | 1587 | 1234 | 1399 | 2283 | 1336 | 826 | 732 | 1075 | 578 | 1992 | 2070 | 677 | 2721 | 1316 | 1650 | 1388 | 1326 |
| | Hot/Wet (miroc) | 474 | 526 | 633 | 425 | 458 | 1538 | 395 | 614 | 364 | 541 | 1321 | 1236 | 332 | 2029 | 436 | 1018 | 771 | 533 |
| | Warm/Wet (giss) | 1154 | 2242 | 1810 | 2012 | 2681 | 1968 | 1590 | 1400 | 1660 | 1112 | 2389 | 2525 | 1360 | 2890 | 2017 | 2328 | 1946 | 1990 |
| | Warm/Dry (ncc) | 974 | 1938 | 1594 | 1877 | 2586 | 2054 | 1368 | 1058 | 1471 | 969 | 2169 | 2418 | 897 | 2873 | 1944 | 2046 | 1765 | 1907 |
| | historical | 550 | 2496 | 1937 | 1417 | 2749 | 2201 | 1673 | 1308 | 1805 | 804 | 2317 | 2537 | 1647 | 2881 | 2135 | 2035 | 1906 | 1986 |
| | Central (canesm) | 140 | 1731 | 1161 | 1007 | 2329 | 1453 | 792 | 566 | 961 | 328 | 1585 | 1957 | 911 | 2692 | 1284 | 1139 | 1252 | 1150 |
| 15-May | Hot/Very Wet (canesm) | 247 | 1537 | 1048 | 835 | 2178 | 1176 | 648 | 509 | 900 | 274 | 1632 | 1797 | 662 | 2538 | 1087 | 1155 | 1136 | 1068 |
| | Hot/Wet (miroc) | 302 | 508 | 346 | 217 | 439 | 1447 | 293 | 531 | 290 | 302 | 1053 | 878 | 565 | 1733 | 352 | 634 | 612 | 473 |
| | Warm/Wet (giss) | 380 | 2199 | 1546 | 1166 | 2560 | 1782 | 1287 | 995 | 1362 | 567 | 2051 | 2286 | 1355 | 2825 | 1693 | 1745 | 1612 | 1620 |
| | Warm/Dry (ncc) | 199 | 1873 | 1301 | 880 | 2438 | 1781 | 986 | 699 | 1106 | 328 | 1692 | 2096 | 879 | 2765 | 1559 | 1708 | 1360 | 1255 |
| | historical | 337 | 1903 | 1089 | 428 | 2156 | 1192 | 1199 | 723 | 845 | 486 | 1140 | 1590 | 1144 | 2782 | 1625 | 1534 | 1261 | 1168 |
| | Central (canesm) | 52 | 1052 | 494 | 202 | 1473 | 563 | 435 | 227 | 310 | 145 | 462 | 810 | 514 | 2353 | 827 | 738 | 666 | 504 |
| 1-Jun | Hot/Very Wet (canesm) | 113 | 1024 | 572 | 258 | 1476 | 585 | 457 | 262 | 398 | 145 | 667 | 956 | 429 | 2254 | 781 | 847 | 699 | 579 |
| | Hot/Wet (miroc) | 90 | 220 | 100 | 36 | 194 | 542 | 104 | 103 | 43 | 158 | 284 | 194 | 185 | 1319 | 194 | 250 | 251 | 190 |
| | Warm/Wet (giss) | 221 | 1545 | 817 | 321 | 1895 | 870 | 928 | 534 | 589 | 346 | 859 | 1262 | 973 | 2646 | 1246 | 1298 | 1022 | 899 |
| | Warm/Dry (ncc) | 97 | 1139 | 567 | 164 | 1598 | 724 | 602 | 294 | 377 | 157 | 552 | 826 | 522 | 2457 | 1049 | 817 | 749 | 584 |

| % change | Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Central (canesm) | -52 | -28 | -33 | -18 | -11 | -26 | -44 | -49 | -40 | -39 | -17 | -13 | -43 | -2 | -34 | -28 | -27 | -28 |
| | Hot/Very Wet (canesm) | -54 | -38 | -44 | -40 | -20 | -44 | -59 | -59 | -49 | -63 | -24 | -24 | -60 | -6 | -46 | -37 | -39 | -44 |
| 1-May | Hot/Wet (miroc) | -70 | -79 | -71 | -82 | -84 | -36 | -81 | -66 | -83 | -66 | -49 | -55 | -80 | -30 | -82 | -61 | -66 | -77 |
| | Warm/Wet (giss) | -28 | -12 | -18 | -13 | -6 | -18 | -22 | -22 | -22 | -29 | -9 | -8 | -20 | 0 | -18 | -11 | -15 | -16 |
| | Warm/Dry (ncc) | -39 | -24 | -28 | -19 | -9 | -14 | -33 | -41 | -31 | -38 | -17 | -11 | -47 | -1 | -21 | -22 | -23 | -19 |
| | Central (canesm) | -75 | -31 | -48 | -29 | -15 | -34 | -53 | -57 | -47 | -59 | -32 | -23 | -45 | -7 | -48 | -44 | -34 | -42 |
| | Hot/Very Wet (canesm) | -55 | -38 | -46 | -41 | -23 | -47 | -61 | -61 | -50 | -66 | -30 | -29 | -60 | -12 | -49 | -43 | -40 | -46 |
| 15-May | Hot/Wet (miroc) | -45 | -80 | -82 | -85 | -84 | -34 | -88 | -59 | -84 | -62 | -55 | -65 | -66 | -40 | -84 | -69 | -68 | -76 |
| | Warm/Wet (giss) | -31 | -12 | -20 | -18 | -7 | -19 | -23 | -24 | -25 | -29 | -11 | -10 | -18 | -2 | -21 | -14 | -15 | -18 |
| | Warm/Dry (ncc) | -64 | -25 | -33 | -37 | -11 | -19 | -41 | -50 | -39 | -59 | -27 | -17 | -47 | -4 | -27 | -41 | -29 | -37 |
| | Central (canesm) | -85 | -45 | -55 | -53 | -32 | -53 | -64 | -69 | -63 | -70 | -59 | -49 | -55 | -15 | -49 | -52 | -47 | -57 |
| | Hot/Very Wet (canesm) | -66 | -46 | -47 | -44 | -32 | -51 | -64 | -64 | -53 | -70 | -42 | -40 | -63 | -19 | -52 | -45 | -45 | -50 |
| 1-Jun | Hot/Wet (miroc) | -73 | -88 | -91 | -92 | -91 | -55 | -91 | -86 | -95 | -67 | -75 | -88 | -84 | -53 | -88 | -84 | -80 | -84 |
| | Warm/Wet (giss) | -34 | -19 | -25 | -25 | -12 | -27 | -23 | -26 | -30 | -29 | -25 | -21 | -15 | -5 | -23 | -15 | -19 | -23 |
| | Warm/Dry (ncc) | -71 | -40 | -48 | -62 | -26 | -39 | -50 | -59 | -55 | -68 | -52 | -45 | -54 | -12 | -35 | -47 | -41 | -50 |

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**Table 5-5: GLAC Snow Covered Area (0.5 m snow depth threshold)** Top: Area (km$^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

## 5.12 ROMO Study Area

**On average, the ROMO study area exhibits a 7 – 64 percent decline in the area of snow depth > 0.5 meters on May 15 for the scenarios considered. Note that the Warm/Wet scenario projects a slight increase in the area of significant snowpack on May 1.**

### 5.12.1 SWE and Snow Covered Area for representative years

Figure 5-15 shows DHSVM model simulated SWE on May 15th for the wet representative year (2011). The historical simulation is shown along with three of the five future scenarios, chosen to represent the central scenario (cnrm), the greatest change in snowpack on average (Hot/Dry (hadgem2) scenario) and the least change (Warm/Wet (giss) scenario). The future scenarios answer the question "what would the snowpack in a wet year (like 2011) look like in the 2040's through 2070's under these scenarios of climate change." Note that the "greatest snowpack change" scenario is different for ROMO than for GLAC. We have included the Hot/Dry scenario for ROMO because a significant number of climate models project drying conditions in ROMO, whereas in GLAC, the vast majority of climate models predict a wetter future.

Figures 5-16 and 5-17 shows SWE for the "Near Normal" (2009) and "Dry" (2002) year. One can see that in the dry year, the snow cover is already very sparse even in the historical simulation.

Figure 5-18 summarizes the results in terms of the total snow covered area ($km^2$) within the study area polygon. In this case, the threshold used is 13mm of SWE, representing a light snow cover, and comparable to the results in McKelvey. Comparing the Wet and Dry years we see, as with GLAC, that dry years are more vulnerable to climate change in terms of percentage of area lost. For the Wet year, the high elevations of the study area result in little loss of snowpack in the study areas under most scenarios of change. The numerical values of snow covered area for all years, as well as percent changes for these quantities are shown in Table 5-7. **On average, the ROMO study area exhibits a 12-52 percent decline in snow covered area on May 15 for the scenarios considered.**

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| ROMO | Snow Covered Area (sq-km) [13mm SWE threshold] | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | historical | 1567 | 1514 | 1574 | 1523 | 1245 | 1524 | 1248 | 1580 | 1573 | 1555 | 1505 | 1578 | 1439 | 1533 | 773 | 1534 | 1472 | 1570 |
| | Central [cnrm] | 1380 | 1216 | 1424 | 1112 | 786 | 1571 | 655 | 1470 | 1376 | 1195 | 1533 | 1396 | 1091 | 1553 | 379 | 1547 | 1234 | 1378 |
| | Hot/Dry [hadgem2] | 1127 | 971 | 1079 | 894 | 418 | 1498 | 429 | 1114 | 1188 | 1081 | 1587 | 1267 | 763 | 1507 | 185 | 1462 | 1033 | 1097 |
| | Hot/Very Wet [miroc] | 963 | 569 | 1045 | 773 | 501 | 1425 | 293 | 1280 | 1215 | 701 | 1582 | 1003 | 837 | 1444 | 112 | 1382 | 945 | 983 |
| | Warm/Wet [gfdl] | 1498 | 1429 | 1510 | 1373 | 944 | 1589 | 964 | 1522 | 1528 | 1461 | 1595 | 1547 | 1385 | 1586 | 583 | 1587 | 1378 | 1504 |
| | Warm/Dry [ncar] | 1462 | 1302 | 1546 | 1353 | 981 | 1584 | 828 | 1519 | 1518 | 1433 | 1595 | 1533 | 1234 | 1584 | 481 | 1580 | 1351 | 1490 |
| | | | | | | | | | | | | | | | | | | | |
| 15-May | historical | 1477 | 1467 | 1146 | 1064 | 989 | 1592 | 831 | 1519 | 1490 | 1421 | 1593 | 1449 | 1372 | 1587 | 588 | 1566 | 1319 | 1438 |
| | Central [cnrm] | 1012 | 1076 | 728 | 935 | 526 | 1546 | 340 | 1206 | 982 | 872 | 1563 | 953 | 951 | 1485 | 245 | 1366 | 959 | 967 |
| | Hot/Dry [hadgem2] | 530 | 688 | 250 | 221 | 213 | 1395 | 119 | 671 | 650 | 569 | 1410 | 470 | 562 | 1320 | 80 | 846 | 625 | 565 |
| | Hot/Very Wet [miroc] | 637 | 483 | 457 | 385 | 327 | 1396 | 141 | 948 | 858 | 491 | 1510 | 635 | 742 | 1395 | 78 | 1193 | 723 | 626 |
| | Warm/Wet [gfdl] | 1235 | 1315 | 877 | 814 | 633 | 1583 | 564 | 1346 | 1312 | 1242 | 1585 | 1246 | 1228 | 1593 | 396 | 1515 | 1156 | 1244 |
| | Warm/Dry [ncar] | 1277 | 1311 | 928 | 756 | 695 | 1573 | 504 | 1361 | 1302 | 1200 | 1588 | 1279 | 1141 | 1556 | 344 | 1505 | 1142 | 1253 |
| | | | | | | | | | | | | | | | | | | | |
| | Snow Covered Area % change [13mm SWE threshold] | | | | | | | | | | | | | | | | | | |
| | Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | Central [cnrm] | -12 | -20 | -10 | -27 | -37 | -1 | -48 | -7 | -13 | -23 | 0 | -12 | -24 | -2 | -51 | -3 | -16 | -12 |
| | Hot/Dry [hadgem2] | -28 | -36 | -31 | -45 | -66 | -6 | -66 | -30 | -24 | -30 | -1 | -20 | -47 | -5 | -76 | -8 | -30 | -30 |
| | Hot/Very Wet [miroc] | -39 | -62 | -34 | -49 | -60 | -11 | -77 | -19 | -23 | -55 | -1 | -36 | -42 | -9 | -86 | -13 | -36 | -37 |
| | Warm/Wet [gfdl] | -4 | -6 | -4 | -10 | -24 | 0 | -23 | -4 | -3 | -6 | 0 | -2 | -7 | 0 | -25 | 0 | -6 | -4 |
| | Warm/Dry [ncar] | -7 | -8 | -2 | -11 | -21 | -1 | -34 | -4 | -3 | -8 | 0 | -3 | -14 | -1 | -38 | -1 | -8 | -5 |
| | | | | | | | | | | | | | | | | | | | |
| 15-May | Central [cnrm] | -29 | -27 | -37 | -53 | -47 | -3 | -59 | -21 | -34 | -39 | -2 | -34 | -31 | -6 | -58 | -13 | -27 | -33 |
| | Hot/Dry [hadgem2] | -63 | -53 | -78 | -79 | -78 | -12 | -86 | -56 | -56 | -60 | -12 | -68 | -59 | -17 | -86 | -46 | -53 | -61 |
| | Hot/Very Wet [miroc] | -55 | -67 | -60 | -64 | -67 | -15 | -83 | -38 | -42 | -65 | -5 | -58 | -46 | -15 | -87 | -24 | -45 | -56 |
| | Warm/Wet [gfdl] | -13 | -10 | -23 | -23 | -30 | -1 | -33 | -11 | -12 | -13 | -1 | -14 | -11 | -2 | -33 | -3 | -12 | -13 |
| | Warm/Dry [ncar] | -14 | -11 | -19 | -29 | -30 | -1 | -39 | -10 | -13 | -16 | 0 | -12 | -17 | -2 | -41 | -4 | -13 | -13 |

**Table 5-6: ROMO Snow Covered Area (13 mm SWE threshold)** Top: Area ($km^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

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### 5.12.2 Area and Number of years with 0.5 m Snow Depth

Because of interest in wolverine denning sites, we analyze snow depth > 0.5 m, which we will refer to here as "significant snow." Figure 5-19 shows the area with snow depth > 0.5 m within the study area. Because of the more stringent threshold for snow, the effects are somewhat larger than for the light snow cover. The numerical values of snow covered area at the > 0.5 m threshold are shown in Table 5-7 for all years, as well as percent changes for these quantities. In this table, we note that dry years such as 2002 see increases in snow covered area for the Hot/Very Wet and Warm/Wet scenarios. As in GLAC, dry years are somewhat buffered against change, and in fact can see increases in high-altitude "significant" snow for scenarios with increased precipitation. This is a result of the elevational dependence of snowpack change that will be discussed in the next sub-section. **On average, the ROMO study area exhibits a 7 – 64 percent decline in the area of snow depth > 0.5 meters on May 15 for the scenarios considered. Note that the Warm/Wet scenario projects a slight increase in the area of significant snowpack on May 1.**

Figure 5-20 shows a map of the number of years (out of 16 possible) where each model pixel had at least 0.5 m of snow depth on May 15th. This summary statistic is analogous to that used by the Copeland study, except that there are more years of data, and these maps use a much higher threshold of snow. The projections show declines in the number of years with significant snow. The areas with frequent (14-16 years) availability of significant snow become concentrated in smaller high elevation areas. The Hot/Dry "greatest change" scenario, illustrates that the combination of drying and warming leads to very large declines in the persistence of snow.

The effects of climate change on snow melt have been presented as analogous to a "time shifting" of the melt season earlier in the year. For example, McKelvey (2011) used the May 31st vs. May 15th snow covered area as a proxy for a 2-week shift in the melt season. Figure 5-21 contrasts the evolution of the snowpack from May 1 to June 1 in the historical simulations (Top Row) with the Warm/Wet scenario (giss, Middle Row) and Hot/Dry (hadgem, Bottom Row) scenarios [Graphics being re-done].

## 5.1 Elevation Dependence of Snowpack Change

Snowpack accumulation and melt depends critically on temperature and hence on elevation. In the Warm/Dry and Hot/Dry scenarios, both the precipitation decrease and the warming act to reduce Spring snowpack. For the scenarios with warming and increased precipitation there are two countervailing forces that play out along an elevational gradient. A warmer, wetter future is one in which the freezing level and snow line tends to be higher, but with the potential for greater snowpack accumulation during the cold season at high elevations. The warming also tends to lead to an earlier snowmelt, so that the increased snowpack is more evident early in the Springtime than later. This scenario of elevation-dependent snowpack change is well supported in the literature (e.g. Ray et al, 2008). Figure 5-22 shows the elevation dependence for the change in May 15th SWE for GLAC and ROMO, computed for 200 m elevation bands. In particular, these two panels show the very large declines in snow at the lower elevations in each study area. For both ROMO and GLAC, the Hot/Very Wet scenarios project an increase in SWE for some of the high elevation regions. In general, the scenarios with increased precipitation

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show a greater contrast between the low and high elevation bands in terms of snow loss. The elevational gradients seen in SWE changes carries over to snow covered area in Figure 5-23 using 0.5 m depth threshold. The potential for increased high-elevation snowpack with the "Very Wet" scenarios is even more apparent if one looks at May 1st snowpack (not shown).

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| ROMO | Snow Covered Area sq-km (0.5 meter snow depth threshold) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | historical | 468 | 249 | 734 | 180 | 26 | 1578 | 90 | 422 | 418 | 746 | 1334 | 594 | 70 | 1356 | 22 | 381 | 542 | 420 |
| | Central [cnrm] | 421 | 185 | 607 | 95 | 38 | 1470 | 102 | 375 | 208 | 398 | 1193 | 451 | 55 | 1253 | 16 | 402 | 457 | 386 |
| | Hot/Dry [hadgem2] | 166 | 57 | 232 | 64 | 10 | 1245 | 33 | 137 | 278 | 314 | 984 | 231 | 14 | 1036 | 2 | 125 | 312 | 152 |
| | Hot/Very Wet [miroc] | 275 | 135 | 375 | 155 | 40 | 1133 | 59 | 320 | 397 | 259 | 1200 | 350 | 130 | 1164 | 3 | 719 | 419 | 297 |
| | Warm/Wet [gfdl] | 453 | 256 | 601 | 210 | 38 | 1552 | 118 | 375 | 514 | 753 | 1417 | 572 | 104 | 1374 | 23 | 481 | 552 | 467 |
| | Warm/Dry [ncar] | 187 | 99 | 483 | 45 | 4 | 1510 | 16 | 172 | 159 | 475 | 946 | 374 | 14 | 1201 | 5 | 176 | 367 | 174 |
| 15-May | historical | 429 | 277 | 288 | 105 | 29 | 1568 | 37 | 474 | 416 | 533 | 1341 | 403 | 227 | 1289 | 25 | 436 | 496 | 409 |
| | Central [cnrm] | 263 | 169 | 177 | 35 | 27 | 1385 | 22 | 352 | 161 | 248 | 988 | 216 | 174 | 1066 | 13 | 267 | 348 | 196 |
| | Hot/Dry [hadgem2] | 56 | 44 | 32 | 12 | 4 | 930 | 3 | 96 | 133 | 114 | 586 | 54 | 35 | 677 | 0 | 45 | 180 | 50 |
| | Hot/Very Wet [miroc] | 174 | 122 | 106 | 58 | 33 | 1051 | 18 | 276 | 263 | 173 | 970 | 184 | 217 | 922 | 4 | 395 | 311 | 179 |
| | Warm/Wet [gfdl] | 351 | 257 | 208 | 94 | 35 | 1519 | 33 | 403 | 433 | 530 | 1292 | 338 | 241 | 1230 | 23 | 404 | 462 | 345 |
| | Warm/Dry [ncar] | 208 | 120 | 168 | 31 | 4 | 1481 | 10 | 211 | 167 | 373 | 1053 | 244 | 87 | 1064 | 6 | 239 | 342 | 188 |

| | Snow Covered Area % change (0.5 meter snow depth threshold) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | Central [cnrm] | -10 | -25 | -17 | -47 | 44 | -7 | 13 | -11 | -50 | -47 | -10 | -24 | -21 | -5 | -27 | 5 | -16 | -8 |
| | Hot/Dry [hadgem2] | -64 | -77 | -68 | -65 | -61 | -21 | -63 | -68 | -33 | -58 | -26 | -61 | -80 | -19 | -91 | -67 | -42 | -64 |
| | Hot/Very Wet [miroc] | -41 | -46 | -49 | -14 | 53 | -28 | -35 | -24 | -5 | -65 | -10 | -41 | 85 | -14 | -85 | 88 | -23 | -29 |
| | Warm/Wet [gfdl] | -3 | 3 | -18 | 16 | 44 | -2 | 31 | -11 | 23 | 1 | 6 | -4 | 48 | 1 | 6 | 26 | 2 | 11 |
| | Warm/Dry [ncar] | -60 | -60 | -34 | -75 | -85 | -4 | -82 | -59 | -62 | -36 | -29 | -37 | -79 | -11 | -79 | -54 | -32 | -59 |
| 15-May | Central [cnrm] | -39 | -39 | -38 | -67 | -5 | -12 | -42 | -26 | -61 | -58 | -26 | -47 | -23 | -17 | -48 | -39 | -30 | -52 |
| | Hot/Dry [hadgem2] | -87 | -84 | -89 | -88 | -85 | -37 | -93 | -80 | -68 | -81 | -56 | -87 | -85 | -47 | -98 | -90 | -64 | -88 |
| | Hot/Very Wet [miroc] | -60 | -56 | -63 | -44 | 13 | -32 | -53 | -42 | -37 | -71 | -28 | -54 | -4 | -28 | -86 | -9 | -37 | -56 |
| | Warm/Wet [gfdl] | -18 | -7 | -28 | -10 | 20 | -3 | -13 | -15 | 4 | -11 | -4 | -16 | 6 | -4 | -8 | -7 | -7 | -16 |
| | Warm/Dry [ncar] | -52 | -56 | -42 | -71 | -85 | -6 | -74 | -55 | -60 | -37 | -22 | -39 | -62 | -17 | -78 | -45 | -31 | -54 |

**Table 5-7: ROMO Snow Covered Area (0.5 m snow depth threshold)** Top: Area (km$^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.



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# 6 Comparing results with McKelvey

An overview of the methodological similarities and differences between this study and McKelvey et al (2011) was presented in section 2.2. The differences in aims of these studies leads to challenges in making a direct comparison. McKelvey investigated persistence of even a snow cover to May 15th as a correlate of wolverine habitat, as noted in Aubry et al (2008). This study focuses on high-elevation terrain and on the persistence of deeper snowpack. Nonetheless some general statements can be made relating the two studies. Figure 5-24 shows McKelvey's historic and "MIROC 2080's" snow cover. The GLAC and ROMO areas have been outlined. A close examination of this figure shows that snow cover persists in our study areas, even for highest-end scenario of change (their "2080's MIROC" scenario). The greatest loss of snow cover in McKelvey occurs at lower elevations than were included in GLAC or ROMO. Because of the increased resolution of this study we are able to ask whether any pockets of snow with depth greater than 0.5 meters will persist.

The choice of future climate scenarios differs somewhat from McKelvey. We have intentionally included scenarios that represent the range of possibilities indicated by the CMIP5 climate models. McKelvey used climate model output from Littell, who chose scenarios based solely on projected warming. For GLAC, this choice fortuitously included a range of precipitation changes as well. For ROMO, however, McKelvey's scenarios include only a narrow range of precipitation change, where we include scenarios with significantly increased wintertime precipitation as well as scenarios with drying. This is a significant factor, given the buffering effect that increased precipitation has on snowpack loss at high elevations.

While McKelvey focused snowpack projections entirely on the long-term average, we investigate how climate variability – the sequences of wet and dry years -- intersects with scenarios of change. For ROMO in particular we find that dry years behave differently than wet years, with dry years benefitting from the increased precipitation in several of our future scenarios. This emphasizes the importance of planning for a range of possible climate scenarios, particularly regarding the direction of change in wintertime precipitation.

The question arises as to how the fine-scale projections of snow persistence in other areas might reasonably be inferred from the two study areas considered here. Figure X indicates many areas in the western United States that show persistence of snow cover in McKelvey's scenarios, even in the more extreme scenarios. We have investigated two study areas: a northern, relatively wet and low-elevation area GLAC, and a southern, relatively dry, and very high elevation area (ROMO). In both areas we find general declines in snow covered area under most future scenarios. The GLAC study area is broadly similar in its climate to much of the high northern Rockies, while ROMO shares features with the high mountain ranges of the Central Rockies. For areas in the McKelvey maps that show retention of snow on the higher mountain ranges it is physically reasonable to presume that a finer scale simulation would show the retention of areas of snow > 0.5 m on May 15th. Extending this beyond the general area of the Rocky Mountains is problematic. Even within the Rockies, in regions where McKelvey's results show widespread loss of snowpack without "islands" of snow persistence it is probably not reasonable to conclude one way or the other whether a finer scale analysis would identify snow refugia.

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# 8 Glossary

- **Aspect:** compass direction that slope faces
- **Baseline period 1916-2000**: Deltas (changes) computed (monthly average delta) for "2040's and "2080's" compared to the 1916-2000 baseline.

- **CanESM:** A CMIP5 climate model the Canadian Centre for Climate Modeling and Analysis (canesm2.1.rcp85), forced with the RCP 8.5 higher emissions pathway, used in this report as a future scenario (Hot/Dry scenario for GLAC only) that has relatively higher increase in temperature (+~4.5 C) and about +20% increase in precipitation (See Figure 5-7)
- **Climate Sensitivity:** Regionally speaking, it is the response of a climate model for a given amount of greenhouse gas increase. More narrowly defined it is the global average temperature increase that results from a doubling of carbon dioxide over pre-industrial values.
- **CMIP3, CMIP5:** Coupled Model Intercomparison Project Phases 3 and 5. "Foundational" collections of climate model projections, used in the Intergovernmental panel on Climate Change (IPCC) 2007 and IPCC 2013 reports, respectively
- **CNRM:** A CMIP5 climate model from the French National Centre of Meteorological Research (cnrm-cm5.1.rcp85),used in this report as a future scenario (Central scenario for both GLAC and ROMO) that is relatively close to the ensemble mean in temperature increase (+~2.5 ºC) and +~5-8% increase in precipitation (See Figure 5-7).
- **DEM:** Digital elevation model
- **DSHVM:** Distributed Hydrology Soil Vegetation Model
- **ESM:** earth system models, see GCM.
- **FIO:** A CMIP5 earth system model from the First Institute of Oceanography, State Oceanic Administration of China (fio-esm.1.rcp85), used in this report as a future scenario (Warm/Dry scenario for both areas) that is relatively lower in temperature increase (+~0.8-1.6 ºC) and -~5% decrease in precipitation (See Figure 5-7).
- **FLH:** Atmospheric freezing level height is the altitude in the free atmosphere at which the temperature is 0 °C
- **GCM:** Global Climate Model, 6 were used for this report from the IPCC 2013 class of models; X of these are actually earth system models (ESM), an advanced type of GCM which have the added capability to explicitly represent biogeochemical processes that interact with the physical climate. GCM is used as a general term referring to both kinds of models, ESM is used specifically for earth system models.
- **GISS:** A CMIP5 climate model from the NASA Goddard Institute for Space Studies (giss-e2-r.1.rcp45), used in this report as a future scenario (Warm/Wet scenario for both areas). Referred to as the "Least Change" scenario because it that is relatively lower temperature increase (+~1-1.3 ºC) and +~7-10% increase in precipitation (See Figure 5-7).
- **GLAC:** An area in Glacier National Park used as a spatial unit of analysis in this report
- **HADGEM:** A CMIP5 earth system model from the United Kingdom Meteorological Office Hadley Center (hadgem2-es.1.rcp85) used in this report as a future scenario (Hot/Very Wet scenario for ROMO only) that has relatively higher temperature increase (+~ 3.5 ºC) and -~5% decrease in precipitation.
- **Internal climate variability**: The variations in the climate, even for 30-year and longer averages, that can occur due to the interactions of the atmosphere, ocean, inland surface and cryosphere. This occurs even in the absence of anthropogenic climate change.
- **MODIS:** Moderate Resolution Imaging Spectroradiometer, a satellite remote sensing instrument carried on the Terra satellite

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- **MIROC:** A CMIP5 earth system model from the Japanese Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies (miroc-esm-chem.1.rcp85), used in this report as a future scenario (Hot/Wet scenario for both areas). Referred to as the "Greatest Change" scenario because it has the highest temperature increase of the scenarios (+~4 ºC) and +~10-18% increase in precipitation (see Figure 5-7). This ESM has an atmospheric chemistry (CHEM) component coupled to the MIROC-ESM (http://maca.northwestknowledge.net/GCMs.php).
- **NDSI:** Normalized Difference Snow Index, a measure of snow cover, has a has a linear relationship to fractional snow cover (FSC)
- **North American Freezing Level Tracker**: NCEP/NCAR Global Reanalysis 2.5º x 2.5º grid data (http://www.wrcc.dri.edu/cwd/products/)
- **Octants:** Topographic aspect, or compass direction, was classified into eight directional bins, each representing 45° of compass arc, e.g; NW, N, NE, E, SE, S, SW, and W
- **ROMO:** An area in and around Rocky Mountain NP used as a spatial unit of analysis in this report
- **SCA:** Snow Covered Area ($km^2$)
- **SDD:** Snow Disappearance Date, the first Day of Year after March 1 where pixel is snow-free, defined as the date which NDSI/100 was less or equal to 0.1.
- **SNODAS:** Snow Data Assimilation System, a product of the NOAA National Weather Service's National Operational Hydrologic Remote Sensing Center (NOHRSC)
- **SWE:** Snow water equivalent (mm).For May, snow depth is assumed to be ~ 2.5 *SWE
- **TopoWx:**
- **Snow covered area, total:**Total area covered by snow within the study boundaries in square kilometers ($km^2$)
- **Snow covered area, fractional:** Percentage of the total land area that is covered by snow; this can be within the study boundaries, aspect area, or elevation bands
- **VIC:** Variable Infiltration Capacity hydrologic model
- **UTM:** Universal Transverse Mercator spatial coordinates

FIGURES – see separate file

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# Wolverine Snow Refugia Study: An analysis of future climate risks

## A Report to the U.S. Fish and Wildlife Service Region 6

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# 1 Introduction

## 1.1 Motivation

This report responds to the United States Fish and Wildlife Service (FWS) need for information on potential climate impacts to snow persistence. The North American wolverine (*Gulo gulo luscus*) is currently being evaluated for listing as a threatened or endangered species under the Endangered Species Act (ESA) and climate change effects on snow persistence was identified as an important factor for the future viability of the wolverine. The species was considered for listing in 2014, but FWS concluded that it did not warrant listing. They further concluded that there is significant uncertainty about how the effects of climate change will affect wolverines and their habitat in the foreseeable future, and that this uncertainty includes information on how fine-scale changes in snow cover and persistence might affect denning site selection.

The U.S. District Court rejected the Service's determination that climate change, small population size (only ~300 wolverines in the northern Rockies and north Cascades), and genetic isolation do not threaten the wolverine's survival in the lower 48 states. The FWS is currently collating the most up to date scientific information to inform the court-ordered re-evaluation of that decision, due in April 2017. This report describes a snow modeling analysis intended to provide FWS with a finer scale assessment of snow extent and depth for future wolverine habitat that extends previous work to finer scales and includes additional snow processes that we believe are critical to future wolverine habitat. Other uncertainties identified by the Service are beyond the scope of this study and report, i.e., whether future snow extent and depth would limit the suitability of habitat within the home range of an individual wolverine, and whether those factors would limit wolverine populations in the foreseeable future.

Funding was provided by the U.S. Fish and Wildlife Service, Region 6 and the NOAA/Earth System Research Lab/Physical Sciences Division. This effort builds on work underway by the project team at NOAA/ESRL/PSD, the NOAA-University of Colorado (CU) Cooperative Institute for Research in Environmental Sciences (CIRES), and CU Department of Civil, Environmental & Architectural Engineering.

## 1.2 Project Objectives

Persistent spring snowpack has been described as an important factor in determining suitable habitat for the wolverine, including Northern boreal forests and subarctic and alpine tundra (Aubry et al, 2007, Peacock et al, 2011). This relationship was the basis for the analysis done by Copeland et al. (2010) and McKelvey et al. (2011) used in the previous FWS decision. In both studies, climate change projections of snowpack were used to characterize potential future wolverine habitat.

Our primary objective is to advance scientific understanding of the current spatial extent of spring snow retention on the landscape, and the future temporal and spatial extent of snow retention through a thirty-year period, 2041-2070, centered on the year 2055. The goal of this effort is to identify the persistence of snow as potential refugia for wolverine denning. Climate

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refugia have been identified as possible targets for conservation in several studies (see Morelli et al. 2016 for a review). We aim to advance snow analysis and modeling to better support assessment of snow-related species, in the following ways:

- Explicitly model the effects of slope and aspect, using fine-scale spatial models to analyze topographic effects on snow
- Better represent of the range of plausible future changes (climate scenarios)
- Analyze extremes: wet and dry years from the historic record and how these might change in the future

Our strategy was to build on previous methods where possible to be comparable to work by McKelvey et al. (2011) and Copeland et al. (2010), and depart from their methods where necessary to take advantage of analysis techniques not feasible at the large scales used in the studies done by those authors. Furthermore, we utilize new scientific data and tools that are now available, including the latest global climate model runs, and conduct Distributed Hydrology Soil Vegetation Model (DHSVM, Wigmosta et al.1994) high resolution hydrologic simulations modeling at highly resolved (250m) spatial scale, as well as analysis of historic snowpack variability to investigate these influences of topography on snowpack, along with the projected physical drivers of snowpack.

First we analyzed historic snow variability from satellite remote sensing of snow extent from the year 2000 to present to determine areas of greater and lesser sensitivity to climate drivers (temperature and precipitation), and identify possible snow refugia. We then did an intercomparison of the satellite observations of snow with that from the DHSVM hydrologic modeling study that includes a representation of slope and aspect (the compass direction that the slope faces) of the terrain and shading on the snowpack. Prior studies also show a relationship between terrain (slope and aspect) and persistence of snow (e.g. Lundquist and Flint, 2006) and the potential importance of this factor under in a changed climate. Finally, the DSHVM hydrologic model was forced with five future scenarios of climate change for each of the two study regions. These future climate scenarios were derived from the latest Coupled Model Inter-comparison Project Phase-5 runs (CMIP5, Taylor et al., 2012) which informed the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC AR5, 2013).

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# 2 Project Overview

## 2.1 Study Areas

High-resolution hydrologic modeling was needed to provide fine scale analysis of snow. However, given time, funding and computational constraints, it was necessary to limit the study domain to two areas of about 1500-3000km$^2$ for high-resolution analysis. Two study areas representing core and peripheral habitat regions in the northern and central Rocky Mountains were identified in consultation with FWS Region 6 personnel (Figures 2-1 and 2-2). The highest priority area is in the "Crown of the Continent" region in the high mountain terrain from the Canadian border south to approx. Helena MT, including Glacier National Park, and adjacent areas. An area within Glacier National Park (GLAC) was chosen (Figure 2-1) area at elevations

higher than about 250 m below tree line. Because we were restricted to smaller areas for analysis, these areas were chosen to bracket a range of habitat conditions for wolverine, from a lower elevation domain in Glacier National Park where wolverines have been observed repeatedly, and a very high elevation domain in ROMO, recently occupied by a male wolverine.

The analysis for the GLAC and ROMO study areas is presented in separate sections, repeating descriptions to make the material self-contained for the reader who may read about only one area; similarly, complete captions are given for each area.

## 2.2 Comparison between our analysis and that of Copeland and McKelvey

This project builds on the analyses done by Copeland et al. (2010) and McKelvey et al. (2011) that was used in the previous FWS decision. Copeland et al. (2010) (hereafter, simply Copeland or the Copeland study) calculated the number of years with snowcover on May 15th as detected by MODIS satellite, postulated as a correlate of wolverine habitat (check cite). They found that most (45 of 75) North American den sites were in areas that snow cover persisted with 6 or 7 out of 7 years on May 15$^{th}$. We also investigated the of number of years of snow persistence for our study areas, however, the new MODIS product has two advantages over that available at the time of their study, 1) improved snow detection (snow covered area, SCA), and 2) 17 years of MODIS data is now available vs the 7 available to Copeland and McKelvey. Furthermore, we investigated the relationships between snow cover persistence and both elevation and aspect (the compass direction of the slope face). A comparison between our work and the studies used previously is summarized in Table 2-1.

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**Table 2-1: Modeling Methods Compared to McKelvey**

| | McKelvey (Littell) | This Study |
|---|---|---|
| Spatial Resolution (modeling) | VIC model – 1/16 degree (~5km x 7 km, ~37km$^2$ cell) | DHSVM model - 250m x 250m UTM grid (~0.0625 km$^2$ cell) |
| Spatial Extent | Westwide except California and Great Basin | ROMO and GLAC study areas, near and above treeline |
| Process differences | ”Flat” pixels, implicit elevation bands. | Slope, aspect, shading, explicit fine scale elevation effects. |
| Validation | None specific to snow | Comparison to SNOTEL (ground stations) and MODIS (satellite) |
| Future Scenarios | Delta Method; “2045”;”2085”; from 3 GCMs selected to span westwide temperature changes. | Delta Method: ”2055” from 5 GCMs spanning regional changes in temperature and precipitation |

| | | |
|---|---|---|
| Analysis | Changes in long-term mean snowpack only | Means and variability, including wet, near normal and dry years. |
| Snow representation | Binary snow/no snow at 13 cm snow depth | Analyzed snow depth at two thresholds: 13mm of SWE ('light snow') and 0.5m depth ('significant snow') |

McKelvey et al. (2011) (hereafter, simply McKelvey or the McKelvey study) used May 1st snow depth simulated by the Variable Infiltration Capacity hydrologic (VIC) hydrology model (1/16 degree, ~5km x 7 km), "flat" gridboxes, or cells, with no slope aspect dependence). The VIC model runs were documented in Littell et al. (2011) and were based on meteorological inputs from Elsner et al. (2010). The present study uses the DHSVM model, which was developed by the same group at the University of Washington for fine-scale simulations, and shares many model components. McKelvey used the "delta method" (described later in Section 5) for the projected changes in climate compared to present day. This study also uses the "delta method." The McKelvey study used a range of temperature change to select GCMs representing the range or spread of future scenarios. As shown below in Section 5.10 and Figure 5.7, their chosen future scenarios reflect a range of precipitation in GLAC, but in ROMO, the three scenarios have similar precipitation changes. This project selected a larger number of future scenarios selected based on changes in both temperature and precipitation.

The McKelvey study calculated a metric for a historic period (1915-2005 average) and two futures, 30-year averages around "2045" and" 2085." This study focused on a 30-year period around mid-century, "2055" to focus on FWS' time horizons for the wolverine and due to time and computational constraints given the project budget. We also reproduce a single future scenario using one of the Littell (2011) "2080's scenarios for direct comparison. Calculations for a later period using the CMIP5 climate models (e.g. ~2100) could easily be made, but were beyond the scope of this project. We provide analysis for two thresholds of snow amount, a "light" snow cover (13mm of snow water equivalent), and significant, or "heavy" snow cover (equivalent to 0.5 m of snow depth). Because McKelvey only had access to May 1st snow depth simulation, they chose to use a 13 cm snow depth on May1st as a proxy for snow disappearance by May 15th. We instead chose to use a much lighter threshold of snow on May 15th itself. Note that SWE is a measure of the water content in the snowpack; to estimate depth, a density of the snow must be assumed, i.e. an approximation of whether the snow is heavy or light. Our threshold of 13mm SWE was originally chosen to be comparable to McKelvey's snow depth. Our assumptions are discussed further in Sec. 5.6.

An important difference between this study and prior work by Copeland et al. (2010) and McKelvey et al. (2011) is the spatial scale of results. McKelvey and Copeland both presented results on a regular 1/16 degree latitude-longitude grid, in which each cell, or gridbox is ~5-7 km on a side. These cells were assumed to be flat in the model-- that is they do not incorporate slope or aspect information in their surface energy balance. The result of this is north-facing slopes are treated identically to south-facing slopes. Our study uses the DHSVM (originally developed by

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Wigmosta et al, 1994, see also http://www.hydro.washington.edu/Lettenmaier/Models/DHSVM/documentation.shtml) for snow at 250m x 250m resolution that incorporates other physical drivers of snowpack (a complete energy balance at the surface, a 2-layer snow model, and a 2-layer vegetation canopy model) and allows analysis of snow at different slopes and aspects (slope directions). The VIC modeling did include the option for elevational snow bands within the VIC grid (Jeremy Littell, pers. comm.) but the snow band information was not explicitly used. Fine-scale elevational effects are implicit in the VIC model whereas it is explicitly modeled in DHSVM. A visual comparison of the gridbox (Fig 2-3).

It should be noted there are tradeoffs between our strategies and the methods of Copeland and McKelvey. The finer scale analysis presented in this report integrates slope and aspect with respect to snow accumulation and retention that are thought to be important for maintaining snow refugia for denning sites (see Fig 2 in McKelvey et al 2011). The disadvantage of this improvement in spatial resolution is we were only able to analyze two study areas due to time and computational constraints. The Copeland and McKelvey projects analyzed a much larger domain, including a significant portion of the wolverine range in the continental US, but does not provide detailed analysis of any habitat area.

## 2.3 A note on description of modeling resolution

The VIC modeling that was the basis for McKelvey was performed on a regular grid in latitude and longitude, with a grid size of 1/16 degree on a side. The distance between degrees of longitude varies due to the curvature of the Earth, and the east-west dimension of a gridbox is smaller than the north-south distance by a factor of the cosine of latitude. At 40°N latitude, the southern extent of Rocky Mountain National Park, the gridbox is ~5km by 7 km (~37km$^2$). Grid boxes at Glacier National Park (~48°N) are slightly smaller. When referring to the McKelvey study we will use the "1/16 degree" notation. The DHSVM modeling used in this study was performed on a uniform grid in the Universal Transverse Mercator (UTM) map projection, which allows a near-uniform grid size of 250m by 250m (0.0625 km$^2$) in both of the study areas.

## 2.4 The Westwide context of future climate

Global climate models (GCMs) are the primary tools used by climate science to examine the nature of climate change during the 21st century. There are currently about 20 modeling centers worldwide that provide output from their best model or models to be considered in the Coupled Model Inter-comparison Project Phase-5 (CMIP5, Taylor et al., 2012) which informed the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC AR5, 2013). When we quantify regional changes in climate variables such as temperature and precipitation by a particular time horizon in the 21st century, we find a large spread in the extent of warming and changes in precipitation, including both increases and decreases in precipitation, as shown in regional maps (Figure 2-4) and described later in Section 5. For temperature change, much of this spread (or uncertainty) is a result of the difference among the formulations of the GCMs (e.g., their climate sensitivities), whereas for precipitation it is both the differences among GCMs and internal climate variability. Some difference also comes out of the choice of future greenhouse gases (GHG) emission scenario. However, the differences among greenhouse gas

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emissions scenarios is less at mid-21st century compared to later in the century, and is much smaller than other sources of uncertainty at the regional scale (IPCC,2013).

Figure 2-4 shows projected annual and seasonal temperature and precipitation changes by 2050 (2035–2064) over the western U.S., including the northern and central Rocky Mountains, from an ensemble of the 34 climate models used for this study under the RCP 8.5, a high-end emissions scenario. The large maps show the average change for all of the models (n=34) for that season, and the small maps show the average changes of the highest 20% and lowest 20% of the models, based on the statewide change for Colorado in temperature or precipitation. For much of the central and northern Rockies, all models show a substantial warming (of +2.5°F to +5.5°F). While fewer models agree about the direction of precipitation change westwide, even the lower (drier) models show an increase in winter precipitation for the area around Glacier National Park, although there is less agreement for the central Rockies area including Rocky Mountain National Park. The GCM output is discussed further in Section 5.

# 3 Observed Climate and Variability

Key Points:

- Both study areas show upward trends in both temperature and freezing level.
- Surface Air Temperature and Atmospheric freezing level are related, with a stronger relationship in ROMO (that is, a greater change in freezing level for a given surface air temperature change)
- Representative years chosen for GLAC: 2011 (cool wet), 2005 (warm dry), 2009 (near normal).
- Representative years chosen for ROMO: 2011 (cool wet), 2002 (warm dry), 2007 (near normal).

## 3.1 Introduction

This section presents a historical analysis of the winter and spring climate variability for the two study regions, GLAC and ROMO. This section presents the following:

- Trends in temperature and freezing level
- Historical variability in cool season (October – May) temperature and precipitation for the study areas.
- Choice of representative years during the simulation period for cool/wet, warm/dry, and near normal conditions for the two areas based on the entire cold season averages
- A ranking of the representative years in a longer climate record to provide context.

A complete description of regional climate is beyond the scope of this project, but may be found in e.g. McWethy et al (2010), Garfin et al (2014), Lukas et al (2014), Shafer et al (2014), and cites therein.

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## 3.2 Trends in Surface Temperature and Freezing Level

Temperature strongly influences hydrologic processes such as evapotranspiration, snowpack accumulation, and timing of snowmelt. Both the Glacier and Rocky Mountain areas show a trend of increasing surface air temperature in the winter season (October-May, Figure 3-1), consistent with trends that have been observed west-wide (Garfin et al 2014; Lukas et al 2014; Shafer et al 2014). While winter season temperatures vary inter-annually, linear regression of these data (not shown) indicates about a 1.4°C increase in temperature from 1948-2015 for an area around Glacier, and about a 1.2°C increase around Rocky Mountain National Park. This report analyzes data by "water year," or Oct 1st-Sept 30th, rather than calendar year, in order to capture precipitation over the contiguous winter months.

Atmospheric freezing level height (FLH) represents the altitude in the free atmosphere (that is, away from the surface and its immediate influence) where the temperature is 0 °C. Above this level, the temperature of the air is typically below freezing. Freezing in the free atmosphere is indicative of the level above which precipitation falls as snow rather than rain. Freezing level height can have a strong influence on freeze-thaw processes in high-elevation regions (Bradley et al 2009). As with winter season temperatures, freezing level varies over time (Figures 3-2, 3-3), but linear regression (not shown) indicates about a 160m increase in the freezing level for Glacier (Fig 3-2), and about a 170 m increase in the freezing level for Rocky Mountain (Fig 3-3).

Figure 3-4 illustrates a strong relationship between freezing levels and surface air temperature change for both regions in October-May with explained variance $R^2$ close to 0.8. For GLAC (3-1, left), a 1°C anomaly in temperature equates to about a 115 m increase in the freezing level, over the period. For ROMO, for 1°C increase in temperature there has been about a 180 m increase in the freezing level (3-1, right).

## 3.3 Choice of Representative Years for Detailed Analysis

The modeling presented later in the report uses all years from 2000-2013 as "base years." While 1998-1999 are modeled, they are not used for most analyses to be consistent with the availability of satellite data. In addition, the first years of a model simulation are often not analyzed because the soil water content is adjusting to the weather forcing, though that is of less concern for this snow-centric analysis). Climate-model derived change factors (the "delta method") were applied to all these years to generate future simulations of snowpack.

McKelvey et al (2011) studied only the effect of climate change on the *average* snowpack. One of the primary study goals is to extend the analysis to include the effects of climate change on extreme years – both for high- and low- spring snowpack. To drive our choice of years modeled, we investigated historical temperature and precipitation anomalies and MODIS-based snow covered area (shown in the next sub-section). Years were chosen within that range to represent a "Cool/Wet" year, a "Near Normal" year, and a "Warm/Dry" year (Table 3-1). When brevity is required these are later called "Wet", "Near Normal", and "Dry." We put special emphasis on these "representative case study" years in the analysis shown in Sections 4 and 5.

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**Table 3-1: Choice of Representative Years**

| Year Type | GLAC | ROMO |
|---|---|---|
| COOL WET (WET) | 2011 | 2011 |
| WARM DRY (DRY) | 2005 | 2002 |
| Near Normal | 2009 | 2007 |

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## 3.4 Historical Year-to-Year variability in Temperature and Precipitation

Year-to-year variations in average cold season (October – May) and melt season (April – June) temperature and precipitation guide the choice of representative years for closer study and also provide the context of these years in the longer climate record. Figure 3-5 shows scatterplots of the anomalous precipitation (as % of average) and temperature (degrees Celsius) for each year of the primary study period (2000-2013) for the two study areas. The larger context of these climate anomalies is indicated by the unlabeled dots that show the data for 1950-1999. For both study areas, the 2011 winter stands out as a particularly large anomaly. The Livneh dataset was chosen because it is the one that is used for the meteorological inputs to the DHSVM model. Other sources with later data indicate that 2015 and 2016 were near average in precipitation, but anomalously warm, with correspondingly low spring snowpack. These years were not included in the DHSVM modeling study.

Examination of the time series of Snow Covered Area (SCA) derived from the MODIS satellite product (Figure 3-6ab) shows the impact of these climate anomalies in terms of springtime snowpack. Because of the high-elevations, the study areas melt late in the Spring. In wet and near normal years, nearly the entire domains are snow-covered. To verify our choices of representative years, we show the SCA as a function of elevation within the study areas (Figure 3-6cd). These time series show that the near-normal years selected closely follow the median profile.

## 3.5 Historical Context

How often did the study years occur in the longer climatological record? The percentiles of October – May precipitation and temperature averaged over the study areas are shown for the representative wet, near normal and dry in Table 3-2 for both study areas. The percentiles are calculated based on the 63 total years in the 1951-2013 period of the Livneh (2014) dataset. For GLAC, October – May 2011 was at the 98$^{th}$ percentile of precipitation and the 6$^{th}$ percentile of temperature, while 2005 was at the 6$^{th}$ percentile of precipitation and 83$^{rd}$ percentile of temperature. For ROMO, 2011 was in the 96$^{th}$ percentile of October – May precipitation, but

only the 36th percentile of temperature, and while anomalously cold was not extreme in temperature. 2002 was in the 4th percentile of precipitation, but only near the median in temperature.

Tables 3-3 (GLAC) and 3-4 (ROMO) show the percentiles of precipitation and temperature for all the years that were simulated using the DHSVM model (see section 5) as well as the percentiels for the April – June melt season. Note that the year 2012 was also considered as a "representative dry year" for ROMO, but difficulty in accurately modeling the spatial pattern of that year's snowpack using DHSVM led us to use 2002 instead. Even though the precipitation was as extreme in 2002 as in 2012, the temperature was not. This is reflected in the MODIS spring snowcover (Figure 3-6), where 2002 was low, but not as nearly extreme as in 2012.

Percentiles were calculated by ranking the data and using the following formula: percentile = (rank – 0.5)/(total number of years). It should be noted that the exact rankings and percentiles would differ based on the underlying dataset and interpolation methods used, as the study areas have relatively few observing stations. Rankings and "representativeness" have been checked against the PRISM dataset and provide qualitatively similar results.

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**Table 3-2: Historical Percentiles of precipitation and temperature for the representative dry, near normal, and wet years for GLAC and ROMO study areas.**

| | Year Type | Year | Oct. - May Precipitation Percentile | Oct. - May Temperature Percentile |
|---|---|---|---|---|
| GLAC | Dry | 2002 | 4 | 45 |
| | Near Normal | 2007 | 56 | 69 |
| | Wet | 2011 | 96 | 36 |
| ROMO | Dry | 2005 | 6 | 83 |
| | Near Normal | 2009 | 45 | 42 |
| | Wet | 2011 | 98 | 6 |

**Table 3-3: Percentile of temperature and precipitation anomalies for GLAC study area based on the 1951-2013 period.** Percentiles are shown for both the October – May cold season and for the April – June melt season.

| GLAC | Percentile 1951-2013 | | | |
|---|---|---|---|---|
| | Oct. - May Precipitation | Oct. - May Temperature | Apr. - June Precipitation | Apr. - June Temperature |
| 2000 | 31 | 96 | 7 | 66 |
| 2001 | 2 | 37 | 47 | 58 |
| 2002 | 61 | 31 | 91 | 12 |
| 2003 | 33 | 87 | 13 | 69 |
| 2004 | 13 | 63 | 33 | 61 |
| 2005 | 6 | 83 | 80 | 47 |
| 2006 | 37 | 82 | 53 | 93 |
| 2007 | 21 | 72 | 6 | 75 |
| 2008 | 39 | 47 | 60 | 17 |
| 2009 | 45 | 42 | 12 | 34 |
| 2010 | 12 | 55 | 85 | 13 |
| 2011 | 98 | 6 | 87 | 4 |
| 2012 | 40 | 74 | 72 | 53 |
| 2013 | 60 | 66 | 56 | 29 |

**Table 3-4: Percentile of temperature and precipitation anomalies for ROMO study area based on the 1951-2013 period.** Percentiles are shown for both the October – May cold season and for the April – June melt season.

| ROMO | Percentile 1951-2013 | | | |
|---|---|---|---|---|
| | Oct. - May Precipitation | Oct. - May Temperature | Apr. - June Precipitation | Apr. - June Temperature |
| 2000 | 45 | 98 | 40 | 98 |
| 2001 | 29 | 33 | 23 | 91 |
| 2002 | 4 | 45 | 2 | 96 |
| 2003 | 75 | 80 | 77 | 64 |
| 2004 | 21 | 91 | 75 | 77 |
| 2005 | 50 | 82 | 82 | 53 |
| 2006 | 28 | 74 | 4 | 94 |
| 2007 | 56 | 69 | 6 | 75 |
| 2008 | 80 | 12 | 45 | 13 |
| 2009 | 77 | 93 | 88 | 44 |
| 2010 | 48 | 13 | 87 | 37 |
| 2011 | 96 | 36 | 93 | 25 |
| 2012 | 10 | 94 | 7 | 99 |
| 2013 | 64 | 26 | 79 | 42 |

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# 4 MODIS Observed Historic Snowpack Variability Analysis

Key points

- In GLAC, even in dry years, NE-facing slopes tend to hold more snow and melt later in the season. Complete snow cover (over 80%) is around 2000 m of elevation on May 1during dry years, and down to 1200 m during wet years. Snow conditions on June 1during wet years resemble those for May 1 during near-normal years.
- In ROMO, NW-facing slopes tend to hold more snow even during dry years. In very dry years, snow cover peaks at intermediate elevations, suggesting that the high-altitude snowpack may be particularly vulnerable in this region under warm/dry conditions.

## 4.1 Introduction

In this chapter we perform an analysis of the variability of snow cover in the historical period 2000-2016 using gridded snow cover data acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Terra satellite. The analysis for the GLAC and ROMO study areas is presented in separate sections, repeating descriptions to make the material self-contained for the reader who may read about only one area. Each section consists of analysis of the following: a) total snow covered area (SCA), b) SCA fractional area as a function of eight compass directions of slope aspect (octants), and d) elevation dependence. MODIS snow cover data serves two purposes in this study – first for the analysis of historical variability in the study areas, and second to serve as a basis for the spatial evaluation of the hydrologic model simulations.

## 4.2 Methods

### 4.2.1 Data subsetting and re-projection

We downloaded selected MODIS/Terra daily snow cover data on a 500m grid from the recently released version 6 (MOD10A1.006) (Hall and Riggs, 2016). All data from geographic tiles h09v04 (ROMO) and h10v04 (GLAC) were downloaded for days between March 1 and July 1 for all years from 2000 to 2016.

The data are available in daily files, one for each tile, and georeferenced to an equal-area sinusoidal projection. Each tile covers 10° x 10° at the equator or approximately 1200 km by 1200 km, with a nominal pixel resolution of 500 m (actual resolution 463.313 m). To bring the data to the same grid as used in the hydrologic modeling necessitated re-projection of the data onto a Universal Transverse Mercator Grid. We used the MODIS Reprojection Tool (https://lpdaac.usgs.gov/tools/modis_reprojection_tool) to subset the daily tiles to the areas of interest and reproject the subsetted areas to UTM grids with a pixel resolution of 250 m using nearest-neighbor resampling. The ROMO study area perimeter falls at the corner of tile h09v04, and extends slightly beyond the tile boundaries at its southern tip. We excluded this extension of the study from our analysis. Parameters for the MODIS data reprojection are provided in Table S4-1.

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### 4.2.2 Normalized Difference Snow Index

In the MODIS product, snow cover is identified using the Normalized Difference Snow Index (NDSI). Snow covered land typically has very high reflectance in visible bands and very low reflectance in the shortwave infrared, and the magnitude of this difference is quantified by the NDSI. A series of screens is also implemented to alleviate errors and flag uncertain snow cover detections. NDSI is reported as a ratio, with values ranging from 0 to 1 (scaled and reported as 0 to 100 in the data files). In the dataset, certain values over 200 are used to classify grid points as "missing data", "night", "inland water", "cloud", etc. The NDSI Snow Cover variable is comparable to the Fractional Snow Cover (FSC) variable used in previous collections of this data. A user could calculate FSC by applying the following linear relationship: FSC = (-0.01 + (1.45 * NDSI))*100.0 for $0.0 \leq NDSI \leq 1.0$.

The prior work by McKelvey and Copeland both used Collection 4 of the MODIS data which provided them with a binary snow cover classification. These data are only available for the years 2000-2007, necessitating the use of the more recent MODIS products. However, collection 6 does not include a binary snow cover product for the daily data. For the purposes of determining binary snow cover, we applied a threshold of NDSI > 0.1. This choice of threshold is the same as that used in the MODIS 8-day composite product.

### 4.2.3 Snow disappearance date and snow cover on a given date

We defined the Snow Disappearance Date (SDD) as the first day after March 1 in which NDSI/100 was less or equal to 0.1. The SDD is denoted by the Day of Year value, in which January 1 is 1, February 1 is 32, March 1 is 60 (or 61 in leap years), etc. Once SDD was defined at each grid point for each year (resulting in 17 annual maps of SDD for the period of record), we were able to derive snow cover maps for any given date. For example, snow cover on May 1 was inferred by marking grid points as "snow-covered" if their SDD was equal or greater than 121 (or 122 for leap years). We repeated the process to infer snow cover maps for May 15 and June 1. This indirect method to infer snow cover allowed us to circumvent the reality of several missing data points due to cloud cover, and offered a conservative estimate of snow disappearance.

### 4.2.4 Snow cover by elevation and aspect

Using a digital elevation model resampled to a 250m resolution grid, we obtained grids for elevation and aspect octants in both study regions. We reclassified the elevation values into 200 m bins. The elevation bins range from 1000 to 3000 m in GLAC and 2600 to 4200 m in ROMO. Both the slope magnitude and the aspect of the slope (that is the compass direction that the slope faces) were analyzed using functionality in the open source Quantum GIS software. We reclassified the aspect grids into eight 45°-wide directional bins (hereafter, octants) centered on the points of the compass. In both types of analyses (elevation and aspect), we computed snow covered area (SCA) on May1, May15, and June1, in terms of the total area in square kilometers and also in terms of the percentage of snow covered area in several elevation bands and aspect octants.

## 4.3 MODIS analysis for GLAC

MODIS snow cover data was analyzed for March1 – July1 for the years 2000-2016. Data for all years was analyzed. We present here some summary statistics of snow cover, including total

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snow covered area, and number of years during the period of study with snow cover on a given date. For more in depth analysis including aspect and elevation-based analyses the report focuses on the representative years defined in Section 3: 2011 ("wet"), 2009 ("near normal"), and 2005 ("dry").

### 4.3.1 Total Snow Covered Area

Total snow covered area was the primary metric that was analyzed in McKelvey et al (2011) and provides an overall summary of availability of snow. Figure 4-1 presents maps of May 15 snow cover for the GLAC study area and vicinity from MODIS. These maps clearly depict the regional character of the year-to-year variations in snowcover. Figure 4-2 shows the total snow covered area within the study area polygon, which is depicted in red on the previous figure. The year-to-year variations are shown for snowcover on three different dates during the melt season. The behavior in individual year varies considerably, including "wet" years such as 2011 with very persistent snow, years with strong melt in early May, such as 2012, or in late May (2009, 2001), and "dry" years (2004, 2005). Though it is beyond the period of the modeling study, it is worth noting that the last two years of the record, 2015 and 2016 show low snowcover. Both these years had near-normal precipitation, but had anomalously warm temperatures.

To summarize all 17 years of the record, Figure 4-3 presents maps of the number of years with snow cover on May 1, May 15, and June 1. These are similar to the analysis done by the Copeland and McKelvey studies. The primary difference is in the use of the newer MODIS products and the extension of the analysis from seven to seventeen years.

Figure 4-4 quantifies the maps in Figure 4-3, showing the area within the GLAC study area polygon with different numbers of years of snow cover. The three colored bars designate different days of the year. Because the study areas were chosen to be in the vicinity of tree line, it is no surprise that in the present climate there are large areas that see snow every year on May 1$^{st}$.

### 4.3.2 Aspect Dependence of Snowpack: Total Area

One of the primary goals of this study is to investigate topographic factors that influence the persistence of snow during the melt season. One such factor is the "slope aspect" or simply "aspect" – the compass direction that the slope faces. Figure 4-5 presents the dependence of total snow covered area (km$^2$) on aspect for each of the 17 years in the MODIS dataset, for May 1, May 15, and June 1. The shape of the curves for individual years is strongly determined by the topography of the region, with more land area available in the northwest and southeast octants. Upon closer inspection, other features become apparent. Comparing the SW and NE octants we see that there is greater year-to-year variability in the SW, indicating a greater sensitivity of SW-facing slopes to variations in the historical climate.

In Figure 4-6 we examine two of the representative years, 2011 and 2005, to see how the total snow covered area progresses from May 1 to June 1. The dry year, 2005, shows that snow cover declines faster on S, SW, and W slopes, as one would expect; this analysis quantifies the magnitude of this effect.

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### 4.3.3 Aspect Dependence of Snowpack: Fractional area

The total land area within each aspect octant varies due to the orientation of ridges and valleys in the study area. As a result, the analysis of total snow covered area is dominated by the topography itself. To focus on the *relative* importance of the snow processes related to aspect, we calculated the fraction of the total land area within each octant that is snow covered for each of the 17 years in the historical record, while in Figure 4-8 we focus on the representative wet and dry years. For example, in Figure 4-7, the asymmetric shape clearly shows that in GLAC, the NE directions ranging from E to N have much larger fractional area covered by snow. Even in dry years, over 60 % of the NE facing slopes are snow-covered on May 15th.

### 4.3.4 Elevation Dependence

Figure 4-9 shows the elevation dependence of MODIS snow cover for the wet, near-normal and dry years, with the median of all years as reference. The results are shown as a percentage of the total area within each 200-meter elevation band within the study area boundaries.

## 4.4 MODIS analysis for ROMO

MODIS snow cover data was analyzed for March1 – July 1 for the years 2000-2016. Data for all years was analyzed. We present here some summary statistics of snow cover, including total snow covered area, and number of years during the period of study with snow cover on a given date. For more in depth analysis including aspect and elevation-based analyses the report focuses on the representative years defined in Section 3: 2011 ("wet"), 2007 ("near normal"), and 2012 ("dry").

The analysis is presented in separate sections for the GLAC and ROMO study areas repeating descriptions as needed to make each section as independent of the other. Each section consists of analysis of the following: a) total snow covered area (SCA), b) SCA as a function of aspect, c) snow covered fractional area as a function of aspect, and d) elevation dependence.

### 4.4.1 Total Snow Covered Area

Total snow covered area was the primary metric that was analyzed in McKelvey et al (2011) and provides an overall summary of availability of snow. Figure 4-10 presents maps of May 15 snow cover for the ROMO study area and vicinity from MODIS. These maps clearly depict the regional character of the year-to-year variations in snowcover. Figure 4-11 shows the total snow covered area within the study area polygon, which is depicted in red on the previous figure. The year-to-year variations are shown for snowcover on three different dates during the melt season. The behavior in individual year varies considerably, including "wet" years such as 2011 with very persistent snow, years with strong melt in early May, such as 2004, or in late May (2001, 2013), and "dry" years (2002, 2012).

To summarize all 17 years of the record, Figure 4-12 presents maps of the number of years with snow cover on May 1, May 15, and June 1. These are similar to the analysis done by Copeland and McKelvey studies. The primary difference is in the use of the newer MODIS products and the extension of the analysis from seven to seventeen years.

Figure 4-13 quantifies the maps shown in Figure 4-12, showing the area within the GLAC study area polygon with different numbers of years of snow cover. The three colored bars designate

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different days of the year. Because the study areas were chosen to be in the vicinity of tree line, it is no surprise that in the present climate there are large areas that see snow every year on May 1.

### 4.4.2 Slope Aspect Dependence of Snowpack: Total Area

One of the primary goals of this study is to investigate topographic factors the influence the persistence of snow during the melt season. One such factor is the "slope aspect" or simply "aspect" – the compass direction that the slope faces. Figure 4-14 presents the dependence of total snow covered area ($km^2$) on aspect for each of the 17 years in the MODIS dataset for May 1, May 15, and June 1. The shape of the curves for individual years is strongly determined by the topography of the region, with less land area available in the NW octant, and more in the NE. Compared to GLAC, the ROMO study area shows more year-to-year variation in the shape of the curves, likely indicating stronger meteorological controls on the directionality of the snowpack compared to the topographic control seen in GLAC.Comparing the SW and NE octants we see that there is greater year-to-year variability in the SW, indicating a greater sensitivity of SW-facing slopes to variations in the historical climate.

In Figure 4-15 we examine two of the representative years, 2011 and 2012, for how the snow cover progresses from May 1 to June 1. The dry year, 2012, shows that snow cover starts out lower on May1 and declines faster on SE, S and SW slopes.

### 4.4.3 Slope Aspect Dependence of Snowpack: Fractional Area

The total land area within each aspect octant varies due to the orientation of ridges and valleys in the study area. As a result, the analysis of total snow covered area is dominated by the topography itself. To focus on the *relative* importance of the snow processes related to aspect, Figure 4-16 presents an analysis of the fraction of the total land area within each directional "bin" that is snow covered. The asymmetric shape shows that the NW-facing slopes have larger fractional area covered by snow. With the exception of 2012, even in dry years over 60 % of the NW facing slopes are snow-covered on May 15th. Figure 4-17 indicates that for the dry year 2012, snow cover was retained preferentially on NW-facing slopes.

### 4.4.4 Elevation Dependence

Figure 4-18 shows the elevation dependence of MODIS snow cover for the wet, near-normal and dry years, with the median of all years as reference. The results are shown as a percentage of the total elevation within each 200-meter elevation band within the study area boundaries. The ROMO area shows that the dry year, 2002 (as well as the other very dry year during the period, 2012), was significantly different from the other two, with a fractional area declining with altitude above 3400m. This may indicate that the meteorology in this region interacts differently with the topography in extremely dry years than in wetter years. The high-altitude snowpack may be particularly vulnerable in this region if conditions like those in 2002 recur.

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# 5 Future Snowpack Projections: DHSVM Modeling

Key Points - Methods

- The Distributed Hydrology Soil Vegetation (DHSVM) model was run for the historic period 1998-2013 and validated against available SNOTEL observing stations. The spatial patterns of snow were validated against MODIS satellite remotely sensed snow cover.
- Five scenarios of the future – a thirty year period centered on 2055 -- were selected from CMIP5 global climate model (GCM) projections based on a moderate (RCP 4.5) and high (RCP 8.5) emissions scenarios. These were chosen to represent a large fraction of the range of the CMIP5 ensemble projections in each study area in terms of precipitation and temperature changes. The scenarios differ somewhat between the two study areas to better represent the range of climate projections in each area.
- The selected GCM projections were downscaled using the "delta method" which applies change factors from the climate models to the historic temperature and precipitation that are used as inputs to the DHSVM model.
- Analysis is presented for light snow cover (Snow Water Equivalent > 13mm) for comparison with MODIS and McKelvey, and for 0.5 m of snow depth.
- To capture climate variability, Wet, Near Normal, and Dry representative case study years are shown for the historical simulations and how each of these years plays out under these five future scenarios.

Key Points – GLAC study area.

- Snow Covered Area in GLAC and area with snow depth greater than 0.5 meters on May 15 declines on average in all scenarios on average and for almost all years.
- On average, projections for the May 15 snowpack in the GLAC study area show a 12-42 percent decline in snow covered area, and a 15-68 percent decline in area with snow depth > 0.5 meters for the scenarios considered.
- All projections show declines in the number of years with significant snow. The areas with frequent (14-16 years) availability of significant snow become concentrated in smaller high elevation areas.
- For wet years, the high elevations of the study areas result in little loss of snowpack in the under most scenarios of change.
- For GLAC the Warm/Wet scenario shows the least change compared to the historic snow cover in terms of the area of significant (0.5 meter) snowpack, comparable to only a small shift in time. Under the Hot/Wet scenario, the May 1st significant snowpack has been diminished below the level of the historic June 1 snowpack – greater than a month shift.

Key Points – ROMO study area.

- Snow Covered Area in ROMO (13mm threshold on May 15) declines on average in all scenarios on average and for almost all years.

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- On average, projections for the May 15 snowpack in the ROMO study area show a 12-52 percent decline in snow covered area, and a 7-64 percent decline in area with snow depth > 0.5 meters for the scenarios considered.
- Snow Covered Area in ROMO (0.5 m threshold on May 15) generally declines in wet years, but may increase in dry years in those scenarios with increased precipitation.
- Scenarios with increased precipitation may show increases in May 15 snowpack at the higher elevations in both study areas, but decreases in snowpack at lower elevations. This can lead to an increase in the area of significant snow for dry years.
- The beneficial effect of increased precipitation on snowpack is more prominent earlier in the Spring. In the Warm/Wet scenario, the area of significant snow on May1 increases on average, though it decreases on May 15.
- For wet years, the high elevations of the study areas result in only modest loss of snow cover in the under all scenarios of change. However even in wet years, the area of significant snowpack can decline by almost 50% for the Hot/Dry climate change scenario.

## 5.1 Introduction

In this section we describe the hydrologic model along with various modeling assumptions, validation of the model, the choice of risk-spanning future climate scenarios, and present results of historical and projected snowpack for the two study areas.

To determine the projected effects of a changing climate on snowpack we ran a physically-based hydrology model. The physical basis of the model – using a full energy and water balance of the snowpack rather than a simple temperature-index model -- is critical to evaluate change in a non-stationary climate. While ambient temperature is a critical factor in whether precipitation falls as rain or snow, the subsequent evolution of the snowpack, and in particular the melt season, is driven primarily by the energy balance at the surface. The energy balance is the result of several processes, including solar and longwave radiation, sensible and latent heat fluxes, and heat flux into the ground, as well as storage of heat in the snowpack. Therefore, including a realistic energy balance helps to understand how the perturbations to climate will affect the snowpack.

## 5.2 Model Description

The Distributed Hydrology Soil Vegetation Model (DHSVM) provides a physically-based simulation of land surface hydrology, including snowpack. The physical processes include a full surface water and energy balance model, a 2-layer canopy model, a multi-layer soil model, a 2-layer snowpack model (Wigmosta et al. 1994). It has been used in many studies that have provided realistic hydrologic simulations in topographically complex areas (e.g. Livneh et al. 2015). The model has explicit treatment of topographic slope, and aspect (the compass direction that the slope faces).

The model was selected for developing snowpack projections because it can be run at a fine spatial scale (250 m x 250m pixels) yet is able to be run over extensive domains. There are both

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finer-scale snow models, for which it would have been impractical to simulate such a large domain, and coarser-scale models, such as the 1/16 degree grid of the VIC model that the McKelvey study used (see section 2.3). Coarser-scale models do not explicitly model the effects of slope and aspect, which is one of the primary goals of this study. Both DHSVM and VIC were primarily developed at the University of Washington, and are available as open-source community models. The two models share many components in common, including similar snow and canopy models. As such it supports the project goal of building on McKelvey study by modelling at a finer scale and treating slope and aspect explicitly.

The model was set up for both study domains on a 250m grid in Universal Transverse Mercator (UTM) coordinates within the modeling domain defined within the polygons shown in Section 2. Soil properties and vegetation type as well as a digital elevation model (DEM) were adapted to the model grid. A soil hydraulic routing network was also determined from the DEM, though in this project we do not investigate the runoff. The effect of slope and aspect on incoming solar radiation is implemented through a computation of the degree of shading for each 250-m pixel that was variable throughout the day and differed from month to month based on the solar angle in the sky and from the DEM.

The model requires inputs of time-varying meteorological fields on sub-daily time scales. Snow water equivalent was output on May 1, May 15, and June 1 for every year of the simulation. As noted below, snow depth was estimated using a typical snowpack density for late Spring.

More details of the model will be included in the Chapter 5 Supplementary Material.

## 5.3 Meteorological Inputs

The DHSVM model inputs were derived in a multi-step process. First, values of daily minimum temperature, daily maximum temperature, and precipitation were extracted from the Livneh (2015) dataset, which has a grid resolution of 1/16$^{th}$ degree in latitude and longitude. These daily values were disaggregated in time. Other forcing variables needed by the model, solar radiation, downwelling longwave radiation, specific humidity were derived from empirical relationships using the MTCLIM algorithms which were evaluated by Livneh et al. (2014) finding small overall biases. The Livneh et al (2015) data was then interpolated to the 250m DHSVM grid using an inverse-distance weighting algorithm along with assumed lapse rates (elevation dependence) in temperature and in precipitation. More details of the Livneh 2015 dataset will be included in the Chapter 5 Supplementary Material.

## 5.4 DHSVM Historical Validation

For the purpose of assessing the effects of climate change it is necessary to have reasonably accurate simulations of the present climate; it is not essential that these be perfect. For the purposes of interpreting the modeled snowpack changes, the future model biases are assumed to be similar to the historical biases. The goal of the model evaluation is to assess the magnitude,

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temporal, and spatial aspects of the modeled snowpack in the Spring. To do this we compared to point observations at the available SNOTEL sites, and the spatial patterns obtained from the MODIS analysis.

### 5.4.1 Comparison to SNOTEL

The DHSVM historical simulation was compared against the snow data from nine SNOTEL sites in the ROMO study area that were in operation during the full time-period of interest, and the 3 SNOTEL sites in and adjacent to the GLAC study area (Table 5-1). Validation against SNOTEL snow data was performed by running the DHSVM model in "point" mode so that it simulated the conditions at the SNOTEL locations only. Because the SNOTEL stations are deliberately sited in clearings, the canopy was assumed to be open for the validation runs, while the actual 250m grid canopy values were used for the production runs. Two metrics were chosen: the meltout day of year (defined as the date when SWE fell to less than 1mm), and the duration of snow cover (total number of days during the water year (October-September) when SWE > 10cm). Figure 5-1a shows the modeled and observed meltout dates for the GLAC and ROMO SNOTEL sites, and Figure 5-1b shows the duration of snowpack. One does not expect exact reproduction of the snowpack at the SNOTEL sites, but rather a scatter about the 1-to-1 line, which is seen. The Copeland Lake, and to some extent the Many Glacier SNOTEL sites are outliers, with the model retaining snowpack significantly longer than in observations. Both these sites are at relatively low elevations, and are quite sensitive to potential temperature biases in the input data. The Livneh (2015) dataset is known to have a cool bias relative to other datasets, which may influence these sites disproportionately.

**Table 5-1 SNOTEL Sites at Study Areas**

| | SNOTEL SITE NAME (Site Number, Abbreviation) |
|---|---|
| Glacier Study Area | Flattop Mountain (482, flat), Many Glacier (613, many), Pike Creek (693, pike) |
| Rocky Mountain Study Area (used for Validation) | Bear Lake (322, bear), Copeland Lake (412, cope), Joe Wright (551, joew), Lake Eldora (564, eldo), Lake Irene (565, iren), Niwot (663, niwo), Phantom Valley (688, phan), University Camp (838, univ), Willow Park (870, will) |
| Rocky Mountain Study Area (installed after 1997, not used) | Never Summer (1031), Wild Basin (1042), Hourglass Lake (1122), Long Draw Reservoir (1123), High Lonesome (1187), Sawtooth (1251) |

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The year-to-year variations of peak snowpack at the GLAC SNOTEL sites are well captured, as illustrated in Figure 5-2 that shows simulated and observed time series of SWE at these stations. Figure 5-3 shows selected SNOTEL sites in the ROMO area. As can be seen in Figure 5-2, the Copeland Lake site is less well simulated than other sites. We attribute this to being located at a lower elevation than other sites, and hence susceptible to small biases in temperature in the meteorological inputs. Other sites in ROMO are well simulated.

Based on this evaluation of DHSVM performance, the standard set of model parameters was adopted for the GLAC domain without modification.

The question arises of the independence of the SNOTEL data from the Livneh (2015) forcing data. The primary observing station data that were used for interpolation by Livneh (2015) did not include SNOTEL. However, a monthly adjustment factor was applied to the interpolated precipitation to reproduce the 1981-2000 climatology of PRISM. The temperature data in Livneh et al (2015) were entirely independent of SNOTEL data. Therefore, we expect that the errors revealed at the SNOTEL sites should be representative of errors at other, unobserved sites in the domain.

### 5.4.2 Comparison to MODIS Snow Cover

The spatial distribution of snow cover was assessed by comparison with MODIS data. Some care must be taken to compare observed NDSI, which indicated fractional snow cover, with modeled SWE, which does not account for fractional snow cover within a pixel. For this evaluation, a threshold to determine "snow covered ground" was chosen for both the MODIS NDSI (0.1) and for the DHSVM SWE. Figures 5-4 and 5-5 snow spatial overlays of the DHSVM simulated snow cover and the MODIS observed snow cover for the representative "dry" years in ROMO and GLAC. In terms of snow cover, dry years were more difficult to simulate than wet years, and the spatial agreement is good for these two examples.

However, initial attempts to model ROMO indicated biases in the spatial patterns of snow cover compared to MODIS. To overcome model errors at ROMO, an adjustment of two DHSVM snow parameters was conducted. The representative values of the physical quantities of these parameters can span a fairly large range, and hence an experiment was conducted to evaluate the appropriate settings of the model for ROMO based on minimizing differences between simulated and MODIS SCA for the historical period, as well as reducing biases with SNOTEL SWE.

The first parameter modified was the snow-surface roughness (SR), which affects the amount of turbulent heat fluxes that occur between the snow and the atmosphere, whereby a small number corresponds to a smoother snowpack that has less heat exchange with the overlying air, while the opposite is true for a large value. The second parameter was the liquid water capacity (LWC) that describes the volume of water that the snowpack can hold before water will leach out of the snowpack. This parameter is important, since it is common for snow to melt during the day and then for liquid water to refreeze at night.

Adjustments were made to SR and LWC within reasonable physical ranges and the DHSVM simulated SCA was compared with MODIS via a threat score. The threat score used, referred to as the Critical Success Index (CSI) by Zappa (2010), is defined as:

$$CSI = \frac{a}{a + b + c}$$

Where $a$ indicates a snow-covered pixel in both the simulation and observed data, $b$ indicates a snow-covered pixel in the simulation but a bare pixel in the observed ("false positive"), and $c$ is a bare pixel for the simulation and a snow-covered pixel shown by the observed data ("false negative"). The objective was to maximize the threat score. Approximately ten unique parameter settings were tested. Additionally, for each parameter setting the mean bias in meltout day and duration of snow cover between DHSVM simulated and SNOTEL SWE was calculated with the

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objective being a minimization of the bias between the two (bias = simulated – observed). The final DHSVM settings for ROMO were identified by the parameter values that corresponded with a combination of a high threat score and a low bias. The table and figure showing the parameter settings and ensuing objective values are included in the supplementary material (Figure S5.X).

## 5.5 Determination of Snow Depth from DHSVM model output

DHSVM does not compute snow depth as a separate quantity, but instead returns snow water equivalent (SWE). To estimate the snow depth from SWE, a bulk density of the snowpack must be assumed. We adopt a density of 0.4 (or equivalently, at 2.5-to-1 ratio of snow depth to SWE) appropriate for the May snowpack in the study areas. Several lines of evidence point to the reasonableness of this assumption. First, SNOTEL stations where both depth and SWE are measured show similar ratios for the two study areas. Second, we investigated the ratio of density from the SNODAS (Snow Data Assimilation System) product from the NOAA National Operational Hydrologic Remote Sensing Center, which points to a very narrow range around 2.6-2.7 for the ratio. Finally, for comparison with the McKelvey et al (2011) work we compared the May 1 Snow Depth and SWE products from the Littell et al (2011) hydrologic model runs (obtained separately from https://cig.uw.edu/datasets/wus/). These all point to an approximate value consistent with a density between 0.35 and 0.4. The results of this study do not depend on a precise value for snow density. Further discussion can be found in the Chapter 5 Supplementary Material.

## 5.6 Choice of thresholds for analysis

While the the McKelvey study analysis was for the presence or absence of snowcover, this modeling effort produces results in terms of SWE. This allows greater flexibility in evaluation of the depth of the snowpack, but presents a problem in comparison. To compare the model-generated SWE with both the McKelvey study results and our own MODIS historical snow cover analysis we investigated several threshold values of SWE: 1mm, 5mm, 13mm. For the purposes of this chapter we use the 13mm SWE threshold. We also were concerned with analyzing the presence of "significant snow" which we defined as 0.5 m of snow depth, or 0.2 m of snow water equivalent using our assumed May snow density. The value of 0.5 m was arrived at by an analysis of the modeled snow depth at known wolverine denning sites in Glacier National Park (Table 5-2). With the exception of one site that had melted out by May 15$^{th}$, the other sites all have snowpack between 0.4 and 1.4 m.

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**Table 5-2: Modeled Snow Depth on May 15 at reported den sites in the Glacier Study Area** (source: John Guinotte, FWS)

| Den site | Date observed | Meltout Date (MODIS) | May 15 snow depth dhsvm (m) | Notes |
|---|---|---|---|---|
| **1** | Apr-03 | 5/25/2003 | 1.036 | |
| **2** | May-03 | 5/25/2003 | 1.045 | |
| **3** | Apr-04 | 6/4/2004 | 0.407 | |
| **4** | Apr-04 | 6/29/2004 | 0.539 | |
| **5** | May-04 | 6/29/2004 | 0.653 | |
| **6** | Mar-05 | 6/11/2005 | 0.531 | |
| **7** | Apr-05 | 6/11/2005 | 0.531 | |
| **8** | May-05 | 6/11/2005 | 0.468 | |
| **9** | Mar-06 | 5/25/2006 | 1.435 | |
| **10** | Apr-06 | 5/14/2006 | 0 | meltout occurred before may 15 |
| **11** | Apr-06 | 6/7/2006 | 1.233 | |
| **12** | May-06 | 5/31/2006 | 0.611 | |
| **13** | May-06 | 5/31/2006 | 0.611 | duplicate |

## 5.7 Delta Method for Future Scenarios

Following McKelvey (2011), we use the "delta method" to downscale the climate model data to the 250m modeling grid.

The steps in this method are as follows:

- Start with historical daily meteorological forcings (inputs to the DSHVM model) for the historical baseline period (1998-2013)
- Run DHSVM with the historical forcings to produce the simulated historical snow and hydrology.
- From climate model output, compute the change in 30-year average temperature for each calendar month over the time frame of interest. Do the same for the percent change in precipitation
- Apply these change factors to the historical daily meteorological inputs to DHSVM to generate future scenarios of meteorological inputs.
- Run DHSVM with these new inputs to generate the projected snow and hydrology.
- Compare the projected snow to the historic DHSVM model simulations to infer changes in snowpack.
- Repeat for a set of change factors from different climate models that adequately sample the uncertainty in climate projections.

**The result of the delta method is a continuous-in-time simulation of the historical period (1998-2013), and an equal length simulation of how this sequence of years would play out in**

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**the future under five different scenarios of climate change.** Figure 5-6 illustrates typical DHSVM model output using the delta method. Figure 5-6a shows a map of May 15, 2011 Snow Water Equivalent for the Glacier Study Area from the historical simulation, while Figure 5-6b shows a single projected future for what that year's SWE would look like under a particular scenario of climate change. The future scenario represents a year similar to 2011, that is, a relatively wet and cool year in the sequence, however the temperature and precipitation have been adjusted to be consistent with the 2041-2070 projected climate from the MIROC climate model.

The advantages and disadvantages of the delta method have been discussed extensively in the literature (e.g. Sofaer et al, 2016, for a recent review). The primary advantages of this method are its long history of use, its simplicity, and its use of the historical observed weather as the baseline. The simplicity allowed for the study to be completed in a short time-frame, while still reaching our primary objectives of finer spatial scale and a more complete exploration of future climate scenarios. The use of the historical baseline allows us to explore how wet, near normal, and dry "representative years" would play out under the different climate futures. However, it is important to keep in mind that we are "parameterizing the future variability in terms of the historical variability." This treatment of daily variability also leads to the primary disadvantage of the delta method: the assumptions that the changes in extremes follow the changes in the means, and that the pattern of daily weather is simply shifted without changing the sequences of weather. This aspect is less of a concern for this study, as snow accumulation and ablation are cumulative processes, so that the daily sequences of storms is less critical to simulate than the monthly and seasonal totals. Another assumption of the delta method is that the large-scale changes in temperature and precipitation apply uniformly to the study area. Equivalently we assume that change factors in ambient (free-air) temperature and precipitation will not depend on the small scale spatial detail. Because we explicitly compute the surface energy balance, we are able to simulate surface temperature differences that depend on fine-scale terrain, mitigating to some extent this limitation of the delta method.

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## 5.8 GCM Uncertainty and Scenario Planning Approach

As noted in Section 2, global climate models (GCMs) are our primary tools to examine the nature of climate change during the 21st century. There are currently about 20 modeling centers worldwide which provided output from their best model(s) to be considered in the Coupled Model Inter-comparison Project Phase-5 (CMIP5, Taylor et al., 2012) which informed the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC AR5). Here we quantify changes in temperature and precipitation for the two study areas for the 2014-2070 time frame. We find a large spread in the extent of warming and changes in precipitation, including both increases and decreases in precipitation, as shown in Figures 5-6. For temperature, much of this spread (or uncertainty) is a result of the difference between GCMs (e.g., their climate sensitivities), whereas for precipitation it is both the difference between GCMs and internal climate variability. Some difference also comes from the choice of future greenhouse gases (GHG) emission scenario. However, these differences among mid-21st century climate responses are limited compared to later in the century (see a discussion in Ray et al., 2010).

For more robust planning and climate adaptation, experts recommend incorporation of these

uncertainties into the assessment of impacts and developing adaptation strategies. The scenario planning approach has been one method that has been recommend and promoted by different entities and experts (National Park Service, 2013; Rowland et al., 2014; Maier et al., 2016; Murphy et al. 2016; Star et al., 2016, Fisicelli et al, 2016 a,b,).

## 5.9 Climate Projections Evaluation and Scenarios Selection

We compiled output for temperature and precipitation projections for 34 CMIP5 GCMs from the Reclamation (2013; http://gdo-dcp.ucllnl.org/) archive of 1-degree Regridded GCM dataset for Representative Concentration Pathways (RCP) 4.5 and 8.5, which are respectively the moderate and high GHG emissions scenarios --- therefore, a total of 68 GCM projections described in Supplementary Material. These data were then analyzed to quantify broad-scale projections for the two study regions by 2055 (i.e. a mid-point centered on the 2041-2070 period) – primarily changes in the cold season (Oct-May) temperature and precipitation by 2055 relative to the 1986-2015 period. Figures 5-7 show these changes for Rocky Mountain and Glacier National Parks, respectively, which are bounded by rectangular latitude/longitude values. As mentioned earlier, we found a large range in temperature increases (1-4 $^{o}$C) and changes in precipitation (-5% to +20%) for these regions by 2055. Table 5-3 shows GCM names, numbers and colors coded in later figures, and relative changes in temperature and precipitation. To incorporate the large range in climate projections, we worked with the ensemble of 68 CMIP5 temperature & precipitation projections, described by the red filled-circles in Figure 5-7, to select five future climate scenarios (black circles) that span the different parts of this projection space. This strategy of selecting multiple divergent future scenarios challenging to the system of interest follows that in Fisichelli et al (2016 a, b). Five GCMs representing these scenarios were identified for both RMNP and GNP. For each of these GCMs, we calculated changes in temperature and precipitation by 2055 for each month of the year, which we call the "monthly delta". These monthly deltas were used to perturb the hydrological models to simulate snow response in RMNP and GNP by 2055.

**Table 5-3. The six future scenarios used** (five for each area) with changes in temperature and precipitation relative to other scenarios (See also Fig 5-7 for an alternate visualization of these changes), and the GCM used as the basis for the deltas for this scenario. More details on the GCMs are in the Glossary.

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| Future Scenario Name and # | Scenario Change in GLAC relative to other scenarios | Scenario Change in ROMO relative to other scenarios | Code and color for GCM used for this scenario |
|---|---|---|---|
| **Central** (#1) | +~2.2 °C increase in temperature (close to the ensemble mean) and +~5% increase in precipitation | +~2.5 °C increase in temperature (close to the ensemble mean) and +~8% increase in precipitation | cnrm, red |
| GLAC: **Hot/ Very Wet** (#2) | relatively higher increase in temperature (+~3.2 C) and the highest increase in precipitation (+20%) for the GLAC scenarios | N/A | canesm, green |
| ROMO: **Hot/Dry** (#2) | N/A | relatively higher temperature increase (+~ 3.5 °C) and -~5% decrease in precipitation. This scenario results in the greatest change (reduction) in snow pack and snowcover. | hadgem, green |
| **Hot/ Wet** (#3) | the highest temperature increase of the GLAC scenarios (+~4.2 °C) and +~10% increase in precipitation | the highest temperature increase of the ROMO scenarios (+~3.7 °C) and the highest increase in precipitation (+~18%). | miroc, purple |
| **Warm/ Wet** (#4) | relatively lower temperature increase (+~1 °C) and +~10% increase in precipitation | relatively lower temperature increase (+~1.3 °C) and +~7% increase in precipitation that appears to partially offset the impacts of the temperature increase. This scenario results in the least change in snow pack and snowcover. | giss, aqua |
| **Warm/ Dry** (#5) | relatively lower temperature increase (+~1.6 °C) and -~5% decrease in precipitation | relatively lower temperature increase (+~0.8 °C) and -~5% decrease in precipitation | fio, orange |

## 5.10 Modeling Caveats

Some processes which may be of relevance not represented in the model include wind and avalanche re-distribution of snowpack. Snow depth is not explicitly modeled, and must be inferred (see below). The meteorological forcing does not take into account cold air pooling or how this may change in the future. While Curtis et al (2014) identify this as a potential process, they do not physically model Cold Air Pooling, but merely include it in their present-day

climatology as a simple "offset" from their unadjusted data. Nonetheless their work provides a complementary approach to the identification of potential snow refugia.

## 5.11 GLAC Study Area Results

### 5.11.1 SWE and Snow Covered Area for representative years

Figures 5-8 shows DHSVM model simulated snow water equivalent (SWE) on May 15 for the wet (2011) representative year. Maps of snow cover derived from SWE by applying a threshold of 13 mm are available in the Supplementary material. Results for thresholds of 1 mm and 5 mm of SWE were also investigated and show similar patterns. Snow covered area with a "light snow cover" threshold was computed primarily for comparison with both the MODIS results from Section 4, and with McKelvey. In Figure 5-8, the historical simulation is shown along with three of the five future scenarios, chosen to represent the central scenario (cnrm), the greatest change in snowpack on average (Hot/Wet (miroc) scenario) and the least change (Warm/Wet (giss) scenario). The projected snow maps answer the question "what would the snowpack in a wet year like 2011 look like in the 2040's through 2070's under these scenarios of climate change."

Figures 5-9 and 5-10 show SWE for the Near Normal (2009) and Dry (2005) representative years. The historical simulation and future scenarios are as in Figure 5-8. Figure 5-11 summarizes the results for snow covered area in terms of the total snow covered area ($km^2$) within the study area polygon. The numerical values of snow covered area for all years in the simulation, as well as percent changes for these quantities are shown in Table 5-4. Table 5-4 indicates that the snowcovered area decreases for all scenarios. **On average, the GLAC study area exhibits a 12-42 percent decline in snow covered area on May 15 for the scenarios considered.**

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Comparing the Wet and Dry representative years we see that dry years are more vulnerable to climate change in terms of percent loss of snow covered area. For the Wet year, the high elevations of the study area result in little loss of snowpack in the study areas under most scenarios of change.

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| GLAC Area (km^2) | Snow Covered Area (13mm SWE threshold) Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | historical | 2552 | 2793 | 2655 | 2802 | 2890 | 2753 | 2533 | 2408 | 2636 | 2491 | 2883 | 2901 | 2524 | 2901 | 2758 | 2851 | 2708 | 2756 |
| | Central (cnrm) | 1768 | 2329 | 2030 | 2459 | 2816 | 2326 | 1812 | 1509 | 1959 | 1816 | 2742 | 2880 | 1886 | 2885 | 2179 | 2561 | 2247 | 2253 |
| | Hot/Very Wet (canesm) | 1394 | 1956 | 1707 | 1955 | 2595 | 1858 | 1303 | 1171 | 1510 | 1174 | 2436 | 2764 | 1293 | 2817 | 1723 | 2127 | 1862 | 1790 |
| | Hot/Wet (miroc) | 1573 | 1646 | 1604 | 1637 | 1518 | 2122 | 998 | 2275 | 1527 | 1517 | 2608 | 2037 | 1618 | 2481 | 1157 | 2165 | 1780 | 1627 |
| | Warm/Wet (giss) | 2197 | 2583 | 2388 | 2599 | 2856 | 2486 | 2191 | 2017 | 2312 | 2109 | 2842 | 2895 | 2170 | 2901 | 2485 | 2705 | 2484 | 2486 |
| | Warm/Dry (fio) | 2112 | 2440 | 2184 | 2586 | 2830 | 2555 | 2089 | 1776 | 2231 | 2070 | 2806 | 2891 | 2127 | 2900 | 2486 | 2659 | 2421 | 2463 |
| 15-May | historical | 1452 | 2718 | 2433 | 2352 | 2873 | 2636 | 2287 | 2087 | 2373 | 1741 | 2807 | 2825 | 2393 | 2900 | 2557 | 2548 | 2436 | 2490 |
| | Central (cnrm) | 636 | 2114 | 1703 | 1780 | 2661 | 2068 | 1409 | 1104 | 1555 | 963 | 2367 | 2479 | 1664 | 2817 | 1763 | 1733 | 1801 | 1748 |
| | Hot/Very Wet (canesm) | 650 | 1835 | 1447 | 1419 | 2449 | 1652 | 1083 | 887 | 1255 | 657 | 2174 | 2218 | 1118 | 2697 | 1473 | 1584 | 1537 | 1460 |
| | Hot/Wet (miroc) | 1079 | 1440 | 977 | 1051 | 1230 | 1958 | 784 | 1451 | 1152 | 1026 | 2307 | 1677 | 1499 | 2305 | 879 | 1760 | 1411 | 1335 |
| | Warm/Wet (giss) | 1079 | 2483 | 2098 | 2062 | 2800 | 2332 | 1963 | 1667 | 1981 | 1299 | 2638 | 2672 | 2034 | 2882 | 2203 | 2247 | 2152 | 2151 |
| | Warm/Dry (fio) | 883 | 2274 | 1913 | 1910 | 2712 | 2372 | 1722 | 1397 | 1851 | 1138 | 2515 | 2600 | 1918 | 2864 | 2125 | 1943 | 2009 | 1931 |
| 1-Jun | historical | 863 | 2360 | 1759 | 1114 | 2599 | 1932 | 1864 | 1375 | 1446 | 1061 | 1923 | 2205 | 1907 | 2863 | 2171 | 2035 | 1842 | 1915 |
| | Central (cnrm) | 250 | 1512 | 948 | 628 | 2049 | 1099 | 897 | 560 | 663 | 417 | 1005 | 1397 | 1025 | 2600 | 1281 | 1114 | 1090 | 1015 |
| | Hot/Very Wet (canesm) | 328 | 1393 | 909 | 590 | 1923 | 966 | 742 | 514 | 689 | 347 | 1172 | 1414 | 794 | 2455 | 1118 | 1134 | 1030 | 937 |
| | Hot/Wet (miroc) | 496 | 813 | 359 | 282 | 682 | 1109 | 417 | 552 | 267 | 511 | 1008 | 682 | 831 | 1862 | 527 | 786 | 699 | 617 |
| | Warm/Wet (giss) | 613 | 2046 | 1392 | 883 | 2401 | 1507 | 1473 | 1046 | 1063 | 759 | 1574 | 1893 | 1580 | 2789 | 1763 | 1747 | 1533 | 1541 |
| | Warm/Dry (fio) | 401 | 1723 | 1137 | 623 | 2217 | 1410 | 1196 | 735 | 810 | 527 | 1222 | 1606 | 1178 | 2691 | 1611 | 1291 | 1274 | 1209 |

| % change | Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | Central (cnrm) | -31 | -17 | -24 | -12 | -3 | -16 | -28 | -37 | -26 | -27 | -5 | -1 | -25 | -1 | -21 | -10 | -17 | -18 |
| | Hot/Very Wet (canesm) | -45 | -30 | -36 | -30 | -10 | -33 | -49 | -51 | -43 | -53 | -15 | -5 | -49 | -3 | -38 | -25 | -31 | -35 |
| | Hot/Wet (miroc) | -38 | -41 | -40 | -42 | -47 | -23 | -61 | -6 | -42 | -39 | -10 | -30 | -36 | -15 | -58 | -24 | -34 | -41 |
| | Warm/Wet (giss) | -14 | -8 | -10 | -7 | -1 | -10 | -13 | -16 | -12 | -15 | -1 | 0 | -14 | 0 | -10 | -5 | -8 | -10 |
| | Warm/Dry (fio) | -17 | -13 | -18 | -8 | -2 | -7 | -18 | -26 | -15 | -17 | -3 | 0 | -16 | 0 | -10 | -7 | -11 | -11 |
| 15-May | Central (cnrm) | -56 | -22 | -30 | -24 | -7 | -22 | -38 | -47 | -34 | -45 | -16 | -12 | -30 | -3 | -31 | -32 | -26 | -30 |
| | Hot/Very Wet (canesm) | -55 | -32 | -41 | -40 | -15 | -37 | -53 | -58 | -47 | -62 | -23 | -22 | -53 | -7 | -42 | -38 | -37 | -41 |
| | Hot/Wet (miroc) | -26 | -47 | -60 | -55 | -57 | -26 | -66 | -30 | -51 | -41 | -18 | -41 | -37 | -21 | -66 | -31 | -42 | -46 |
| | Warm/Wet (giss) | -26 | -9 | -14 | -12 | -3 | -12 | -14 | -20 | -17 | -25 | -6 | -5 | -15 | -1 | -14 | -12 | -12 | -14 |
| | Warm/Dry (fio) | -39 | -16 | -21 | -19 | -6 | -10 | -25 | -33 | -22 | -35 | -10 | -8 | -20 | -1 | -17 | -24 | -18 | -22 |
| 1-Jun | Central (cnrm) | -71 | -36 | -46 | -44 | -21 | -43 | -52 | -59 | -54 | -61 | -48 | -37 | -46 | -9 | -41 | -45 | -41 | -47 |
| | Hot/Very Wet (canesm) | -62 | -41 | -48 | -47 | -26 | -50 | -60 | -63 | -52 | -67 | -39 | -36 | -58 | -14 | -49 | -44 | -44 | -51 |
| | Hot/Wet (miroc) | -42 | -66 | -80 | -75 | -74 | -43 | -78 | -60 | -82 | -52 | -48 | -69 | -56 | -35 | -76 | -61 | -62 | -68 |
| | Warm/Wet (giss) | -29 | -13 | -21 | -21 | -8 | -22 | -21 | -24 | -27 | -28 | -18 | -14 | -17 | -3 | -19 | -14 | -17 | -20 |
| | Warm/Dry (fio) | -54 | -27 | -35 | -44 | -15 | -27 | -36 | -47 | -44 | -50 | -36 | -27 | -38 | -6 | -26 | -37 | -31 | -37 |

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**Table 5-4: GLAC Snow Covered Area (13mm SWE threshold)** Top: Area ($km^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

However, in Figures 5-10 and 5-11 we notice an anomaly – for the dry year, the Hot/Wet scenario does not have the greatest loss of snow covered area. The increase in precipitation in this scenario has somewhat compensated for the loss of snowpack due to warming.

### 5.11.2 Area and Number of years with 0.5 m Snow Depth

Because of interest in wolverine denning sites, we analyze snow depth > 0.5 m, which we will refer to as "significant snow." Figure 5-12 shows the area with snow depth > 0.5 m within the study area for the dry. Near normal, and wet years. Because of the more stringent threshold for snow, the effects are somewhat larger than for the light snow threshold. This is particularly evident in the dry year, which has a 50% decline on May 15 for four of the future scenarios. The numerical values of snow covered area at the > 0.5 m threshold are shown in Table 5-5 for all years, as well as percent changes for these quantities. **On average, the GLAC study area exhibits a 15 – 68 percent decline in the area of snow depth > 0.5 meters for the scenarios considered.**

Figure 5-13 shows a map of the number of years (out of 16 possible) where each model pixel had at least 0.5 m of snow depth on May 15. This number-of-years statistic is analogous to that used by the Copeland study, except that there are more years of data, and these maps use a much higher threshold of snow. The projections show declines in the number of years with significant snow. The areas with frequent (14-16 years) availability of significant snow become concentrated in smaller high elevation areas.

The effects of climate change on snow melt have been presented as analogous to a "time shifting" of the melt season earlier in the year. For example, McKelvey used the May 31 vs. May 15 snow covered area as a proxy for a 2-week shift in the melt season. Figure 5-14 contrasts the evolution of the snowpack from May 1 to June 1 in the historical simulations (Top Row) with the Warm/Wet scenario (Middle Row) and Hot/Wet (Bottom Row) scenarios. We see that the Warm/Wet scenario, shows the least change compared to the historic snow cover in terms of the availability of significant snow. In contrast, under the Hot/Wet scenario, the May 1$^{st}$ significant snowpack has been diminished below the level of the historic June 1 snowpack – greater than a month shift.

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Snow Covered Area (0.5 m depth threshold)

| Area (km^2) | Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | historical | 1594 | 2545 | 2204 | 2326 | 2844 | 2392 | 2032 | 1800 | 2124 | 1571 | 2613 | 2731 | 1692 | 2901 | 2453 | 2625 | 2278 | 2359 |
| | Central (cnrm) | 770 | 1826 | 1477 | 1912 | 2530 | 1766 | 1137 | 912 | 1283 | 951 | 2160 | 2383 | 965 | 2847 | 1630 | 1893 | 1653 | 1698 |
| | Hot/Very Wet (canesm) | 733 | 1587 | 1234 | 1399 | 2283 | 1336 | 826 | 732 | 1075 | 578 | 1992 | 2070 | 677 | 2721 | 1316 | 1650 | 1388 | 1326 |
| | Hot/Wet (miroc) | 474 | 526 | 633 | 425 | 458 | 1538 | 395 | 614 | 364 | 541 | 1321 | 1236 | 332 | 2029 | 436 | 1018 | 771 | 533 |
| | Warm/Wet (giss) | 1154 | 2242 | 1810 | 2012 | 2681 | 1968 | 1590 | 1400 | 1660 | 1112 | 2389 | 2525 | 1360 | 2890 | 2017 | 2328 | 1946 | 1990 |
| | Warm/Dry (fio) | 974 | 1938 | 1594 | 1877 | 2586 | 2054 | 1368 | 1058 | 1471 | 969 | 2169 | 2418 | 897 | 2873 | 1944 | 2046 | 1765 | 1907 |
| 15-May | historical | 550 | 2496 | 1937 | 1417 | 2749 | 2201 | 1673 | 1308 | 1805 | 804 | 2317 | 2537 | 1647 | 2881 | 2135 | 2035 | 1906 | 1986 |
| | Central (cnrm) | 140 | 1731 | 1161 | 1007 | 2329 | 1453 | 792 | 566 | 961 | 328 | 1585 | 1957 | 911 | 2692 | 1284 | 1139 | 1252 | 1150 |
| | Hot/Very Wet (canesm) | 247 | 1537 | 1048 | 835 | 2128 | 1176 | 648 | 509 | 900 | 274 | 1632 | 1797 | 662 | 2538 | 1087 | 1155 | 1136 | 1068 |
| | Hot/Wet (miroc) | 302 | 508 | 346 | 217 | 439 | 1447 | 203 | 531 | 290 | 302 | 1053 | 878 | 565 | 1733 | 352 | 634 | 612 | 473 |
| | Warm/Wet (giss) | 380 | 2199 | 1546 | 1166 | 2560 | 1782 | 1287 | 995 | 1362 | 567 | 2051 | 2286 | 1355 | 2825 | 1693 | 1745 | 1612 | 1620 |
| | Warm/Dry (fio) | 199 | 1873 | 1301 | 890 | 2438 | 1781 | 986 | 659 | 1106 | 328 | 1692 | 2096 | 879 | 2765 | 1559 | 1208 | 1360 | 1255 |
| 1-Jun | historical | 337 | 1903 | 1089 | 428 | 2156 | 1192 | 1199 | 723 | 845 | 486 | 1140 | 1590 | 1144 | 2782 | 1625 | 1534 | 1261 | 1168 |
| | Central (cnrm) | 52 | 1052 | 494 | 202 | 1473 | 563 | 435 | 227 | 310 | 145 | 462 | 810 | 514 | 2353 | 827 | 738 | 666 | 504 |
| | Hot/Very Wet (canesm) | 113 | 1024 | 572 | 238 | 1476 | 585 | 437 | 262 | 398 | 145 | 667 | 956 | 429 | 2254 | 781 | 847 | 699 | 579 |
| | Hot/Wet (miroc) | 90 | 220 | 100 | 36 | 194 | 542 | 104 | 103 | 43 | 158 | 284 | 194 | 185 | 1319 | 194 | 250 | 251 | 190 |
| | Warm/Wet (giss) | 221 | 1545 | 817 | 321 | 1895 | 870 | 928 | 534 | 589 | 346 | 859 | 1262 | 973 | 2646 | 1246 | 1298 | 1022 | 899 |
| | Warm/Dry (fio) | 97 | 1139 | 567 | 164 | 1598 | 724 | 602 | 294 | 377 | 157 | 552 | 876 | 522 | 2457 | 1049 | 817 | 749 | 584 |

| % change | Year | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | Central (cnrm) | -52 | -28 | -33 | -18 | -11 | -26 | -44 | -49 | -40 | -39 | -17 | -13 | -43 | -2 | -34 | -28 | -27 | -28 |
| | Hot/Very Wet (canesm) | -54 | -38 | -44 | -40 | -20 | -44 | -59 | -59 | -49 | -63 | -24 | -24 | -60 | -6 | -46 | -37 | -39 | -44 |
| | Hot/Wet (miroc) | -70 | -79 | -71 | -82 | -84 | -36 | -81 | -66 | -83 | -66 | -49 | -55 | -80 | -30 | -82 | -61 | -66 | -77 |
| | Warm/Wet (giss) | -28 | -12 | -18 | -13 | -6 | -18 | -22 | -22 | -22 | -29 | -9 | -8 | -20 | 0 | -18 | -11 | -15 | -16 |
| | Warm/Dry (fio) | -39 | -24 | -28 | -19 | -9 | -14 | -33 | -41 | -31 | -38 | -17 | -11 | -47 | -1 | -21 | -22 | -23 | -19 |
| 15-May | Central (cnrm) | -75 | -31 | -40 | -29 | -15 | -34 | -53 | -57 | -47 | -59 | -32 | -23 | -45 | -7 | -40 | -44 | -34 | -42 |
| | Hot/Very Wet (canesm) | -55 | -38 | -46 | -41 | -23 | -47 | -61 | -61 | -50 | -66 | -30 | -29 | -60 | -12 | -49 | -43 | -40 | -46 |
| | Hot/Wet (miroc) | -45 | -80 | -82 | -85 | -84 | -34 | -88 | -59 | -84 | -62 | -55 | -65 | -66 | -40 | -84 | -69 | -68 | -76 |
| | Warm/Wet (giss) | -31 | -12 | -20 | -18 | -7 | -19 | -23 | -24 | -25 | -29 | -11 | -10 | -18 | -2 | -21 | -14 | -15 | -18 |
| | Warm/Dry (fio) | -64 | -25 | -33 | -37 | -11 | -19 | -41 | -50 | -39 | -59 | -27 | -17 | -47 | -4 | -27 | -41 | -29 | -37 |
| 1-Jun | Central (cnrm) | -85 | -45 | -55 | -53 | -32 | -53 | -64 | -69 | -63 | -70 | -59 | -49 | -55 | -15 | -49 | -52 | -47 | -57 |
| | Hot/Very Wet (canesm) | -66 | -46 | -47 | -44 | -32 | -51 | -64 | -64 | -53 | -70 | -42 | -40 | -63 | -19 | -52 | -45 | -45 | -50 |
| | Hot/Wet (miroc) | -73 | -88 | -91 | -92 | -91 | -55 | -91 | -86 | -95 | -67 | -75 | -88 | -84 | -53 | -88 | -84 | -80 | -84 |
| | Warm/Wet (giss) | -34 | -19 | -25 | -25 | -12 | -27 | -23 | -26 | -30 | -29 | -25 | -21 | -15 | -5 | -23 | -15 | -19 | -23 |
| | Warm/Dry (fio) | -71 | -40 | -48 | -62 | -26 | -39 | -50 | -59 | -55 | -68 | -52 | -45 | -54 | -12 | -35 | -47 | -41 | -50 |

**Table 5-5: GLAC Snow Covered Area (0.5 m snow depth threshold)** Top: Area ($km^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

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## 5.12 ROMO Study Area

**On average, the ROMO study area exhibits a 7 – 64 percent decline in the area of snow depth > 0.5 meters on May 15 for the scenarios considered. Note that the Warm/Wet scenario projects a slight increase in the area of significant snowpack on May 1.**

### 5.12.1 SWE and Snow Covered Area for representative years

Figure 5-15 shows DHSVM model simulated SWE on May 15th for the wet representative year (2011). The historical simulation is shown along with three of the five future scenarios, chosen to represent the central scenario (cnrm), the greatest change in snowpack on average (Hot/Dry (hadgem2) scenario) and the least change (Warm/Wet (giss) scenario). The future scenarios answer the question "what would the snowpack in a wet year (like 2011) look like in the 2040's through 2070's under these scenarios of climate change." Note that the "greatest snowpack change" scenario is different for ROMO than for GLAC. We have included the Hot/Dry scenario for ROMO because a significant number of climate models project drying conditions in ROMO, whereas in GLAC, the vast majority of climate models predict a wetter future.

Figures 5-16 and 5-17 shows SWE for the "Near Normal" (2009) and "Dry" (2002) year. One can see that in the dry year, the snow cover is already very sparse even in the historical simulation.

Figure 5-18 summarizes the results in terms of the total snow covered area ($km^2$) within the study area polygon. In this case, the threshold used is 13mm of SWE, representing a light snow cover, and comparable to the results in McKelvey. Comparing the Wet and Dry years we see, as with GLAC, that dry years are more vulnerable to climate change in terms of percentage of area lost. For the Wet year, the high elevations of the study area result in little loss of snowpack in the study areas under most scenarios of change. The numerical values of snow covered area for all years, as well as percent changes for these quantities are shown in Table 5-7. **On average, the ROMO study area exhibits a 12-52 percent decline in snow covered area on May 15 for the scenarios considered.**

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| ROMO | Snow Covered Area sq-km (13mm SWE threshold) Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1-May | historical | 1567 | 1514 | 1574 | 1523 | 1245 | 1594 | 1248 | 1580 | 1573 | 1555 | 1595 | 1578 | 1439 | 1593 | 779 | 1594 | 1472 | 1570 |
| | Central (cnrm) | 1380 | 1216 | 1424 | 1112 | 786 | 1571 | 655 | 1470 | 1376 | 1195 | 1593 | 1396 | 1091 | 1553 | 379 | 1547 | 1234 | 1378 |
| | Hot/Dry (hadgem2) | 1127 | 971 | 1079 | 844 | 418 | 1498 | 429 | 1114 | 1188 | 1081 | 1587 | 1267 | 763 | 1507 | 185 | 1462 | 1033 | 1097 |
| | Hot/Very Wet (miroc) | 963 | 569 | 1045 | 773 | 501 | 1425 | 293 | 1280 | 1215 | 701 | 1582 | 1003 | 837 | 1444 | 112 | 1382 | 945 | 983 |
| | Warm/Wet (giss) | 1498 | 1429 | 1510 | 1373 | 944 | 1589 | 964 | 1522 | 1528 | 1461 | 1595 | 1547 | 1335 | 1586 | 583 | 1587 | 1378 | 1504 |
| | Warm/Dry (fio) | 1462 | 1392 | 1546 | 1353 | 981 | 1584 | 828 | 1519 | 1518 | 1433 | 1595 | 1533 | 1234 | 1584 | 481 | 1580 | 1351 | 1490 |
| | | | | | | | | | | | | | | | | | | | |
| 15-May | historical | 1427 | 1467 | 1146 | 1064 | 989 | 1592 | 831 | 1519 | 1490 | 1421 | 1593 | 1449 | 1372 | 1587 | 588 | 1566 | 1319 | 1438 |
| | Central (cnrm) | 1012 | 1076 | 728 | 495 | 526 | 1546 | 340 | 1206 | 982 | 872 | 1563 | 953 | 951 | 1485 | 245 | 1366 | 959 | 967 |
| | Hot/Dry (hadgem2) | 530 | 688 | 250 | 221 | 213 | 1395 | 119 | 671 | 650 | 569 | 1410 | 470 | 562 | 1320 | 80 | 846 | 625 | 565 |
| | Hot/Very Wet (miroc) | 637 | 483 | 457 | 385 | 327 | 1346 | 141 | 948 | 858 | 491 | 1510 | 615 | 742 | 1355 | 78 | 1193 | 723 | 626 |
| | Warm/Wet (giss) | 1235 | 1315 | 877 | 814 | 693 | 1583 | 554 | 1346 | 1312 | 1242 | 1585 | 1246 | 1228 | 1559 | 396 | 1515 | 1156 | 1244 |
| | Warm/Dry (fio) | 1227 | 1311 | 928 | 755 | 695 | 1573 | 504 | 1361 | 1302 | 1200 | 1588 | 1279 | 1141 | 1556 | 344 | 1505 | 1142 | 1253 |
| | Snow Covered Area % change (13mm SWE threshold) Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | Central (cnrm) | -12 | -20 | -10 | -27 | -37 | -1 | -48 | -7 | -13 | -23 | 0 | -12 | -24 | -2 | -51 | -3 | -16 | -12 |
| | Hot/Dry (hadgem2) | -28 | -36 | -31 | -45 | -66 | -6 | -66 | -30 | -24 | -30 | -1 | -20 | -47 | -5 | -76 | -8 | -30 | -30 |
| | Hot/Very Wet (miroc) | -39 | -62 | -34 | -49 | -60 | -11 | -77 | -19 | -23 | -55 | -1 | -36 | -42 | -9 | -86 | -13 | -36 | -37 |
| | Warm/Wet (giss) | -4 | -6 | -4 | -10 | -24 | 0 | -23 | -4 | -3 | -6 | 0 | -2 | -7 | 0 | -25 | 0 | -6 | -4 |
| | Warm/Dry (fio) | -7 | -8 | -2 | -11 | -21 | -1 | -34 | -4 | -3 | -8 | 0 | -3 | -14 | -1 | -38 | -1 | -8 | -5 |
| | | | | | | | | | | | | | | | | | | | |
| 15-May | Central (cnrm) | -29 | -27 | -37 | -53 | -47 | -3 | -59 | -21 | -34 | -39 | -2 | -34 | -31 | -6 | -58 | -13 | -27 | -33 |
| | Hot/Dry (hadgem2) | -63 | -53 | -78 | -79 | -78 | -12 | -86 | -56 | -56 | -60 | -12 | -68 | -59 | -17 | -86 | -46 | -53 | -61 |
| | Hot/Very Wet (miroc) | -55 | -67 | -60 | -64 | -67 | -15 | -83 | -38 | -42 | -65 | -5 | -58 | -46 | -15 | -87 | -24 | -45 | -56 |
| | Warm/Wet (giss) | -13 | -10 | -23 | -23 | -30 | -1 | -33 | -11 | -12 | -13 | -1 | -14 | -11 | -2 | -33 | -3 | -12 | -13 |
| | Warm/Dry (fio) | -14 | -11 | -19 | -29 | -30 | -1 | -39 | -10 | -13 | -16 | 0 | -12 | -17 | -2 | -41 | -4 | -13 | -13 |

**Table 5-6: ROMO Snow Covered Area (13 mm SWE threshold)** Top: Area ($km^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

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### 5.12.2 Area and Number of years with 0.5 m Snow Depth

Because of interest in wolverine denning sites, we analyze snow depth > 0.5 m, which we will refer to here as "significant snow." Figure 5-19 shows the area with snow depth > 0.5 m within the study area. Because of the more stringent threshold for snow, the effects are somewhat larger than for the light snow cover. The numerical values of snow covered area at the > 0.5 m threshold are shown in Table 5-7 for all years, as well as percent changes for these quantities. In this table, we note that dry years such as 2002 see increases in snow covered area for the Hot/Very Wet and Warm/Wet scenarios. As in GLAC, dry years are somewhat buffered against change, and in fact can see increases in high-altitude "significant" snow for scenarios with increased precipitation. This is a result of the elevational dependence of snowpack change that will be discussed in the next sub-section. **On average, the ROMO study area exhibits a 7 – 64 percent decline in the area of snow depth > 0.5 meters on May 15 for the scenarios considered. Note that the Warm/Wet scenario projects a slight increase in the area of significant snowpack on May 1.**

Figure 5-20 shows a map of the number of years (out of 16 possible) where each model pixel had at least 0.5 m of snow depth on May 15th. This summary statistic is analogous to that used by the Copeland study, except that there are more years of data, and these maps use a much higher threshold of snow. The projections show declines in the number of years with significant snow. The areas with frequent (14-16 years) availability of significant snow become concentrated in smaller high elevation areas. The Hot/Dry "greatest change" scenario, illustrates that the combination of drying and warming leads to very large declines in the persistence of snow.

The effects of climate change on snow melt have been presented as analogous to a "time shifting" of the melt season earlier in the year. For example, McKelvey (2011) used the May 31st vs. May 15th snow covered area as a proxy for a 2-week shift in the melt season. Figure 5-21 contrasts the evolution of the snowpack from May 1 to June 1 in the historical simulations (Top Row) with the Warm/Wet scenario (giss, Middle Row) and Hot/Dry (hadgem, Bottom Row) scenarios [Graphics being re-done].

## 5.1 Elevation Dependence of Snowpack Change

Snowpack accumulation and melt depends critically on temperature and hence on elevation. In the Warm/Dry and Hot/Dry scenarios, both the precipitation decrease and the warming act to reduce Spring snowpack. For the scenarios with warming and increased precipitation there are two countervailing forces that play out along an elevational gradient. A warmer, wetter future is one in which the freezing level and snow line tends to be higher, but with the potential for greater snowpack accumulation during the cold season at high elevations. The warming also tends to lead to an earlier snowmelt, so that the increased snowpack is more evident early in the Springtime than later. This scenario of elevation-dependent snowpack change is well supported in the literature (e.g. Ray et al, 2008). Figure 5-22 shows the elevation dependence for the change in May 15th SWE for GLAC and ROMO, computed for 200 m elevation bands. In particular, these two panels show the very large declines in snow at the lower elevations in each study area. For both ROMO and GLAC, the Hot/Very Wet scenarios project an increase in SWE for some of the high elevation regions. In general, the scenarios with increased precipitation

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show a greater contrast between the low and high elevation bands in terms of snow loss. The elevational gradients seen in SWE changes carries over to snow covered area in Figure 5-23 using 0.5 m depth threshold. The potential for increased high-elevation snowpack with the "Very Wet" scenarios is even more apparent if one looks at May 1st snowpack (not shown).

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| ROMO | Snow Covered Area sq-km (0.5 meter snow depth threshold) | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | historical | 468 | 249 | 734 | 180 | 26 | 1578 | 90 | 422 | 418 | 746 | 1334 | 594 | 70 | 1356 | 22 | 381 | 542 | 420 |
| | Central (cnrm) | 421 | 185 | 607 | 95 | 38 | 1470 | 102 | 375 | 208 | 398 | 1199 | 451 | 55 | 1293 | 16 | 402 | 457 | 386 |
| | Hot/Dry (hadgem2) | 166 | 57 | 232 | 64 | 10 | 1245 | 33 | 137 | 278 | 314 | 984 | 231 | 14 | 1096 | 2 | 125 | 312 | 152 |
| | Hot/Very Wet (miroc) | 275 | 135 | 375 | 155 | 40 | 1133 | 59 | 320 | 397 | 259 | 1200 | 350 | 130 | 1164 | 3 | 719 | 419 | 297 |
| | Warm/Wet (giss) | 453 | 256 | 601 | 210 | 38 | 1552 | 118 | 375 | 514 | 753 | 1417 | 572 | 104 | 1374 | 23 | 481 | 552 | 467 |
| | Warm/Dry (fio) | 187 | 99 | 483 | 45 | 4 | 1510 | 16 | 172 | 159 | 475 | 946 | 374 | 14 | 1201 | 5 | 176 | 367 | 174 |
| | | | | | | | | | | | | | | | | | | | |
| 15-May | historical | 429 | 277 | 288 | 105 | 29 | 1568 | 37 | 474 | 416 | 593 | 1341 | 403 | 227 | 1289 | 25 | 436 | 496 | 409 |
| | Central (cnrm) | 263 | 169 | 177 | 35 | 27 | 1385 | 22 | 352 | 161 | 248 | 988 | 216 | 174 | 1066 | 13 | 267 | 348 | 196 |
| | Hot/Dry (hadgem2) | 56 | 44 | 32 | 12 | 4 | 990 | 3 | 96 | 133 | 114 | 586 | 54 | 35 | 677 | 0 | 45 | 180 | 50 |
| | Hot/Very Wet (miroc) | 174 | 122 | 106 | 58 | 33 | 1061 | 18 | 276 | 263 | 173 | 970 | 184 | 217 | 922 | 4 | 395 | 311 | 179 |
| | Warm/Wet (giss) | 351 | 257 | 208 | 94 | 35 | 1519 | 33 | 403 | 433 | 530 | 1292 | 338 | 241 | 1239 | 23 | 404 | 462 | 345 |
| | Warm/Dry (fio) | 208 | 120 | 168 | 31 | 4 | 1481 | 10 | 211 | 167 | 373 | 1053 | 244 | 87 | 1064 | 6 | 239 | 342 | 188 |
| | | | | | | | | | | | | | | | | | | | |
| | Snow Covered Area % change (0.5 meter snow depth threshold) | | | | | | | | | | | | | | | | | | |
| | Scenario | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average | Median |
| 1-May | Central (cnrm) | -10 | -25 | -17 | -47 | 44 | -7 | 13 | -11 | -50 | -47 | -10 | -24 | -21 | -5 | -27 | 5 | -16 | -8 |
| | Hot/Dry (hadgem2) | -64 | -77 | -68 | -65 | -61 | -21 | -63 | -68 | -33 | -58 | -26 | -61 | -80 | -19 | -91 | -67 | -42 | -64 |
| | Hot/Very Wet (miroc) | -41 | -46 | -49 | -14 | 53 | -28 | -35 | -24 | -5 | -65 | -10 | -41 | 85 | -14 | -85 | 88 | -23 | -29 |
| | Warm/Wet (giss) | -3 | 3 | -18 | 16 | 44 | -2 | 31 | -11 | 23 | 1 | 6 | -4 | 48 | 1 | 6 | 26 | 2 | 11 |
| | Warm/Dry (fio) | -60 | -60 | -34 | -75 | -85 | -4 | -82 | -59 | -62 | -36 | -29 | -37 | -79 | -11 | -79 | -54 | -32 | -59 |
| | | | | | | | | | | | | | | | | | | | |
| 15-May | Central (cnrm) | -39 | -39 | -38 | -67 | -5 | -12 | -42 | -26 | -61 | -58 | -26 | -47 | -23 | -17 | -48 | -39 | -30 | -52 |
| | Hot/Dry (hadgem2) | -87 | -84 | -89 | -88 | -85 | -37 | -93 | -80 | -68 | -81 | -56 | -87 | -85 | -47 | -98 | -90 | -64 | -88 |
| | Hot/Very Wet (miroc) | -60 | -56 | -63 | -44 | 13 | -32 | -53 | -42 | -37 | -71 | -28 | -54 | -4 | -28 | -86 | -9 | -37 | -56 |
| | Warm/Wet (giss) | -18 | -7 | -28 | -10 | 20 | -3 | -13 | -15 | 4 | -11 | -4 | -16 | 6 | -4 | -8 | -7 | -7 | -16 |
| | Warm/Dry (fio) | -52 | -56 | -42 | -71 | -85 | -6 | -74 | -55 | -60 | -37 | -22 | -39 | -62 | -17 | -78 | -45 | -31 | -54 |

**Table 5-7: ROMO Snow Covered Area (0.5 m snow depth threshold)** Top: Area ($km^2$) in historical and five future scenarios. Bottom: percent change in future simulations compared to historical. Average and Median values also shown.

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# 6 Comparing results with McKelvey

An overview of the methodological similarities and differences between this study and McKelvey et al (2011) was presented in section 2.2. The differences in aims of these studies leads to challenges in making a direct comparison. McKelvey investigated persistence of even a snow cover to May 15th as a correlate of wolverine habitat, as noted in Aubry et al (2008). This study focuses on high-elevation terrain and on the persistence of deeper snowpack. Nonetheless some general statements can be made relating the two studies. Figure 5-24 shows McKelvey's historic and "MIROC 2080's" snow cover. The GLAC and ROMO areas have been outlined. A close examination of this figure shows that snow cover persists in our study areas, even for highest-end scenario of change (their "2080's MIROC" scenario). The greatest loss of snow cover in McKelvey occurs at lower elevations than were included in GLAC or ROMO. Because of the increased resolution of this study we are able to ask whether any pockets of snow with depth greater than 0.5 meters will persist.

The choice of future climate scenarios differs somewhat from McKelvey. We have intentionally included scenarios that represent the range of possibilities indicated by the CMIP5 climate models. McKelvey used climate model output from Littell, who chose scenarios based solely on projected warming. For GLAC, this choice fortuitously included a range of precipitation changes as well. For ROMO, however, McKelvey's scenarios include only a narrow range of precipitation change, where we include scenarios with significantly increased wintertime precipitation as well as scenarios with drying. This is a significant factor, given the buffering effect that increased precipitation has on snowpack loss at high elevations.

While McKelvey focused snowpack projections entirely on the long-term average, we investigate how climate variability – the sequences of wet and dry years -- intersects with scenarios of change. For ROMO in particular we find that dry years behave differently than wet years, with dry years benefitting from the increased precipitation in several of our future scenarios. This emphasizes the importance of planning for a range of possible climate scenarios, particularly regarding the direction of change in wintertime precipitation.

The question arises as to how the fine-scale projections of snow persistence in other areas might reasonably be inferred from the two study areas considered here. Figure X indicates many areas in the western United States that show persistence of snow cover in McKelvey's scenarios, even in the more extreme scenarios. We have investigated two study areas: a northern, relatively wet and low-elevation area GLAC, and a southern, relatively dry, and very high elevation area (ROMO). In both areas we find general declines in snow covered area under most future scenarios. The GLAC study area is broadly similar in its climate to much of the high northern Rockies, while ROMO shares features with the high mountain ranges of the Central Rockies. For areas in the McKelvey maps that show retention of snow on the higher mountain ranges it is physically reasonable to presume that a finer scale simulation would show the retention of areas of snow > 0.5 m on May 15th. Extending this beyond the general area of the Rocky Mountains is problematic. Even within the Rockies, in regions where McKelvey's results show widespread loss of snowpack without "islands" of snow persistence it is probably not reasonable to conclude one way or the other whether a finer scale analysis would identify snow refugia.

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- snow depth, cold air pooling

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Data Center Distributed Active Archive Center. doi: http://dx.doi.org/10.5067/MODIS/MOD10A1.006. Accessed on 09/06/2016.
- reference for MODIS collection 6 data
- more MODIS references needed --(technical documents, papers?)

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Final Draft 14April 17

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- Used Littell et al (2011) climate and hydrology data as well as analyzing MODIS snow cover to investigate wolverine habitat. Our study attempts to extend the science in this study.

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# 8 Glossary

- **Aspect:** compass direction that slope faces
- **Baseline period 1916-2000**: Deltas (changes) computed (monthly average delta) for "2040's and "2080's" compared to the 1916-2000 baseline.

- **CanESM:** A CMIP5 climate model the Canadian Centre for Climate Modeling and Analysis (canesm2.1.rcp85), forced with the RCP 8.5 higher emissions pathway, used in this report as a future scenario (Hot/Dry scenario for GLAC only) that has relatively higher increase in temperature (+~4.5 C) and about +20% increase in precipitation (See Figure 5-7)
- **Climate Sensitivity:** Regionally speaking, it is the response of a climate model for a given amount of greenhouse gas increase. More narrowly defined it is the global average temperature increase that results from a doubling of carbon dioxide over pre-industrial values.
- **CMIP3, CMIP5:** Coupled Model Intercomparison Project Phases 3 and 5. "Foundational" collections of climate model projections, used in the Intergovernmental panel on Climate Change (IPCC) 2007 and IPCC 2013 reports, respectively
- **CNRM:** A CMIP5 climate model from the French National Centre of Meteorological Research (cnrm-cm5.1.rcp85),used in this report as a future scenario (Central scenario for both GLAC and ROMO) that is relatively close to the ensemble mean in temperature increase (+~2.5 $^{o}$C) and +~5-8% increase in precipitation (See Figure 5-7).
- **DEM:** Digital elevation model
- **DSHVM:** Distributed Hydrology Soil Vegetation Model
- **ESM:** earth system models, see GCM.
- **FIO:** A CMIP5 earth system model from the First Institute of Oceanography, State Oceanic Administration of China (fio-esm.1.rcp85), used in this report as a future scenario (Warm/Dry scenario for both areas) that is relatively lower in temperature increase (+~0.8-1.6 $^{o}$C) and -~5% decrease in precipitation (See Figure 5-7).
- **FLH:** Atmospheric freezing level height is the altitude in the free atmosphere at which the temperature is 0 °C
- **GCM:** Global Climate Model, 6 were used for this report from the IPCC 2013 class of models; X of these are actually earth system models (ESM), an advanced type of GCM which have the added capability to explicitly represent biogeochemical processes that interact with the physical climate. GCM is used as a general term referring to both kinds of models, ESM is used specifically for earth system models.
- **GISS:** A CMIP5 climate model from the NASA Goddard Institute for Space Studies (giss-e2-r.1.rcp45), used in this report as a future scenario (Warm/Wet scenario for both areas). Referred to as the "Least Change" scenario because it that is relatively lower temperature increase (+~1-1.3 $^{o}$C) and +~7-10% increase in precipitation (See Figure 5-7).
- **GLAC:** An area in Glacier National Park used as a spatial unit of analysis in this report
- **HADGEM:** A CMIP5 earth system model from the United Kingdom Meteorological Office Hadley Center (hadgem2-es.1.rcp85) used in this report as a future scenario (Hot/Very Wet scenario for ROMO only) that has relatively higher temperature increase (+~ 3.5 $^{o}$C) and -~5% decrease in precipitation.
- **Internal climate variability**: The variations in the climate, even for 30-year and longer averages, that can occur due to the interactions of the atmosphere, ocean, inland surface and cryosphere. This occurs even in the absence of anthropogenic climate change.
- **MODIS:** Moderate Resolution Imaging Spectroradiometer, a satellite remote sensing instrument carried on the Terra satellite

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- **MIROC:** A CMIP5 earth system model from the Japanese Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies (miroc-esm-chem.1.rcp85), used in this report as a future scenario (Hot/Wet scenario for both areas). Referred to as the "Greatest Change" scenario because it has the highest temperature increase of the scenarios (+~4 $^{o}$C) and +~10-18% increase in precipitation (see Figure 5-7). This ESM has an atmospheric chemistry (CHEM) component coupled to the MIROC-ESM (http://maca.northwestknowledge.net/GCMs.php).
- **NDSI:** Normalized Difference Snow Index, a measure of snow cover, has a has a linear relationship to fractional snow cover (FSC)
- **North American Freezing Level Tracker**: NCEP/NCAR Global Reanalysis 2.5$^{o}$ x 2.5$^{o}$ grid data (http://www.wrcc.dri.edu/cwd/products/)
- **Octants:** Topographic aspect, or compass direction, was classified into eight directional bins, each representing 45° of compass arc, e.g; NW, N, NE, E, SE, S, SW, and W
- **ROMO:** An area in and around Rocky Mountain NP used as a spatial unit of analysis in this report
- **SCA:** Snow Covered Area (km$^2$)
- **SDD:** Snow Disappearance Date, the first Day of Year after March 1 where pixel is snow-free, defined as the date which NDSI/100 was less or equal to 0.1.
- **SNODAS:** Snow Data Assimilation System, a product of the NOAA National Weather Service's National Operational Hydrologic Remote Sensing Center (NOHRSC)
- **SWE:** Snow water equivalent (mm).For May, snow depth is assumed to be ~ 2.5 *SWE
- **TopoWx:**
- **Snow covered area, total:**Total area covered by snow within the study boundaries in square kilometers (km$^2$)
- **Snow covered area, fractional:** Percentage of the total land area that is covered by snow; this can be within the study boundaries, aspect area, or elevation bands
- **VIC:** Variable Infiltration Capacity hydrologic model
- **UTM:** Universal Transverse Mercator spatial coordinates

FIGURES – see separate file

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| | |
|---|---|
| **From:** | Guinotte, John |
| **To:** | Joseph Barsugli - NOAA Affiliate |
| **Cc:** | Andrea Ray; Stephen Torbit; Imtiaz Rangwala; Candida Dewes; Aaron Joseph Heldmyer; Ben Livneh; Kevin Doherty |
| **Subject:** | Re: FINAL DRAFT of the Wolverine Report |
| **Date:** | Monday, April 17, 2017 8:39:33 AM |

Hi All,
I was out of the office Friday. I will read through this today and get back to you. Also, please cc Kevin Doherty on the emails regarding the report and any updates. He will be reviewing the docs as well.
Thanks,
John

John Guinotte
Fish and Wildlife Biologist
Ecological Services
U.S. Fish and Wildlife Service
Mountain Prairie Region 6
134 Union Blvd., Lakewood, CO 80228
303-236-4264
john_guinotte@fws.gov

On Fri, Apr 14, 2017 at 9:45 PM, Joe Barsugli <joseph.barsugli@noaa.gov> wrote:

> All
>
> Andrea and I came pretty darn close to making all the requested revisions/comments, adding the text for ROMO, and the elevational analysis, as well as a qualitative assessment of the differences with McKelvey, and relabeling most of the figures. I have put a version of the Wolverine Report on the Google Drive that I am -- perhaps presumptuously -- calling FINAL DRAFT 14 APR 2017. It really is a quantum leap from the previous draft. As before the figures and text are in separate files. I am also attaching the text as it is small. There are PDF versions on the drive as well. The requested revisions have taken more effort than we anticipated, and there are still some small issues to deal with -- particularly a couple of figures that still need to be redone. These are not terribly substantive changes, but will need to be done. The Supplementary Material is not ready for wider distribution yet. At this point I am not comfortable going with the latest runs from Aaron (the MIROC 2080's McKelvey delta runs) until we understand them better. We can discuss later as to how far we want to go on the McKelvey comparison in this Report.
>
> Happy Weekend, and I hope Steve has a quick recovery!
>
> Yours,
>
> Joe
>
> --

Joseph Barsugli, Research Scientist III
CIRES, UCB216
University of Colorado Boulder
Boulder CO 80309
303-497-6042
PSD Science Board and
Attribution and Predictability Assessments Team Member

**From:** Doherty, Kevin
**To:** Guinotte, John
**Subject:** Re: FINAL DRAFT of the Wolverine Report
**Date:** Monday, April 17, 2017 8:45:29 AM

---

roger that.  I am working from home until I go to the funeral at 11

On Mon, Apr 17, 2017 at 8:42 AM, Guinotte, John <john_guinotte@fws.gov> wrote:

> Sounds good. Kales was just in here looking for you.
>
> John Guinotte
> Fish and Wildlife Biologist
> Ecological Services
> U.S. Fish and Wildlife Service
> Mountain Prairie Region 6
> 134 Union Blvd., Lakewood, CO 80228
> 303-236-4264
> john_guinotte@fws.gov
>
> On Mon, Apr 17, 2017 at 8:40 AM, Doherty, Kevin <kevin_doherty@fws.gov> wrote:
>
> > OK,
> >
> > I will likely start on it tomorrow because I have Sagebrush Science Initiative Calls this morning and then off from 11 on for the funeral.  Instead of edits on edits, I can read and think, but I will wait until you have your edits done so we do not have to reconcile them.
> >
> > Cheers
> > Kevin
> >
> > On Mon, Apr 17, 2017 at 8:37 AM, Guinotte, John <john_guinotte@fws.gov> wrote:
> >
> > > Hey Kevin,
> > >
> > > This was in my inbox this am. I'm planning to read it today sometime and start editing over the next couple of days.
> > >
> > > Best, J
> > >
> > >
> > > ---------- Forwarded message ----------
> > > From: **Joe Barsugli** <joseph.barsugli@noaa.gov>
> > > Date: Fri, Apr 14, 2017 at 9:45 PM
> > > Subject: FINAL DRAFT of the Wolverine Report
> > > To: Andrea Ray <Andrea.Ray@noaa.gov>, "Guinotte, John" <john_guinotte@fws.gov>, Stephen Torbit <Stephen_Torbit@fws.gov>, Imtiaz Rangwala <Imtiaz.Rangwala@noaa.gov>, Candida Dewes <Candida.Dewes@noaa.gov>, Aaron Joseph Heldmyer <Aaron.Heldmyer@colorado.edu>, Ben Livneh <ben.livneh@colorado.edu>
> > >
> > >
> > > All

Andrea and I came pretty darn close to making all the requested revisions/comments, adding the text for ROMO, and the elevational analysis, as well as a qualitative assessment of the differences with McKelvey, and relabeling most of the figures. I have put a version of the Wolverine Report on the Google Drive that I am -- perhaps presumptuously -- calling FINAL DRAFT 14 APR 2017. It really is a quantum leap from the previous draft. As before the figures and text are in separate files. I am also attaching the text as it is small. There are PDF versions on the drive as well. The requested revisions have taken more effort than we anticipated, and there are still some small issues to deal with -- particularly a couple of figures that still need to be redone. These are not terribly substantive changes, but will need to be done. The Supplementary Material is not ready for wider distribution yet. At this point I am not comfortable going with the latest runs from Aaron (the MIROC 2080's McKelvey delta runs) until we understand them better. We can discuss later as to how far we want to go on the McKelvey comparison in this Report.

Happy Weekend, and I hope Steve has a quick recovery!

Yours,

Joe

--
Joseph Barsugli, Research Scientist III
CIRES, UCB216
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--

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--

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**From:** Joe Barsugli
**To:** Kevin Doherty; Guinotte, John
**Cc:** Andrea Ray
**Subject:** Wolverine Report Addendum
**Date:** Monday, April 17, 2017 4:45:51 PM
**Attachments:** Wolverine Report Figures Addendum 17apr2017.docx

---

This addendum has Figure 5-24 which was missing from the original draft. -- Joe

--
Joseph Barsugli, Research Scientist III
CIRES, UCB216
University of Colorado Boulder
Boulder CO 80309
303-497-6042
PSD Science Board and
Attribution and Predictability Assessments Team Member

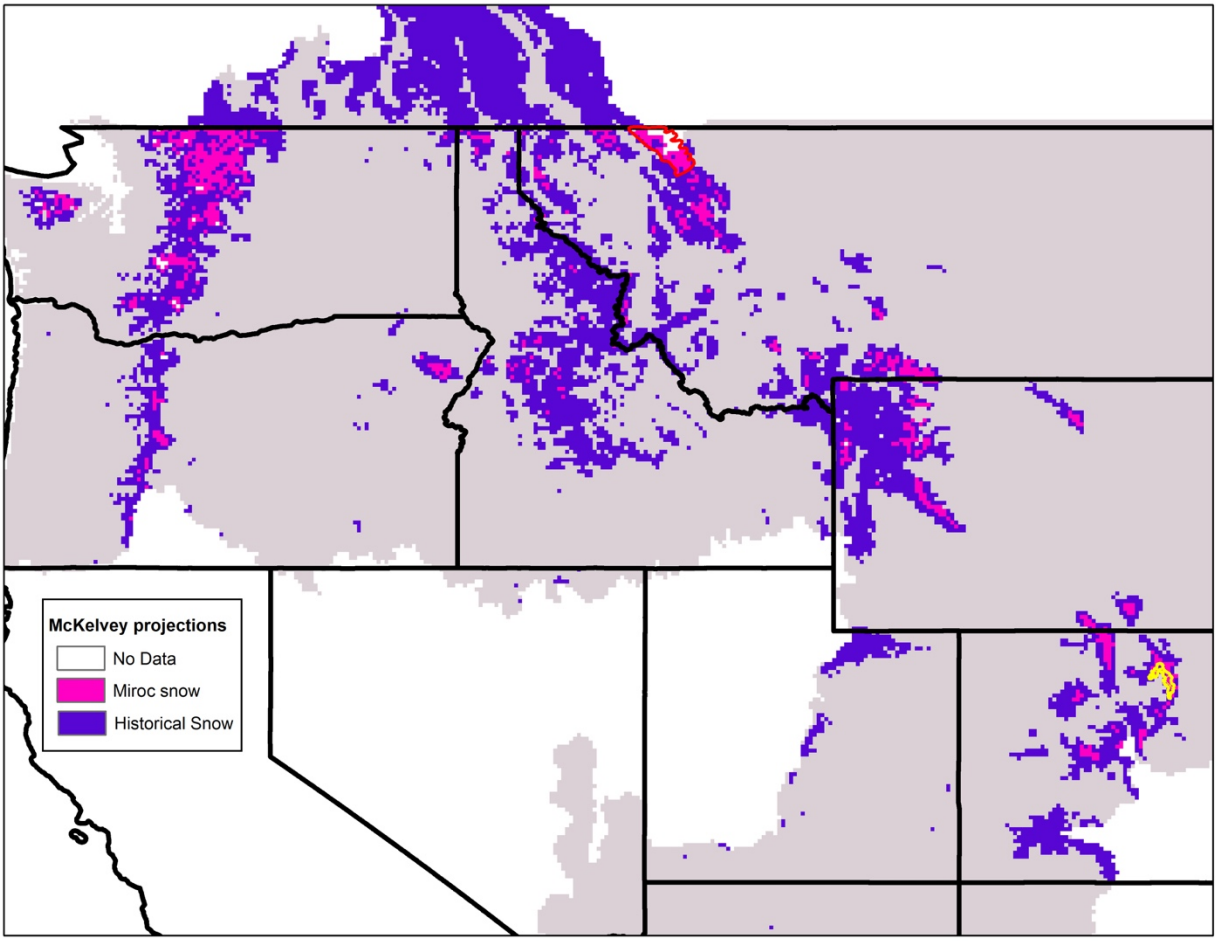


**Figure 5-24: Simulated May 15 average snow cover inferred from 13cm snow depth on May 1 from McKelvey et al. (2011). Historical simulation and "MIROC 2080s" projection are shown. No projection data were included for Canada. Outlined areas are shown from the present study: GLAC (red), ROMO (yellow). Note that the domain simulated in McKelvey et al. (2011) did not include all of the GLAC study area. (Data were generously provided by Jeff Copeland. Graphic prepared by John Guinotte).**

DRAFT

**From:** Grizzle, Betty
**To:** Shoemaker, Justin
**Subject:** Ecoregion map - DRAFT
**Date:** Tuesday, April 18, 2017 2:58:25 PM
**Attachments:** Wolverine_Crrent_Range_EPA_Portrait_new.pdf

---

A first draft of how defined ecoregions relate to our current range for North American wolverine. John has the shape files, which are available from this website
- https://www.epa.gov/eco-research/ecoregions-north-america

--

Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

U.S. Fish & Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave. Suite 250, Carlsbad, California 92008

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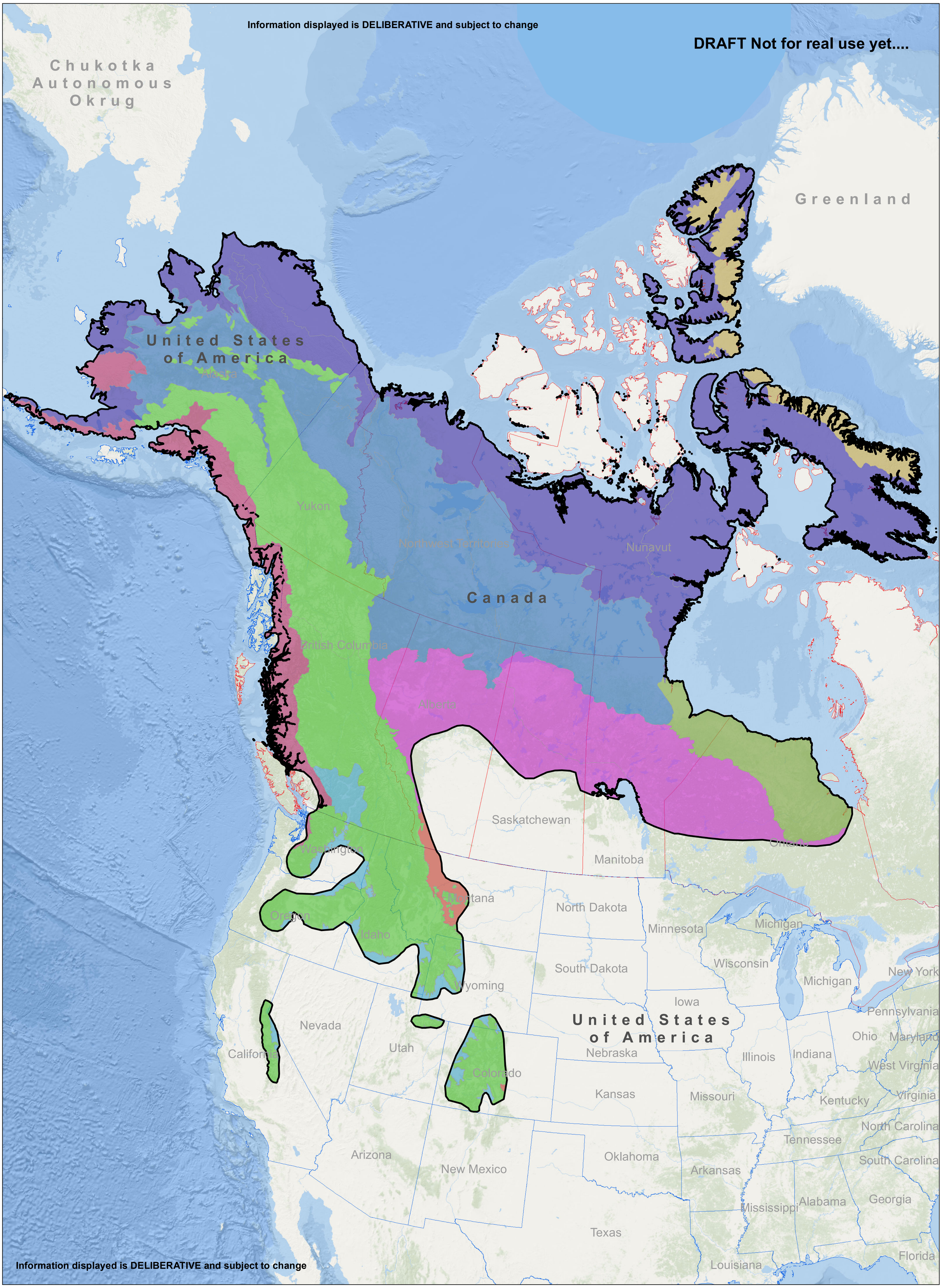


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DRAFT Not for real use yet....

PRODUCED BY GIS SERVICES
CARLSBAD FIELD OFFICE
GIS CONTACT: ED TURNER
BIOLOGY CONTACT: BETTY GRIZZLE
(760) 431-9440
DATA SOURCE: USFWS,
IMAGE SOURCE: ESRI Online Mapper
Apr 17, 2017
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**NA_L1NAME**

- ARCTIC CORDILLERA
- GREAT PLAINS
- HUDSON PLAIN
- MARINE WEST COAST FOREST
- MEDITERRANEAN CALIFORNIA
- NORTH AMERICAN DESERTS
- NORTHERN FORESTS
- NORTHWESTERN FORESTED MOUNTAINS
- TAIGA
- TUNDRA
- North American Wolverine (*Gulo gulo luscus*) Current Range

**From:** Grizzle, Betty
**To:** John Guinotte
**Subject:** Fwd: emails discussions
**Date:** Tuesday, April 18, 2017 3:41:32 PM
**Attachments:** The McKelvey Email.docx
The McKelvey Email Response.docx

---

---------- Forwarded message ----------
From: **A J** <222wsheridan@gmail.com>
Date: Tue, Apr 18, 2017 at 2:20 PM
Subject: emails discussions
To: "Grizzle, Betty" <betty_grizzle@fws.gov>

Betty
I don't know if you have already seen these from Shawn's files, but these emails contain a discussion I had with Copeland and McKelvey after some reluctance on my part to get into such an exchange post-status review. I was pretty burned out by then on the whole subject. But you may find parts help answer some of the questions you recently sent. The McKelvey Email file is emails between Jeff and I until it became apparent that it was better to talk directly to Kevin and so his responses to me are in blue type in that email. The McKelvey Email Response file holds my answers back to him in black type. As you will see, there is little consensus on the matters under discussion. I had permission from both to share these emails and Shawn received copies. He had encouraged us to discuss these issues (and others) hoping to get some resolution of the differences of opinion, but as I suspected from the start, I don't think anyone changed their minds on anything.

--

Betty J. Grizzle, D.Env.
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2177 Salk Ave, Suite 250
Carlsbad, CA  92008
760-431-9440, ext. 215
760-431-5901 fax

Ok. Let's go through the science and see where that leads us. I will start with a published statement by you:

"We believe a critical feature of wolverine denning habitat is dependability of deep snow throughout the denning period." (Magoun and Copeland 1998 pg. 1318).

If this statement is true, then there are a number of consequences.

1) As this is "critical", areas lacking this property should be unsuitable for denning

2) If denning is limited to sites having this characteristic, then the range of the breeding population of wolverines can be defined by this property.

3) Climate change has reduced the depth (APR 1 SWE) of spring snow by about 40% across those areas of the western U. S. currently occupied by wolverines when compared to the mid 20$^{th}$ century (Mote et al. 2005). Climate change models all show continuing declines in spring snow depth and SWE. Given 1 and 2, this will lead to a reduction in the areal extent of areas having deep persistent snow throughout the denning period.

4) Because female wolverines don't really pack into areas (fairly consistent home range size, little overlap), this reduction in areal extent will lead to declines both in range and in local population size.

Note that the entire case for climate dependency, the precise nature of that dependency, and the inevitable consequences of that dependency are all fully defined by this statement—you don't actually need Copeland et al. (2010) or McKelvey et al. (2011).

So, what did Copeland et al. (2010) add to this? Copeland et al. (2010) explored 3 issues: Was this critical relationship to snow in fact a universal property? Could you map it sufficiently using current satellite data? And were the consequences as expected: dens range limited to areas with evidence of persistent spring snow?

The short answers were: Yes, Yes, and Yes. You sort of went out on a limb in 1998, suggesting a general biological limit based on a very limited dataset and one might have thought that you would be happy

that your premise was so strongly supported by Jeff's work. However, you were concerned about the details of the mapping. Below I discuss your concerns as best I understand them and make a case that your concerns are off target: not that the mapping is perfect, but that its imperfections differ from those you have identified.

First, you seem to feel that Jeff's use of persistent spring snow cover rather than persistent spring snow depth represents is a big issue. At least in this context, it isn't. During the spring snow melt, persistence for any patch of snow is directly related to its depth (e. g. the deepest drifts persist the longest). To persist, snow has to be deep. Therefore, if you were on the ground during spring melt measuring these two metrics (average snow depth and average areal extent), you would find them to be highly correlated. A much bigger deal is that the measurements were made by satellites and that snow pixels (500x500m) were identified based on binary classification (snow, no snow)—more on that below.

Secondly, you were very upset by the choice of May 15 as the final day in the denning period. Based on the literature, this is not an unreasonable date to end the denning period (See Inman et al. 2012) and I could make a perfectly valid case that in the sort of correlational work represented by Copeland et al. (2010) the exact start and stop dates will always be arbitrary and are largely irrelevant. I'm not going to do this, because I think that the data in Copeland et al. are actually telling us something meaningful about the nature of the relationship between wolverine den choices and snow. Specifically, I think that the location of den sites in areas much snowier than would be strictly necessary to provide natal den requirements likely indicates broader dependencies on snow covered landscapes that extend beyond the denning period. But to get there, I need to discuss what a snow pixel is more formally.

In Copeland et al. (2010) we evaluated daily data which had been classified on a per-pixel basis as snow or not snow. This classification was based on the spectral signature of the pixel, exposed to a model that reported the likelihood that the pixel was snow or not—pixels were classified based on whichever likelihood was greatest. We insisted that, for a period of 21 days, that a pixel classified as snow every day is was visible: a single "not-snow" classification any time within this 21 day period would remove that pixel from being considered snow covered in that year. Thinking about this process, the only way that it was likely that a pixel would be typed as being snow covered this consistently was if the spectral signature was very "white". As a pixel dropped to ~50% snow covered, the chances of being typed as a snow pixel consistently across 21 trials becomes insignificant; pixels with scattered snow drifts never classify as snow pixels. So even pixels that only classified as being snow covered 1 year out of 7 were actually pretty snowy places. The idea that because a pixel was not classified as a snow pixel meant that it contained no snow is simply wrong. You can't make that case using these data.

This discussion relates to a third identified concern: that because a few den sites fell outside of the persistent spring snow layer as evaluated using the above method, the method is somehow fundamentally flawed. There are 2 explanations for these dens: one is that these few den sites indicate greater plasticity –that is in some areas dependable deep snow throughout the denning period is not critical in some places. A second explanation is that the satellite doesn't correctly map snow under certain circumstances. There are a number of reasons to believe that the latter rather than the former is the cause. First, we contacted the scientists that located all of these dens and confirmed that all were snow dens—this supported the idea that these dens didn't represent exceptions to the assumed snow dependency. Secondly, all of these den sites occurred in flat boreal tiaga composed of heavy canopied species such as spruce: it is well documented that the snow classification algorithms don't work well when all of the snow occurs under heavy canopies. This is especially true when you demand, as we did, on consistent classification as snow pixels across a 21 day period. Probably the best understanding therefore is that the satellite imagery-based underestimates the extent of spring snow in the tiaga and in other areas where conifer canopies are heavy and have few gaps. However, the overall success of Jeff's mapping suggests that this phenomena was localized. Importantly, it does not appear to be a problem in the western U. S.

And this leads to a final understanding from Jeff's work. Because of the extremely conservative nature of the snow/no snow calls, areas that were identified as being snow pixels 7 out of 7 years had to be classified as snow up to 147 times with no failures—6 of 7 perhaps only a single failure. To do this, these pixels really needed to not just contain snow, but to be snow covered (nearly pure white) through a period extending to mid-May. A very consistent majority of den sites (67% in Sweden, 68% in Norway, and 71% in North America) occur in pixels that were classified as being snow covered at least 6 out of the 7 years. I would agree with you that this far exceeds the thermal requirements for denning. In many cases it exceeds the needs for successful natal dens. It suggests, in fact, that wolverines are choosing to den in sites that, when families emerge from the natal den, are still covered with deep and fairly contiguous snow and in areas where this condition persists into the spring. It therefore suggests additional snow associations other than those formally associated with the needs for successful natal dens. Two that have been posited (though with little data support) are predator avoidance and refrigerated food caching (Inman et al. 2012).

There is no evidence that wolverines den in warmer locations that might have snow drifts through April but which have lost their snow cover by mid-May. Quite the contrary. In the western U. S., where the population has been steadily expanding, one might think that, even if a bit sub-optimal, sub adult females seeking to establish home ranges would set up shop in adjacent lower elevation areas rather than take the long hike to adjacent mountain ranges. There's a lot of this sort of habitat available. The fact that there is no evidence that this ever happens is really rather remarkable.

Bottom line: Copeland et al. (2010) provided strong evidence to support your assumption that snow dependency was universal. Further, it implies that this dependency is stronger and extends further in their life history than what you initially thought. Given this, the understanding that you published in 1998 is THE critical for defining the macro-scale ecology of wolverines, and sets hard limits on where

they can live and where they can't. It also fully defines a specific and unavoidable impact of warming climates on wolverines. Dens exterior to the snow coverage were few, were in very specific topographic locations and forest types, and likely reflect the well-documented inability of satellites to see through conifer canopies.

Now we come to McKelvey et al. (2011). Concerning your statement that it is "invalid", I can't really comment as the stream of emails almost exclusively discusses the findings of Copeland et al. (2010); I have no idea what this putative lack of validity stems from. However, I believe that the validity of tracking patterns of persistent spring snow is well established—both by your 1998 paper and by Copeland et al. (2010). I also believe that that we did a good and careful job both of modeling snow, and matching those data to Jeff's MODIS data. I insisted that we go the extra mile to be transparent and to back-check our modeling as much as possible. Comparing modeled data to MODIS data later in the spring and including a specific section that explicitly stated assumptions and caveats are examples of the care we took. K.

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http://scholar.google.com/citations?user=CmG2R0QAAAAJ&hl=en

**From:** A Magoun [/src/compose.php?send_to=222wsheridan@gmail.com]
**Sent:** Friday, March 14, 2014 2:49 PM
**To:** Jeff Copeland

**Cc:** McKelvey, Kevin -FS; Shawn Sartorius
**Subject:** Re: Den data

Jeff

Where my questions were heading was towards a better understanding of your viewpoint and an examination of whether there is any convincing evidence that my position, that the McKelvey et al. 2011 model predicting loss of wolverine habitat under climate change is not based on the best available science, is invalid. I have been reading many climate papers and bioclimatic envelope papers and communicating with other wolverine biologists since your review of my peer review of the wolverine listing proposal and so far I haven't found anything that has convinced me to change my position, in fact on the whole just the opposite. After our extended discussion over the last few days, it appears that we have come full circle and are right back to disagreeing about our interpretations of the best available science.

To address the specific question of my problem with the May 15 date, I refer you to my comment submitted to the FWS in the second comment period, which is on the FWS peer review page. I don't have it with me as I am traveling. I assumed you had already read it but perhaps not, however, based on our recent discussions, I don't expect that it will convince you to alter your position.

I prefer to end this discussion here as I've already spent a great deal of time thinking about and reading the "science" and discussing the various aspects as I'm sure you have. If I find that I have changed my position before the review panel meets, I will let you and Shawn Sartorius know. Likewise, if after the panel meets I change my mind, I will also let you know. I will also copy you on any further comments I submit to the FWS before the end of this comment period on May 6.

All the best

Audrey

Sent from my iPhone

On Mar 13, 2014, at 10:43 PM, Jeff Copeland <jcopeland224@gmail.com> wrote:

1) It is a bit difficult to answer that question because it assumes, or I believe the question assumes, that our snow model possibly represents 1 meter of snow on the 15th of May, which is probably does not across the extent of the model. But all things equal, a model that represented the extent of 1 meter snow in April would be larger in extent than a model for May 15. Using April rather than May snow would have probably produced a different model in terms of where snow remained but I suspect that the change in snow loss over time would be very similar.

An important consideration here, Audrey, and much of the reason we engaged in this process is that wolverine weaning occurs at the same time as spring snow melt. If you recall from the snotel charts the buildup of snow is a gradual process when compared with spring snow melt, which generally happens across a very short period of time, and coincides with wolverine weaning. We (or I) did assume that the den is important throughout the denning period. As global warming pushes spring runoff back 2 or 3 weeks it is pushing snowline up the mountain and degrading the den earlier. This was an important premise in the development of the model. If you believe that den integrity is not important during the latter stages of denning then you might assume that an earlier spring thaw will have less of an impact on denning success. The problem with that assumption is that what we know about wolverine denning does not support that. They den in places that provide long lasting snow, not in places that melt out early. There is really no difference between April, March, or February snow for that matter. It is basically everywhere and adequately deep. It is in late April and early May that she needs the deep snow to persist, and I say this not because I am simply speculating. I say it because that is where the dens are.

2) In thinking about it now, Audrey, I believe the first date we used was May 21 not May 28. I came up with May 28 because I was thinking 28 days. The first models were 28 days which went from April 24 to May 21. Anyway, as I recall the extent of the model only changed by about 3% but it shifted the dens a bit. In N.A. there were dens in 1-year and 2-year snow with the 28 day model. When we changed to 21 days there were no dens in 1-2 year snow.

3) The climate model was queried based on snow depth values it provided until we found a minimum depth that spatially matched the snow model fairly well. The snow depth parameter that provided the best match was >13 cm snow depth. Once that was determined our snow model was left behind. But in the sense that the climate model was "trained" on the snow model, I guess one could say that the future climate models would approximate May 15 snow.

4) The snow model depicts the wolverine's fundamental niche. I am thinking about "habitat" relationships more in terms of "life zones" than what we might think of as habitat. Guess it is a matter of terminology. I believe that wolverine "habitat" in the Brooks Range is not much

different than wolverine "habitat" in Glacier National Park, from a wolverine's perspective. As such, I believe the wolverine is a very habitat specific animal. That habitat, or niche, or life zone occurs pretty much everywhere at northern latitudes while as southern latitudes it resides in a very narrow elevational band.

You still haven't answered my question in regard to your issue with May 15. Your questions all seem to be leading somewhere. It would be most helpful if I understood where this is headed.

jeff

On Thu, Mar 13, 2014 at 9:40 PM, A Magoun <222wsheridan@gmail.com> wrote:

Jeff

I have some questions to help me understand this:

1) if, rather than MODIS May 15 snow cover, you could have measured snow depth (for discussion sake, let's say snow depth of 1 meter or more on April 1), had that data been widely available on the scale you needed it, do you think the resulting snow map coverage would have been larger, smaller, or just the same as the one produced by the May 15 analysis? Do you think the climate model, had it used this snow metric instead of May 15 snow cover to train the model, that the predicted future extent of wolverine habitat would have looked the same?

2) if you had used May 28 instead of May 15, do you think the concordance of expert-derived wolverine distribution and the resulting snow map would have been better (e.g., 100% of dens and all known breeding populations in 5-6 out of 7 years)?

3) by saying that "the May 15 date had no bearing on the future predictions", do you mean the various maps of predicted wolverine habitat in the McKelvey et al. 2011 paper do not show where MODIS May 15 snow cover (or snow depth >13 cm on May 1) can be expected to occur in the respective time periods?

4) I understand how the bioclimatic envelope depicts current distribution (give or take a little) but I don't see why you are saying it depicts habitat relationships since in our other email below you seem to agree that the model is about WHERE wolverine habitat currently is not WHAT wolverine habitat is (I.e., "the model is less about snow than it is about where wolverine habitat is"). What habitat relationships does the bioclimatic model depict?

Thanks

Audrey

Sent from my iPhone

On Mar 13, 2014, at 7:19 PM, Jeff Copeland <jcopeland224@gmail.com> wrote:

I have no objections whatsoever to you including Kevin in this discussion.

The May 15 date had no bearing on the future predictions. It was only used to train the climate model to match our model of wolverine distribution. The future predictions were created with the climate models only using our model as a beginning point. The predictions then suggest that if the bioclimatic envelope accurately depicts current wolverine distribution and habitat relationships - or the animal's niche, then that niche will decrease in extent. We were actually fairly pleased with the predictions in that most of the large, contiguous blocks of wolverine habitat remain pretty much intact throughout the century. It is really not the gloom and doom scenario that some might suggest.

In regards to your statement, ***Until someone shows me the link between May 15 snow cover and a change in winter snow pack so severe that wolverines cannot find a secure den (assuming that denning habitat is the key), then I think a climate model based on MODIS May 15*** ***snow cover that predicts loss of wolverine habitat has little scientific merit without an explanation of why,*** you are getting way out in front of what this represents, Audrey. The snow model is very congruent with our best understanding of the wolverine's current and historical distribution so we are calling it a model of the wawolverine's distribution. The climate analysis then simply projects that distribution of snow (wolverine habitat) into the future. However precisely it represents actual wolverine habitat the futuring of the model is simply a change-estimation exercise. There is this much now, there will be this much later. We made no attempt to speculate what that meant other than increased resistance to movement.

Further, how much do we really know about what a female wolverine prefers, or needs for denning habitat. No one has ever documented a wolverine population - or a single wolverine, for that matter - that chose a den site away from snow. Our N.A. wolverines, as you can see in the chart I sent you, didn't den on the periphery of the model, they prefered to be in the 5-6 year snow - way higher and deeper than was necessary if they didn't want deep snow to the end of denning, or about May 15. Please explain what it is that bothers you so much about May 15? We would have produced an even more precise model - a better fit to known wolverine distribution in N.A. had we used May 28. May 15 captured 99% of dens and about 90% of year-around habitat use. Seems to me that that is a pretty good indication that this is not a bad date. Could you be more explicit as to what your concerns are regarding that date.

Jeff

On Thu, Mar 13, 2014 at 6:05 PM, A Magoun <222wsheridan@gmail.com> wrote:

Jeff

Thanks for taking the time to write this lengthy response. There's some interesting points to ponder here. I will take some time later to respond after I think about them more thoroughly, but for now let me just point out that my apology below was for my specific statement in my FWS peer review that the bioclimate envelope paper stated that MODIS snow cover on May 15 was obligatory for wolverines. I now understand that our paper did not make that claim. I also realize that the bioclimate envelope paper, when taken simply as such, is a scientifically acceptable way to look at snow as an integral part of the wolverine's niche (I.e., a way to map current wolverine distribution using a snow metric that can be applied at a worldwide scale). My problem with the May 15 date is that it was used in McKelvey et al. 2011 to predict wolverine habitat into the future. This paper relied on our bioclimatic envelope paper for the May 15 date, despite the fact that the authors stated that they did not know why that date worked so well in showing a concordance of wolverine distribution and May 15 snow cover. I believe that, because the authors did not demonstrate a specific link between the wolverine's need for snow and the May 15 date, there is no way to know if May 15 is the appropriate date to model future habitat (using either the MODIS data or the May 29 forward projection of snow cover). The May 15 date was useful in modeling worldwide wolverine distribution now (or more specifically in 2000-2006), but may not be useful in the future. If the earlier spring melting that is projected to occur in the future with climate change (i.e., the McKelvey et al. climate model) cannot be linked to a decline in snow pack earlier in the winter (or some other critical underlying variable) that is severe enough to cause wolverines to abandon habitats used today, then the use of May 15 is not valid for projecting changes in occupied habitat with climate warming. Until someone shows me the link between May 15 snow cover and a change in winter snow pack so severe that wolverines

cannot find a secure den (assuming that denning habitat is the key), then I think a climate model based on MODIS May 15 snow cover that predicts loss of wolverine habitat has little scientific merit without an explanation of why. What the McKelvey et al. 2011 model says to me is that we need to find out what aspects of snow wolverines are dependent upon for habitat and viable populations. In that respect the paper is useful because it is a heads up that, unless we understand wolverine habitat requirements more specifically, we cannot know their conservation needs or plan appropriately. I hope you do not mind me sending this on to Kevin as we are now discussing a paper on which he is the first author. In fact, it would be good to send this exchange to all the other authors in case they share your concerns about a new review panel. Let me know if you have any objections to that.
Audrey

Sent from my iPhone

On Mar 13, 2014, at 11:01 AM, Jeff Copeland <jcopeland224@gmail.com> wrote:

Yes ! In fact, we have been a bit disappointed that the model has come to be known as the "snow" model because it is less about snow than it is about where wolverine habitat is, as you state. When we began developing it we were focused on snow and denning. Our goal was to see how well spring snow correlated with dens - nothing beyond that. It wasn't until later and we began looking at the spatial relationship between the model and year-around presence that we realized this might represent a fundamental niche more so than simply denning habitat.

I do need to clarify a bit regarding your comments about May 15. May 15 date was not a random choice, either in this paper or the earlier Aubry et al. paper. We were thinking denning and I wanted to be sure we defined the distribution of snow at least to the end of the denning period. I was assuming (and still see no reason not to believe) that snow was important to the end of denning, and May 15 seemed to be a good date to capture the entirety of the denning period while allowing for enough spring snow melt to move the persistent spring snow line up the mountain a ways. So in that sense the date is based on wolverine biology. We knew that that date, in terms of denning cessation, would vary around the world, which is why we don't focus on that date as some defined, or obligate, denning break-point for the wolverine.

I think you might be looking at this a bit backwards, Audrey. If we felt that deep snow was important to denning wolverines only to, say, mid April, then the best way to model the distribution of deep April snow, using MODIS data, would be to run the model out to maybe mid-June or July. By doing so you would allow more pixels to show bare ground, which would eliminate them, and you would move the persistent snowpack much farther up the mountain. In this context the date leaves the biology realm and becomes important only in the modeling process. In our case May 15 not only worked well for the modeling but it also has a biological

tie to the animal as representing the end of denning. This is a bit fortunate but it is as much coincidence as anything. Remember, our model is not simply showing where snow is on May 15, it is meant to be a representation of where deep, persistent show occurs at that time. As was the case in your Ontario study area, as well as in Scandinavia, there were places where wolverines were denning that were outside the model. What was important is that we know they were not outside of snow. Their lack of concordance with the model was only a reflection of the model's limitations rather than wolverine choice. As I have said, we conclude from this that the wolverine is a snow-obligate rather than a model-obligate animal.

I tried to find some the the analyses from when I first modeled the data out to May 28, but haven't been able to just yet, but as I recall there were a few North American dens that occurred in 1-year data. When we moved the date back to May 15 it extended the distribution of snow enough that there we no dens in 1 or 2-year data so it might have been even better to have used the May 28 date in terms of how it fit the data (I have included a chart of the N.A. data that was not in the paper), but because this was not a fitting exercise we left it at May 15, largely due to your concerns. I guess what this suggests is that it is more about deep snow than it is about dates. We did not include this graphic in the paper as we felt the distribution of N.A. dens was not representative across the continent - at least not to the degree that it was for Scandinavia.

With that said, I do, very much, appreciate your apology but what concerns me is that this "misunderstanding" has been perpetuated way beyond a simple exercise in interpretation among scientists. The FWS is convening a science panel next month to discuss the merits of the science used in the listing decision based solely on the concerns you and Bob Inman have raised, most of which revolve around this May 15th thing. MWFP and IDFG have focused their objections to listing on the fact that two of the peer reviewers have vehemently argued that the science used in the analysis is flawed, and in some cases that the scientists that created it are biased. Your recognition that you misunderstood this is certainly gratifying to me personally, but I have to wonder what can be done to correct this image of flawed science and biased scientists that this has created and perpetuated on a much larger scale?

I would like it very much if you could clarify something for me. Have you focused on this because you disagree with the need to list the wolverine, or is this simply about concerns you have had regarding the bioclimatic envelope paper?

Jeff

On Wed, Mar 12, 2014 at 3:31 PM, A J <222wsheridan@gmail.com> wrote:

Jeff

I agree there is no reason we should not be able to resolve this and hope this response does so. I have read over your attached emails a number of times, and some others as well, to be sure I understand the Copeland et al. 2010 paper, the spring snow cover model, and the correct interpretation of it. I think one of your statements in your March 9 email below helped me in particular to better understand the model: i.e., what I "need to do to is try and separate the model from the biology." I thought about this and it did help me to come to a better understanding of the model I think. I will lay out my understanding here and you can let me know if I have it right.

The MODIS May 15 snow cover for 2000-2007 produced a model that defined ***where*** wolverine habitat is not ***what*** wolverine habitat is. You selected May 15 to model persistent spring snow. You did not select May 15 because it was necessarily linked to wolverine biology, but because it was one of a number of metrics related to snow cover (snow depth) that one might use to compare to wolverine distribution. The MODIS May 15 snow cover was the metric that worked best for mapping worldwide spring snow cover with some refinements to eliminate ephemeral spring snow, clouds, etc . The reason you wanted to map snow cover is that wolverines are a snow-dependent species and in fact a snow-obligate denner. You are not claiming that wolverines need snow cover for denning up to May 15 and such a conclusion would be a misinterpretation of the snow model and the paper. The MODIS May 15 snow cover is simply a way to model worldwide persistent spring snow cover and the snow cover layer in Copeland et al. 2010 should simply be considered a map of persistent spring snow cover for the period you measured it. You overlaid all known wolverine dens on the May 15 snow cover map and found that the resulting bioclimatic envelope model defines the wolverine's distribution at 86% in winter (the summer portion of the bioclimatic envelope model is 95%). This level of concordance between May 15 snow cover and dens sites need not be 100% to use the model to show where wolverine habitat is on a worldwide scale. You are not claiming the wolverines need snow on May 15 for denning and those who see the bioclimatic envelope model this way are misinterpreting the model. For instance, the following statement in my peer review to FWS is incorrect: "*Copeland et al. (2010) assumed that a suitable surrogate for where wolverine habitat occurs on a global scale is obligate snow cover on 15 May as determined by MODIS snow cover data.*" Indeed, after a careful reading of Copeland et al. 2010, I could not find a statement where you specifically said that MODIS May 15 snow cover is obligatory for wolverine habitat. For that, I do apologize and hope you understand how I and the FWS and others misunderstood this concept. Please let me know if I have made any errors in this paragraph that you wish to clarify.

---------- Forwarded message ----------
From: **Jeff Copeland**<gulo@wolverinefoundation.org>
Date: Mon, Mar 10, 2014 at 7:35 PM
Subject: Re: Den data
To: A J <222wsheridan@gmail.com>

Audrey,

I will begin by saying that I am pleased that you are willing to communicate on this. I don't see any reason you and I cannot resolve this.

I did not say that you agreed specifically to the May 15 date. I stated that you expressed concern regarding the May 28 date so I moved it to May 15. I can't recall how you responded to May 15 but assume there would have been additional dialog if you had expressed a problem. You make it sound in your review like I ignored your concern. I cannot imagine I would have done so.

I don't recall the conversation you claim we had about the May 15 date and your idea about redoing the analysis. The pixel examination that resulted in either keeping or eliminating pixels occurred on each image for each of the 21 days. Had we made the end date earlier we would have produced a map with a much larger snow coverage. An important characteristic of the model is that it does miss in a few areas. Had it resulted in 100% coverage of dens and year-around use I would have worried that it over-estimates the wolverine's niche. Had it missed to a greater extent I would have worried that it was too conservative. Because it misses by only a few percent, it suggests that it is probably about as good a representation as one could expect. You are too focused on the model missing in places such as Alberta and Finland. The conclusion reached by what the model provides is that the wolverine is a snow-obligate denner. If you want to question the conclusions of the paper you should be looking for wolverine's that den in non-snow conditions. The model only represents our best guess at the wolverine's world-wide distribution. Also, please remember that the model was a hypothesis, which was then tested with den and telemetry data. This was not a fitting exercise such as what Bob Inman did to develop his habitat model.

And, as far as the May 15 date not having biological support, it really doesn't need to for the model development. We were trying to develop a model that reflected snow depth using data that did not provide snow depth. We could have used any date whatsoever - April 1 or August 1 - to develop the model - whatever it took to produce a persistent spring snow layer. I just wanted to make certain we were including snow that occurred at least to May 15. You are going to have to tell me what is wrong with that date because I think it is biologically sound. Every den I have ever found was actively being used late into the first week of May. There is every reason to believe the dens would have remained in use to some time close to May 15. I'm sorry but I still do not understand your obsession with this date. Had I used an earlier date, as you suggest, the model would have extended way into areas that we know are not wolverine habitat. Why do you feel that would be preferred?

Jeff

On Mon, Mar 10, 2014 at 12:34 PM, A J <222wsheridan@gmail.com> wrote:

Jeff

I am traveling right now and cannot address many of the points in your email without looking at my files at home on my computer. However, I would like to clear up one point. In your email you stated:

"In you peer review comments you state that you tried to convince me with no success to change to an earlier date, as an excuse for why you are now questioning a paper in which you are a co-author. The truth is the original date we planned to use for the analysis was May 28. At your request we moved it to May 15, which you accepted so what you state in your review is untrue."

I find it very difficult to believe that I would have requested that we move the date to May 15 and that I accepted that date. So if you have some written confirmation of this, please send it to me. I realize that memory is often unreliable and miscommunication occurs all the time but I have a couple of reasons for feeling confident that I did not suggest we use May 15:

1) As you may recall, I presented a map of spring snow cover in North America at the Wolverine Workshop in Monterey CA many years ago. I presented the map as a talking point to discuss wolverine habitat. The date that I used for that map was May 1. What I didn't mention at the time was that I had been working with the snow data off and on for a couple of years before the workshop. By the time the workshop came around, I had already decided that May was not a good match (to me that means 100% of breeding populations) for wolverine distribution and had decided to start looking at April. I had ordered the data from the snow center but had not analyzed it yet before the workshop, so I threw out the May 1 map as a starting point. I was initially hesitant to even present the map at the workshop because I had not finished the analysis, but I thought it would provide some background for opening a discussion. We never did have much of a discussion (I think I still have the audio tapes of the meeting). However, Kevin McKelvey came up to me after my presentation and asked for the source of the snow data in the map I had presented. I gave that to him and that was the last time that I discussed snow cover and a specific date as far as I can recall. I would not have suggested May 15 in any event because I had already determined for myself that sometime in April would likely provide a better fit if I wanted to examine snow cover and wolverine distribution.

2. In a face-to-face discussion with you at a meeting (perhaps at the Elk Ranch near Ennis, I don't recall exactly), I asked you why you had chosen May 15 for the bioclimate paper. This I believe was after you withdrew the manuscript from the Journal of Biogeography and

resubmitted it to the Canadian Journal of Zoology. At that time you did not say it was because I had suggested that we use that date, rather you said it was because the MODIS snow cover data was problematic because of the ephemeral spring snow that sometimes occurred in May that redeposited snow across wide areas including areas where you knew wolverines didn't occur. You said (again as I recall) that in order to eliminate pixels that were once snow-free, but covered again in ephemeral snow, you had to draw the analysis out to May 15. At that point I suggested that perhaps a better way to eliminate those early snow-free pixels was to start at the beginning of the denning season and progress through the denning season eliminating any snow-free pixels as they occurred. The response from you to this suggestion was that you had already spent an enormous amount of time analyzing the data and preparing the paper for publication, which I took to mean that you did not intend to go back and reanalyze the data. I decided not to pursue the point any further.

I did not keep earlier drafts of the bioclimate paper or my review comments to you on those drafts. Perhaps you still have those and can send them to me if there is anywhere in my comments (or anywhere else) that indicates I suggested May 15.

Jeff, I suspect you probably will not take this well, but I did consider removing my name as an author on the paper while leaving my den data in. I gave it a lot of thought and decided against it because I did not want to alienate the authors (not a good reason, I admit) and I did not want to potentially cause a problem with the editors when they saw that an author had dropped out at that point (again, not a good reason I suppose). Whether you believe it or not, I was being genuine in my review comments when I wrote that I had not considered that the May 15 date specifically would be the basis for modeling future climate effects on wolverine habitat. Had I realized that or been given a chance to review the McKelvey et al. 2011 paper before it was published, I would have certainly suggested that additional dates be considered that might have more biological support.

Please, if you have it, send me any corroborating evidence you might have that I suggested you use May 15 in the bioclimate paper. I will be happy to apologize if I find that you are correct and will try to rectify it to the degree that I can.

Audrey

On Sun, Mar 9, 2014 at 9:46 PM, Jeff Copeland <gulo@wolverinefoundation.org> wrote:

Audrey, your effort to discredit this paper is not about a differing of interpretation. If it was, you and I would be discussing it directly, so don't patronize me. You have initiated a world-wide effort to discredit the paper by spreading misinformation. Why you are so intent on doing this, I have no idea, but I will try one more time: The bioclimatic envelope model attempts to define the wolverine's distribution. It does so at about 95% for summer and 86% for winter. Because neither of these numbers are 100%, a wolverine may actually live outside the area. But, 95% and 86% are pretty good for a one variable model on a world-wide scale. Do you know of another model that does as well? Because you can find a den, or a wolverine, or a population of wolverines that occur outside the model does not discredit the value of the model, by any means. What you need to do is try and separate the model from the biology. Because of the precision of the model we concluded that the wolverine is snow obligate. We didn't conclude that the wolverine is obligated to snow until May 15, although all of the data ever collected and published indicates such, we only concluded that it needs spring snow. YOU interpreted it to mean May 15, not me. When you find a population of wolverines that are denning in a non-snow environment, then we might should consider something different. The fact that Anni Koskela's wolverines occur outside the bioclimatic envelope means the model misses somewhat in that part of the world. If her wolverines are denning in the absence of snow (not the absence of the model) THEN we might want to consider what this means regarding the wolverine's obligate relationship with snow.

Regarding the den data you requested. I would suggest you secure these data in the same manner in which I did. When the researchers provided those data I promised them I would not distribute it any further so I need to honor that. You should not have any difficulty gathering those data for yourself. If you have some specific questions as to how I used those data in the analysis, I would be happy to provide whatever you need in that regard.

A couple of additional items: In you peer review comments you state that you tried to convince me with no success to change to an earlier date, as an excuse for why you are now questioning a paper in which you are a co-author. The truth is the original date we planned to use for the analysis was May 28. At your request we moved it to May 15, which you accepted so what you state in your review is untrue.

Secondly, Dorothy Hall was deeply involved in our analysis. She assigned a technician (acknowledged in the paper) to help us throughout the analysis. Only version 4 data was available at the time. Version 5 was still being developed. You phrased your questions to

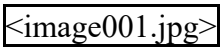
Dorothy in such as way that you led her to criticize our use of V.4. Were she to be reminded of what you were referring to (and hiding from her) I doubt she would be pleased.

Jeff

Jeffrey P. Copeland

Executive Director

The Wolverine Foundation




On Fri, Mar 7, 2014 at 12:31 PM, A J <222wsheridan@gmail.com> wrote:

Thanks, Jeff. Next week would work for the data.

Regarding your reference to slander, I think you should reread my comments. In nearly all cases, I referred only to Copeland et al. 2010 not to you as an individual. The only reference to you as an individual was in a couple of places where I quoted you from your individual response to my inquiries or comments. I'm sorry if you are taking this personally. Scientists offer differ in their interpretation of data and often only more science can resolve the differences.

All the best

Audrey

On Wed, Mar 5, 2014 at 3:04 PM, Jeff Copeland <gulo@wolverinefoundation.org> wrote:

Audrey,

I am at a conference in Boise this week and do not have access to those data from here, but will be back in Driggs next week and can get it to you then. Will that work?

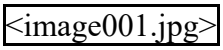
It is clear from all your comments that you, and Bob Inman as well, are having a lot of difficulty understanding the bioclimatic envelope paper, which is unfortunate. The paper is much simpler than you are trying to make it, Audrey. I would be happy to explain any aspect of it that is still troubling you. I would much rather do that than continue to be subjected to the misrepresentation and slander that has characterized this campaign to discredit me and my work. I have never experienced anything so unprofessional.

jeff

Jeffrey P. Copeland

Executive Director

The Wolverine Foundation



On Wed, Mar 5, 2014 at 12:28 PM, A Magoun <222wsheridan@gmail.com> wrote:

Hello Jeff
I like the look of your new website. My reason for writing is to get the den data used in our Copeland et al. 2010 paper. Can you send the data or is it better to contact the Forest Service? I would like to get the metadata if the data file includes year, elevation, lat/long, and which snow layer the dens were in if you have it. I have no specific plans for the data other than to get a more complete idea of the data behind the paper.
Thanks much
Audrey

Sent from my iPhone

This electronic message contains information generated by the USDA solely for the intended recipients. Any unauthorized interception of this message or the use or disclosure of the information it contains may violate the law and subject the violator to civil or criminal penalties. If you believe you have received this message in error, please notify the sender and delete the email immediately.

Kevin

Here are my responses to your email. I will continue to send any pertinent references that I come across that might shed some light on the science and I welcome the same from you.

Ok. Let's go through the science and see where that leads us. I will start with a published statement by you:

"We believe a critical feature of wolverine denning habitat is dependability of deep snow throughout the denning period." (Magoun and Copeland 1998 pg. 1318).

First let me say that Magoun and Copeland (1998) was published over 15 years ago and we hopefully have progressed further in our knowledge of wolverines and their habit by now, so care should be taken in citing older references. That being said, I have made few revisions in my thinking since that paper was published regarding what we can conclude about wolverines and denning without more data on den selection and kit survival. One thing that I have come to realize over the last 15 years is that Vivian Banci was quite correct in saying that the lack of dens found in lowland boreal forest habitat was likely due to failure to look for dens there. That was written in 1994 and is largely still the case; in fact, still the only published record for North America is the Ontario den. This isn't because there are no more dens there but no one has looked anywhere else in lowland boreal forest across Canada. It appears that the Finnish dens outside the reindeer herding area, in what AnniKoskela's thesis refers to as the eastern population, are also in lower elevation boreal forest and according the thesis, the eastern population is about 50% of the entire Finnish population.

Also, note that in my Attachment A of my peer review I addressed the definition of deep snow used in the statement above and also the definition of denning period. In the 1998 paper deep snow referred to snow equal or greater than 1 meter (meaning that snow depth could be problematic if it dropped below a meter at the den site during the denning period). Of course, we were referring to snow at an individual's den site (i.e., from the wolverine's viewpoint not from the viewpoint of MODIS satellite snow extent across the female's home range cross-walked to a hydrologic model of snow depth on May 1 that matched the MODIS snow cover). This "deep snow" could include what I usually refer to as remnant snowdrifts in spring and would not require additional deep snow in the home range by May 15 outside of these remnant snowdrifts.

Denning period referred to a period from initiation of denning to no later than April 30 (up to May), only because abandonment of one of the dens in my study area observed was on or before April 29. Of course, the denning period for each individual wolverine will vary depending on when the young are born and probably other things. We don't have much information on the variability of initiation of denning for any particular female home range (or community of females) in any particular region within the wolverine's distribution because our sample of dens for which we know the initiation and ending dates for denning is quite limited. However, my Attachment A (and other attachments referred to therein) presents the best available science for what this might be in the mountain habitat in the western states.

Over 15 years my thinking has evolved since the "den paper" and I would even consider a snow depth of 70 cm as the minimum snow depth needed during the cold period (temperatures still dropping below freezing most days and no loss of snow accumulation) and April 15 as the end of the period that

wolverines might need snow cover for thermal protection (see discussion in Attachment A and other attachments referred to therein). The question if they still need snow cover for other purposes will depend upon where the wolverine is living. If a denning female lives where there is avalanche debris, large blow downs, and boulder fields, she may no longer need snow cover because she can get that from these other structures that afford protection from predators and wind. On the North Slope tundra area where I worked, some wolverines had no such structural features in their home ranges, and in those cases they used icy caves formed by melt water running under dense, hard-packed remnant snowdrifts in drainage lines during the rapid melt period. These remnant snowdrifts lasted well into summer and were used the whole time they were available (at least into July), but I wouldn't claim that wolverines need snow cover until July even on the tundra. Use of a habitat feature is not evidence that it is an obligatory feature. More information would be needed to determine that. Consider, wolverines use trees to escape predators (White et al. ) and even sometimes to cache food (at least temporarily; personal observation), but we wouldn't accept that as evidence that wolverines need trees.

If this statement is true, then there are a number of consequences.

1) As this is "critical", areas lacking this property should be unsuitable for denning

First one would have to define the term explicitly, for the application they are citing the reference, to be sure their interpretation of that term is the same as in the den paper. Quoting a general term like "dependability of deep snow throughout the denning period" from one paper and then redefining it another way for a new paper and then citing the old paper as a reference is unacceptable in my opinion.

For that matter, the term "critical" should also be defined if it is used in this context and the den paper didn't do that, which is also a failure in that paper, but at that time I was thinking that, if there wasn't at least a meter of snow someplace in a female's home range (or probably in at least several places in case she needs to move the den) during the cold period, then wolverine kits would not survive the cold period, and in addition some tundra areas may require the snow for protection from wind and predators if no other structures are available.

2) If denning is limited to sites having this characteristic, then the range of the breeding population of wolverines can be defined by this property.

Again, what is the specific (explicit) characteristic you are referring to here when you wrote "this characteristic"; is it 1) snow at least a meter deep lasting to the end of April including remnant snowdrifts, or is it 2) MODIS-measured snow cover on May 15 (or >13 cm of snow depth on May 1) with no measure of areas with only remnant snowdrifts? Once you define it explicitly, we can consider whether we can use it to define the range of the breeding population of wolverines.

3) Climate change has reduced the depth (APR 1 SWE) of spring snow by about 40% across those areas of the western U. S. currently occupied by wolverines when compared to the mid 20$^{th}$ century (Mote et al. 2005). Climate change models all show continuing declines in spring snow depth and SWE. Given 1 and 2, this will lead to a reduction in the areal extent of areas having deep persistent snow throughout the denning period.

First of all, 1 and 2 are not a given because you have not specified a) or b). Secondly, 40% of how much, i.e., what initial (present day) accumulated snow depth (based on SWE) are you starting from to determine if snow in wolverine habitat will fall below 1 meter on April 30 (or any other period before this while wolverines are denning)? Thirdly, you are talking about a reduction in areal extent of areas having as yet undefined "deep persistent snow", measured by the MODIS satellite, which does not measure where fractional snow occurs on the landscape or even snow under conifer cover under certain conditions as you mention below. Wolverines experience real snow on the ground in all its many forms, not just what MODIS can measure. While it may seem so obvious that a snow-dependent species like the wolverine must eventually be affected by climate warming in the future (and the future for the purposes of the listing document appears to be until 2100), we don't know the effects of predicted warming on the particular snow that wolverines actually depend upon (the severity may not be anywhere near what some predict it will be ondownstream agriculture, or stream hydrology, or fish habitat). The climate model only predicts where snow depth >13 cm will be on the landscapeon May 1. To project loss of wolverine habitat in 2100, one must stipulate the "extinction risk" to wolverines in habitats where they currently breed, feed, and shelter. I use the term "extinction risk" loosely here but the assumption is that eventually we must be talking about "extinction risk" in the classical sense if the climate keeps warming and warming. But that must be true for all species currently adapted to and only occupying boreal habitats. In the timeframe of the listing document, it is counterintuitive to me,with the current best available science that we have, that simply a predicted 2-week earlier spring melt can cause wolverines living in the mountains to abandon habitats they currently use. No scientific evidence that I could find shows that snow depths over the denning season will be insufficient for denning, especially in the topographically complex landscape of the western mountains where remnant snowdrifts last well into spring (May) and even early summer in many places.

4) Because female wolverines don't really pack into areas (fairly consistent home range size, little overlap), this reduction in areal extent will lead to declines both in range and in local population size.

The climate model only predicts the change in areal extent of putative snow depth >13 cm on May 1. There is no biological mechanism offered for why this would make any difference to a wolverine. In addition, errorsin sampling are problematic, i.e., few areas across the wolverine's distribution were sampled for dens and home rangesto develop the bioclimatic envelope upon which the prediction of habitat loss was based. The failure to consider the presence of wolverines outside the fundamental niche is problematic because it indicates that the niche model is misspecified (Araujo and Peterson 2012) with consequences for predicting the effects of climate change. Home range size is fairly large for wolverines (~225 $km^2$ used in the climate model). Even if the occupying wolverine needs to move a den upslope within a home range in the future to find >1 meter of snow when she starts denning, she need only move about 1 km to go 2000 feet higher on a mountain slope of 30 degrees. This is only 1/18 of her home range diameter. And again, there is no evidence that she would need to do this with the predicted change underlined above and snowdrifts scattered in the topographically complex environment of the western mountains.

Note that the entire case for climate dependency, the precise nature of that dependency, and the inevitable consequences of that dependency are all fully defined by this statement—you don't actually need Copeland et al. (2010) or McKelvey et al. (2011).

But that's the problem. The statement is not defined and neither are the inevitable consequences of an undefined dependency.

So, what did Copeland et al. (2010) add to this? Copeland et al. (2010) explored 3 issues: Was this critical relationship to snow in fact a universal property? Could you map it sufficiently using current satellite data? And were the consequences as expected: dens range limited to areas with evidence of persistent spring snow?

The short answers were: Yes, Yes, and Yes. You sort of went out on a limb in 1998, suggesting a general biological limit based on a very limited dataset and one might have thought that you would be happy that your premise was so strongly supported by Jeff's work. However, you were concerned about the details of the mapping. Below I discuss your concerns as best I understand them and make a case that your concerns are off target: not that the mapping is perfect, but that its imperfections differ from those you have identified.

On the contrary, the short answers are: No, No, and It Depends. No, the critical relationship of wolverines to the May 15 MODIS derived snow model was not defined nor was it a universal property. No, the satellite data used in the model was not sufficient for mapping the areal extent of the fundamental niche, which is important for predicting future wolverine habitat. Finally, the consequences would be as expected if one accepts that the fundamental niche defined in the Copeland et al. 2010 model is not sufficient to capture all known dens and home ranges, but instead misses across the southern portion of boreal Canada (and other areas globally) where 1) at least one den was identified in the first ever attempt to find one there, and 2) home range size, overlap, and configuration of radiocollared wolverines and sex ratio fit the pattern of what we expect from a resident breeding population (research project at Red Lake, Ontario)and 3) the pattern of annual trapping records in the other provinces, from the lower elevation boreal forest outside the fundamental niche, indicate a consistently present resident population rather than occasional dispersers(based on my years of working with trappers in Alaska on harvest numbers and rates and sex ratios and necropsying hundreds of female wolverine carcasses). Rather than discounting wolverine presence outside the fundamental niche, that presence could have been used to validate (or invalidate) the niche model [although I believe the model nevertheless has value as a first attempt at delineating the fundamental abiotic niche for the wolverine because it suggests further areas of research] ORthe presence of wolverines outside the snow model indicates that the model is misspecified, suggesting methodological changes could be used to strengthen the model (which is what I believe Jeff was alluding to in one of his recent emails).

First, you seem to feel that Jeff's use of persistent spring snow cover rather than persistent spring snow depth represents is a big issue. At least in this context, it isn't. During the spring snow melt, persistence for any patch of snow is directly related to its depth (e. g. the deepest drifts persist the longest). To persist, snow has to be deep. Therefore, if you were on the ground during spring melt measuring these two metrics (average snow depth and average areal extent), you would find them to be highly correlated. A much bigger deal is that the measurements were made by satellites and that snow pixels (500x500m) were identified based on binary classification (snow, no snow)—more on that below.

I agree that "persistence for any patch of snow is directly related to its depth", in fact, the science shows that snow depth in May is related to maximum accumulated winter snow (generally accepted as being around April 1) rather than directly related to the climate drivers that determine snow depth in the other winter months. The averages may be correlated but wolverines don't pay attention to averages but to specific snow depths in specific places in spring when snow is melting. If you were on the ground

during spring melt (late April??) (May???), say at a SNOTEL site, you would find that there is a highly variable relationship over the years between snow depth at the site on May 1 and the date that snow disappears at the site on May 15. I checked ~30 years of snow melt data at the Banner Summit SNOTEL site near where one of Jeff's females denned; at this particular site for those 30 years, the May 1 snow depth >13 cm was not a particularly accurate predictor of when snow would be gone at the site on May 15 (i.e., the snow for the two dates was not correlated at this scale).Snow around the site is also variable, so using SNOTEL sites and hydrologic models to get at snow that is important to wolverines in the spring to model wolverine habitat now or in the future is problematic if what wolverines key into is not measured by the MODIS satellite.I'm not sure that even if snow depth had been used for the bioclimatic envelope and measured at the scale of the VIC hydrologic model on a global scale that it would have captured what wolverines are looking for in the snowmelt period. Nevertheless, use of either metric is not problematic if the goal is to model the fundamental abiotic niche of the wolverine but is problematic when using the bioclimatic envelope to project future wolverine habitat.

Secondly, you were very upset by the choice of May 15 as the final day in the denning period. Based on the literature, this is not an unreasonable date to end the denning period (See Inman et al. 2012) and I could make a perfectly valid case that in the sort of correlational work represented by Copeland et al. (2010) the exact start and stop dates will always be arbitrary and are largely irrelevant. I'm not going to do this, because I think that the data in Copeland et al. are actually telling us something meaningful about the nature of the relationship between wolverine den choices and snow. Specifically, I think that the location of den sites in areas much snowier than would be strictly necessary to provide natal den requirements likely indicates broader dependencies on snow covered landscapes that extend beyond the denning period. But to get there, I need to discuss what a snow pixel is more formally.

As you say, and I don't disagree, the end date of the denning period is largely irrelevant, depending on the purpose for assigning an end date. No matter what end date one chooses, wolverine kits of different ages will be hidden away under snowregardless of their age and development if the snow "cavity" (I won't call it a "den" after May 15 if you choose that as the end date for denning) is available. We refer to natal dens, maternal dens, and rendezvous sites based on dens used for birth and approximate date of weaning, if we have an idea of birth date of the kits. Again, this is all rather arbitrary; there is no reason a wolverine would abandon a den because the kits are weaned (which is a gradual process anyway apparently ending sometime in June). So far there is no evidence that the wolverine sees any of these dens differently and chooses one over the other depending on birth date, weaning date, or maturation of kits. The old den paper suggested that natal dens might be more secure, but if a wolverine uses an avalanche debris field as a place to birth her kits and moves them to another avalanche debris field as a maternal den or rendezvous site later, what is the difference to her? Why did she pick one over the other? In the higher elevations in "areas much snowier than would be strictly necessary to provide natal den requirements", all such sites have adequate snow so the snow is not helping to differentiate between one den choice or another, and she doesn't know if it will have snow cover in the spring (I may be underestimating her ability to remember and choose based on whether she remembers snow is there in spring). She probably chooses based on her familiarity with all the possible den sites in her home range and the relative security she feels at these sites because of the structures there that have sheltered her previously, and possibly sites that are closer to caching areas where she has stored up food, or possibly areas where she has run into the least number of predators, or possibly all of the above. Now if avalanche debris and boulder piles are most numerous and well distributed at the higher elevations, which is what I would expect in mountainous habitat, then the correlation of the location of dens sites may be just that, a correlation, but the cause may be avalanche debris and boulders (maybe or maybe something else). The interesting thing is that wolverines in the eastern boreal forest don't

have high elevations or very deep snow, but they do have boulder piles scattered all over the forest (see Attachment J in my peer review) and surprisingly the boulder den in Ontario looked almost exactly like one found by Keith Aubry in the Cascades in Washington. Ontario also has enormous amounts of blowdown in the wolverine habitat I surveyed there at the southern edge of their distribution. The areal extent of some of these individual blowdown events are incredible, caused by microbursts that are like small tornadoes that level whole sections of the forest in a long narrow swathe. My first thought when I saw them was "Wow, I bet wolverines like those!" My point here is that the correlation of dens to high elevations (largely in the "5 and 6 out of 7" layers) in the mountains of the west may not be due to differences in snow between elevations at all, otherwise how do we explain the majority of wolverines in Ontario (Attachment U), Saskatchewan (Attachment S), and Manitoba (Attachment T) that occur in Layers 1-3, and even outside these layers in areas designated by the snow model as "not wolverine habitat,"i.e., not within the proposed fundamental abiotic niche of the wolverine. In Manitoba, wolverines occur all through the boreal forest outside the snow model and lactating females were found there (Attachment R). Wolverines in the Scandinavian mountains may select for habitat with "persistent spring snow" (MODIS snow) 5-6 years out of 7 and in the Rocky Mountains too, but not so over much of Canada, not just the southern edge.

In Copeland et al. (2010) we evaluated daily data which had been classified on a per-pixel basis as snow or not snow. This classification was based on the spectral signature of the pixel, exposed to a model that reported the likelihood that the pixel was snow or not—pixels were classified based on whichever likelihood was greatest. We insisted that, for a period of 21 days, that a pixel classified as snow every day is was visible: a single "not-snow" classification any time within this 21 day period would remove that pixel from being considered snow covered in that year. Thinking about this process, the only way that it was likely that a pixel would be typed as being snow covered this consistently was if the spectral signature was very "white". As a pixel dropped to ~50% snow covered, the chances of being typed as a snow pixel consistently across 21 trials becomes insignificant; pixels with scattered snow drifts never classify as snow pixels. So even pixels that only classified as being snow covered 1 year out of 7 were actually pretty snowy places. The idea that because a pixel was not classified as a snow pixel meant that it contained no snow is simply wrong. You can't make that case using these data.

EXACTLY!! I never said, nor has anyone else that I know of, said that a pixel not classified as a snow pixel meant that it contained no snow. Just the opposite may be true, in fact. Many pixels that were not classified as snow cover indeed have snow and, if your ~50% is correct, there are even more than I thought. I have been thinking of these types of pixels as "fractional snow pixels." Some may appear fractional because of conifer cover or because snow really is fragmented across the pixel. I believe that these pixels account for a considerable amount of wolverine habitat that lies outside the abiotic fundamental niche in the bioclimatic envelope paper. Furthermore, I think there are ways to include at least some of these in the fundamental niche to improve on its accuracy (e.g., see Deems et al. 2008, Arsenault et al. 2012), providing fractional snow is an important feature of wolverine habitat and continued use of wolverine habitat relies on at least some amount of fractional snow being present after April 1. In fact, there is probably a way to manipulate the current bioclimatic envelope to include the area of sparsely distributed snow pixelsbelow Layer 1 that are currently considered outside the envelope. This is where all the anomalous (outside the envelope) dens and wolverine home ranges are in the current snow map in Copeland et al. 2010 including Ontario, Finland, Sweden, and probably others that we don't know about. If one had drawn the edges of the envelope to include what appears as small dots of snow("MODIS fractional snow") in the envelope paper (the areas with the little dots of snow could be in part frozen lakes or gaps in the canopy), it would more likely have captured the entire abiotic fundamental niche of the wolverine. The fact that wolverines do not use all of the area within

the fundamental niche defined this way is OK because fundamental niches, especially those based on a single abiotic factor, will almost always include areas where the species does not occur because the realized niche is only a subset of the fundamental niche (the opposite is never true). A realized niche can be further defined by bringing in additional abiotic and biotic factors.

This discussion relates to a third identified concern: that because a few den sites fell outside of the persistent spring snow layer as evaluated using the above method, the method is somehow fundamentally flawed. There are 2 explanations for these dens: one is that these few den sites indicate greater plasticity –that is in some areas dependable deep snow throughout the denning period is not critical in some places. A second explanation is that the satellite doesn't correctly map snow under certain circumstances. There are a number of reasons to believe that the latter rather than the former is the cause. First, we contacted the scientists that located all of these dens and confirmed that all were snow dens—this supported the idea that these dens didn't represent exceptions to the assumed snow dependency. Secondly, all of these den sites occurred in flat boreal tiaga composed of heavy canopied species such as spruce: it is well documented that the snow classification algorithms don't work well when all of the snow occurs under heavy canopies. This is especially true when you demand, as we did, on consistent classification as snow pixels across a 21 day period. Probably the best understanding therefore is that the satellite imagery-based underestimates the extent of spring snow in the tiaga and in other areas where conifer canopies are heavy and have few gaps. However, the overall success of Jeff's mapping suggests that this phenomena was localized. Importantly, it does not appear to be a problem in the western U. S.

See above regarding tree canopies but also see Ford et al.2013. It doesn't appear localized to me if your explanation of tree canopy explains some of the "MODIS fractional snow" discussed above. In the Western States it indeed may not be as much of a problem but for a different reason than you are implying. There is very little "outside-the-envelope" MODIS fractional snow (as distinguished from on-the-ground real fractional snow) in the western mountains compared to the boreal forest across Canada, but that doesn't mean that "outside-the-envelope" fractional snow (whether MODIS or real) is not important in Canada (lots of wolverines must live there based on actual harvest records and other evidence such as the den and home ranges in Ontario and the Shevenell report from which we obtained the Alberta map in Attachment R) and it may be important in the future in the western mountains for maintaining wolverine habitat at the lower elevations where they now occur. Elevation gradients are comparatively tight in the mountains. A wolverine would often not have to go far to cross from one snow layer to the next, or from MODIS fractional snow to a snow layer, unlike in Canada where many wolverines must live within a single layer because of how broad the snow layers are in Canada compared to the western mountains.

And this leads to a final understanding from Jeff's work. Because of the extremely conservative nature of the snow/no snow calls, areas that were identified as being snow pixels 7 out of 7 years had to be classified as snow up to 147 times with no failures—6 of 7 perhaps only a single failure. To do this, these pixels really needed to not just contain snow, but to be snow covered (nearly pure white) through a period extending to mid-May. A very consistent majority of den sites (67% in Sweden, 68% in Norway, and 71% in North America) occur in pixels that were classified as being snow covered at least 6 out of the 7 years. I would agree with you that this far exceeds the thermal requirements for denning. In many cases it exceeds the needs for successful natal dens. It suggests, in fact, that wolverines are choosing to den in sites that, when families emerge from the natal den, are still covered with deep and fairly contiguous snow and in areas where this condition persists into the spring. It therefore suggests additional snow associations other than those formally associated with the needs for successful natal

dens. Two that have been posited (though with little data support) are predator avoidance and refrigerated food caching (Inman et al. 2012).

See again my response above discussing correlative approaches. In my opinion the posited needs of predator avoidance and refrigerated food caching are much more likely than snow cover on May 15 (or >13 cm on May 1) because the latter is not supported by any biological explanation of why it should matter to a wolverine.

There is no evidence that wolverines den in warmer locations that might have snow drifts through April but which have lost their snow cover by mid-May. Quite the contrary. In the western U. S., where the population has been steadily expanding, one might think that, even if a bit sub-optimal, sub adult females seeking to establish home ranges would set up shop in adjacent lower elevation areas rather than take the long hike to adjacent mountain ranges. There's a lot of this sort of habitat available. The fact that there is no evidence that this ever happens is really rather remarkable.

Actually there is some evidence that wolverines den in "warmer locations that might have snow drifts through April but which have lost their snow cover by mid-May [do you mean MODIS snow cover or real snow cover at the den??, again, be explicit]." Jens Persson has a photograph taken with a motion-detection camera of young wolverines with their mother at a den on April 24 where there is no longer snow at the den site, which appears to be a cavity under a large rock or boulder, and there may be even more evidence in the future as wolverines seem to be expanding their ranges in other areas of their distribution.

By the way, I don't think female wolverines have a problem taking a long hike up the mountain since that is where they live in the western states and there's lots of elevation change in their home ranges to help them stay in shape. Besides, as I mentioned, I calculated how far one would have to go to cover 2000 feet of elevation change where the slope is 30 degrees, the most common slope degree in the Sawtooths in Idaho (Swanson 2012), which was about a kilometer, barely enough to work up a sweat for a wolverine.

Bottom line: Copeland et al. (2010) provided strong evidence to support your assumption that snow dependency was universal. Further, it implies that this dependency is stronger and extends further in their life history than what you initially thought. Given this, the understanding that you published in 1998 is THE critical for defining the macro-scale ecology of wolverines, and sets hard limits on where they can live and where they can't. It also fully defines a specific and unavoidable impact of warming climates on wolverines. Dens exterior to the snow coverage were few, were in very specific topographic locations and forest types, and likely reflect the well-documented inability of satellites to see through conifer canopies.

See all comments above; I don't dispute that snow dependency is universal. But again, what snow are we talking about, what kind, how deep, when, how is it distributed, what is it used for, etc.? And most importantly why.

Now we come to McKelvey et al. (2011). Concerning your statement that it is "invalid", I can't really comment as the stream of emails almost exclusively discusses the findings of Copeland et al. (2010); I have no idea what this putative lack of validity stems from. However, I believe that the validity of tracking patterns of persistent spring snow is well established—both by your 1998 paper and by

Copeland et al. (2010). I also believe that that we did a good and careful job both of modeling snow, and matching those data to Jeff's MODIS data. I insisted that we go the extra mile to be transparent and to back-check our modeling as much as possible. Comparing modeled data to MODIS data later in the spring and including a specific section that explicitly stated assumptions and caveats are examples of the care we took. K.

Again, "persistent spring snow" is not defined the same in those two papers and therefore, tracking the patterns will not be the same. Unfortunately, the MODIS satellite technology is not as equally transparent as you were, i.e., the technology cannot see through trees sometimes, it cannot detect real fractional snow very well, it does not directly measure what is important to wolverines on the landscape, it is not at fine enough scale requiring downscaling, etc. To "define wolverine habitat" the envelope model had to use MODIS satellite data at a global scale, place the geographically limited sample of dens and home ranges on the resulting 7-year layered map, lump the layers together to define where wolverine habitat is, and then hand the "lumped" habitat map to the climate model to downscale to the western mountains, and then project into the future where wolverine habitat will be based on a limited number of climate ensembles. It would have been interesting to see the habitat map broken into two parts at least, the selected 5,6, and 7 layers( plus the 4 layer) and the non-selected 1,2, and 3 layers and downscale separately to see where the snow depth fit best for each of the two groups. Climate warming will almost certainly affect the lower elevations (lower layers) differently than theupper elevations and we really have no idea if the landscape as viewed by a wolverine will have all the snow, fractional or otherwise, in the foreseeable future (and the other abiotic and biotic factors) that it needs to keep using its current habitat in the western states.

I will gather together the references cited above and others that support statements above and send them to you.

I leave you with this quote from ARAU´JO and PETERSON"S 2012 paper "Uses and Misuses of Bioclimatic Envelope Modeling" in Ecology:

*……let us consider a few applications of bioclimatic envelopes that can be considered useful or not. For example, if models are used to estimate the potential distribution of an endangered species, perhaps in the context of a translocation experiment to save the species from climate warming, modeled climatic envelopes may be used to characterize areas to which the species can be reintroduced. In a counterexample, however, if the challenge is to estimate extinction risk for species over coming decades in the face of changing climates (e.g., Thomas et al. 2004), the models only estimate the empirical relationships between species' present-day distribution and climate variables, and use the inferred relationships to identify potential distributional areas of the species under future climate scenarios. Here, the quantity of interest (extinction risk), however, is not represented among the input data and thus is not the*

*target of the modeling exercise (Ladle et al. 2004); the usefulness of this model is thus open to debate, because only partial evidence exists that shifting climate suitabilities within the modeled time frame could speak to the reasons for which the species might go extinct (e.g., Thuiller et al. 2004a, Akcakaya et al. 2006, Botkin et al. 2007, Hampe and Jump 2011). This pair of examples illustrates how inappropriate application of bioclimatic envelopes can cause problems with interpretation and conclusions, emphasizing the importance of proper framing of their use in appropriate biological questions.*

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http://scholar.google.com/citations?user=CmG2R0QAAAAJ&hl=en

**From:** A Magoun [/src/compose.php?send_to=222wsheridan@gmail.com]
**Sent:** Friday, March 14, 2014 2:49 PM
**To:** Jeff Copeland
**Cc:**McKelvey, Kevin -FS; Shawn Sartorius
**Subject:** Re: Den data

Jeff

Where my questions were heading was towards a better understanding of your viewpoint and an examination of whether there is any convincing evidence that my position, that the McKelvey et al. 2011 model predicting loss of wolverine habitat under climate change is not based on the best available science, is invalid. I have been reading many climate papers and bioclimatic envelope papers and communicating with other wolverine biologists since your review of my peer review of the wolverine listing proposal and so far I haven't found anything that has convinced me to change my position, in fact on the whole just the opposite. After our extended discussion over the last few days, it appears that we have come full circle and are right back to disagreeing about our interpretations of the best available science.

To address the specific question of my problem with the May 15 date, I refer you to my comment submitted to the FWS in the second comment period, which is on the FWS peer review page. I don't have it with me as I am traveling. I assumed you had already read it but perhaps not, however, based on our recent discussions, I don't expect that it will convince you to alter your position.

I prefer to end this discussion here as I've already spent a great deal of time thinking about and reading the "science" and discussing the various aspects as I'm sure you have. If I find that I have changed my position before the review panel meets, I will let you and Shawn Sartorius know. Likewise, if after the panel meets I change my mind, I will also let you know. I will also copy you on any further comments I submit to the FWS before the end of this comment period on May 6.

All the best

Audrey

Sent from my iPhone

On Mar 13, 2014, at 10:43 PM, Jeff Copeland <jcopeland224@gmail.com> wrote:

1) It is a bit difficult to answer that question because it assumes, or I believe the question assumes, that our snow model possibly represents 1 meter of snow on the 15th of May, which is probably does not across the extent of the model. But all things equal, a model that represented

the extent of 1 meter snow in April would be larger in extent than a model for May 15. Using April rather than May snow would have probably produced a different model in terms of where snow remained but I suspect that the change in snow loss over time would be very similar.

An important consideration here, Audrey, and much of the reason we engaged in this process is that wolverine weaning occurs at the same time as spring snow melt. If you recall from the snotel charts the buildup of snow is a gradual process when compared with spring snow melt, which generally happens across a very short period of time, and coincides with wolverine weaning. We (or I) did assume that the den is important throughout the denning period. As global warming pushes spring runoff back 2 or 3 weeks it is pushing snowline up the mountain and degrading the den earlier. This was an important premise in the development of the model. If you believe that den integrity is not important during the latter stages of denning then you might assume that an earlier spring thaw will have less of an impact on denning success. The problem with that assumption is that what we know about wolverine denning does not support that. They den in places that provide long lasting snow, not in places that melt out early. There is really no difference between April, March, or February snow for that matter. It is basically everywhere and adequately deep. It is in late April and early May that she needs the deep snow to persist, and I say this not because I am simply speculating. I say it because that is where the dens are.

2) In thinking about it now, Audrey, I believe the first date we used was May 21 not May 28. I came up with May 28 because I was thinking 28 days. The first models were 28 days which went from April 24 to May 21. Anyway, as I recall the extent of the model only changed by about 3% but it shifted the dens a bit. In N.A. there were dens in 1-year and 2-year snow with the 28 day model. When we changed to 21 days there were no dens in 1-2 year snow.

3) The climate model was queried based on snow depth values it provided until we found a minimum depth that spatially matched the snow model fairly well. The snow depth parameter that provided the best match was >13 cm snow depth. Once that was determined our snow model was left behind. But in the sense that the climate model was "trained" on the snow model, I guess one could say that the future climate models would approximate May 15 snow.

4) The snow model depicts the wolverine's fundamental niche. I am thinking about "habitat" relationships more in terms of "life zones" than what we might think of as habitat. Guess it is a matter of terminology. I believe that wolverine "habitat" in the Brooks Range is not much different than wolverine "habitat" in Glacier National Park, from a wolverine's perspective. As such, I believe the wolverine is a very habitat specific animal. That habitat, or niche, or life zone

occurs pretty much everywhere at northern latitudes while as southern latitudes it resides in a very narrow elevational band.

You still haven't answered my question in regard to your issue with May 15. Your questions all seem to be leading somewhere. It would be most helpful if I understood where this is headed.

jeff

On Thu, Mar 13, 2014 at 9:40 PM, A Magoun<222wsheridan@gmail.com> wrote:

Jeff

I have some questions to help me understand this:

1) if, rather than MODIS May 15 snow cover, you could have measured snow depth (for discussion sake, let's say snow depth of 1 meter or more on April 1), had that data been widely available on the scale you needed it, do you think the resulting snow map coverage would have been larger, smaller, or just the same as the one produced by the May 15 analysis? Do you think the climate model, had it used this snow metric instead of May 15 snow cover to train the model, that the predicted future extent of wolverine habitat would have looked the same?

2) if you had used May 28 instead of May 15, do you think the concordance of expert-derived wolverine distribution and the resulting snow map would have been better (e.g., 100% of dens and all known breeding populations in 5-6 out of 7 years)?

3) by saying that "the May 15 date had no bearing on the future predictions", do you mean the various maps of predicted wolverine habitat in the McKelvey et al. 2011 paper do not show where MODIS May 15 snow cover (or snow depth >13 cm on May 1) can be expected to occur in the respective time periods?

4) I understand how the bioclimatic envelope depicts current distribution (give or take a little) but I don't see why you are saying it depicts habitat relationships since in our other email below

you seem to agree that the model is about WHERE wolverine habitat currently is not WHAT wolverine habitat is (I.e., "the model is less about snow than it is about where wolverine habitat is"). What habitat relationships does the bioclimatic model depict?

Thanks

Audrey

Sent from my iPhone

On Mar 13, 2014, at 7:19 PM, Jeff Copeland <jcopeland224@gmail.com> wrote:

I have no objections whatsoever to you including Kevin in this discussion.

The May 15 date had no bearing on the future predictions. It was only used to train the climate model to match our model of wolverine distribution. The future predictions were created with the climate models only using our model as a beginning point. The predictions then suggest that if the bioclimatic envelope accurately depicts current wolverine distribution and habitat relationships - or the animal's niche, then that niche will decrease in extent. We were actually fairly pleased with the predictions in that most of the large, contiguous blocks of wolverine habitat remain pretty much intact throughout the century. It is really not the gloom and doom scenario that some might suggest.

In regards to your statement, ***Until someone shows me the link between May 15 snow cover and a change in winter snow pack so severe that wolverines cannot find a secure den (assuming that denning habitat is the key), then I think a climate model based on MODIS May 15*** ***snow cover that predicts loss of wolverine habitat has little scientific merit without an explanation of why,*** you are getting way out in front of what this represents, Audrey. The snow model is very congruent with our best understanding of the wolverine's current and historical distribution so we are calling it a model of the wawolverine's distribution. The climate analysis then simply projects that distribution of snow (wolverine habitat) into the future. However precisely it represents actual wolverine habitat the futuring of the model is simply a change-estimation exercise. There is this much now, there will be this much later. We made no attempt to speculate what that meant other than increased resistance to movement.

Further, how much do we really know about what a female wolverine prefers, or needs for denning habitat. No one has ever documented a wolverine population - or a single wolverine, for that matter - that chose a den site away from snow. Our N.A. wolverines, as you can see in the chart I sent you, didn't den on the periphery of the model, they prefered to be in the 5-6 year snow - way higher and deeper than was necessary if they didn't want deep snow to the end of denning, or about May 15. Please explain what it is that bothers you so much about May 15? We would have produced an even more precise model - a better fit to known wolverine distribution in N.A. had we used May 28. May 15 captured 99% of dens and about 90% of year-around habitat use. Seems to me that that is a pretty good indication that this is not a bad date. Could you be more explicit as to what your concerns are regarding that date.

Jeff

On Thu, Mar 13, 2014 at 6:05 PM, A Magoun<222wsheridan@gmail.com> wrote:

Jeff

Thanks for taking the time to write this lengthy response. There's some interesting points to ponder here. I will take some time later to respond after I think about them more thoroughly, but for now let me just point out that my apology below was for my specific statement in my FWS peer review that the bioclimate envelope paper stated that MODIS snow cover on May 15 was obligatory for wolverines. I now understand that our paper did not make that claim. I also realize that the bioclimate envelope paper, when taken simply as such, is a scientifically acceptable way to look at snow as an integral part of the wolverine's niche (I.e., a way to map current wolverine distribution using a snow metric that can be applied at a worldwide scale). My problem with the May 15 date is that it was used in McKelvey et al. 2011 to predict wolverine habitat into the future. This paper relied on our bioclimatic envelope paper for the May 15 date, despite the fact that the authors stated that they did not know why that date worked so well in showing a concordance of wolverine distribution and May 15 snow cover. I believe that, because the authors did not demonstrate a specific link between the wolverine's need for snow and the May 15 date, there is no way to know if May 15 is the appropriate date to model future habitat (using either the MODIS data or the May 29 forward projection of snow cover). The May 15 date was useful in modeling worldwide wolverine distribution now (or more specifically in 2000-2006), but may not be useful in the future. If the earlier spring melting that is projected to occur in the future with climate change (i.e., the McKelvey et al. climate model) cannot be linked to a decline in snow pack earlier in the winter (or some other critical underlying variable) that is severe enough to cause wolverines to abandon habitats used today, then the use of May 15 is not valid for projecting changes in occupied habitat with climate warming. Until someone shows me the link between May 15 snow cover and a change in winter snow pack so severe that wolverines cannot find a secure den (assuming that denning habitat is the key), then I think a climate model based on MODIS May 15 snow cover that predicts loss of wolverine habitat has little scientific

merit without an explanation of why. What the McKelvey et al. 2011 model says to me is that we need to find out what aspects of snow wolverines are dependent upon for habitat and viable populations. In that respect the paper is useful because it is a heads up that, unless we understand wolverine habitat requirements more specifically, we cannot know their conservation needs or plan appropriately. I hope you do not mind me sending this on to Kevin as we are now discussing a paper on which he is the first author. In fact, it would be good to send this exchange to all the other authors in case they share your concerns about a new review panel. Let me know if you have any objections to that.
Audrey

Sent from my iPhone

On Mar 13, 2014, at 11:01 AM, Jeff Copeland <jcopeland224@gmail.com> wrote:

Yes ! In fact, we have been a bit disappointed that the model has come to be known as the "snow" model because it is less about snow than it is about where wolverine habitat is, as you state. When we began developing it we were focused on snow and denning. Our goal was to see how well spring snow correlated with dens - nothing beyond that. It wasn't until later and we began looking at the spatial relationship between the model and year-around presence that we realized this might represent a fundamental niche more so than simply denning habitat.

I do need to clarify a bit regarding your comments about May 15. May 15 date was not a random choice, either in this paper or the earlier Aubry et al. paper. We were thinking denning and I wanted to be sure we defined the distribution of snow at least to the end of the denning period. I was assuming (and still see no reason not to believe) that snow was important to the end of denning, and May 15 seemed to be a good date to capture the entirety of the denning period while allowing for enough spring snow melt to move the persistent spring snow line up the mountain a ways. So in that sense the date is based on wolverine biology. We knew that that date, in terms of denning cessation, would vary around the world, which is why we don't focus on that date as some defined, or obligate, denning break-point for the wolverine.

I think you might be looking at this a bit backwards, Audrey. If we felt that deep snow was important to denning wolverines only to, say, mid April, then the best way to model the distribution of deep April snow, using MODIS data, would be to run the model out to maybe mid-June or July. By doing so you would allow more pixels to show bare ground, which would eliminate them, and you would move the persistent snowpack much farther up the mountain. In this context the date leaves the biology realm and becomes important only in the modeling process. In our case May 15 not only worked well for the modeling but it also has a biological tie to the animal as representing the end of denning. This is a bit fortunate but it is as much coincidence as anything. Remember, our model is not simply showing where snow is on May

15, it is meant to be a representation of where deep, persistent show occurs at that time. As was the case in your Ontario study area, as well as in Scandinavia, there were places where wolverines were denning that were outside the model. What was important is that we know they were not outside of snow. Their lack of concordance with the model was only a reflection of the model's limitations rather than wolverine choice. As I have said, we conclude from this that the wolverine is a snow-obligate rather than a model-obligate animal.

I tried to find some the the analyses from when I first modeled the data out to May 28, but haven't been able to just yet, but as I recall there were a few North American dens that occurred in 1-year data. When we moved the date back to May 15 it extended the distribution of snow enough that there we no dens in 1 or 2-year data so it might have been even better to have used the May 28 date in terms of how it fit the data (I have included a chart of the N.A. data that was not in the paper), but because this was not a fitting exercise we left it at May 15, largely due to your concerns. I guess what this suggests is that it is more about deep snow than it is about dates. We did not include this graphic in the paper as we felt the distribution of N.A. dens was not representative across the continent - at least not to the degree that it was for Scandinavia.

With that said, I do, very much, appreciate your apology but what concerns me is that this "misunderstanding" has been perpetuated way beyond a simple exercise in interpretation among scientists. The FWS is convening a science panel next month to discuss the merits of the science used in the listing decision based solely on the concerns you and Bob Inman have raised, most of which revolve around this May 15th thing. MWFP and IDFG have focused their objections to listing on the fact that two of the peer reviewers have vehemently argued that the science used in the analysis is flawed, and in some cases that the scientists that created it are biased. Your recognition that you misunderstood this is certainly gratifying to me personally, but I have to wonder what can be done to correct this image of flawed science and biased scientists that this has created and perpetuated on a much larger scale?

I would like it very much if you could clarify something for me. Have you focused on this because you disagree with the need to list the wolverine, or is this simply about concerns you have had regarding the bioclimatic envelope paper?

Jeff

<image.png>

On Wed, Mar 12, 2014 at 3:31 PM, A J <222wsheridan@gmail.com> wrote:

Jeff

I agree there is no reason we should not be able to resolve this and hope this response does so. I have read over your attached emails a number of times, and some others as well, to be sure I understand the Copeland et al. 2010 paper, the spring snow cover model, and the correct interpretation of it. I think one of your statements in your March 9 email below helped me in particular to better understand the model: i.e., what I "need to do to is try and separate the model from the biology." I thought about this and it did help me to come to a better understanding of the model I think. I will lay out my understanding here and you can let me know if I have it right.

The MODIS May 15 snow cover for 2000-2007 produced a model that defined *where* wolverine habitat is not *what* wolverine habitat is. You selected May 15 to model persistent spring snow. You did not select May 15 because it was necessarily linked to wolverine biology, but because it was one of a number of metrics related to snow cover (snow depth) that one might use to compare to wolverine distribution. The MODIS May 15 snow cover was the metric that worked best for mapping worldwide spring snow cover with some refinements to eliminate ephemeral spring snow, clouds, etc . The reason you wanted to map snow cover is that wolverines are a snow-dependent species and in fact a snow-obligate denner. You are not claiming that wolverines need snow cover for denning up to May 15 and such a conclusion would be a misinterpretation of the snow model and the paper. The MODIS May 15 snow cover is simply a way to model worldwide persistent spring snow cover and the snow cover layer in Copeland et al. 2010 should simply be considered a map of persistent spring snow cover for the period you measured it. You overlaid all known wolverine dens on the May 15 snow cover map and found that the resulting bioclimatic envelope model defines the wolverine's distribution at 86% in winter (the summer portion of the bioclimatic envelope model is 95%). This level of concordance between May 15 snow cover and dens sites need not be 100% to use the model to show where wolverine habitat is on a worldwide scale. You are not claiming the wolverines need snow on May 15 for denning and those who see the bioclimatic envelope model this way are misinterpreting the model. For instance, the following statement in my peer review to FWS is incorrect: *"Copeland et al. (2010) assumed that a suitable surrogate for where wolverine habitat occurs on a global scale is obligate snow cover on 15 May as determined by MODIS snow cover data."* Indeed, after a careful reading of Copeland et al. 2010, I could not find a statement where you specifically said that MODIS May 15 snow cover is obligatory for wolverine habitat. For that, I do apologize and hope you understand how I and the FWS and others misunderstood this concept. Please let me know if I have made any errors in this paragraph that you wish to clarify.

---------- Forwarded message ----------
From: **Jeff Copeland**<gulo@wolverinefoundation.org>
Date: Mon, Mar 10, 2014 at 7:35 PM
Subject: Re: Den data
To: A J <222wsheridan@gmail.com>

Audrey,

I will begin by saying that I am pleased that you are willing to communicate on this. I don't see any reason you and I cannot resolve this.

I did not say that you agreed specifically to the May 15 date. I stated that you expressed concern regarding the May 28 date so I moved it to May 15. I can't recall how you responded to May 15 but assume there would have been additional dialog if you had expressed a problem. You make it sound in your review like I ignored your concern. I cannot imagine I would have done so.

I don't recall the conversation you claim we had about the May 15 date and your idea about redoing the analysis. The pixel examination that resulted in either keeping or eliminating pixels occurred on each image for each of the 21 days. Had we made the end date earlier we would have produced a map with a much larger snow coverage. An important characteristic of the model is that it does miss in a few areas. Had it resulted in 100% coverage of dens and year-around use I would have worried that it over-estimates the wolverine's niche. Had it missed to a greater extent I would have worried that it was too conservative. Because it misses by only a few percent, it suggests that it is probably about as good a representation as one could expect. You are too focused on the model missing in places such as Alberta and Finland. The conclusion reached by what the model provides is that the wolverine is a snow-obligate denner. If you want to question the conclusions of the paper you should be looking for wolverine's that den in non-snow conditions. The model only represents our best guess at the wolverine's world-wide distribution. Also, please remember that the model was a hypothesis, which was then tested with den and telemetry data. This was not a fitting exercise such as what Bob Inman did to develop his habitat model.

And, as far as the May 15 date not having biological support, it really doesn't need to for the model development. We were trying to develop a model that reflected snow depth using data that did not provide snow depth. We could have used any date whatsoever - April 1 or August 1 - to develop the model - whatever it took to produce a persistent spring snow layer. I just wanted to make certain we were including snow that occurred at least to May 15. You are going to have to tell me what is wrong with that date because I think it is biologically sound. Every den I have ever found was actively being used late into the first week of May. There is every reason to believe the dens would have remained in use to some time close to May 15. I'm sorry but I still do not understand your obsession with this date. Had I used an earlier date, as you suggest, the model would have extended way into areas that we know are not wolverine habitat. Why do you feel that would be preferred?

Jeff

On Mon, Mar 10, 2014 at 12:34 PM, A J <222wsheridan@gmail.com> wrote:

Jeff

I am traveling right now and cannot address many of the points in your email without looking at my files at home on my computer. However, I would like to clear up one point. In your email you stated:

"In you peer review comments you state that you tried to convince me with no success to change to an earlier date, as an excuse for why you are now questioning a paper in which you are a co-author. The truth is the original date we planned to use for the analysis was May 28. At your request we moved it to May 15, which you accepted so what you state in your review is untrue."

I find it very difficult to believe that I would have requested that we move the date to May 15 and that I accepted that date. So if you have some written confirmation of this, please send it to me. I realize that memory is often unreliable and miscommunication occurs all the time but I have a couple of reasons for feeling confident that I did not suggest we use May 15:

1) As you may recall, I presented a map of spring snow cover in North America at the Wolverine Workshop in Monterey CA many years ago. I presented the map as a talking point to discuss wolverine habitat. The date that I used for that map was May 1. What I didn't mention at the time was that I had been working with the snow data off and on for a couple of years before the workshop. By the time the workshop came around, I had already decided that May was not a good match (to me that means 100% of breeding populations) for wolverine distribution and had decided to start looking at April. I had ordered the data from the snow center but had not analyzed it yet before the workshop, so I threw out the May 1 map as a starting point. I was initially hesitant to even present the map at the workshop because I had not finished the analysis, but I thought it would provide some background for opening a discussion. We never did have much of a discussion (I think I still have the audio tapes of the meeting). However, Kevin McKelvey came up to me after my presentation and asked for the source of the snow data in the map I had presented. I gave that to him and that was the last time that I discussed snow cover and a specific date as far as I can recall. I would not have suggested May 15 in any event because I had already determined for myself that sometime in April would likely provide a better fit if I wanted to examine snow cover and wolverine distribution.

2. In a face-to-face discussion with you at a meeting (perhaps at the Elk Ranch near Ennis, I don't recall exactly), I asked you why you had chosen May 15 for the bioclimate paper. This I believe was after you withdrew the manuscript from the Journal of Biogeography and resubmitted it to the Canadian Journal of Zoology. At that time you did not say it was because I had suggested that we use that date, rather you said it was because the MODIS snow cover data

was problematic because of the ephemeral spring snow that sometimes occurred in May that redeposited snow across wide areas including areas where you knew wolverines didn't occur. You said (again as I recall) that in order to eliminate pixels that were once snow-free, but covered again in ephemeral snow, you had to draw the analysis out to May 15. At that point I suggested that perhaps a better way to eliminate those early snow-free pixels was to start at the beginning of the denning season and progress through the denning season eliminating any snow-free pixels as they occurred. The response from you to this suggestion was that you had already spent an enormous amount of time analyzing the data and preparing the paper for publication, which I took to mean that you did not intend to go back and reanalyze the data. I decided not to pursue the point any further.

I did not keep earlier drafts of the bioclimate paper or my review comments to you on those drafts. Perhaps you still have those and can send them to me if there is anywhere in my comments (or anywhere else) that indicates I suggested May 15.

Jeff, I suspect you probably will not take this well, but I did consider removing my name as an author on the paper while leaving my den data in. I gave it a lot of thought and decided against it because I did not want to alienate the authors (not a good reason, I admit) and I did not want to potentially cause a problem with the editors when they saw that an author had dropped out at that point (again, not a good reason I suppose). Whether you believe it or not, I was being genuine in my review comments when I wrote that I had not considered that the May 15 date specifically would be the basis for modeling future climate effects on wolverine habitat. Had I realized that or been given a chance to review the McKelvey et al. 2011 paper before it was published, I would have certainly suggested that additional dates be considered that might have more biological support.

Please, if you have it, send me any corroborating evidence you might have that I suggested you use May 15 in the bioclimate paper. I will be happy to apologize if I find that you are correct and will try to rectify it to the degree that I can.

Audrey

On Sun, Mar 9, 2014 at 9:46 PM, Jeff Copeland <gulo@wolverinefoundation.org> wrote:

Audrey, your effort to discredit this paper is not about a differing of interpretation. If it was, you and I would be discussing it directly, so don't patronize me. You have initiated a world-wide effort to discredit the paper by spreading misinformation. Why you are so intent on doing this, I have no idea, but I will try one more time: The bioclimatic envelope model attempts to define the wolverine's distribution. It does so at about 95% for summer and 86% for winter. Because neither of these numbers are 100%, a wolverine may actually live outside the area. But, 95% and 86% are pretty good for a one variable model on a world-wide scale. Do you know of another model that does as well? Because you can find a den, or a wolverine, or a population of wolverines that occur outside the model does not discredit the value of the model, by any means. What you need to do is try and separate the model from the biology. Because of the precision of the model we concluded that the wolverine is snow obligate. We didn't conclude that the wolverine is obligated to snow until May 15, although all of the data ever collected and published indicates such, we only concluded that it needs spring snow. YOU interpreted it to mean May 15, not me. When you find a population of wolverines that are denning in a non-snow environment, then we might should consider something different. The fact that AnniKoskela's wolverines occur outside the bioclimatic envelope means the model misses somewhat in that part of the world. If her wolverines are denning in the absence of snow (not the absence of the model) THEN we might want to consider what this means regarding the wolverine's obligate relationship with snow.

Regarding the den data you requested. I would suggest you secure these data in the same manner in which I did. When the researchers provided those data I promised them I would not distribute it any further so I need to honor that. You should not have any difficulty gathering those data for yourself. If you have some specific questions as to how I used those data in the analysis, I would be happy to provide whatever you need in that regard.

A couple of additional items: In you peer review comments you state that you tried to convince me with no success to change to an earlier date, as an excuse for why you are now questioning a paper in which you are a co-author. The truth is the original date we planned to use for the analysis was May 28. At your request we moved it to May 15, which you accepted so what you state in your review is untrue.

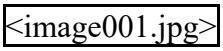
Secondly, Dorothy Hall was deeply involved in our analysis. She assigned a technician (acknowledged in the paper) to help us throughout the analysis. Only version 4 data was available at the time. Version 5 was still being developed. You phrased your questions to Dorothy in such as way that you led her to criticize our use of V.4. Were she to be reminded of what you were referring to (and hiding from her) I doubt she would be pleased.

Jeff

Jeffrey P. Copeland

Executive Director

The Wolverine Foundation



On Fri, Mar 7, 2014 at 12:31 PM, A J <222wsheridan@gmail.com> wrote:

Thanks, Jeff. Next week would work for the data.

Regarding your reference to slander, I think you should reread my comments. In nearly all cases, I referred only to Copeland et al. 2010 not to you as an individual. The only reference to you as an individual was in a couple of places where I quoted you from your individual response to my inquiries or comments. I'm sorry if you are taking this personally. Scientists offer differ in their interpretation of data and often only more science can resolve the differences.

All the best

Audrey

On Wed, Mar 5, 2014 at 3:04 PM, Jeff Copeland <gulo@wolverinefoundation.org> wrote:

Audrey,

I am at a conference in Boise this week and do not have access to those data from here, but will be back in Driggs next week and can get it to you then. Will that work?

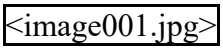
It is clear from all your comments that you, and Bob Inman as well, are having a lot of difficulty understanding the bioclimatic envelope paper, which is unfortunate. The paper is much simpler than you are trying to make it, Audrey. I would be happy to explain any aspect of it that is still troubling you. I would much rather do that than continue to be subjected to the misrepresentation and slander that has characterized this campaign to discredit me and my work. I have never experienced anything so unprofessional.

jeff

Jeffrey P. Copeland

Executive Director

The Wolverine Foundation




On Wed, Mar 5, 2014 at 12:28 PM, A Magoun<222wsheridan@gmail.com> wrote:

Hello Jeff
I like the look of your new website. My reason for writing is to get the den data used in our Copeland et al. 2010 paper. Can you send the data or is it better to contact the Forest Service? I would like to get the metadata if the data file includes year, elevation, lat/long, and which snow layer the dens were in if you have it. I have no specific plans for the data other than to get a more complete idea of the data behind the paper.
Thanks much
Audrey

Sent from my iPhone

This electronic message contains information generated by the USDA solely for the intended recipients. Any unauthorized interception of this message or the use or disclosure of the information it contains may violate the law and subject the violator to civil or criminal penalties. If you believe you have received this message in error, please notify the sender and delete the email immediately.

**From:** A J
**To:** Grizzle, Betty
**Subject:** Re: emails discussions
**Date:** Tuesday, April 18, 2017 3:57:19 PM

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Let me know what you need. You should have the following items:
1) my comments made directly on the status review, of which there were many
2) Appendices A, which cites all the other appendices and summarized my thoughts
3) a follow-up comment in the second round
4) emails between Shawn and I including the ones I just sent between Copeland and Mckelvey and me

On Tue, Apr 18, 2017 at 1:33 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> Thanks Audrey. I found a few things, but not these (yet). I am looking at your peer review comments on previous proposed rule and haven't found your "Attachment B" yet....will keep looking.
>
> I apologize for having you search for and resend your earlier comments; I am trying to be thorough in this new assessment and have many questions about several analyses.
> Betty
>
> On Tue, Apr 18, 2017 at 2:20 PM, A J <222wsheridan@gmail.com> wrote:
>
> > Betty
> > I don't know if you have already seen these from Shawn's files, but these emails contain a discussion I had with Copeland and McKelvey after some reluctance on my part to get into such an exchange post-status review. I was pretty burned out by then on the whole subject. But you may find parts help answer some of the questions you recently sent. The McKelvey Email file is emails between Jeff and I until it became apparent that it was better to talk directly to Kevin and so his responses to me are in blue type in that email. The McKelvey Email Response file holds my answers back to him in black type. As you will see, there is little consensus on the matters under discussion. I had permission from both to share these emails and Shawn received copies. He had encouraged us to discuss these issues (and others) hoping to get some resolution of the differences of opinion, but as I suspected from the start, I don't think anyone changed their minds on anything.

--

Betty J. Grizzle, D.Env.
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U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

**From:** A J
**To:** Grizzle, Betty
**Subject:** Re: emails discussions
**Date:** Tuesday, April 18, 2017 3:57:50 PM

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best to read the emails from bottom to top on the Copeland exchange

On Tue, Apr 18, 2017 at 1:33 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> Thanks Audrey. I found a few things, but not these (yet). I am looking at your peer review comments on previous proposed rule and haven't found your "Attachment B" yet....will keep looking.
>
> I apologize for having you search for and resend your earlier comments; I am trying to be thorough in this new assessment and have many questions about several analyses.
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**From:** A J
**To:** Grizzle, Betty
**Subject:** Re: emails discussions
**Date:** Tuesday, April 18, 2017 4:34:02 PM
**Attachments:** USFWS wolverine listing rule_with comments_Magoun.doc

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Betty
Here are the comments I made on the status review that was sent to the 7 peer reviewers. Even some of these comments are probably out of date now. I assume you have this for all 7 reviewers, but just in case.....

On Tue, Apr 18, 2017 at 2:23 PM, A J <222wsheridan@gmail.com> wrote:
> i'm not sure Frances ever completed that thesis; I got that draft from his advisor Dr. Cook
>
> On Tue, Apr 18, 2017 at 2:20 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > Thanks again. Also, just wanted to let you know that the photos in your "Associations and Movement Patterns of Reproductive Female Wolverines (*Gulo gulo luscus*) on the Southeast Alaska Mainland" (Final Report February 2010) were very interesting. But more importantly, I had been searching (without success) for the Frances 2008 MS Thesis that is included in that document as an Appendix (the UNM library said it was missing from their collection!).
> >
> > On Tue, Apr 18, 2017 at 3:15 PM, A J <222wsheridan@gmail.com> wrote:
> > > here it is
> > >
> > > On Tue, Apr 18, 2017 at 2:08 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > > > Looking for Attachment (appendix?) A right now.
> > > >
> > > > On Tue, Apr 18, 2017 at 3:05 PM, A J <222wsheridan@gmail.com> wrote:
> > > > > Here Attachment B; do you need any others?
> > > > >
> > > > > On Tue, Apr 18, 2017 at 1:33 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > > > > > Thanks Audrey. I found a few things, but not these (yet). I am looking at your peer review comments on previous proposed rule and haven't found your "Attachment B" yet....will keep looking.
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> > > > > > I apologize for having you search for and resend your earlier comments; I am trying to be thorough in this new assessment and have many questions about several analyses.
> > > > > > Betty
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> > > > > > > Betty
> > > > > > > I don't know if you have already seen these from Shawn's files, but these emails contain a discussion I had with Copeland and McKelvey after some reluctance on my part to get into such an exchange post-status review. I was pretty burned out by then on the whole subject. But you may find parts help answer some of the questions you recently sent. The McKelvey Email file is emails between Jeff and I until it became apparent that it was better to talk directly to Kevin and so his responses to me are in blue type in that email. The McKelvey Email Response file holds my answers back to him in black type. As you will see,

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**DEPARTMENT OF THE INTERIOR**

**Fish and Wildlife Service**

**[FWS–R6–ES–2012–0107]**

**[4500030113]**

**RIN 1018–AY26**

**Endangered and Threatened Wildlife and Plants; Threatened Status for the Distinct Population Segment of the North American Wolverine Occurring in the Contiguous United States**

**AGENCY:** Fish and Wildlife Service, Interior.

**ACTION:** Proposed rule.

**SUMMARY:** We, the U.S. Fish and Wildlife Service, propose to list the distinct population segment of the North American wolverine occurring in the contiguous United States, as a threatened species under the Endangered Species Act. If we finalize this rule as proposed, it would extend the Act's protections to this species. The effect of this regulation is to add the distinct population segment of the North

American wolverine occurring in the contiguous United States to the List of Endangered and Threatened Wildlife (50 CFR 17.11). We also propose a special rule under section 4(d) of the Act to apply the specific prohibitions of the Act necessary to protect the wolverine. We find that critical habitat is not determinable at this time. The Service seeks data and comments from the public on this proposed listing rule, the proposed special rule under section 4(d) of the Act, and our finding that the designation of critical habitat for the species is not determinable at this time.

**DATES:** We will accept comments received or postmarked on or before [INSERT DATE 90 DAYS AFTER DATE OF PUBLICATION IN THE FEDERAL REGISTER]. Comments submitted electronically using the Federal eRulemaking Portal (see **ADDRESSES** section, below) must be received by 11:59 p.m. Eastern Time on the closing date. We must receive requests for public hearings, in writing, at the address shown in the **ADDRESSES** section by [INSERT DATE 45 DAYS AFTER DATE OF PUBLICATION IN THE FEDERAL REGISTER].

*Public Informational Sessions and Public Hearing*: We will hold 3 public informational sessions and public hearings on this proposed rule. Public informational sessions will occur from 2:00 p.m. to 5:00 p.m. and public hearings will be held from 7:00 p.m. to 9:00 p.m. at each location. Public informational sessions and public hearings will occur in Boise, ID, on March 13, 2013, from 7:00 p.m. to 9:00 p.m.; in Lakewood, CO, on March 19, 2013, from 7:00 p.m. to 9:00 p.m.; and in Helena, MT, on March 27, 2013, from 7:00 p.m. to 9:00 p.m., all times local (see **ADDRESSES**). Registration for those providing testimony in the public hearings will begin at 6:00 p.m. at each location.

**ADDRESSES:** You may submit comments by one of the following methods:

(1) *Electronically*: Go to the Federal eRulemaking Portal: *http://www.regulations.gov*. In the Keyword box, enter Docket No. FWS–R6–ES–2012–0107, which is the docket number for this rulemaking. Then, in the Search panel on the left side of the screen, under the Document Type heading, click on the Proposed Rules link to locate this document. You may submit a comment by clicking on Comment Now!"

(2) *By hard copy*: Submit by U.S. mail or hand-delivery to: Public Comments Processing, Attn: FWS–R6–ES–2012–0107; Division of Policy and Directives Management; U.S. Fish and Wildlife Service; 4401 N. Fairfax Drive, MS 2042–PDM; Arlington, VA 22203.

(3) *At a public hearing*: We are holding three public hearings on this proposed rule (see **ADDRESSES** for location information). You may provide your comments at any of the three hearings.

We request that you send comments **only** by the methods described above. We will post all comments on *http://www.regulations.gov*. This generally means that we will post any personal information you provide us (see the **Public Comments** section below for more information).

*Public Informational Sessions and Public Hearings*: Public informational sessions and public hearings will be held on March 13, 2013, at the Boise Centre on the Grove, 850 West Front Street, Boise, ID 83702. The second is scheduled on March 19, 2013, at the Hampton Inn, 137 Union Boulevard, Lakewood, CO 80228. The third is scheduled on March 27, 2013, at the Red Lion Colonial Inn, 2301 Colonial Drive, Helena, MT 59601. At all three locations the public informational session will run from 2:00 p.m. to 5:00 p.m., followed by public speaker registration at 6:00 p.m., and then the public hearing for oral testimony from 7:00 p.m. to 9:00 p.m. People needing reasonable accommodations in order to attend and participate in the public hearing should contact Brent Esmoil,

Montana Ecological Services Field Office, as soon as possible (see **FOR FURTHER INFORMATION CONTACT**).

Any additional tools or supporting information that we may develop for this rulemaking will be available at http://www.fws.gov/mountain-prairie/species/mammals/wolverine/, at http://www.regulations.gov at Docket No. FWS–R6–ES–2012–0107, and at the Montana Field Office (see **FOR FURTHER INFORMATION CONTACT**).

**FOR FURTHER INFORMATION CONTACT:** Brent Esmoil, Field Supervisor (Acting), U.S. Fish and Wildlife Service, Montana Field Office, 585 Shepard Way, Helena, Montana 59601, by telephone (406) 449-5225. Persons who use a telecommunications device for the deaf (TDD) may call the Federal Information Relay Service (FIRS) at 800-877-8339.

**SUPPLEMENTARY INFORMATION:**

**Executive Summary**

**Why we need to publish a rule.** Under the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 et seq.) (Act or ESA), if a species is determined to be an endangered or threatened species throughout all or a significant portion of its range, we are required to promptly publish a proposal in the **Federal Register** and make a determination on our proposal within 1 year. Critical habitat shall be designated, to the maximum extent prudent and determinable, for any species determined to be an

endangered or threatened species under the Act. Listing a species as an endangered or threatened species and designations and revisions of critical habitat can only be completed by issuing a rule.

**This rule consists of:**

- A proposed rule to list the distinct population segment (DPS) of the North American wolverine occurring in the contiguous United States as a threatened species; and
- A proposed special rule under section 4(d) of the Act that outlines the prohibitions necessary and advisable for the conservation of the wolverine.

A proposed rule under section 10(j) of the Act to establish an experimental non-essential population of wolverine in Colorado is published concurrently in this issue of the **Federal Register**. Also, a draft Recovery Outline for the wolverine DPS is available on our website at http://www.fws.gov/mountain-prairie/species/mammals/wolverine/ or on http://www.regulations.gov.

**The basis for our action.** Under the Act, we can determine that a species is an endangered or threatened species based on any of five factors: (A) The present or threatened destruction, modification, or curtailment of its habitat or range; (B) Overutilization for commercial, recreational, scientific, or educational purposes; (C) Disease or predation; (D) The inadequacy of existing regulatory mechanisms; or (E) Other natural or manmade factors affecting its continued existence.

We have determined that habitat loss due to increasing temperatures and reduced late spring snowpack due to climate change is likely to have a significant negative population-level impact on wolverine populations in the contiguous United States. In the future, wolverine habitat is likely to be reduced to the point that the wolverine in the contiguous United States is in danger of extinction.

**We will seek peer review.** We are seeking comments from knowledgeable individuals with scientific expertise to review our analysis of the best available science and application of that science and to provide any additional scientific information to improve this proposed rule. Because we will consider all comments and information received during the comment period, our final determinations may differ from this proposal.

**Information Requested**

We intend that any final action resulting from this proposed rule will be based on the best scientific and commercial data available and be as accurate and as effective as possible. Therefore, we request comments or information from the public, other concerned governmental agencies, Native American tribes, the scientific community, industry, or any other interested parties concerning this proposed rule. We particularly seek comments concerning:

(1) Biological, commercial trade, or other relevant data concerning any threats (or lack thereof) to this species and regulations that may be addressing those threats.

(2) Additional information concerning the historical and current status, range, distribution, and population size of this species, including the locations of any additional populations of this species.

(3) Any information on the biological or ecological requirements of the species, and ongoing conservation measures for the species and its habitat.

(4) Current or planned activities in the areas occupied by the species and possible impacts of these activities on this species.

(5) The reasons why we should or should not designate habitat as "critical habitat" under section 4 of the Act (16 U.S.C. 1531 *et seq*.) including whether and how the wolverine may benefit from such a designation; whether there are threats to the species from human activity, the degree to which it can be expected to increase due to a critical habitat designation, and whether that increase in threat outweighs the benefit of designation such that the designation of critical habitat may not be prudent;

(6) Specific information on the amount and distribution of wolverine habitat,

(7) Information on the projected and reasonably likely impacts of climate change on the wolverine and its habitat;

(8) Suitability of the proposed 4(d) rule for the conservation, recovery, and management of the DPS of the North American wolverine occurring in the contiguous United States.

(9) Additional information concerning whether it is appropriate to prohibit incidental take of wolverine in the course of legal trapping activities directed at other species in the proposed 4(d) rule, including any information about State management plans related to trapping regulations and any

measures within those plans that may avoid or minimize the risk of wolverine mortality from incidental trapping for other species.

(10) Additional provisions the Service may wish to consider to conserve, recover, and manage the DPS of the North American wolverine occurring in the contiguous United States.

We will consider all comments and information received during the comment period on this proposed listing rule and special rule under section 4(d) of the Act during our preparation of a final determination. Accordingly, the final decision may differ from this proposal.

Please note that submissions merely stating support for or opposition to the action under consideration without providing supporting information, although noted, will not be considered in making a determination, as section 4(b)(1)(A) of the Act directs that determinations as to whether any species is an endangered or threatened species must be made "solely on the basis of the best scientific and commercial data available."

You may submit your comments and materials concerning this proposed rule by one of the methods listed in the **ADDRESSES** section. We request that you send comments **only** by the methods described in the **ADDRESSES** section.

If you submit information via *http://www.regulations.gov*, your entire submission—including any personal identifying information—will be posted on the website. If your submission is made via a hardcopy that includes personal identifying information, you may request at the top of your document

that we withhold this information from public review. However, we cannot guarantee that we will be able to do so. We will post all hardcopy submissions on *http://www.regulations.gov*. Please include sufficient information with your comments to allow us to verify any scientific or commercial information you include.

Comments and materials we receive, as well as supporting documentation we used in preparing this proposed rule, will be available for public inspection on *http://www.regulations.gov*, or by appointment, during normal business hours, at the U.S. Fish and Wildlife Service, Montana Field Office (see **FOR FURTHER INFORMATION CONTACT**).

**Previous Federal Actions**

On April 19, 1995, we published a finding (60 FR 19567) that a previous petition, dated August 3, 1994, submitted by the Predator Project (now named the Predator Conservation Alliance) and Biodiversity Legal Foundation to list the wolverine in the contiguous United States as an endangered or threatened species, did not provide substantial information indicating that listing the wolverine in the contiguous United States may be warranted.

On July 14, 2000, we received a petition dated July 11, 2000, submitted by the Biodiversity Legal Foundation, Predator Conservation Alliance, Defenders of Wildlife, Northwest Ecosystem Alliance, Friends of the Clearwater, and Superior Wilderness Action Network, to list the wolverine within the contiguous United States as an endangered or threatened species and designate critical habitat for the species.

On October 21, 2003, we published a 90-day finding that the petition failed to present substantial scientific and commercial information indicating that listing may be warranted (68 FR 60112).

On September 29, 2006, as a result of a complaint filed June 8, 2005 by Defenders of Wildlife and others alleging we used the wrong standards to assess the July 11, 2000, wolverine petition, the U.S. District Court, Montana District, ruled that our 90-day petition finding (68 FR 60112) was in error and ordered us to submit to the **Federal Register** a 12-month finding for the wolverine by September 29, 2007. On April 6, 2007, the deadline for this 12-month finding was extended to February 28, 2008.

On March 11, 2008, we published a 12-month finding of "not warranted" for the wolverine in the contiguous United States (73 FR 12929). In that finding we determined that the wolverine in the contiguous United States did not constitute a distinct population segment or a significant portion of the range of a listable entity of the wolverine in North America and so was not a listable entity under the Act.

On July 8, 2008 we received a Notice of Intent to Sue from Earthjustice alleging violations of the Act in our March 11, 2008, 12-month finding. On September 30, 2008, Earthjustice filed a complaint in the U.S. District Court, District of Montana, seeking to set aside and remand the 12-month finding back to the Service for reconsideration.

On March 6, 2009, the Service agreed to settle the case with Earthjustice by voluntarily remanding the 12-month finding and issuing a new 12-month finding by December 1, 2010. Following the settlement agreement, the court dismissed the case on June 15, 2009, and ordered the Service to comply with the settlement agreement.

On April 15, 2010, the Service published a Notice of Initiation of a 12-month finding for wolverines in the contiguous United States (75 FR 19591). That finding was published on December 14, 2010, and determined that the wolverine in the contiguous United States constituted a Distinct Population Segment and that the DPS warranted listing under the Act, but that listing was precluded by higher priority listing actions (75 FR 78030).

On September 9, 2011, we reached an agreement with plaintiffs in *Endangered Species Act Section 4 Deadline Litig.,* Misc. Action No. 10-377 (EGS), MDL Docket No. 2165 (D. D.C.) (known as the "MDL case") on a schedule to publish proposed rules or to withdraw warranted findings for the species on our list of candidate species. This agreement stipulated that we would submit for publication in the **Federal Register** a proposed listing rule for the wolverine, or withdraw the warranted 12-month finding, no later than the end of the 2013 Fiscal Year.

On April 13, 2012, several parties filed an action challenging the Service's December 14, 2010 warranted but precluded finding for wolverine. *Cottonwood Envtl. Law Ctr., et al. v. Salazar, et al.,* 9:12-cv-00057-DLC (D. Mont.) On September 20, 2012, the court granted the Service's motion to stay that litigation based on the Service's representation to the Court that it expected to submit this rule or withdraw the warranted finding to the **Federal Register** by January 18, 2013.

**THREATENED STATUS FOR THE CONTIGUOUS UNITED STATES WOLVERINE DPS:**

**Background**

It is our intent to discuss below only those topics directly relevant to the listing of the contiguous United States DPS of the North American wolverine as a threatened species in this section of the proposed rule.

*Species Information*

Taxonomy and Life History

The wolverine has a Holarctic (habitats found in the northern continents) distribution including northern portions of Europe, Asia, and North America. The currently accepted taxonomy classifies wolverines worldwide as a single species, *Gulo gulo*, with two subspecies. Old World wolverines are found in the Nordic countries of Europe, Russia, Mongolia, and Siberia and are part of the subspecies *Gulo gulo gulo*. New World wolverines occur in North America. The wolverines in the contiguous United States are a part of the New World subspecies, *G. g. luscus*: the North American wolverine (Kurten and Rausch 1959 p. 19; Pasitschniak-Arts and Lariviere 1995, p. 1). The species is known by several common names, including mountain devil, glutton, caracajou, quickhatch, gulon, skunk bear, as well as wolverine.

The wolverine is the largest terrestrial member of the family Mustelidae. Adult males weigh 12 to 18 kilograms (kg) (26 to 40 pounds (lb)), and adult females weigh 8 to 12 kg (17 to 26 lb) (Banci 1994, p. 99). The wolverine resembles a small bear with a bushy tail. It has a broad, rounded head; short, rounded ears; and small eyes. Each foot has five toes with curved, semi-retractile claws used for digging and climbing (Banci 1994, p. 99).

A large number of female wolverines (40 percent) are capable of giving birth at 2 years old, become pregnant most years, and produce average litter sizes of 1 to 2 kits. In one study of known-aged females, none reproduced at age 2; 3 of 10 first reproduced at age 3; and 2 did not reproduce until age 4. The average age at first reproduction was 3.4 years (Persson *et al*. 2006, pp. 76-77). Another study indicated that the average age at first reproduction is likely more than 3 years (Inman *et al*. 2007c, p. 70). Pregnant females commonly resorb or spontaneously abort litters prior to giving birth (Magoun 1985, pp. 30-31; Copeland 1996, p. 43; Persson *et al*. 2006, p. 77; Inman *et al*. 2007c, p. 70). This may in turn preserve resources to increase reproductive success in subsequent years (Persson 2005, p. 1456). By age 3, nearly all female wolverines become pregnant every year, but energetic constraints due to low food availability result in loss of pregnancy in about half of them each year. It is likely that, in many places in the range of wolverines, it takes 2 years of foraging for a female to store enough energy to successfully reproduce (Persson 2005, p. 1456). It is likely that, despite the high rate of initiation of pregnancy, due to the spontaneous abortion of litters resulting from resource limitation, actual rates of successful reproduction in wolverines are among the lowest known for mammals (Persson 2005, p. 1456).

**Commented [O1]:** Up to 29 in Petersburg Alaska; A. Magoun unpub. data

**Commented [O2]:** Wolverines do NOT have semi-retractile claws; don't know where this originally came from but it keeps getting repeated.

**Commented [O3]:** Incorrect statement; check your reference for this and put it here; Persson et al. 2006 does not state this; in fact no 2 year olds in his study gave birth; you may have gotten this from Inman 2007c instead, p. 70, but I'm not sure it is correct without reviewing the 3 papers that Inman cited. Suggest going to the original 3 papers for the correct information.

**Commented [O4]:** Reference? Cite the reference and the actual number, which I believe is an average litter size of 1.88 from Perrson

**Commented [O5]:** State whether this is average litter size based on placental scars or emerging from the den; this is low for placental scars

**Commented [O6]:** There is no way to know if this is a true statement; Magoun 1985 does NOT state this on pp. 30-31; Copeland 1996 also does not state this but only that Mead et al. 1993 (not the 1991 paper) found absorption of unimplanted blastocysts in mustelids (not woverines); Mead was never able to get wolverines to breed or become pregnant; Persson et al. (2006) also do NOT state this, rather they say that "young are lost during pregnancy, early after parturition, or both. Losses probably do not occur before implantation, because a unique feature of delayed implantation in mustelids is that there is minimal intrauterine death of embryos during the prolonged preimplantation period (Mead et al. 1993), and the number of corpora lutea approximates the number of unimplanted blastocysts (e.g., Liskop et al. 1981; Rausch and Pearson 1972). However, pregnancy failure at implantation might occur (Arthur and Krohn 1991)." Suggest that you check with the Mead et al. 1993 paper for the exact information. If any of the female wolverines conceived in their study (unknown), the embryos "either died during preimplantation, were resorbed during postimplantation, or the kits were eaten shortly after birth." Finally, Inman et al. 2007c does not refer to abortion of litters prior to birth. Check original citations that he cites. The fact is that no one knows why wolverines do not give birth in some years because any of these may occur: failure to breed, pseudopregnancy, failure to implant, absorption of implanted fetuses, stillbirth, death before den emergence, including infanticide.

**Commented [O7]:** What does this refer to? Persson 1985 does not say that resorbtion or abortion prior to birth preserves resources, rather ANY reason wolverines fail to reproduce in a given year (and this would include any of the above plus early death of kits after den emergence)

**Commented [O8]:** No scientific data to support this; just say failure to reproduce for unknown reasons

Supplemental feeding of females increases reproductive potential (Persson 2005, p. 1456). Food-supplemented females were also more successful at raising kits to the time of weaning, suggesting that wolverine reproduction and ultimately population growth rates and viability are food-limited. Female wolverines appear to use a complex strategy of food accumulation and caching to attain enough resources to successfully raise a litter (Inman *et al*. 2012b, pp. 640-641).

Breeding generally occurs from late spring to early fall (Magoun and Valkenburg 1983, p. 175; Mead *et al*. 1991, pp. 808-811). Females undergo delayed implantation until the following winter or spring, when active gestation lasts from 30 to 40 days (Rausch and Pearson 1972, pp. 254-257; Mead et al. 1993, Inman2012 (J of Mamm paper) = 45 days average ). Litters are born from mid-February through March, containing one to five kits, with an average in North America of between one and two kits (Magoun 1985, pp. 28-31; Copeland 1996, p. 36; Krebs and Lewis 1999, p. 698; Copeland and Yates 2006, pp. 32-36; Inman *et al*. 2007c, p. 68).

Female wolverines use natal (birthing) dens that are excavated in snow. Persistent, stable snow greater than 1.5 meters (m) (5 feet (ft)) deep appears to be a requirement for natal denning, because it provides security for offspring and buffers cold winter temperatures (Pulliainen 1968, p. 342; Copeland 1996, pp. 92-97; Magoun and Copeland 1998, pp. 1317-1318; Banci 1994, pp. 109-110; Inman *et al*. 2007c, pp. 71-72; Copeland *et al*. 2010, pp. 240-242). Female wolverines go to great lengths to find secure den sites, suggesting that predation is a concern (Banci 1994, p. 107). Natal dens consist of tunnels that contain well-used runways and bed sites and may naturally incorporate shrubs, rocks, and downed logs as part of their structure (Magoun and Copeland 1998, pp. 1315-1316; Inman *et al*. 2007c, pp. 71-72). In Idaho, natal den sites occur above 2,500 m (8,200 ft) on rocky sites, such as north-facing

**Commented [O9]:** As early as January and as late as April (Inman et al. 2012 paper) and give peak parturition

**Commented [O10]:** Although 5 fetuses have been found, I know of no verified live births of 5 kits; give reference if you have one

**Commented [O11]:** Must state whether from examination of carcasses or from observed kits after leaving the den or dug from dens; most litters at birth probably have at least 2 kits, but one or both may die before they can be counted; an average litter of between 1 and 2 "AT BIRTH" is unmeasured and unknown for wild wolverines; only mean litter size at the time they are counted

**Commented [O12]:** Define terms

**Commented [O13]:** Not accurate; see lengthy discussion in Attachment A; snow ≥1 m and possibly less (e.g., 70 cm)

**Commented [O14]:** What does "great lengths" mean? there are often lots of potential den sites in a female's home range and the females are probably very familiar with them well before denning begins; this statement by Banci is opinion, not scientific fact; most carnivores find secure den sites because predation is almost always a concern

boulder talus or subalpine cirques (steep-walled semicircular basin carved by a glacier) in forest openings (Magoun and Copeland 1994, pp. 1315-1316). In Montana, natal dens occur above 2,400 m (7,874 ft) and are located on north aspects in avalanche debris, typically in alpine habitats near timberline (Inman *et al*. 2007c, pp. 71-72). Offspring are born from mid-February through March and the dens are typically used through late April or early May (Myrberget 1968, p. 115; Magoun and Copeland 1998, pp. 1314-1317; Inman *et al*. 2007b, pp. 55-59). Occupation of natal dens is variable, ranging from approximately 9 to 65 days (Magoun and Copeland 1998, pp. 1316-1317).

Females may move kits to multiple secondary (maternal) dens as they grow during the month of May (Pulliainen 1968, p. 343; Myrberget 1968, p. 115), although use of maternal dens may be minimal (Inman *et al*. 2007c, p. 69). Timing of den abandonment is related to accumulation of water in dens (due to snow melt), the maturation of offspring, disturbance, and geographic location (Myrberget 1968, p. 115; Magoun 1985, p. 73). After using natal and maternal dens, wolverines may also use rendezvous sites through early July. These sites are characterized by natural (unexcavated) cavities formed by large boulders, downed logs (avalanche debris), and snow (Inman *et al*. 2007c, pp. 55-56). Male wolverines likely mate with several females, and although they are not known to directly contribute to rearing young, they do tolerate subadult wolverines in their territories (usually their own offspring) until they reach maturity (Copeland 1996, p. 72).

Habitat, Space, and Food

In North America, wolverines occur within a wide variety of alpine, boreal, and arctic habitats, including boreal forests, tundra, and western mountains throughout Alaska and Canada. The southern

**Commented [O15]:** Born from January to mid-April but the peak of parturition is February to mid-March (Inman et al. 2012-J of Mamm. Vol. 93, p. 637-638

**Commented [O16]:** Use Inman et al. 2012- J of Mamm. Vol. 93, p. 637-638 for your reference here as it is comprehensive and includes the others listed here; also, Myrberget 1968 is not a good reference here because they did not know birth date

**Commented [O17]:** Use Magoun and Copeland 1998 for reference; the two references cited here did not know birth date and therefore could not know if dens being used at the time the kits were dug out were natal, maternal, or rendezvous sites; although they mention moves, Pulliainen 1968 , p..343 stated it was due to disturbance; Myrberget 1968 (p. 115) also does not say they move kits to multiple dens; only that moves were observed and may have been influenced by disturbance from man---check your references.

**Commented [O18]:** "the thaw that has occurred" is more accurate (Myrberget 1968, p. 115; Magoun 1985, p. 1985 mentions "spring melt conditions"; neither observed accumulation of water in dens; spring melt conditions might include slumping of snow tunnels (Magoun, personal observation)

**Commented [O19]:** Not enough data on whether the subadults in a male's territory are their own offspring in all cases; they may tolerate unrelated subadults between ~1-2 years old in general; more information is needed on this topic; unrelated males do occur in the home ranges of other males (pers. observ., SE AK study)and there is not enough data on the social behavior of unrelated males

portion of the species' range extends into the contiguous United States, including high-elevation alpine portions of Washington, Idaho, Montana, Wyoming, California, and Colorado (Wilson 1982, p. 644; Hash 1987, p. 576; Banci 1994, p. 102, Pasitschniak-Arts and Lariviere 1995, p. 499; Aubry *et al*. 2007, p. 2152; Moriarty *et al*. 2009, entire; Inman *et al*. 2009, pp. 22-25). Wolverines do not appear to specialize on specific vegetation or geological habitat aspects, but instead select areas that are cold and receive enough winter precipitation to reliably maintain deep persistent snow late into the warm season (Copeland *et al*. 2010, entire). The requirement of cold, snowy conditions means that, in the southern portion of the species' range where ambient temperatures are warmest, wolverine distribution is restricted to high elevations, while at more northerly latitudes, wolverines are present at lower elevations and even at sea level in the far north (Copeland *et al*. 2010, Figure 1).

**Commented [O20]:** Include Oregon if you are including California and Colorado based on Magoun et al. 2013 final report on the Wallowa study

**Commented [O21]:** So how are you defining the wolverine's range; looks as though you mean anywhere wolverines are occurring as residents even if there is no evidence of reproduction ???

**Commented [O22]:** Define terms

**Commented [O23]:** What is the "warm season"; be specific and use documented dates; see discussion in Attachment A

**Commented [O24]:** This is true if you are referring to the western US but not if you are referring to the entire N.A. population because wolverines at the southern extent of their range in eastern Canada do not have high elevation habitat

**Commented [O25]:** What is "far North"; wolverines occur at sea level in SE Alaska (Magoun et al. 2010) and in British Columbia (current research project by Canadian researchers; Aubry, pers. comm..)

In the contiguous United States, wolverines likely exist as a metapopulation (Aubry *et al*. 2007, p. 2147, Figures 1, 3). A population is a group of interbreeding individuals of the same species. A metapopulation is a population composed of a network of semi-isolated subpopulations, each occupying a suitable patch of habitat in a landscape of otherwise unsuitable habitat (Pulliam and Dunning 1997, pp. 212-214). Metapopulations require some level of regular or intermittent migration and gene flow among subpopulations, in which individual subpopulations support one-another by providing genetic and demographic enrichment through mutual exchange of individuals (Meffe and Carroll 1997, p. 678). Individual subpopulations may go extinct or lose genetic viability, but are then "rescued" by immigration from other subpopulations, thus ensuring the persistence of the metapopulation as a whole. If metapopulation dynamics break down, either due to changes within subpopulations or loss of connectivity, then the entire metapopulation may be jeopardized due to subpopulations becoming unable to persist in the face of inbreeding or demographic and environmental

stochasticity (Pulliam and Dunning 1997, pp. 221-222). The wolverine metapopulation in the DPS consists of a network of small subpopulations on mountain tops, some consisting of less than ten individuals. Persistence of subpopulations under these conditions requires movement between subpopulations across both suitable and unsuitable wolverine habitat. Wolverines prefer to move across suitable habitat (as defined by persistent spring snow cover) rather than to cross unsuitable habitats during dispersal movements (Schwartz et al. 2009, p. 3230). Therefore, we would expect that changes resulting in reduction of suitable habitat conditions would result in reduced movement rates between habitat patches if distances between them became greater. This could affect the metapopulation as a whole if movement rates became too low to ensure subpopulation demographic or genetic health.

Wolverines are opportunistic feeders and consume a variety of foods depending on availability. They primarily scavenge carrion, but also prey on small animals and birds, and eat fruits, berries, and insects (Hornocker and Hash 1981, p. 1290; Hash 1987, p. 579; Banci 1994, pp. 111-113). Wolverines have an excellent sense of smell that enables them to find food beneath deep snow (Hornocker and Hash 1981, p. 1297).

Wolverines require a lot of space; the availability and distribution of food is likely the primary factor in determining female wolverine movements and home range size (Hornocker and Hash 1981, p. 1298; Banci 1994, pp. 117-118). Male wolverine home range size and location is likely tied to the presence of active female home ranges and breeding opportunities (Copeland 1996, p. 74). Female wolverines forage close to den sites in early summer, progressively ranging further from dens as kits become more independent (May *et al*. 2010, p. 941). Wolverines travel long distances over rough

**Commented [O26]:** There are few documented accounts of wolverines eating fruits, berries, and insects; not probably a major part of their diet; not even listed in Banci 1994 or Hornocker and Hash 1290; Rausch and Pearson 1972 gives one of the only first-hand account of berries in the diet (p. 266); the emphasis should be on mice, ground squirrels, marmots, and hares, which are the primary small prey documented (multiple literature sources).

**Commented [O27]:** They also prey on large mammals to varying degrees; domestic sheep in Norway, semi-domesticated reindeer in Sweden; Dall sheep, personal observation; also Gill 1978-see Banci 1994, p. 113 for citations; moose (Magoun, poster paper reporting 3 accounts of wolverines killing moose—; see Banci 1994 for other species and citations; Haglund 1974)

**Commented [O28]:** Other instances of wolverines passing by bait at <300 m do not support this statement (Magoun pers. observation) and experiments I did with young wolverines indicated that their ability to smell bait at relatively close distance (~5) buried under moss was poor; there is no scientific data that support the supposition that wolverine's ability to smell is unusually keen for a carnivore; they do have good memories for where they have found food before or where they have cached food (pers. observ.) so maybe the "excellent" sense of smell is actually an "excellent" memory, similar to other animals that cache food like Clark's nutcracker (supported by research).

**Commented [O29]:** Do you mean rendezvous sites? Or do you mean in the denning season? I don't see where May actually states this on p. 941; he discusses foraging intensity and preferences, not distance

**Commented [O30]:** This is not what this reference actually says; especially when considering night-time movements; nothing about distance just elevation ; e.g., "In spring, wolverines showed restricted movement patterns around rendezvous sites at high elevations by day, whereas during the night animals were active at lower elevations." (see abstract)

terrain and deep snow, and adult males generally cover greater distances than females (Hornocker and Hash 1981, p. 1298; Banci 1994, pp. 117-118; Moriarty *et al*. 2009, entire; Inman *et al*. 2009, pp. 22-28; Brian 2010, p. 3; Copeland and Yates 2006, Figure 9). Home ranges of wolverines are large, and vary greatly in size depending on availability and distribution of food and gender and age of the animal. Home ranges of adult wolverines also vary in size depending on geographic location. Home ranges in Alaska were approximately 100 square kilometers ($km^2$) to over 900 $km^2$ (38.5 square miles ($mi^2$) to 348 $mi^2$) (Banci 1994, p. 117). Average home ranges of resident adult females in central Idaho were 384 $km^2$ (148 $mi^2$), and average home ranges of resident adult males were 1,522 $km^2$ (588 $mi^2$) (Copeland 1996, p. 50). Wolverines in Glacier National Park had average adult male home ranges of 496 $km^2$ (193 $mi^2$) and adult female home ranges of 141 $km^2$ (55 $mi^2$) (Copeland and Yates 2006, p. 25). Wolverines in the Greater Yellowstone Ecosystem had average adult male home ranges of 797 $km^2$ (311 $mi^2$), and average adult female home ranges of 329 $km^2$ (128 $mi^2$) (Inman *et al*. 2007a, p. 4). These home range sizes are large relative to the body size of wolverines, and may indicate that wolverines occupy a relatively unproductive niche in which they must forage over large areas to consume the amount of calories needed to meet their life-history requirements (Inman *et al*. 2007a, p. 11).

**Commented [O31]:** use published reference Inman et al. 2012 J of Mammalogy

Across their worldwide distribution, wolverines are dependent on persistent spring snow cover for successful reproduction (Pulliainen 1968, pp. 338-341; Myrberget 1968, p. 115; Copeland 1996, pp. 93-94; Magoun and Copeland 1998, pp. 1315-1319; Aubry *et al*. 2007, p. 2153; Inman *et al*. 2012a, p.785; Copeland *et al*. 2010, entire). No records exist of wolverines denning anywhere but in snow, despite the wide availability of snow-free denning opportunities within the species' geographic range. The snow tunnels and complex structure associated with dens are likely required to protect young from

**Commented [O32]:** few records; there are 1 or 2 but they may be unusual circumstances; see Pulliainen 1968 and Rausch and Pearson 1972

interspecific and intraspecific predation (Persson *et al*. 2003, pp. 25-26; Magoun and Copeland 1998, p. 1318). A layer of deep snow may also add crucial insulation from cold temperatures and wind prevalent in wolverine habitat (Pulliainen 1968, p. 342; Bjärvall *et al*. 1978, p. 24-25; Copeland 1996, p. 100; Magoun and Copeland 1998, p. 1318).

Female wolverines have been observed to abandon reproductive dens when temperatures warm and snow conditions become wet (Magoun and Copeland 1998, p. 1316); this response indicates that the condition of the snow is also important to successful reproduction, and that the onset of spring snowmelt forces female wolverines to move kits into alternate denning sites with better snow conditions, if they are available. These movements may be energetically costly and subject females and kits to predation risk. The deep, persistent spring snow layer in the Copeland et al. (2010) model captures all known wolverine den sites in the DPS; however, on average, most denning occurs at higher elevations within the area defined by the model. Female wolverines establish reproductive dens at elevations higher than average elevations used by nonreproductive wolverines (Copeland 1996, p. 94; Magoun and Copeland 1998, pp. 1315-1316; Inman *et al*. 2007c, p. 71), suggesting that females find the conditions necessary for successful denning in the upper portion of their home range where snow is most persistent and occurs in the heaviest accumulations.

Wolverine year-round habitat use also takes place almost entirely within the area defined by deep persistent spring snow (Copeland et al. 2010, pp. 242-243). Within the DPS, this area is generally centered on the alpine tree line (the maximum elevation beyond which tree growth is precluded and only low-growing vegetation is found). In the contiguous United States, wolverine year-round habitat is found at high elevations centered near the tree line in conifer forests (below tree line) and rocky

**Commented [O33]:** actually says when spring snow melt begins; dens were not actually excavated until ~ a week after the den was abandoned so we don't know if there was standing water at that time; slumping snow tunnels could be the reason for den abandonment

**Commented [O34]:** Copeland et al. 2010 did not measure depth nor used it to construct the snow model; no measurement of depth for the DPS provided in Copeland et al. 2010

**Commented [O35]:** Should note though that the authors state they did not attempt to fit the snow coverage to the data (i.e., actual locations of the dens against actual snow cover during the years the dens were used) and the snow coverage was based on snow cover in 1-7 years out of 7 years in only 2000-2006 (see Attachment A for more detailed discussion).

**Commented [O36]:** Cite page number

**Commented [O37]:** In the western US

**Commented [O38]:** Again, depth was not measured or used in Copeland et al. 2010

alpine habitat (above tree-line) and in cirque basins and avalanche chutes that have food sources such as marmots, voles, and carrion (Hornocker and Hash 1981, p. 1296; Copeland 1996, p. 124; Magoun and Copeland 1998, p. 1318; Copeland *et al*. 2007, p. 2211; Inman *et al*. 2007a, p. 11). In the southern portion of wolverine range in North America which includes the DPS, wolverines are constrained by their need for cold conditions and persistent spring snow to using only the coldest available landscapes (Copeland *et al*. 2010, Figure 6).

Mean seasonal elevations used by wolverines in the northern Rocky Mountains and North Cascades vary between 1,400 and 2,600 m (4,592 and 8,528 ft) depending on location, but are always relatively high on mountain slopes (Hornocker and Hash 1981, p. 1291; Copeland *et al*. 2007, p. 2207, Aubry *et al*. 2007, p. 2153; Inman et al. 2012, p.782). Elevation ranges used by historical wolverine populations in the Sierra Nevada and southern Rocky Mountains are unknown, but presumably wolverines used higher elevations, on average, than more northerly populations to compensate for the higher temperatures found at lower latitudes. In the contiguous United States, valley bottom habitat appears to be used only for dispersal movements and not for foraging or reproduction (Inman *et al*. 2009, pp. 22-28). Wolverine reproductive dens have been located in alpine, subalpine, taiga, or tundra habitat (Myrberget 1968, p. 115; Pulliainen 1968, pp. 338-341; Bjärvall 1982, p. 318; Lee and Niptanatiak 1996, p. 349; Landa *et al*. 1998, pp. 451-452; Magoun and Copeland 1998, pp. 1317-1318). Wolverines rarely, or never, den in lower elevation forested habitats, although they may occupy these habitats occasionally (Magoun and Copeland 1998, p. 1317).

**Commented [O39]:** Lowland boreal (Dawson et al. 2010)

**Commented [O40]:** They did NOT say that wolverines "occupy these habitats occasionally" rather that they "occupy these habitats" and in fact, they occupy quite a bit of this habitat in boreal Canada and are denning in lowland boreal in Sweden (see Attachment A); be careful to cite your references accurately

**Commented [O41]:** Magoun and Copeland 1998 did not say this; what they said was "rarely have dens been reported in low-elevation densely forested habitats.." p. 1317; they acknowledge that this could be an artifact of where researchers have searched for dens citing Banci 1994; the best available science now indicates that wolverines do den in lowland boreal forest (see Attachment A).

Wolverine Densities

Wolverines naturally occur in low densities with a reported range from one animal per 65 $km^2$ (25 $mi^2$), to one animal per 337 $km^2$ (130 $mi^2$) (Hornocker and Hash 1981, pp. 1292-1295; Hash 1987, p. 578; Copeland 1996, pp. 31-32; Copeland and Yates 2006, p. 27; Inman *et al*. 2007a, p. 10; Squires *et al*. 2007, p. 2218). No systematic population census exists over the entire current range of wolverines in the contiguous United States, so the current population level and trends are not known with certainty. However, based on our current knowledge of occupied wolverine habitat and wolverine densities in this habitat, it is reasonable to estimate that the wolverine population in the contiguous United States numbers approximately 250 to 300 individuals (Inman 2010b, pers. comm.). The bulk of the current population occurs in the northern Rocky Mountains, with a few individuals in the North Cascades and one known individual each in the Sierra Nevada and southern Rocky Mountains. Within the area known to currently have wolverine populations, relatively few wolverines can coexist due to their naturally low population densities, even if all areas were occupied at or near carrying capacity. Given the natural limitations on wolverine population density, it is likely that historical wolverine population numbers were also low (Inman et al. 2007a, Table 6). Because of these natural limitations, it is possible that densities and population levels in the northern Rocky Mountains and North Cascades where populations currently exist may not be substantially lower than population densities were in these areas prior to European settlement. However, historically, the contiguous United States population would likely have been larger than it is today due to the larger area occupied by populations when the southern Rocky Mountains, Bighorn Mountains, Sierra Nevada, and possibly also the Oregon Cascades and mountains of Utah, were occupied at full capacity.

Wolverine Status in Canada and Alaska

**Commented [O42]:** Copeland and Yates 2006 do not report on density on p. 27

**Commented [O43]:** More recent and complete references include Inman et al. 2012 JWM 76:778-792 (Table 5)

The bulk of the range of North American wolverines is found in Canada and Alaska, where wolverines inhabit alpine tundra, boreal forest, and arctic habitats (Slough 2007, p. 78). Wolverines in Canada have been divided into two populations for management by the Canadian Government: an eastern population in Labrador and Quebec, and a western population that extends from Ontario to the Pacific coast, and north to the Arctic Ocean. The eastern population is currently listed as endangered under the Species At Risk Act in Canada, and the western population is designated as a species of special concern (COSEWIC 2003, p. 8).

**Commented [O44]:** Mention that a new COSEWIC is currently under review (Graham Forbes, Univ. of New Brunswick, pers. comm..) and status could change

The current status of wolverines in eastern Canada is uncertain. Wolverines have not been confirmed to occur in Quebec since 1978 (Fortin *et al*. 2005, p. 4). Historical evidence of wolverine presence in eastern Canada is also suspect because no evidence exists to show that wolverine pelts attributed to Quebec or Labrador actually came from that region; animals were possibly trapped elsewhere and the pelts shipped through the eastern provinces (COSEWIC 2003, p. 20). Wolverines in eastern Canada may currently exist in an extremely low-density population, or may be extirpated. Wolverines in eastern Canada, both historically and currently, could represent migrants from western populations that never became resident animals (COSEWIC 2003, pp. 20-21). The Federal Government of Canada has completed a recovery plan for the eastern population with the goal of establishing a self-sustaining population through reintroduction and protection (Fortin *et al*. 2005, p. 16).

**Commented [O45]:** What historical evidence? Records of harvests? What do you consider historical?

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**Commented [O46]:** This statement is misleading because it suggests that wolverines may never have been present, but the COSEWIC 2003 report does not say that historical presence is suspect, only that harvests said to be from those provinces may not have been trapped there; there IS historical evidence of presence of wolverines in Labrador and Quebec; see Attachments Labrador; in addition see the Fortin et al. 2005 National Recovery Plan for the Wolverine (Eastern population) in your list of references, p. 4 ("Prior to the arrival of Europeans, wolverines were present throughout Labrador and Quebec (Kelsall 1981). The wolverine's historical distribution appears to have coincided with the distribution of caribou within the taiga ecoregion of the Canadian Shield (van Zyll de Jong 1972). However, the historical population size is not known. At the beginning of the 20th century, the geographic range of wolverine was thought to extend to the 66th parallel and perhaps beyond (de Puyjalon 1900)."

**Commented [O47]:** Again, this is a misleading statement, indicating that even historic occurrences of wolverines in eastern Canada may have been migrants and so giving the impression you are saying that wolverines never were established in eastern Canada and this is not true. This should be reworded with better information on on historic wolverine populations and references.

Wolverines in western Canada and Alaska inhabit a variety of habitats from sea level to high elevations (Slough 2007, pp. 77-78). They occur in Alaska, Ontario, Manitoba, Saskatchewan, Alberta, British Columbia, Yukon, Northwest Territories, and Nunavut (Slough 2007, pp. 77-78). Since

European colonization, a generally recognized range contraction has taken place in boreal Ontario and the aspen parklands of Manitoba, Saskatchewan, and Alberta (COSEWIC 2003, pp. 20-21; Slough 2007, p. 77). This range contraction occurred concurrently with a reduction in wolverine records for the Great Lakes region in the contiguous United States (Aubry *et al*. 2007, pp. 2155-2156). Causes of these changes are uncertain, but may be related to increased harvest, habitat modification, or climate change (COSEWIC 2003, pp. 20-21; Aubry *et al*. 2007, pp. 2155-2156; Slough 2007, pp. 77-78). Analysis supports climate change as a factor contributing to population declines in southern Ontario, because snow conditions necessary to support wolverines do not currently exist in the Great Lakes region of the contiguous United States, and are marginal in southern Ontario (Aubry *et al*. 2007, p. 2154). It is not known if these snow conditions existed historically in the Great Lakes of the contiguous United States; however, the small number of wolverine records from this area suggests that they did not. It is possible that suitable snow conditions did reach further south in eastern Canada in 1850 than they do today, making wolverine dispersal attempts from Canada to the Great Lakes region of the contiguous United States more likely than they are now. Wolverines occurred historically on Vancouver Island and have been given status as a separate subspecies by some (Hall 1981, p. 109). The Vancouver Island population is now regarded as possibly extirpated; no sightings have occurred since 1992 (COSEWIC 2003, p. 18).

Wolverines in western Canada and Alaska appear to persist everywhere that habitat and climate conditions are suitable (COSEWIC 2003, pp. 13-21; Aubry *et al*. 2007, pp. 2152-2155; Slough 2007, p. 79; Copeland *et al*. 2010, Figure 2). Throughout this area, wolverines are managed by regulated harvest at the Provincial and State level. Population estimates for Canada and Alaska are rough because no wolverine surveys have taken place at the State or Provincial scale. However, the population in western

**Commented [O48]:** It is not possible to tease apart the contribution of climate change from that of habitat conversion during human settlement, logging and railroad construction and the overharvest of ungulates that occurred all at the same time; information on historic snow depths is not available (Russ Brown, Climate Research Branch, Atmospheric Environment Service, Canada, pers. comm..) It seems you are using circular reasoning: saying changes in snow conditions may have led to declines in wolverines and then saying low number of wolverine records indicate that snow conditions were not able to support wolverines historically. Just say we don't know for sure what caused wolverines to disappear from the Great Lakes Region

**Commented [O49]:** Same comment as 047 above; also snow conditions in southern Ontario may be sufficient for denning but anthropogenic change may be at least one of the causes of retraction in wolverine range in Ontario in the south (possibly even more important than climate change); furthermore, Aubry et al. 2007 is inconclusive on the role of climate change on wolverine range in southern Ontario

**Commented [O50]:** Or that wolverines historically occurred in the extreme northern areas of Minnesota where they did not often encounter people and therefore not many records would be expected even if they occurred there; even today snow conditions around Lake Superior could be suitable snow cover for denning in some years (snow cover maps from the National Operational Hydrologic Remote Sensing Center).

Canada is estimated to include approximately 15,089 to 18,967 individuals (COSEWIC 2003, p. 22). The number of wolverines in Alaska is unknown, but they appear to exist at naturally low densities in suitable habitats throughout the state (Alaska Department of Fish and Game 2004, pp. 1-359). We have no information to indicate that wolverine populations have been reduced in numbers or geographic range in Alaska.

The Complexity of Geographic Range Delineation

Information on the nature of historical and current locations of wolverine is lacking for several reasons. Wolverines tend to live in remote and inhospitable places away from human settlements, where they are seldom encountered, documented, or studied. Wolverines naturally occur at low population densities and are rarely and unpredictably encountered where they do occur. Wolverines often move long distances in short periods of time; for example, when dispersing from natal ranges, wolverines may transit through habitats that are unsuitable for long-term survival (Aubry *et al*. 2007, p. 2147; Moriarty *et al*. 2009, entire; Inman *et al*. 2009, pp. 22-28; Brian 2010, p. 3). Such movements make it difficult to distinguish with certainty between occurrence records that represent established populations in suitable habitats and records that represent short-term occupancy or exploratory movements without the potential for establishment of home ranges, reproduction, or populations. These natural attributes of wolverines make it difficult to precisely determine their present range, or trends in range expansion or contraction, that may have occurred in the past. Therefore, we are cautious and use multiple lines of evidence when trying to determine where past wolverine populations occurred.

Throughout the remainder of this proposed rule, we focus on the use of verifiable and documented wolverine occurrence records to define historical and present range as we have determined that these records constitute the best scientific information available on the past and present distribution of wolverines (see Aubry *et al*. 2007, p. 2148; McKelvey *et al*. 2008, entire). Verifiable records are records supported by physical evidence such as museum specimens, harvested pelts, DNA samples, and diagnostic photographs. Documented records are those based on accounts of wolverines being killed or captured. Use of only verifiable and documented records avoids mistakes of misidentification often made in eyewitness accounts of visual encounters of unrestrained animals in the wild. Visual-encounter records often represent the majority of occurrence records for elusive forest carnivores, and they are subject to inherently high rates of misidentification of the species involved, including wolverines (McKelvey *et al*. 2008, pp. 551-552). These misidentifications can result in wildly inaccurate conclusions about species occurrence (McKelvey *et al*. 2008, pp. 550-553).

Aubry *et al*. (2007, entire) used only verifiable and documented records to investigate wolverine distribution through time. This paper is the only available comprehensive treatment of these distribution patterns that attempts to distinguish between records that represent resident animals versus animals that have dispersed outside of suitable habitat. For these reasons, we find that Aubry *et al.* (2007, entire) represents the best available summary of wolverine occurrence records in the contiguous United States at this time. Since the publication of Aubry *et al*. (2007, entire), verified records of wolverines have also been documented in Colorado and California, which we will describe in greater detail below.

Aubry *et al*. (2007, entire) used verifiable and documented records from museum collections, literature sources, and State and Federal institutions to trace changes in geographic distribution of wolverines in the historical record. They then used an overlay of suitable wolverine habitats to determine which records represent wolverines in habitats that may support residency, and, by extension, populations, and which records likely represent wolverines outside the range of suitable habitats, so called "extralimital" records. Aubry *et al*.'s (2007, entire) focus on verifiable and documented records corrected past overly broad approaches to wolverine range mapping (Nowak 1973, p. 22; Hall 1981, p. 1009; Wilson 1982, p. 644; Hash 1987, p. 576), which used a more inclusive but potentially misleading approach when dealing with occurrence records. Many of the extralimital records used in these publications represented individuals that dispersed from natal ranges but ended up in habitats that could not support wolverines. Use of these data to determine the historical geographic range of wolverines results in gross overestimation of the area that can actually be used successfully by wolverines for the establishment of populations. Subsequent to publication of Aubry *et al*. (2007, entire), two publications (Copeland *et al*. 2010, entire; Brock *et al*. 2007, entire) further refined our understanding of wolverine habitat needs and corroborated the approach of Aubry *et al*. (2007, entire). Thus, despite the paucity of verifiable records, we now have strong information on the areas that are currently suitable to be occupied by wolverine based on habitat and climate conditions.

We agree with Aubry *et al*. (2007, p. 2149) that the most appropriate method to determine the current and historical range of wolverines is to use a combination of occurrence records and habitat suitability, along with other information, such as documented successful reproduction events, indicating where reproductive and potentially self-sustaining populations may occur. We also generally agree with their conclusions about the historical and current range of the species. We find that the species' range is

the area that may support viable populations, and does not include extralimital occurrences outside of habitat that is likely to support wolverine life-history needs. Areas that can support wolverine populations may be referred to as potential "source" populations because they provide surplus individuals through reproduction beyond what is needed for replacement. Areas that have some of the habitat attributes of wolverine habitat but do not have enough habitat to support viable populations may be referred to as population "sinks" because wolverines may disperse to these areas and remain for some time, but will either die there without reproducing, leave the area in search of better habitat conditions, or may actually reproduce, but at a rate lower than that needed for replacement of individuals lost to mortality or emigration, leading to eventual population extinction.

For a widely dispersing species like the wolverine, we expect many locality records to represent dispersal attempts into sink habitats or nonhabitat. The value to the population (and thus the DPS) of dispersers in these areas is unclear; it is likely that most dispersers into sink habitats or nonhabitat will be lost to the population unless they are able to move back into source habitats. Therefore, it is our conclusion that population sink areas and areas of non-wolverine habitat, here defined as places where wolverines may be found but where habitat is not suitable for long-term occupancy and reproduction, do not represent part of the species historical range and have little conservation value for the DPS, other than possibly serving as temporary stop-overs for attempted dispersers as they search for suitable habitats. Compared with broader approaches to defining historical geographic range, this focused approach (1) results in reducing the bias of extralimital dispersers and (2) concentrates conservation attention on areas capable of maintaining populations.

**Commented [O51]:** This statement seems inconsistent with statements elsewhere regarding the need for dispersal habitat and genetic exchange

Aubry *et al*. (2007, pp. 2147-2148) divided records into "historical" (recorded prior to 1961), "recent" (recorded between 1961 and 1994), and "current" (recorded after 1994). Historical records occurred before systematic surveys. Historical records encompass the time during which wolverine numbers and distribution were hypothesized to be at their highest (prior to European settlement) and also at their lowest (early 20$^{th}$ century) (Wright and Thompson 1935; Grinnell *et al*. 1937; Allen 1942; Newby and Wright 1955, all as cited in Aubry *et al*. 2007, p. 2148). The recent time interval covers a hypothesized population expansion and rebound from the early 20$^{th}$ century low. Current records offer the most recent evidence available for wolverine occurrences and potential populations. All occurrence records must be individually analyzed in light of their context in terms of habitat conditions conducive to wolverine population establishment and whether or not they occur clustered with other records, which might indicate that populations have historically occurred in the area. The authors of Aubry *et al.* (2007) did such an analysis as they compiled their records.

*Wolverine Distribution*

We assessed the historical, recent, and current distribution data for each of the regions below to determine the likelihood of the presence of historical populations (rather than extralimital dispersers). Of 729 mappable records (those records with precise location information) compiled by Aubry *et al*. (2007, p. 2150), 188 were from the historical time interval (see Table 1). The discussion below draws heavily from both Aubry *et al*. (2007, entire) and Copeland *et al*. (2010, entire).

Table 1. Wolverine records from three time periods from Aubry *et al*. 2007. Numbers represent total documented and verifiable records with the subset of those records that were verifiable in parentheses.

□Historical (<1964)□Recent (1961-1994)□Current (>1994)□□Northeast □13 (1)□0□0□□Upper Midwest□4 (2)□0□0□□Great Lakes□36 (4)□1□0□□Central Great Plains□71* (2)□1□0□□Rocky Mountains□147 (45)□332 (283)□215 (210)□□Pacific Coast□89 (14)□23 (15)□7□□TOTALS□362 (68)□357 (298)□222 (210)□□* 35 records from a single source (the journals of Alexander Henry).

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Northeast and Upper Midwest—The low number of records and scattered nature of their distribution combined with a lack of suitable habitat indicate that wolverines were likely only occasional transients to the area and not present as a reproducing population after 1800.

Great Lakes—The lack of large numbers of verifiable records in this area of relatively high human population density and the lack of suitable habitat suggests that wolverines did not exist in this area as a viable population after 1900. Widely scattered records generally before 1900, along with occasional subsequent records suggest that if a reproducing population existed in the Great Lakes, it predated 1900, and that any post-1900 records represent dispersal from a receding Canadian population. Wolverine distribution in Ontario, Canada, appears to have receded north from the Great Lakes region since the 1800s, and currently wolverines occupy only the northern portion of the province, a distance of over 644 km (400 mi) from the United States border (COSEWIC 2003, p. 9). The distribution pattern of record illustrated in Aubry *et al*. (2007, p. 2152) is consistent with what would be expected if those records were of dispersing individuals from a Canadian population that receded progressively further north into Canada after 1800, possibly due to natural climate changes (COSEWIC 2003, p. 28).

Central Great Plains—The lack of precise locality records and suitable habitat from the Great Plains States leads us to conclude that reproducing populations of wolverines did not historically inhabit this area. Of thirty-six records from North Dakota, 35 are from the journals of a single fur trader (see Table 1), and it is not clear that the records represent actual collection localities or are localities where trades or shipments occurred (Aubry 2007, pers. comm.). Given the habitat relationships of wolverines (e.g., Copeland *et al*. 2010, Figure 1), it is unlikely that these records represent established wolverines or that this area served as wolverine habitat.

Rocky Mountains—Five Rocky Mountains States (Idaho, Montana, Wyoming, Colorado, and Utah) contained numerous wolverine records. Records with precise locality information appear to coalesce around several areas that may have been population centers, such as central Colorado, the greater Yellowstone region, and northern Idaho-northwestern Montana. The large number of verifiable and documented records for this region, along with the suggestion of population centers or strongholds, suggests that wolverines existed in reproducing populations throughout much of the Rocky Mountains during the historical time interval. The lack of records for Colorado and Utah after 1921 suggests that the southern Rocky Mountains population of wolverines was extirpated in the early 1900s, concurrent with widespread systematic predator control by government agencies and livestock interests. The northern Rocky Mountains population (north of Wyoming) was reduced to historical lows or possibly even extirpated during the early 1900s, and then increased dramatically in the second half of the 1900s (see Table 1) as predator control efforts subsided and trapping regulations became more restrictive (Aubry *et al*. 2007, p. 2151). This increase likely indicates a population rebound from historical lows in this period.

Wolverine records from 1995 to 2005 indicate that wolverine populations currently exist in the northern Rocky Mountains (see Table 1). Legal trapping in Montana in the recent past removed an average of 10.5 individuals from this population each year (Montana Department of Fish, Wildlife, and Parks 2007, p. 2), but harvest mortality has been reduced due to regulatory changes in 2008 (Montana Department of Fish, Wildlife and Parks 2008, p. 8). Populations in British Columbia and Alberta, Canada, are extant (COSEWIC 2003, pp. 18-19), and may have been a source of surplus wolverines to the contiguous United States population during population lows. Recently, a male wolverine moved on its own from the southern Greater Yellowstone Area of Wyoming into the southern Rocky Mountains of Colorado, where it still persisted as of November 2012 (Inman *et al*. 2009, pp. 22-26; Odell 2012, pers. comm.). This attempted dispersal event is the first verified wolverine occurrence in Colorado since 1919 and may represent a continuation of the wolverine expansion in the Rocky Mountains detailed above. It is possible that other wolverines have traveled to the southern Rocky Mountains and have remained undetected. There is no evidence that Colorado currently hosts a wolverine population or that female wolverines have made, or are likely to make, similar movements. Female dispersal movements tend to be much shorter than males, usually occupying home ranges adjacent to their natal range, and dispersal is documented only for lesser distances than males routinely travel (Hornocker and Hash 1981, p. 1290; Copeland 1996, p. 91; Kyle and Strobeck 2001, p. 338; Tomasik and Cook 2005, p. 390; Cegelski *et al.* 2006, p. 206, Inman *et al*. 2011, p. 7). The largest documented female movement occurred in 2010 in the North Cascades of Washington (Aubry *et al*. 2011, pp. 21-22). In that instance, a radio-collared female wolverine moved an air-line distance of approximately 233 km (145 mi) over a 44-day period. During this movement, her course generally stayed within suitable wolverine habitat (as defined by Copeland *et al*. (2010, p. 242)) and was never more than about 19 km (12 mi) from suitable wolverine habitat.

**Commented [O52]:** Distance of ~300 km (airline kilometers) for an ear-tagged young female wolverine in Alaska (Magoun 1985, p. 55-57); although the ear-tags were not retrieved from the trapper, there was no one else tagging wolverines in NW Alaska or anywhere in Alaska, especially not with yellow ear tags.

**Commented [O53]:** Mulders 2000 documented movement of 225 km, and 4 other movements of 69, 83, 97, and 189 so these should be stated here because you do not define the term "much shorter than males" and you state they usually occupy ranges adjacent to their natal area; what distances do Males "routinely travel"; Flagstand et al. 2004 stated that both sexes have the capacity to disperse 100-200 km

**Commented [O54]:** This is not how I interpret the path of this female on a map of the snow cover layer; much of her course was outside the snow cover layer of Copeland et al. 2010, even though the 15 May MODIS snow cover habitat was near enough that she could have selected it but didn't.

Pacific Coast—Historical records show that wolverines occurred in two population centers in the North Cascades Range and the Sierra Nevada. However, records do not show occurrences between these centers from southern Oregon to northern California, indicating that the historical distribution of wolverines in this area is best represented by two disjunct populations rather than a continuous peninsular extension from Canada. This conclusion is supported by genetic data indicating that the Sierra Nevada and Cascades wolverines were separated for at least 2,000 years prior to extirpation of the Sierra Nevada population (Schwartz *et al*. 2007, p. 2174).

**Commented [O55]:** Most recent scientific data invalidate this statement; McKelvey et al. in review (K. Aubry, pers. comm..)

Only one Sierra Nevada record exists after 1930, indicating that this population was likely extirpated in the first half of the 1900s, concurrent with widespread systematic predator control programs. In 2008, a male wolverine was discovered in the Sierra Nevada Range of California, the first verified record from California since 1922 (Moriarty *et al*. 2009, entire). Genetic testing revealed that this wolverine was not a descendant of the endemic Sierra Nevada wolverine population, but was likely derived from wolverines in the Rocky Mountains (Moriarty *et al*. 2009, p. 159). This attempted dispersal event may represent a continuation of the wolverine expansion in the contiguous United States as detailed above. Other wolverines may have travelled to the Sierra Nevada and remain undetected. There is no evidence that California currently hosts a wolverine population or that female wolverines have made, or are likely to make, similar dispersal movements.

**Commented [O56]:** Contradicts statement above about isolation for 2000 years; why would one accept that they were isolated for 2000 years but can now disperse there in a modern era with more anthropogenic "barriers to dispersal"; but see comment 052 above

Wolverines were likely extirpated from the North Cascades in the early 20th century and then recently recolonized from Canada. Currently, a small population persists in this area (Aubrey *et al*. 2011, entire). In 2012, reproduction was documented for the first time in the North Cascades (Aubry *et*

*al*. 2012, p. 2). Wolverines have also been documented in the southern portion of the North Cascades, near Mount Adams, since 2009 (Akins 2010, p. 4). The North Cascades population may be connected with, and is possibly dependent on, the larger Canadian population for future expansion and long-term persistence.

**Commented [O57]:** Should say "is connected" since some of the home ranges and dispersal movements of tagged wolverines span the border

*Summary of Wolverine Distribution*

Historical wolverine records were found across the northern tier of the contiguous United States, with convincing evidence of wolverine populations in the northern and southern Rocky Mountains, Sierra Nevada Mountains, and North Cascades Mountains (Aubry *et al*. 2007, p. 2152).

Currently, wolverines appear to be distributed as functioning populations in two regions in the contiguous United States: the North Cascades in Washington, and the northern Rocky Mountains in Idaho, Montana, and Wyoming (this area also includes the Wallowa Range in Oregon). Wolverines were likely extirpated, or nearly so, from the entire contiguous United States in the first half of the 20th century (Aubry *et al*. 2007, Table 1). Although the reasons for this extirpation are not known with certainty, unregulated trapping and widespread indiscriminant predator control likely contributed to population declines. The available evidence suggests that, in the second half of the 20th century and continuing into the present time, wolverine populations have expanded in the North Cascades and the northern Rocky Mountains from sources in Canada, but that populations have not been reestablished in the Sierra Nevada Range or the southern Rocky Mountains, despite the known movement of single individual males to each of these areas. We conclude that the current range of the species in the contiguous United States includes the North Cascades Mountains, the northern Rocky Mountains, the

southern Rocky Mountains, and the Sierra Nevada Mountains, but that reestablishment of populations in the southern Rocky Mountains and Sierra Nevada Mountains has not yet occurred.

We also conclude that wolverines either did not exist as established populations, or were extirpated prior to settlement and the compilation of historical records, in the Great Lakes region, possibly due to climate changes that occurred through the 1800s and 1900s. The Great Lakes region lacks suitable wolverine habitat, and suitable habitat does not appear to exist in adjacent Canada (Copeland *et al.* 2010, Figure 1). The widely scattered records from this region are consistent with dispersing individuals from a Canadian population that receded north early in the 1800s. We cannot rule out the possibility that wolverines existed as established populations prior to the onset of trapping in this area, but we have no evidence of this.

**Commented [O58]:** What evidence do you base this on that specifically indicates that snow conditions (depth and timing) for denning changed from historical times; I've tried to chase this down but haven't succeeded

**Commented [O59]:** Or expansion of humans, which happened concurrently with warming temperatures; unfortunately, there actually is no conclusive evidence of climate change [ie., decrease in snow depth in the denning season and duration in the 1800s and 1900s] that would explain the disappearance of wolverines any better than expansion of human developments; warming temperatures do not necessarily mean less winter snow (Russ Brown, climatologist, pers. comm..)

No evidence in the historical records indicates that wolverines were ever present as established populations in the Great Plains, Midwest, or Northeast.

*Habitat Relationships and Wolverine Distribution*

Deep, persistent, and reliable spring snow cover (April 15 to May 14) is the best overall predictor of wolverine occurrence in the contiguous United States (Aubry *et al*. 2007, pp. 2152-2156; Copeland *et al.* 2010, entire). Deep, persistent snow correlates well with wolverine year-round habitat use across wolverine distribution in North America and Eurasia at both regional and local scales (Copeland *et al*. 2010, entire; Inman *et al*. 2012a, p. 785). It is uncertain why spring snow cover so accurately predicts wolverine habitat use; however, it is likely related to wolverines' need for deep

**Commented [O60]:** Define terms

**Commented [O61]:** From Aubry not Copeland

**Commented [O62]:** I disagree; see Attachment A

**Commented [O63]:** Dates are 24 April to 15 May from Copeland

**Commented [O64]:** "Deep" has not been defined; Copeland did not use depth. And on p. 785 of the Inman et al. paper cited, Inman only states "deep snow exists during winter"; when defining year-round habitat, Inman used distance to snow of depth >2.5 cm (Inman et al. 2013, Paper III, p. 6); no definition of what depth is required so it remains a subjective statement (see Attachment A for further discussion)

snow during the denning period. In addition, wolverines appear to take advantage of a cold, low-productivity niche by using food caching in cold habitats to survive food-scarce winters that other carnivores cannot (Inman *et al*. 2012b, pp. 640-642). Wolverines' physiological requirement for year-round cold temperatures may also play a role in habitat use (Copeland *et al*. 2010, pp. 242-243). Snow cover during the denning period is essential for successful wolverine reproduction range-wide (Hatler 1989, p. iv; Magoun and Copeland 1998, p. 1317; Inman *et al*. 2007c, pp. 71-72; Persson 2007; Copeland *et al*. 2010, p. 244). Wolverine dens tend to be in areas of high structural diversity such as logs and boulders with deep snow (Magoun and Copeland 1998, p. 1317; Inman *et al*. 2007c, pp. 71-72; Persson 2007, entire). Reproductive females dig deep snow tunnels to reach the protective structure provided by logs and boulders. This behavior presumably protects the vulnerable kits from predation by large carnivores, including other wolverines (Pulliainen 1968, p. 342; Zyryanov 1989, pp. 3-12), but may also have physiological benefits for kits by buffering them from extreme cold, wind, and desiccation (Pullianen 1968, p. 342, Bjärvall *et al*. 1978, p. 23). Wolverines live in low-temperature conditions and appear to select habitats in part to avoid high summer temperatures (Copeland *et al*. 2010, p. 242). Wolverine distribution is likely affected by climatic conditions at two different scales. Wolverines require deep persistent snow for denning, and this likely determines where wolverine populations can be found at the grossest range-wide scale (Copeland *et al*. 2010, p. 244). At smaller scales, wolverines likely select habitats to avoid high summer temperatures. These cool habitats also tend to retain snow late into spring, leading to wolverines' year-round association with areas of persistent spring snow (Copeland *et al*. 2010, p. 244).

All of the areas in the contiguous United States for which good evidence of persistent wolverine populations (either present or historical) exists (i.e., North Cascades, Sierra Nevada, northern and

**Commented [O65]:** Inman et al. 2012 proposes other plausible explanations (J of Mamm. , Vol. 93) and could be the more proximate factors explaining spring snow cover relationships to wolverine habitat use; in other words, do wolverines use areas with spring snow cover because they have to den in snow, or do they den in snow because they use areas with spring snow cover because of the resources and nature of competition and predation risk that occur there.

**Commented [O66]:** Summer temperatures in the Rockies and WA Cascades can hardly be considered "cold"; be specific on what this means; (i.e, average MAXIMUM August temperatures <22 degrees C?); there is no measure of upper thermal limits for wolverines and may not be the reason for the southern limit of wolverine distribution. Copeland e al. cites upper therrmal limits for arctic foxes (in winter pelage) as 26-28 degrees C because they overlap on wolverine range, but the fox study also shows that red foxes have an upper thermal limit (summer and winter pelages tested) of 30-32 degrees C and this species actually overlaps on more of the wolverine distribution than do arctic foxes. In other studies the thermoneutral zone of arctic animals extends from +30 degrees C to -30 degrees C (e.g., arctic fox and husky pups). However, the more important point is that all these studies are testing the animals at rest (or nearly so) and do not consider ways that animals deal with heat (besides resting and panting); e.g., shedding the winter coat; seeking cool places to rest; swimming; drinking water; waiting until late in the day to move around; exposing the thinly-furred areas; etc. Average daily minimum temperatures may have been a better metric for matching with wolverine distribution.

**Commented [O67]:** In the DPS not in the tundra areas

**Commented [O68]:** Again, define; can be as little as 1 m (or even less); is that "deep"?

**Commented [O69]:** I don't know of any reference that states that snow dens protect kits from predation by other wolverines; other wolverines have been documented in dens that have later failed to produce kits (Magoun 1985) a nd infanticide may happen in dens (Swedish study)

**Commented [O70]:** See comment 060 above; the data were not clear on this in Copeland et al. and the "low-temperatures" in wolverine habitat may be selected for other reasons (Inman et al. 2012 J. Mamm.)

**Commented [O71]:** Define deep; again, Copeland does not consider depth of snow

**Commented [O72]:** Other reasons have been proposed (Inman et al. 2012, J. Mamm.)

**Commented [O73]:** I don't see this mentioned on p. 244 specifically

southern Rocky Mountains) contain large and well-distributed areas of deep snow cover that persists through the wolverine denning period (Inman *et al*. 2011, Fig. 3; Aubry *et al*. 2007, p. 2154; Copeland *et al*. 2010, Figure 1). The Great Plains, Great Lakes, Midwest, and Northeast lack the spring snow conditions and low summer temperatures thought to be required by wolverines for successful reproduction and year-round occupancy (Aubry *et al*. 2007, p. 2154; Copeland *et al*. 2010, Figure 1). The lack of persistent spring snow conditions in the Great Plains, Great Lakes, Midwest, and Northeast supports the exclusion of these areas from the current range of wolverines. Whether wolverines once existed as established populations in any of these regions is uncertain, but the current climate appears to preclude their presence as reproducing populations, and the sparse historical record of wolverine presence in this area makes historical occupation of these areas by wolverine populations doubtful. It is our conclusion that the ecosystem that supports wolverines does not exist in these areas currently, and may not have existed at the time of European settlement of these areas.

**Commented [O74]:** But what is "deep" and what is the "denning period"; see detailed discussion in Attachment A

**Commented [O75]:** Contradicts Aubry et al. 2007 for the Great Lakes region, p. 2155; i.e., the Great Lakes region probably was the southern extent of wolverine range

Large areas of habitat with characteristics suitable for wolverines still occur in the southern Rocky Mountains and Sierra Nevada, despite the extirpation of wolverines from those areas (Aubry *et al*. 2007, p. 2154, Inman et al. 2011, Fig. 4; Copeland *et al*. 2010, Figure 1). Wolverine extirpations in these areas were coincident with unregulated trapping and systematic predator eradication efforts in the early 1900s, which have been discontinued for many years. Each of these areas has received at least one and possibly more migrants from adjacent populations in the northern Rocky Mountains; however, there is no evidence that females have migrated to these areas or that populations of wolverines currently exist there (Aubry *et al*. 2007, *Table 1*; Moriarty *et al*. 2009, entire; Inman *et al*. 2009, entire).

We conclude that areas of wolverine historical occurrence can be placed in one of three categories: (1) Areas where wolverines are extant as reproducing and potentially self-sustaining populations (North Cascades, northern Rocky Mountains); (2) areas where wolverines historically existed as reproducing and potentially self-sustaining populations prior to human-induced extirpation, and where reestablishment of those populations is possible given current habitat conditions and management (the Sierra Nevada Mountains in California and southern Rocky Mountains in Colorado, New Mexico, Wyoming, Uinta Mountains and surrounding ranges in Utah, Bighorn Mountains in Wyoming, and possibly the Oregon Cascades Mountains); and (3) areas where historical presence of wolverines in reproducing and potentially self-sustaining populations is doubtful, and where the current habitat conditions preclude the establishment of populations (Great Plains, Midwest, Great Lakes, and Northeast). We, therefore, consider the current range of wolverines to include suitable habitat in the North Cascades of Washington, the northern Rocky Mountains of Idaho, Wyoming, Montana, and eastern Oregon, the southern Rocky Mountains of Colorado and Wyoming, and the Sierra Nevada of California. We here include the Sierra Nevada and southern Rocky Mountains in the current range of wolverines despite the probability that functional populations do not exist in these areas. They are included due to the known existence of one individual in each area and the possibility that more, as yet undetected, individuals inhabit these areas.

**Distinct Population Segment**

Pursuant to the Act, we must consider for listing any species, subspecies, or, for vertebrates, any Distinct Population Segment (DPS) of these taxa, if there is sufficient information to indicate that such action may be warranted. To interpret and implement the DPS provision of the Act and Congressional

guidance, the Service and the National Marine Fisheries Service published, on February 7, 1996, an interagency Policy Regarding the Recognition of Distinct Vertebrate Population Segments under the Act (61 FR 4722). This policy addresses the recognition of DPSs for potential listing actions. The policy allows for more refined application of the Act that better reflects the biological needs of the taxon being considered, and avoids the inclusion of entities that do not require its protective measures.

Under our DPS policy, three elements are considered in a decision regarding the status of a possible DPS as endangered or threatened under the Act. These are applied similarly for additions to the list of endangered and threatened species, reclassification, and removal from the list. They are: (1) Discreteness of the population segment in relation to the remainder of the taxon; (2) the biological or ecological significance of the population segment to the taxon to which it belongs; and (3) the population segment's conservation status in relation to the Act's standards for listing (i.e., whether the population segment is, when treated as if it were a species or subspecies, an endangered or threatened species). Discreteness refers to the degree of isolation of a population from other members of the species, and we evaluate this factor based on specific criteria. If a population segment is considered discrete, we must consider whether the discrete segment is "significant" to the taxon to which it belongs by using the best available scientific and commercial information. If we determine that a population segment is both discrete and significant, we then evaluate it for endangered or threatened species status based on the Act's standards. The DPS evaluation in this proposed rule concerns the segment of the wolverine species occurring within the contiguous 48 States, including the northern and southern Rocky Mountains, Sierra Nevada Range, and North Cascades Range.

**Distinct Population Segment Analysis for Wolverine in the Contiguous United States**

*Analysis of Discreteness*

Under our DPS Policy, a population segment of a vertebrate species may be considered discrete if it satisfies either one of the following conditions: (1) It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors (quantitative measures of genetic or morphological discontinuity may provide evidence of this separation); or (2) it is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act (inadequacy of existing regulatory mechanisms). The wolverine within the contiguous United States meets the second DPS discreteness condition because of differences in conservation status as delimited by the Canadian-United States international governmental boundary.

In our 12-month finding for the North American wolverine DPS (75 FR 78030) we conducted a complete analysis of the discreteness of the wolverine DPS that we incorporate here by reference. In that analysis we concluded that the international boundary between Canada and the United States currently leads to division of the control of exploitation and conservation status of the wolverine. This division is significant because it allows for potential extirpation of the species within the contiguous United States through loss of small populations and lack of demographic and genetic connectivity of the two populations. This difference in conservation status is likely to become more significant in light of threats discussed in the five factors analyzed below. Therefore, we find that the difference in the conservation statuses in Canada and the United States result in vulnerability to the significant threat

(discussed below) in the U.S. wolverine population but not for the Canadian population. Existing regulatory mechanisms are inadequate to ensure the continued existence of wolverines in the contiguous United States in the face of these threats. Therefore, it is our determination that the difference in conservation status between the two populations is significant in light of section 4(a)(1)(D) of the Act, because existing regulatory mechanisms appear sufficient to maintain the robust conservation status of the Canadian population, while existing regulatory mechanisms in the contiguous United States are insufficient to protect the wolverine from threats due to its depleted conservation status. As a result, the contiguous United States population of the wolverine meets the discreteness criterion in our DPS Policy (61 FR 4725). Consequently, we use the international border between the United States and Canada to define the northern boundary of the contiguous United States wolverine DPS.

*Analysis for Significance*

If we determine a population segment is discrete, its biological and ecological significance will then be considered in light of Congressional guidance that the authority to list DPSs be used sparingly while encouraging the conservation of genetic diversity. In carrying out this examination, we consider available scientific evidence of the population's importance to the taxon to which it belongs (i.e., the North American wolverine (*Gulo gulo luscus*)). Our DPS policy states that this consideration may include, but is not limited to: (1) Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon; (2) evidence that loss of the discrete population segment would result in a significant gap in the range of the taxon; (3) evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an

introduced population outside its historical range; or (4) evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

In our 12-month finding (75 FR 78030), we conducted an exhaustive analysis of the significance of the contiguous United States population of the North American wolverine that we incorporate here by reference. In that analysis we concluded that the wolverine population in the contiguous United States is significant because its loss would result in a significant gap in the range of the taxon.

*Summary of the Distinct Population Segment Analysis*

We conclude that the wolverine population in the contiguous United States is both discrete and significant under our DPS policy. The conservation status of wolverines in the contiguous United States is less secure than wolverines in adjacent Canada due to fragmented habitat, small population size, reduced genetic diversity, and their vulnerability to threats analyzed in this finding. Loss of the contiguous United States wolverines would result in a significant gap in the range of the taxon. Therefore, we determine that the population of wolverines in the contiguous 48 States, as currently described, meets both the discreteness and significance criteria of our DPS policy, and is a listable entity under the Act as a DPS.

**Summary of Factors Affecting the Species**

Section 4 of the Act (16 U.S.C. 1533), and its implementing regulations at 50 CFR part 424, set forth the procedures for adding species to the Federal Lists of Endangered and Threatened Wildlife and Plants. Under section 4(a)(1) of the Act, we may list a species based on any of the following five factors: (A) The present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; and (E) other natural or manmade factors affecting its continued existence. Listing actions may be warranted based on any of the above threat factors, singly or in combination. Each of these factors is discussed below.

*Factor A. The Present or Threatened Destruction, Modification, or Curtailment of Its Habitat or Range*

Under Factor A we will discuss a variety of impacts to wolverine habitat including: (1) Climate change, (2) human use and disturbance, (3) dispersed recreational activities, (4) infrastructure development, (5) transportation corridors, and (6) land management. Many of these impact categories overlap or act in concert with each other to affect wolverine habitat. Climate change is discussed under Factor A because although climate change may affect wolverines directly by creating physiological stress, the primary impact of climate change on wolverines is expected to be through changes to the availability and distribution of wolverine habitat.

Two efforts to map wolverine habitat in the contiguous United States have been completed (Inman et al. 2012, entire; Copeland *et al*. 2010, entire). Both of these habitat models rely on snow as a primary input. The Copeland *et al*. (2010) model defines wolverine habitat as simply the area continuously covered by snow from mid-winter until mid-May. The Inman *et al*. (2012) model is based

**Commented [O76]:** No; it defines it as continuously cover by snow from 24 April (not mid winter) to mid-May in only 1 of 7 years from 2000-2006 as measured by MODIS (Version 4); and also states that the 15 May MODIS should be viewed as an "*approximation of underlying bioclimatic requirements*" (p. 244); see Attachment A

on snowpack and also incorporates other habitat variables, such as terrain ruggedness and some aspects of human development. The two models result in estimates of wolverine habitat that are very similar across most of the range of wolverines in the contiguous United States. Areas of significant departure between the models are the California Sierras and Oregon Cascades where the Copeland *et al*. (2010) model predicts significantly greater habitat area than does the Inman *et al*. (2012) model. Given the general agreement between the two models, we combined the areas depicted by them into a composite wolverine habitat model that includes all areas described by one or both of these models. This composite model serves as the basis for our estimates of wolverine habitat below. Within the four States that currently harbor wolverines (Montana, Idaho, Oregon (Wallowas) and Wyoming), an estimated 124,014 $km^2$ (47,882 $mi^2$) of wolverine habitat exists. Habitat in the North Cascades and Eastern Washington (Kettle Range and associated habitat) add approximately 20,356 $km^2$ (7859 $mi^2$). Ninety-four percent (135,396 $km^2$; 52,277 $mi^2$) of total wolverine habitat is in Federal ownership with most of that managed by the U.S. Forest Service (Forest Service).

**Commented [O77]:** None considered more important than another so snowpack should not be singled out

**Commented [O78]:** Primary /maternal habitat but not dispersal habitat; only Inman considers dispersal habitat

**Commented [O79]:** Not greater habitat area in general; just greater maternal habitat as it still has the same primary habitat for both models

**Commented [O80]:** State that these estimates do not include "dispersal habitat" as defined by Inman's map, or do they?

***Reduction in Habitat due to Climate Change***

Our analyses under the Act include consideration of ongoing and projected changes in climate. The terms "climate" and "climate change" are defined by the Intergovernmental Panel on Climate Change (IPCC). "Climate" refers to the mean and variability of different types of weather conditions over time, with 30 years being a typical period for such measurements, although shorter or longer periods also may be used (IPCC 2007, p. 78). The term "climate change" thus refers to a change in the mean or variability of one or more measures of climate (e.g., temperature or precipitation) that persists for an extended period, typically decades or longer, whether the change is due to natural variability,

human activity, or both (IPCC 2007, p. 78). Various types of changes in climate can have direct or indirect effects on species. These effects may be positive, neutral, or negative and they may change over time, depending on the species and other relevant considerations, such as the effects of interactions of climate with other variables (e.g., habitat fragmentation) (IPCC 2007, pp. 8–14, 18–19).

**Commented [O81]:** This would be a good place to mention what would be considered the timeframe for projecting climate effects on species; i.e., define "foreseeable future" as defined or used by the ESA

We recognize that there are scientific uncertainties on many aspects of climate change, including the role of natural variability in climate. In our analysis, we rely both on synthesis documents (e.g., IPCC 2007; Karl *et al*. 2009) that present the consensus view of a very large number of experts on climate change from around the world, and on five analyses that relate the effects of climate changes directly to wolverines (Gonzalez *et al*. 2008, entire; Brodie and Post 2009, entire; Peacock 2011, entire; McKelvey *et al*. 2011, entire, Johnston *et al*. 2012, entire). To date, McKelvey *et al*. (2011) is the most sophisticated analysis regarding climate change effects to wolverines. This report is based on data from global climate models including both temperature and precipitation, downscaled to reflect the regional climate patterns and topography found within the range of wolverines in the contiguous United States. For this reason we find that McKelvey *et al*. (2011, entire) represents the best scientific information available regarding the impacts of climate change to wolverine habitat.

**Commented [O82]:** I do not agree; See lengthy and detailed comments in Attachment A

Snowpack changes as well as concomitant changes to wolverine habitat suitability result from both changes in temperature (negative relationship) and changes in snowfall (positive relationship). Because many climate models predict higher precipitation levels associated with climate warming, the interaction between these two variables can be quite complex. Consequently, predictions about snow coverage that rely only on temperature projections are less reliable than those that rely on both

**Commented [O83]:** Changes in spring temperatures and their effect on NDVI may not all be negative; see Attachment A

temperature and precipitation. McKelvey *et al*. (2011, entire) report projections for wolverine habitat and dispersal routes through the time interval from 2070 to 2099.

Commented [O84]: Are these dates then considered to be "the foreseeable future" for projections of climate change on wolverine habitat; specifically, is "the foreseeable future" the end of the 21st century? McKelvey indicates that after that, projections are more uncertain

Climate Effects to Wolverines

Due to dependence of wolverines on deep snow that persists into late spring both for successful reproduction and for year-round habitat, and their restricted distribution to areas that maintain significant snow late into the spring season, we conclude that deep snow maintained through the denning period is required for wolverines to successfully live and reproduce. Reduction of this habitat feature would proportionally reduce wolverine habitat, or to an even greater extent if habitat reduction involved increasing fragmentation.

Commented [O85]: define

Commented [O86]: define

Commented [O87]: define, define, define, define

Commented [O88]: these two terms must be defined specifically, otherwise, it can be misinterpreted and there would be no way to determine when the conditions change because they were not defined from the start; strongly suggest a list of definitions of terms at the beginning of the document

Commented [O89]: probably not proportionally; some high elevation habitat not currently used by wolverines could become useable

Based on the information described above, we analyzed the effects of climate change on wolverines through three primary mechanisms: (1) Reduced snowpack and earlier spring runoff, which would reduce suitable habitat for wolverine denning; (2) increase in summer temperatures beyond the physiological tolerance of wolverines; and (3) ecosystem changes due to increased temperatures, which would move lower elevation ecosystems to higher elevations, thereby eliminating high-elevation ecosystems on which wolverines depend and increasing competitive interactions with species that currently inhabit lower elevations. These mechanisms would tend to push the narrow elevation band that wolverines use into higher elevation. Due to the conical structure of mountains, this upward shift would result in reduced overall suitable habitat for wolverines.

Commented [O90]: but over what time period; would this likely happen in the "foreseeable future" or beyond the 21st century when uncertainty increases concerning the effects of climate warming; my review of the literature does not show any evidence that a significant upward shift will occur in the foreseeable future; nor that an upward shift in tree line in mountain habitats will have a negative influence on wolverine habitat; your statement is supposition at this point and somewhat simplistic given the complexities of climate change in mountains and subsequent changes in mountain ecosystems; there is no indication at this point that wolverines will discontinue use of lower elevations

Reduced Snow Pack and Earlier Spring Runoff

Warmer winter temperatures are reducing snow pack in western North American mountains through a higher proportion of precipitation falling as rain and higher rates of snowmelt during winter (Hamlet and Lettenmaier 1999, p. 1609; Brown 2000, p. 2347; Mote 2003, p. 3-1; Christensen *et al*. 2004, p. 347; Knowles *et al*. 2006, pp. 4548-4549). This trend is expected to continue with future warming (Hamlet and Lettenmaier 1999, p. 1611; Christensen *et al*. 2004, p. 347; Mote *et al*. 2005, p. 48). Shifts in the initiation of spring runoff toward earlier dates are also well documented (Hamlet and Lettenmaier 1999, p. 1609; Brown 2000, p. 2347; Cayan *et al*. 2001, pp. 409-410; Christensen *et al*. 2004, p. 347; Mote *et al*. 2005, p. 41; Knowles *et al*. 2006, p. 4554). Earlier spring runoff leads to lack of snow or degraded snow conditions during April and May, the critical time period for wolverine reproductive denning. In addition, a feedback effect hastens the loss of snow cover due to the reflective nature of snow and the relative heat-absorbing properties of non-snow-covered ground. This effect leads to the highest magnitude of warming occurring at the interface of snow-covered and exposed areas, increasing the rate at which melting occurs in spring (Groisman *et al*. 1994a, pp. 1637-1648; Groisman *et al*. 1994b, pp. 198-200). Due to the importance of deep snow cover in spring for wolverine reproduction, currently suitable habitat that loses this feature would be rendered unsuitable for wolverines.

Ecosystem Changes Associated with Climate Change

Changes in temperature and rainfall patterns are expected to shift the distribution of ecosystems northward (IPCC 2007c, p. 230) and up mountain slopes (McDonald and Brown 1992, pp. 411-412; Danby and Hik 2007, pp. 358-359; IPCC 2007c, p. 232). As climate changes over a landscape, the

**Commented [O91]:** must define "winter"; a reduction in snowpack is not necessarily detrimental if it occurs late in the denning period and if reduction is not below what is required for wolverine denning; see Attachment A

**Commented [O92]:** not necessarily detrimental to wolverines see (Attachment A) or even perhaps to summer food items

**Commented [O93]:** I disagree that April and May comprise the "critical time period for wolverine reproductive denning"; see Attachment A; no evidence that May is critical

**Commented [O94]:** The definition of "deep" and "spring" is very important in this discussion because the data must show that the reduction in snow pack and melt must occur at a time and at a level that would affect wolverine denning and neither of these papers present evidence that this is likely to happen in the 21st century or perhaps longer; see Attachment A

**Commented [O95]:** It is very important when discussing reduction in snow pack and spring melt that the time periods and the amounts relative to wolverine denning are defined specifically; in other words, how much of a reduction in snow pack and when? How soon is the spring snow melt and how does it affect wolverines, either positively or negatively; see Attachment A; the general concensus of the papers that you cite and others that I have read indicates that there will be more snow in winter and an earlier spring melt and this is not necessarily detrimental to wolverines (Attachment A). Even more rain-on-snow events may not be detrimental because this is quite common in wolverine habitat in SE Alaska where we have documented one of the highest reported densities of wolverines

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**Commented [O96]:** The goal of McDonal and Brown 1992 was "not to make definitive predictions about future extinctions" but to present one model that could be used "*given certain assumptions"* and p. 411-412 is simply a list of the assumptions

**Commented [O97]:** Danby and Hik 2007 show that advancement of spruce did not occur on north-facing slopes, only density of the stands; an increase in elevation and density on south-facing slopes only in high mountain areas cannot be interpreted as a negative impact on wolverines without evidence of what the direct detrimental effects would be, or for that matter, possible beneficial effects such as nmore trees for cover, for more avalanche debris, fallen trees for den sites, etc.

**Commented [O98]:** Very important here to talk about the timeframe for these changes and at what level the change has to occur before it affects wolverines or the ecosystem features important to wolverines. As mentioned in the next sentence, there are time lags, so what are the projected time lags relative to the features of wolverine habitat that matter? Are they decades or centuries? And what is the timeframe relative to the certainty of the climate models? The cited literature does not indicate an imminent DEGREE OF change in ecosystems RELATIVE TO WOLVERINE HABITAT FEATURES THAT ARE LIKELY TO AFFECT WOLVERINE POPULATIONS at least in the 21st century. For example, McDonald and Brown 1992, referring to smaller mammals, acknowledged that more complex models might give more accurate predictions of extinctions in mountain regions with climate warming in their model, but "it is beyond the scope of this simple heuristic exercise. Given the uncertainties in the expected magnitude and kind of climatic change, there is little justification for going to the effort of constructing a more elaborate model at present." Hall and Fagre 2003 emphasize the uncertainty in their models: "The pattern is more varied than we hypothesized, however. Rather than predicting clear bands of vegetation progressing altitudinally, the model predicts considerable spatial variation in the distributions." "In the carbon dioxide–doubling scenario, forests reach their maximum extent around 2020–2050 and decline for 4 ...

ecosystems that support wolverines are likely to move according to the change of temperature, but with a time lag depending on the ability of individual plant species to migrate (McDonald and Brown 1992, pp. 413-414; Hall and Fagre 2003, p. 138; Peterson 2003, p. 652). Wolverines are not dependent on any particular ecosystem in the sense that they do not appear to depend on a certain vegetative component or other biological ecosystem attribute; however, it is likely that wolverines would respond to similar climatic cues as other members of the alpine ecosystem such that changes in tree-line location up or down slope would predict a similar change in wolverine distribution. Because of their reliance on mountainous habitat, wolverines in the contiguous United States will most likely adjust to climate changes by using higher elevations on mountain slopes, not by shifting their latitudinal distribution. Along a latitudinal gradient through the historical distribution of wolverines, records tend to be found at higher elevations in southern latitudes (Aubry *et al*. 2007, p. 2153), suggesting that wolverines compensate for increased temperature at low latitudes by selecting higher elevations. Therefore, the regional availability of suitable habitat is not likely to significantly change (i.e., at least some wolverine habitat will continue to be available in all regions where wolverines currently occur), but within these landscapes, smaller areas will remain suitable for wolverines. Mountain ranges with maximum elevations within the elevation band that wolverines currently use, such as much of the wolverine habitat in central Idaho, may become entirely unsuitable for wolverines with the projected level of warming reported in McKelvey *et al*. (2011, Figure 3; see below for discussion).

Timing of Climate Effects

Unlike snow conditions, which respond directly to temperature change without a time lag, ecosystem responses to temperature change do lag, with the magnitude of the lag depending on

**Commented [O99]:** What is the time lag relative to wolverines not plant species???

**Commented [O100]:** The literature you cite and other papers indicate that effects of climate change on mountain habitat in the western states is not clear , either on snow or on vegetation, especially at regional or local scales; moreover, changes in tree-line in the foreseeable future are more related to changes in density of trees and changes in types of tree stands, not by appreciable advances in forest cover up-slope; again, without discussing the exact changes relative to what wolverines use now and the timeframe in which they are predicted to occur, the generalizations stated in this section are not elucidating relative to "Ecosystem Changes Associated with Climate Change" and you do not discuss ecosystem changes that could be positive (e.g. NDVI in spring; bigger trees that provide large down logs for dens or mor avalanche debris fields with larger trees, etc).

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**Commented [O101]:** This does not agree with Copeland et al. 2007 where elevations range to 3,279 m but use by wolverines was in a band up to 2,600 m

**Commented [O102]:** See Attachment A

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constituent species' individual migratory abilities. Wolverines are described as a "tree-line" species because they are most often found in an elevation band that is approximately centered on the alpine tree-line at any given locality within their range (Inman *et al*. 2012a, p. 785). Alpine tree lines are maintained by a complex set of climactic and biotic factors, of which temperature is significantly important (Cogbill and White 1991, p. 169; Hättenschwiler and Körner 1995, p. 367; Jobbágy and Jackson 2000, p. 259; Pellat *et al*. 2000, pp. 80-81). However, the conditions that favor tree establishment and lead to elevation advance in the tree line may exist only sporadically, increasing time lags associated with tree line response to warming beyond the species-specific generation time of the trees involved (Hessl and Baker 1997, p. 181; Klasner and Fagre 2002, p. 54). Within wolverine habitats, tree lines have advanced up mountain slopes since 1850, due to climate warming, and this trend is expected to continue into the future (Hessl and Baker 1997, p. 176; Hall and Fagre 2003, p. 138). We expect that species reliant on resources associated with this biome, such as wolverines, will need to shift accordingly, not necessarily due to their dependence on the specific vegetation conditions, but due to wolverines likely being keyed into similar climatic variables. Since wolverine association with tree-line location is likely coincident with their dependence on climatic conditions, and the fact that wolverines can move about in response to climate changes, it is not likely that wolverines would respond to climate changes with a similar time lag. More likely, wolverines would respond to climate changes in real time, shifting habitat use more rapidly than tree-line shifts would occur. Given the irregular nature of tree-line response to warming, tree-line migration is likely to lag behind the climate warming that causes it.

Magnitude of Climate Effects on Wolverine

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**Commented [O103]:** I see no reference to advance of tree line on p. 176 or in the body of the reference cited here; this study was for tree invasion in patch forest openings at treeline not advancement of treeline; furthermore, the study was equivocal on whether even this invasion, if climate driven, would continue; please be sure to use citations that support your statements

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**Commented [O104]:** This study concerns the melting of glaciers in Glacier National Park and the predicted change in vegetation; from Fig. 7 it is possible to conclude that a net increase in wolverine habitat should occur where before much of the area was covered in ice; since, as you state, there are no studies that indicate a particular vegetation type to which wolverines are tied, and presuming the snow depth will still be >1m in winter in this area, this paper does not appear to support a reduction in wolverine habitat, simply a revegetation of land that was once covered in ice and possibly an increase in wolverine habitat including denning habitat

**Commented [O105]:** Wolverines may increase use of more of the high elevation habitat with an upward shift in treeline, but that doesn't mean they will decrease the use of lower elevations that are currently forested, especially since no one has addressed why wolverines would stop using lower elevation habitats; no studies on changes in wolverine habitat due to climate warming are addressing the changes that occur at lower elevations (or even the present day use of lower elevation forests by wolverines); it is much too simplistic to assume that because wolverines have been defined by some as a "treeline" species, that any advance of treeline will will reduce wolverine habitat, since wolverines have also been described as a species that does not depend on any particular vegetation type

**Commented [O106]:** See Attachment A (entire) for detailed discussion of McKelvey et al. 2011 and the science on which they base their conclusions

Several studies relating the effects of climate changes on wolverines in the past, present, and future are now available (Brock and Inman Personal Communication 2007, entire; Gonzales *et al*. 2008, pp. 1-5; Brodie and Post 2010, entire; McKelvey *et al*. 2011, entire; Peacock 2011, entire; Johnston *et al*. 2012, entire). The Gonzalez *et al*. report and the report by Brock and Inman (Personal Communication 2007) were both preliminary attempts to analyze climate change impacts to wolverines, but are not currently considered the best available science because they did not consider the effects of both changes in temperature and precipitation that may affect the distribution of persistent spring snow cover (McKelvey 2011, entire). The analysis by Peacock (2011) is a sophisticated look at climate change impacts to wolverines, but suffers from the large-scale data presentation used. This large scale makes relating specific impacts to wolverines difficult, because the montane habitat inhabited by wolverines is climatologically complex on a small scale, and without significant downscaling of climate results, it is not possible to determine how much habitat may be left after climate change impacts have occurred. Both Brock and Inman (Personal Communication 2007) and Gonzalez *et al.* (2008) have been superseded by a more sophisticated analysis provided by McKelvey *et al.* (2011, entire). The course-grain scale of the analysis in Peacock (2011, entire) limits its use to that of supporting the conclusion that wolverine habitat is likely to decline. Likewise, the limited area analyzed by Johnston *et al*. (2012) also limits its use for this wide-ranging species. The McKelvey *et al.* (2011, entire) analysis includes climate projections at a local scale for wolverine habitats and analyzes the effects of both temperature changes and changes to precipitation patterns. Lack of accounting for changes in precipitation was a weakness of their own work cited by the authors of both Brock and Inman (Personal Communication 2007) and Gonzalez *et al.* (2008).

Brodie and Post (2010, entire) correlate the decline in wolverine populations in Canada over the past century with declining snowpack due to climate change over the same period. However, correlation does not infer causation; other factors could have caused the decline. The Brodie and Post (2010, entire) analysis used harvest data to infer population trends in addition to its reliance on correlation to infer causation (McKelvey *et al*. 2010a, entire); in this case, historic climate changes are inferred to have caused the declines in harvest returns, which are thought by the authors to reflect actual population declines. Due to the above-stated concerns, we view the analysis of Brodie and Post (2010, entire) with caution, although we do agree that the posited mechanism, of loss of snowpack affecting wolverine populations and distribution, likely has merit.

McKelvey *et al*. (2011, entire) used downscaled global climate models to project the impacts of changes in temperature and precipitation to wolverine habitat as modeled by Copeland *et al*. (2010, entire). The authors also present an alternative method for evaluating climate impacts on wolverine habitat, by merely projecting onset of spring snowmelt to occur 2 weeks earlier than it currently does. Based on this information, wolverine habitat in the contiguous United States, which supports approximately 250 to 300 wolverines, is shrinking and is likely to continue to shrink with increased climate warming (McKelvey *et al*. 2011, Figure 4). Habitat losses are likely to occur throughout the range of the DPS and are projected to be most severe in central Idaho. However, large areas of snow cover are likely to remain in the North Cascades, Greater Yellowstone Area (GYA), and the Glacier Park-Bob Marshall Wilderness of Montana (McKelvey *et al*. 2011 Figures 4, 13). The southern Rocky Mountains of Colorado retained significant high-elevation snow in some models but not others, and so may be another area that could support wolverine populations in the face of climate changes (McKelvey *et al*. 2011, p. 2889).

**Commented [O107]:** Based on erroneous biological assumptions about wolverine denning requirements; see full discussion in Attachment A

Overall, wolverine habitat in the contiguous United States is expected to get smaller and more highly fragmented as individual habitat islands become smaller and the intervening areas between wolverine habitats become larger (McKelvey *et al*. 2011, Figures 4, 13). McKelvey et al. (2011) predict that 31 percent of current wolverine habitat in the contiguous United States will be lost due to climate warming by the time interval centered on 2045 (2030-2059) (McKelvey *et al*. 2011, pp. 2887-2888). That loss expands to 63 percent of wolverine habitat by the time interval centered on 2085 (2070 to 2099). Estimates for the northern Rocky Mountain States (Montana, Idaho, and Wyoming) are similar, with an estimated 32 percent and 63 percent of persistent spring snow lost for the 2045 and 2085 intervals respectively. Central Idaho is predicted to be especially sensitive to climate change effects losing 43 percent and 78 percent of wolverine habitat for the 2045 and 2085 intervals respectively. Conversely, the mountains of Colorado appear to be slightly less sensitive to climate changes in their analysis losing 31 percent and 57 percent of habitat over the same intervals. Given the spatial needs of wolverines and the limited availability of suitable wolverine habitat in the contiguous United States, this projected gross loss of habitat area is likely to result in a loss of wolverine numbers that is greater than the overall loss of habitat area.

**Commented [O108]:** Predictions are questionable because the basis of the model (critical snow requirements) is in error; Appendix A

We expect wolverine populations to be negatively affected by changes in the spatial distribution of habitat patches as remaining habitat islands become progressively more isolated from each other due to climate changes (McKelvey *et al*. 2011, Figure 8). Currently, wolverine habitat in the contiguous United States can be described as a series of habitat islands. Some of these groups of islands are large and clumped closely together, such as in the North Cascades, Glacier Park-Bob Marshall Wilderness complex in Montana, and the GYA. Other islands are smaller and more isolated, such as the island

mountain ranges of central and southwestern Montana. Inbreeding and consequent loss of genetic diversity have occurred in the past within these smaller islands of habitat (Cegelski *et al*. 2006, p. 208), and genetic exchange between subpopulations is difficult to achieve (Schwartz *et al*. 2009, Figure 4). Climate change projections indicate that, as warming continues, large contiguous blocks of habitat will decrease in size and become isolated to the extent that their ability to support robust populations becomes questionable (McKelvey *et al*. 2010b, Figure 8). Under the moderate climate change scenarios analyzed by McKelvey *et al*. (2011, entire), the current wolverine stronghold in central Idaho begins to look similar to the current situation in the more isolated mountain ranges of southwestern Montana (McKelvey *et al*. 2011, Figure 4) where wolverines persist, but subpopulations are small. These subpopulations are essentially family groups, which require connectivity with other groups for genetic and possibly demographic enrichment. This habitat alteration would result in a high likelihood of reduced genetic diversity due to inbreeding within a few generations (Cegelski *et al*. 2006, p. 209). Further isolation of wolverines on small habitat islands with reduced connectivity to other subpopulations would also increase the likelihood of subpopulations loss due to demographic stochasticity, impairing the functionality of the wolverine metapopulation in the contiguous United States.

**Commented [O109]:** Based on erroneous assumptions about habitat requirements for wolverines in the denning and den abandonment seasons; see Attachment A

We find that McKelvey *et al*. (2011, entire) represents the best available science for projecting the future impacts of climate change on wolverine habitat for four primary reasons. First, their habitat projections are based on global climate models that are thought to be the most reliable predictors of future climate available (IPCC 2007a, p. 12). Second, they conducted downscaling analyses to infer geographic climate variation at a scale relevant to wolverine habitat. Third, they used a hydrologic model to predict snow coverage during the spring denning period (the strongest correlate with

wolverine reproductive success). Fourth, they used the habitat model developed by Copeland *et al.* (2010, entire), to relate projected climate changes to wolverine habitat. Based on our analysis of the methods and analysis used by the authors, we conclude it constitutes the best available information on the likely impact of climate change on wolverine distribution in the contiguous United States. Other analyses of climate change discussed above (Brock and Inman Personal Communication 2007, entire; Gonzales *et al.* 2008, entire; Brodie and Post 2010, entire; Peacock 2011, entire) all support the conclusion that climate changes caused by warming are likely to negatively affect wolverine habitat in the future. Based on the analysis presented, we conclude that climate changes are likely to result in permanent loss of a significant portion of wolverine habitat in the future. Additional impacts of climate change will be increased habitat fragmentation as habitat islands become smaller and intervening habitat disappears. Eventually, habitat fragmentation will likely lead to a breakdown of wolverine metapopulation dynamics, as subpopulations are no longer able to rescue each other after local extinctions due to a lack of connectivity. It is also likely that loss of genetic diversity resulting in lower fitness will occur as population isolation increases.

**Commented [O110]:** See comment 101 above

*Summary of Impacts of Climate Changes*

Wolverine habitat is projected to decrease in area and become more fragmented in the future as a result of climate changes that result in increasing temperatures, earlier spring snowmelt, and loss of deep, persistent, spring snowpack. These climate change impacts are expected to have direct and indirect effects to wolverine populations in the contiguous United States including reducing the number of wolverines that can be supported by available habitat and reducing the ability of wolverines to travel between patches of suitable habitat. This reduction in population size and connectivity is likely to

**Commented [O111]:** Predictions of increases in winter snow and an earlier spring melt in the mountains of the western United States do not support this conclusion for the period when wolverines den (Feb-April) (see detailed discussion in Attachment A)

affect metapopulation dynamics, making it more difficult for subpopulations to recolonize areas where wolverines have been extirpated and to bolster the genetics or demographics of adjacent subpopulations.

***Habitat Impacts Due to Human Use and Disturbance***

Because wolverine habitat is generally inhospitable to human use and occupation and most wolverine habitat is also federally managed in ways that must consider environmental impacts, wolverines are somewhat insulated from impacts of human disturbances from industry, agriculture, infrastructure development, or recreation. Human disturbance in wolverine habitat in the contiguous United States has likely resulted in the loss of some minor amount of wolverine habitat, although this loss has not yet been quantified. Sources of human disturbance to wolverines has been speculated to include winter and summer recreation, housing and industrial development, road corridors, and extractive industry, such as logging or mining. In the contiguous United States, these human activities and developments sometimes occur within or immediately adjacent to wolverine home ranges, such as in alpine or boreal forest environments at high elevations on mountain slopes. They can also occur in a broader range of habitats that are occasionally used by wolverines during dispersal or exploratory movements—habitats that are not suitable for the establishment of home ranges and reproduction.

Little is known about the behavioral responses of individual wolverines to human presence, or about the species' ability to tolerate and adapt to repeated human disturbance. Some speculate that disturbance may reduce the wolverine's ability to complete essential life-history activities, such as foraging, breeding, maternal care, routine travel, and dispersal (Packila *et al*. 2007, pp. 105-110).

However, wolverines have been documented to persist and reproduce in areas with high levels of human use and disturbance including developed alpine ski areas and areas with motorized use of snowmobiles (Heinemeyer 2012, entire). This suggests that wolverines can survive and reproduce in areas that experience human use and disturbance. How or whether effects of disturbance extend from individuals to characteristics of subpopulations and populations, such as vital rates (e.g., reproduction, survival, emigration, and immigration) and gene flow, and ultimately to wolverine population or metapopulation persistence, remains unknown at this time.

Wolverine habitat is characterized primarily by spring snowpack, but also by the absence of human presence and development (Hornocker and Hash 1981 p. 1299; Banci 1994, p. 114; Landa *et al*. 1998, p. 448; Rowland *et al*. 2003 p. 101; Copeland 1996, pp. 124-127; Krebs *et al*. 2007, pp. 2187-2190). This negative association with human presence is sometimes interpreted as active avoidance of human disturbance, but it may simply reflect the wolverine's preference for cold, snowy, and high-elevation habitat that humans avoid. In the contiguous United States, wolverine habitat is typically associated with high-elevation (e.g., 2,100 m to 2,600 m (6,888 ft to 8,528 ft)) subalpine forests that comprise the Hudsonian Life Zone (weather similar to that found in northern Canada), environments not typically used by people for housing, industry, agriculture, or transportation. However, a variety of activities associated with extractive industry, such as logging and mining, as well as recreational activities in both summer and winter are located in a small amount of occupied wolverine habitat.

For the purposes of this rulemaking, we analyze human disturbance in four categories: (1) Dispersed recreational activities with primary impacts to wolverines through direct disturbance (e.g., snowmobiling and heli-skiing); (2) disturbance associated with permanent infrastructure such as

**Commented [O112]:** Define "high levels" of human use; areas with motorized snowmobile use cannot be classified as high use relative to developed areas through which wolverines might have to disperse, especially since snowmobile use is usually daylight hours only compared to major highways and housing developments; perhaps better to say "periodic" high levels of use

**Commented [O113]:** I couldn't find anything in this reference to support this statement; do you mean Heinemeyer and Squires 2012

**Commented [O114]:** Results of this project are not finalized but in Heinemeyer and Squires 2012, the authors state that they have only a small sample of wolverines in areas exposed to highly recreated landscapes and that "one female we have monitored for 3 years in a highly recreated landscape attempted to den but failed in the first year and has not denned in the subsequent 2 years of monitoring." P. 17; they go on to say they need more data on females in highly recreated areas; this suggests there could be problems with these landscapes but it still has to be sorted out

**Commented [O115]:** Define; Copeland did not measure spring snowpack; Inman's model included many other factors

**Commented [O116]:** Add Inman 2013 papers

residential and commercial developments, mines, and campgrounds; (3) disturbance and mortality associated with transportation corridors; and (4) disturbance associated with land management activities such as forestry, or fire/fuels reduction activities. Overlap between these categories is extensive, and it is often difficult to distinguish effects of infrastructure from the dispersed activities associated with that infrastructure. However, we conclude that these categories account for most of the human activities that occur in occupied wolverine habitat.

Dispersed Recreational Activities

Dispersed recreational activities occurring in wolverine habitat include snowmobiling, heli-skiing, hiking, biking, off- and on-road motorized use, hunting, fishing, and other uses.

One study documented (in two reports) the extent that winter recreational activity spatially and temporally overlapped modeled wolverine denning habitat in the contiguous United States (Heinemeyer and Copeland 1999, pp. 1-17; Heinemeyer *et al*. 2001, pp. 1-35). This study took place in the Greater Yellowstone Area (GYA) in an area of high dispersed recreational use. The overlap of modeled wolverine denning habitat and dispersed recreational activities was extensive. Strong temporal overlap existed between snowmobile activity (February–April) and the wolverine denning period (February–May). During 2000, six of nine survey units, ranging from 3,500 to 13,600 (ha) (8,645 to 33,592 (ac)) in size, showed evidence of recent snowmobile use. Among the six survey units with snowmobile activity, the highest use covered 20 percent of the modeled denning habitat, and use ranged from 3 to 7 percent over the other survey units. Snowmobile activity was typically intensive where detected.

Three of nine survey units in this study showed evidence of skier activity (Heinemeyer and Copeland 1999, p. 10; Heinemeyer *et al*. 2001, p. 16). Among the three units with activity, skier use covered 3 to 19 percent of the survey unit. Skiers also intensively used the sites they visited. Combined skier and snowmobile use covered as much as 27 percent of potential denning habitat in one unit where no evidence of wolverine presence was detected. We conclude from this study that in some areas, high recreational use may coincide substantially with wolverine habitat. The authors of the study cited above chose the study area based on its unusually high level of motorized recreational use. Although we do not have information on the overlap of wolverine and winter recreation in the remaining part of the contiguous United States range, it is unlikely that any of the large areas of wolverine habitat such as the southern Rocky Mountains, Northern Rocky Mountains, GYA, or North Cascades get the high levels of recreational use seen in the portion of the GYA examined in this study across the entire landscape. Rather, each of these areas has small (relative to wolverine home range size) areas of intensive recreational use (ski resorts, motorized play areas) surrounded by a landscape that is used for more dispersed recreation such as backcountry skiing or snowmobile trail use.

Although we can demonstrate that recreational use of wolverine habitat is heavy in some areas, we do not have any information to suggest that these activities have negative effects on wolverines. No rigorous assessments of anthropogenic disturbance on wolverine den fidelity, food provisioning, or offspring survival have been conducted. Disturbance from foot and snowmobile traffic associated with historical wolverine control activities (Pulliainen 1968, p. 343), and field research activities, have been purported to cause maternal females to abandon natal dens and relocate kits to maternal dens (Myrberget 1968, p. 115; Magoun and Copeland 1998, p. 1316; Inman *et al*. 2007c, p. 71). However, this behavior appears to be rare, even under intense disturbance associated with capture of family

**Commented [O117]:** perhaps for natal dens, depending on type of disturbance, but not for maternal dens (e.g., Magoun and Copeland 1998 p. 1318)

groups at the den site (Persson et al. 2006, p. 76), and other causes of den abandonment may have acted in these cases. Preliminary results from an ongoing study on the potential impacts of winter recreation on wolverines in central Idaho indicate that wolverines are present and reproducing in this area in spite of heavy recreational use, including a developed ski area, dispersed winter and summer recreation, and dispersed snowmobile use (Heinemeyer *et al*. 2012, entire). The security of the den and the surrounding foraging areas (i.e., protection from predation by carnivores) is an important aspect of den site selection. Abandonment of natal and maternal dens may be a preemptive strategy that females use in the absence of predators (i.e. females may abandon dens without external stimuli), as this may confer an advantage to females if prolonged use of the same den makes that den more evident to predators. Evidence for effects to wolverines from den abandonment due to human disturbance is lacking. The best scientific information available does not substantiate dispersed recreational activities as a threat to wolverine.

Most roads in wolverine habitat are low-traffic volume dirt or gravel roads used for local access. Larger, high-volume roads are dealt with below in the section "transportation corridors. At both a site-specific and landscape scale, wolverine natal dens were located particularly distant from public (greater than 7.5 km (4.6 mi)) and private (greater than 3 km (1.9 mi)) roads (May 2007, p. 14-31; Dawson et al. 2010). Placement of dens away from public roads (and away from associated human-caused mortality) was also a positive influence on successful reproduction. It is not known if the detected correlation is due to the influence of the roads but we find it unlikely that wolverines avoid the type of low-use forest roads that generally occur in wolverine habitat. Other types of high-use roads are rare in wolverine habitat and are not likely to affect a significant amount of wolverine habitat (see transportation corridors section below).

**Commented [O118]:** Not sure what you mean here; Persson was not referring to capture of family groups at a den site in this case; just examining on the ground to verify a den; capture was later at rendezvous sites; digging young from dens almost always resulted in den abandonment (Magoun, personal observation and Persson, personal commun.)

**Commented [O119]:** I don't know of a reference that suggests females select *foraging areas* for security from predators, just dens

**Commented [O120]:** No references for this statement; doesn't explain why some females use the same den throughout the denning season; I doubt if this statement is true

**Commented [O121]:** But wolverines have been hit and killed on such roads, including forestry roads in Ontario and the pipeline haul road in northern Alaska

**Commented [O122]:** Doesn't this statement contradict the one above that states that natal dens are located away from roads? Generalization about roads is probably not advisable because avoidance of roads depends on the density of roads (and probably activity level); see Bowman et al. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. C. J. Zool. 88:454-467.

Infrastructure Development

Infrastructure includes all residential, industrial, and governmental developments such as buildings, houses, oil and gas wells, and ski areas. Infrastructure development on private lands in the Rocky Mountain West has been rapidly increasing in recent years and is expected to continue as people move to this area for its natural amenities (Hansen *et al*. 2002, p. 151). Infrastructure development may affect wildlife directly by eliminating habitats, or indirectly, by displacing animals from suitable habitats near developments.

**Commented [O123]:** Or inhibiting dispersal

Wolverine home ranges generally do not occur near human settlements, and this separation is largely due to differential habitat selection by wolverines and humans (May *et al*. 2006, pp. 289-292; Copeland *et al*. 2007, p. 2211). In one study, wolverines did not strongly avoid developed habitat within their home ranges (May *et al* 2006, p. 289). Wolverines may respond positively to human activity and developments that are a source of food. They scavenge food at dumps in and adjacent to urban areas, at trapper cabins, and at mines (LeResche and Hinman 1973 as cited in Banci 1994 p. 115; Banci 1994, p. 99). Based on the best available science, we conclude that wolverines do not avoid human development of the types that occur within suitable wolverine habitat.

**Commented [O124]:** What does near mean? On the outskirts of town? Within 2, 5, or 10 km? doesn't it depend on how near the settlement is to wolverine habitat? And also what the surrounding area consists of? In wolverine habitat in Ontario, the effect is not due to differential habitat selection by wolverines and humans (they occur in the same habitat); also depends on whether wolverines are trapped in the area or not

**Commented [O125]:** Unlike your definition of infrastructure above, May differentiates between infrastructure and human development; i.e., "Within their home ranges wolverines used the available area *randomly with regard to infrastructure*. The available habitat within their home ranges tended to be used *non-randomly with regard to human development*"

**Commented [O126]:** doesn't this contradict your statement above that they do not occur near human settlements (generally)

There is no evidence that wolverine dispersal is affected by infrastructure development. Linkage zones are places where animals can find food, shelter, and security while moving across the landscape between suitable habitats. Wolverines prefer to travel in habitat that is most similar to habitat they use for home-range establishment, i.e., alpine habitats that maintain snow cover well into the

**Commented [O127]:** what do you mean by "affected by"; the dispersing wolverine moving to Colorado avoided a small subdivision and moved around it; what would have been the effect if a much larger area was covered in subdivisions, etc.; would the dispersal not have happened through that area? Wouldn't that have affected dispersal? How would you prove that wolverines are not affected by infrastructure? You can't prove what you can't observe if wolverines are avoiding infrastructure (e.g., large towns).

**Commented [O128]:** if this is true, why did the young female wolverine Eowyn (Northern Cascades study) disperse through habitat that did not fall in the snow cover layer that Schwartz et al. 2009 states they should prefer during dispersal; this wolverine had areas defined by the Copeland snow layer <20 km to the east and west of where she dispersed, yet much of her dispersal appeared to be outside of the "preferred" habitat

spring (Schwartz *et al*. 2009, p. 3227). Wolverines may move large distances in an attempt to establish new home ranges, but the probability of making such movements decreases with increased distance between suitable habitat patches, and the degree to which the characteristics of the habitat to be traversed diverge from preferred habitat in terms of climatic conditions (Copeland *et al*. 2010, entire; Schwartz *et al*. 2009, p. 3230).

**Commented [O129]:** are you referring to mountains in western states here; because wolverines don't prefer alpine habitats in Ontario

**Commented [O130]:** and other conditions based on Inman's habitat model

The level of development in these linkage areas that wolverines can tolerate is unknown, but it appears that the current landscape does allow wolverine dispersal (Schwartz *et al*. 2009, Figures 4, 5; Moriarty *et al*. 2009, entire; Inman *et al*. 2009, pp. 22-28). For example, wolverine populations in the northern Rocky Mountains appear to be connected to each other at the present time through dispersal routes that correspond to habitat suitability (Schwartz *et al*. 2009, Figures 4, 5). However, gene flow between wolverine subpopulations in the contiguous United States may not be high enough to prevent genetic drift (Cegelski *et al*. 2006, p. 208). To ensure long-term genetic viability, each subpopulation within the contiguous United States would need an estimated 400 breeding pairs, or 1 to 2 effective migrants per generation (Cegelski *et al*. 2006, p. 209). Our current understanding of wolverine ecology suggests that no subpopulation historically or presently at carrying capacity would approach 400 breeding pairs within the contiguous United States (Brock *et al*. 2007, p. 26); nor is the habitat capable of supporting anywhere near this number. It is highly unlikely that 400 breeding pairs exist in the entire contiguous United States. Because no wolverine subpopulations are likely to be large enough to maintain genetic diversity over time on their own, long-term viability of wolverines in the contiguous United States requires exchange of individuals between subpopulations.

Wolverines are capable of long-distance movements through variable and anthropogenically altered terrain, crossing numerous transportation corridors (Moriarty *et al*. 2009, entire; Inman *et al*. 2009, pp. 22-28). Wolverines are able to successfully disperse between habitats, despite the level of development that is currently taking place in the current range of the DPS (Copeland 1996, p. 80; Copeland and Yates 2006, pp. 17-36; Inman *et al*. 2007a, pp. 9-10; Pakila *et al*. 2007, pp. 105-109; Schwartz *et al*. 2009, Figures 4, 5). Dispersal between populations is needed to avoid further reduction in genetic diversity; however, there is no evidence that human development and associated activities are preventing wolverine movements between suitable habitat patches. Rather, wolverine movement rates are limited by suitable habitat and proximity of suitable habitat patches, not the characteristics of the intervening unsuitable habitat (Schwartz *et al*. p. 3230).

**Commented [O131]:** unless the characteristics include transportation corridors; see next section

Transportation Corridors

Transportation corridors are places where transportation infrastructure and other forms of related infrastructure are concentrated together. Examples include interstate highways and high-volume secondary highways. These types of highway corridors often include railroads, retail, industrial, and residential development and also electrical and other types of energy transmission infrastructure. Transportation corridors may affect wolverines if located in wolverine habitat or between habitat patches. If located in wolverine habitat, transportation corridors result in direct loss of habitat. Direct mortality due to collisions with vehicles is also possible (Packila *et al*. 2007, Table 1).

The Trans Canada Highway at Kicking Horse Pass in southern British Columbia, an important travel corridor over the Continental Divide, has a negative effect on wolverine movement (Austin 1998,

p. 30). Wolverines partially avoided areas within 100 m (328 ft) of the highway, and preferred to use distant sites (greater than 1,100 m (3,608 ft)). Wolverines that approached the highway to cross repeatedly retreated, and successful crossing occurred in only half of the attempts (Austin 1998, p. 30). Highway-related mortality was not documented in the study. Where wolverines did successfully cross, they used the narrowest portions of the highway right-of-way. A railway with minimal human activity, adjacent to the highway, had little effect on wolverine movements. Wolverines did not avoid, and even preferred, compacted, lightly used ski trails in the area. The extent to which avoidance of the highway may have affected wolverine vital rates or life history was not measured.

In the tri-State area of Idaho, Montana, and Wyoming, most crossings of Federal or State highways were done by subadult wolverines making exploratory or dispersal movements (ranges of resident adults typically did not contain major roads) (Packila *et al*. 2007, p. 105). Roads in the study area, typically two-lane highways or roads with less improvement, were not absolute barriers to wolverine movement. The individual wolverine that moved to Colorado from Wyoming in 2008 successfully crossed Interstate 80 in southern Wyoming (Inman *et al*. 2008, Figure 6). Wolverines in Norway successfully cross deep valleys that contain light human developments such as railway lines, settlements, and roads (Landa *et al*. 1998, p. 454). Wolverines in central Idaho avoided portions of a study area that contained roads, although this was possibly an artifact of unequal distribution of roads that occurred at low elevations and peripheral to the study site (Copeland *et al*. 2007, p. 2211). Wolverines frequently used un-maintained roads for traveling during the winter, and did not avoid trails used infrequently by people or active campgrounds during the summer (Copeland *et al*. 2007, p. 2211).

At both a site-specific and landscape scale, wolverine natal dens were located particularly distant from public (greater than 7.5 km (4.6 mi)) and private (greater than 3 km (1.9 mi)) roads (May 2007, p. 14-31). Placement of dens away from public roads (and away from associated human-caused mortality) was a positive influence on successful reproduction (May 2007, p. 14-31). Predictive, broad-scale habitat models, developed using historical records of wolverine occurrence, indicated that roads were negatively associated with wolverine occurrence (Rowland *et al*. 2003, p. 101). Although wolverines appear to avoid transportation corridors in their daily movements, studies of the few areas where transportation corridors are located in wolverine habitat leads us to conclude that the effects are most likely local in scale. There are no studies that address potential effects of transportation corridors in linkage areas (i.e. outside of wolverine habitat). In the few documented long-distance movements by wolverines, the animals successfully crossed transportation corridors (Inman *et al*. 2009, Fig. 6). The available evidence indicates that dispersing wolverines can successfully cross transportation corridors.

**Commented [O132]:** some wolverines don't cross successfully and have been killed crossing transportation corridors; see Krebs et al. 2004, unpublished data used by Keith Aubry for his Aubry et al. 2007 paper; road in Kluane National Park in Canada and the pipeline haul road, P. Mickelson, pers. commun.; forestry roads in Ontarion (N. Dawson, pers. comm..), and these are only the ones we know about

Land Management

Few effects to wolverines from land management actions such as grazing, timber harvest, and prescribed fire have been documented. Wolverines in British Columbia used recently logged areas in the summer and moose winter ranges for foraging (Krebs *et al*. 2007, pp. 2189-2190). Males did not appear to be influenced strongly by the presence of roadless areas (Krebs *et al*. 2007, pp. 2189-2190). In Idaho, wolverines used recently burned areas despite the loss of canopy cover (Copeland 1996, p. 124).

**Commented [O133]:** not female wolverines in the Omineca Mountains, p. 2186

**Commented [O134]:** but females were, p. 2186

Intensive management activities such as timber harvest and prescribed fire do occur in wolverine habitat; however, for the most part, wolverine habitat tends to be located at high elevations and in rugged topography that is unsuitable for intensive timber management. Much of wolverine habitat is managed by the U.S. Forest Service or other Federal agencies and is protected from some practices or activities such as residential development. In addition, much of wolverine habitat within the contiguous United States is already in a management status such as wilderness or national park (see Factor D for more discussion) that provides some protection from management, industrial, and recreational activities. Wolverines are not thought to be dependent on specific vegetation or habitat features that might be manipulated by land management activities, nor is there evidence to suggest that land management activities are a threat to the conservation of the species.

***Summary of Factor A***

The threat of current, and future impacts to wolverine habitat due to climate change occurs over the entire range of the contiguous United States population of the wolverine. This threat is likely to have already reduced the overall areal extent and distribution of wolverine suitable habitat. Determining whether or not wolverine populations have been impacted by this threat is complicated by the historical extirpation of wolverines in the early 20th century followed by recolonization and expansion. It is possible that expansion of wolverine populations through the second half of the 20th century has masked climate change effects that would have otherwise reduced populations had they existed at presettlement levels. Despite the lack of detectable population-level impacts, it is still likely that habitat is already reduced from historic levels due to this threat.

**Commented [O135]:** state that you are talking about the western US because this is not true for wolverines in lowland boreal habitats

**Commented [O136]:** British Columbia logs in high elevation habitats where wolverines occur (Krebs et al. 2007, p. 2181)

**Commented [O137]:** In the DPS

**Commented [O138]:** Again, see Krebs et al. 2007 and Bowman et al. 2010

**Commented [O139]:** In what areas? Aubry et al. 2007 do not indicate habitat loss has occurred except perhaps for Great Lakes, and they suggest that area may not have been wolverine habitat even in the past but are equivocal on this point

**Commented [O140]:** I don't know what you are basing this on; reference or explanation is needed here

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Suitable wolverine habitat is projected to be reduced by 31 percent in the contiguous United States by 2045 and 63 percent by the time interval 2070 to 2099 due to climate warming. This reduction will likely result in suitable wolverine habitat shifting up mountain slopes, and becoming smaller and more isolated due to the conical structure of mountains. Because wolverine home ranges tend to be so large, some small mountain ranges are likely to lose the ability to support wolverine populations. We expect that the secondary effects of this habitat loss, such as increased habitat fragmentation and isolation, will intensify the overall impacts of habitat loss on wolverines.

Deep snow that persists into the month of May is essential for wolverine reproduction. This life-history parameter for the species (reproductive rate) is likely to be most sensitive to climate changes. Wolverine are vulnerable to habitat modification (specifically, reduction in persistent spring snow cover) due to climate warming in the contiguous United States. Further, it is likely that year-round wolverine habitat, not just denning habitat, will also be significantly reduced due to the effects of climate warming. Reductions in habitat would result in greater habitat isolation, thereby likely reducing the frequency of dispersal between habitat patches and the likelihood of recolonization after local extinction events. This reduced dispersal ability, if not compensated for by higher population levels or assisted dispersal, is likely to result in loss of genetic diversity within remaining habitat patches and population loss due to demographic stochasticity. The contiguous United States population of wolverines is already very small and fragmented and is, therefore, particularly vulnerable to these impacts.

Human activities, including dispersed recreation activities, infrastructure, and the presence of transportation corridors occur in occupied wolverine habitat. However, the alpine and subalpine

**Commented [O141]:** Reference here; if this is based on McKelvey et al. 2011, see Attachment A

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**Commented [O142]:** This is speculation not based on any scientific evidence because we don't know what limits wolverine distribution in lower elevation forests. Moreover, you must state over what time frame this would happen relative to wolverine habitat requirements and what evidence there is that the lower slopes would not remain wolverine habitat.

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**Commented [O143]:** No evidence that this is true; see Attachment A; also define "deep"

**Commented [O144]:** Define "reproductive rate"; do you mean the proportion of females reproducing annually (e.g., Persson et al. 2006)? I don't think the proposed effects of climate change would necessarily change this parameter; just the total number of females reproducing, if that

**Commented [O145]:** Define persistent spring snow; if you are referring to the Copeland snow cover layer, then it is unlikely that earlier melting of snow cover on 15 May will reduce or modify wolverine habitat; see Attachment A

**Commented [O146]:** See Attachment A

habitats preferred by wolverine typically receive little human use relative to lower elevation habitats. The majority of wolverine habitat (over 90 percent) occurs within Forest Service and National Park Service lands that are subject to activities, but usually not direct habitat loss to infrastructure development. The best available science leads us to determine that human activities and developments do not pose a current threat to wolverines in the contiguous United States.

Wolverines coexist with some modification of their environment, as wilderness characteristics such as complete lack of motorized use or any permanent human presence are likely not critical for maintenance of populations. It is clear that wolverines coexist with some level of human disturbance and habitat modification.

We know of no examples where human activities such as dispersed recreation have occurred at a scale that could render a large enough area unsuitable so that a wolverine home range would be likely to be rendered unsuitable or unproductive. Given the large size of home ranges used by wolverine, most human activities affect such a small portion that negative effects to individuals are unlikely. These activities do not occur at a scale that is likely to have population-level effects to wolverine.

Little scientific or commercial information exists regarding effects to wolverines from development or human disturbances associated with them. What little information does exist suggests that wolverines can adjust to moderate habitat modification, infrastructure development, and human disturbance. In addition, large amounts of wolverine habitat are protected from human disturbances and development, either legally through wilderness and National Park designation, or by being located at remote and high-elevation sites. Therefore, wolverines are afforded a relatively high degree of

protection from the effects of human activities by the nature of their habitat. Wolverines are known to successfully disperse long distances between habitats through human-dominated landscapes and across transportation corridors. The current level of residential, industrial, and transportation development in the western United States does not appear to have precluded the long-distance dispersal movements that wolverines require for maintenance of genetic diversity. We do not have information to suggest that future levels of residential, industrial, and transportation development would be a significant conservation concern for the DPS.

**Commented [O147]:** Does this apply to both male and female long-distance dispersal? is it possible that female wolverines might be more sensitive to this type of disturbance, as information on grizzly bear females suggests? How do you know that some wolverines have not been precluded from long-distance dispersal?

In summary, the best scientific and commercial information available indicates that only the projected decrease and fragmentation of wolverine habitat or range due to future climate change is a threat to the species now and in the future. The available scientific and commercial information does not indicate that other potential stressors such as land management, recreation, infrastructure development, and transportation corridors pose a threat to the DPS.

**Commented [O148]:** Restate this sentence because a "projected decrease and fragmentation" cannot be a threat currently

**Commented [O149]:** We know that wolverines have been killed on roads and railroads in the past and will probably continue to be; why isn't this considered a current threat to the DPS? How does one know how many wolverines are killed this way?

*Factor B. Overutilization for Commercial, Recreational, Scientific, or Educational Purposes*

Over much of recent history, trapping has been a primary cause of wolverine mortality (Banci 1994, p. 108; Krebs *et al*. 2004, p. 497; Lofroth and Ott 2007, pp. 2196-2197; Squires *et al*. 2007, p. 2217). Unregulated trapping is believed to have played a role in the historical decline of wolverines in North America in the late 1800s and early 1900s (Hash 1987, p. 580). Wolverines are especially vulnerable to targeted trapping and predator reduction campaigns due to their habit of ranging widely in search of carrion, bringing them into frequent contact with poison baits and traps (Copeland 1996, p. 78; Inman *et al*. 2007a, pp. 4-10; Packila *et al*. 2007, p. 105; Squires *et al*. 2007, p. 2219).

Human-caused mortality of wolverines is likely additive to natural mortality due to the low reproductive rate and relatively long life expectancy of wolverines (Krebs *et al*. 2004, p. 499; Lofroth and Ott 2007, pp. 2197-2198; Squires *et al*. 2007, pp. 2218-2219). This means that trapped subpopulations likely live at densities that are lower than carrying capacity, and may need to be reinforced by recruits from untrapped subpopulations to maintain population viability and persistence.

**Commented [O150]:** Some can be additive, and some compensatory; this is logical considering that a relatively large proportion of mortality in wolverines has been starvation (Krebs et al. 2004); a starving wolverine would be more likely to be trapped or hit by vehicles if moving around more in search of food; since it may have died from starvation anyway, this mortality could be compensatory under some circumstances (e.g,, in harvested populations)

A study in British Columbia determined that, under a regulated trapping regime, trapping mortality in 15 of 71 wolverine population units was unsustainable, and that populations in those unsustainable population units were dependent on immigration from neighboring populations or untrapped refugia (Lofroth and Ott 2007, pp. 2197-2198). Similarly, in southwestern Montana, legal trapping in isolated mountain ranges accounted for 64 percent of documented mortality and reduced the local wolverine subpopulation (Squires *et al*. 2007, pp. 2218-2219). The observed harvest levels, which included two pregnant females in a small mountain range, could have significant negative effects on a small subpopulation (Squires *et al*. 2007, p. 2219). Harvest refugia, such as jurisdictions with closed seasons, national parks, and large wilderness areas, are important to wolverine persistence on the landscape because they can serve as sources of surplus individuals to bolster trapped populations (Squires *et al*. 2007, p. 2219; Krebs and Ott 2004, p. 500). Due to their large space requirements, wolverine population refuges must be large enough to provide protection from harvest mortality; and complete protection is only available for wolverines whose entire home range occurs within protected areas. Glacier National Park, though an important refuge for a relatively robust population of wolverines, was still vulnerable to trapping because most resident wolverine home ranges extended into large areas outside the park (Squires *et al*. 2007, p. 2219). It is likely that the largerscale refuges

provided by the states of Idaho and Wyoming (which do not permit wolverine trapping) provide wolverine habitat that is fully protected from legal harvest in Montana; however, wolverines with home ranges that partially overlap Montana and dispersers that move into Montana would be vulnerable to harvest. Due to the restrictive, low level of harvest now allowed by Montana, the number of affected wolverines would be correspondingly small.

Despite the impacts of trapping on wolverines in the past, trapping is no longer a threat within most of the wolverine range in the contiguous United States. Montana is the only State where wolverine trapping is still legal. Before 2004, average wolverine harvest was 10.5 wolverines per year. Due to preliminary results of the study reported in Squires *et al*. (2007, pp. 2213-2220), the Montana Department of Fish, Wildlife, and Parks adopted new regulations for the 2004–2005 trapping season that divided the State into three units, with the goal of spreading the harvest more equitably throughout the State.

**Commented [O151]:** Why do you indicate "Most"; where is trapping still a threat? Reference? Are you referring to legal trapping or incidental take?

For the 2008–2009 trapping season, the Montana Department of Fish, Wildlife, and Parks adjusted its wolverine trapping regulations again to further increase the geographic control on harvest to prevent concentrated trapping in any single area, and to completely stop trapping in isolated mountain ranges where small populations are most vulnerable (Montana Department of Fish Wildlife and Parks 2010, pp. 8-11). Their new regulations spread harvest across three geographic units (the Northern Continental Divide area, the Greater Yellowstone area, and the Bitterroot Mountains), and established a statewide limit of five wolverines. In the four trapping seasons that have occurred since these rules were implemented, wolverine take averaged 3.25 wolverines annually (Montana Department of Fish Wildlife and Parks 2010, pp. 8-11; Brian Giddings Pers. Comm. August 30, 2012), with reduced

harvest being due to season closure rather than lack of wolverines. Under the current regulations, no more than three female wolverines can be legally harvested each year, and harvest in the more vulnerable isolated mountain ranges is prohibited. The size of the wolverine population subjected to trapping in this area is not known precisely but is likely not more than about 300 animals in states of Montana, Idaho, and Wyoming combined (Bob Inman pers. comm. 2010b).

The Montana Department of Fish, Wildlife, and Parks conduct yearly furbearer monitoring using track surveys. These surveys involve snowmobiling along transect routes under good tracking conditions and visually identifying all carnivore tracks encountered. The protocol does not use verification methods such as DNA collection or camera stations to confirm identifications. Consequently, misidentifications are likely to occur. Given the relative rarity of wolverines and the relative abundance of other species with which they may be confused, such as bobcats (*Lynx rufus*), Canada lynx (*Lynx canadensis*), and mountain lions (*Felis concolor*), lack of certainty of identifications of tracks makes it highly likely that the rare species is overrepresented in unverified tracking records (McKelvey *et al.* 2008, entire). The Montana Department of Fish, Wildlife, and Parks wolverine track survey information does not meet our standard for reliability described in the geographic distribution section, and we have not relied on this information in this finding.

Montana wolverine populations have rebounded from historic lows in the early 1900s while at the same time being subjected to regulated trapping (Aubry *et al*. 2007, p. 2151; Montana Department of Fish, Wildlife, and Parks 2007, p. 1). In fact, much of the wolverine expansion that we have described above took place under less-restrictive (i.e., higher harvest levels) harvest regulations than are in place today. The extent to which wolverine population growth has occurred in Montana as a result of

within-Montana population growth, versus population growth attributable to surrounding states where wolverines are not trapped, i.e., population growth driven by the entire metapopulation versus just the portion of the metapopulation found in Montana, is unknown.

Current levels of incidental trapping (i.e., capture in traps set for species other than wolverine) have been suggested by the petitioners to be a threat to wolverines. In the 2008–2009 trapping season, two wolverines were incidentally killed in traps set for other species in Beaverhead and Granite Counties, Montana (Montana Fish, Wildlife, and Parks 2010, p. 2). These two mortalities occurred within the portion of southwestern Montana that is currently closed to legal wolverine trapping to ensure that wolverines are not unsustainably harvested in this area of small, relatively isolated mountain ranges. Four cases of incidental wolverine trapping have occurred in Idaho in recent years. One wolverine was trapped by a coyote/bobcat trapper in 2006 and was collared and released after all of its toes and a portion of its left front foot were amputated (Inman et al. 2008, p. 1). That animal (a female) survived and successfully reproduced after release. The Department of Agriculture Wildlife Services trapped three wolverines (one each in 2004, 2005, and 2010) incidental to trapping wolves involved in livestock depredations. One of these sustained severe injuries and was euthanized. The other two were released without visible injury. Another wolverine was trapped in Wyoming in 2006. This animal was released unharmed (Inman 2012, pers. comm.). The three documented mortalities are possibly locally significant for wolverines in these areas because local populations in each of the mountain ranges are small and relatively isolated from nearby source populations.

Summary of Factor B

Legal wolverine harvest occurs in one state, Montana, within the range of the DPS. The extent to which this harvest affects populations occurring outside of Montana is unknown. However, the State of Montana contains most of the habitat and wolverines that exist in the current range of the DPS, and regulates trapping to reduce the impact of harvest on wolverine populations. Incidental harvest also occurs within the range of the DPS; however, the level of mortality from incidental trapping appears to be low. Harvest,when combined with the likely effects of climate change, may contribute to the likelihood that the wolverine will become extirpated in the future. This may occur by increasing the speed with which small populations of wolverine are lost from isolated habitats, and also by increasing mortality levels for dispersing wolverines, with the result of reducing dispersal rates. Regular dispersal and exchange of genetic material are required to maintain the genetics and demographics of wolverine subpopulations in the contiguous United States.

The current known level of incidental trapping mortality is low. We note that it is unknown whether or not increased trapping of wolves associated with wolf trapping regulations recently approved by the states of Idaho and Montana would be likely to result in increased incidental trapping of wolverines. Idaho began its wolf trapping program in the winter of 2011–2012, and Montana began theirs in the winter of 2012–2013. These wolf trapping activities are relatively new in the DPS area, and we do not yet have reliable information on the level of incidental take of wolverines that may result from them.

Based on the best scientific and commercial information available, we conclude that trapping, including known rates of incidental trapping in Montana and Idaho, result in a small number of wolverine mortalities each year and that this level of mortality by itself would not be a threat to the

wolverine DPS. However, by working in concert with habitat loss resulting from climate change, mortality due to harvest and incidental trapping may contribute to population declines. Therefore, we conclude that trapping, when considered cumulatively with habitat loss resulting from climate change, is likely to become a threat to the DPS (see discussion under Synergistic Interactions Between Threat Factors, below).

*Factor C. Disease or Predation*

No information is currently available on the potential effects of disease on wild wolverine populations. Wolverines are sometimes killed by wolves (*Canis lupus*), black bears (*Ursus americanus*), and mountain lion (White et al. Can. Field nat. 116:132-134;Burkholder 1962, p. 264; Hornocker and Hash 1981, p. 1296; Copeland 1996, p. 44-46; Inman *et al*. 2007d, p. 89). In addition, wolverine reproductive dens are likely subject to predation, although so few dens have been discovered in North America that determining the intensity of this predation is not possible.

**Commented [O152]:** Add this reference

**Commented [O153]:** Dens are not subject to predation, kits are??. Are you including intraspecific predation by other wolverines?

Summary of Factor C

We have no information to suggest that wolverine mortality from predation and disease is above natural or sustainable levels. The best scientific and commercial information available indicates that disease or predation is not a threat to the species now or likely to become so in the future.

*Factor D. Inadequacy of Existing Regulatory Mechanisms*

Based on our calculations using a composite map showing the coverage of both the Copeland *et al*. (2010, entire) and Inman et al. (2012, entire) wolverine habitat models, the majority (94 percent) of wolverine habitat currently occupied by wolverine populations in the lower contiguous United States is Federally owned and managed, mostly by the U.S. Forest Service. An estimated 144,371 $km^2$ (49,258 $mi^2$) of wolverine habitat occurs in the occupied area in Montana, Idaho, Oregon (Wallowa Range), and Wyoming. Of that, 135,396 $km^2$ (46,332 $mi^2$) is in Federal ownership. Additionally, 47,150 $km^2$ (12,973 $mi^2$) (32.7 percent) occurs in designated wilderness, and 23,062 $km^2$ (1,630 $mi^2$) (16.0 percent) occurs in inventoried roadless areas. An additional 13,784 $km^2$ (3,288 $mi^2$) (9.5 percent) are within national parks.

None of the existing Federal or State regulatory mechanisms were designed to address the threat of modification of wolverine habitat due to the loss of snowpack associated with climate change. Several existing regulatory mechanisms protect wolverine from other forms of disturbance and from overutilization from harvesting; these are described in more detail below.

Federal Laws and Regulations

The Wilderness Act

The Forest Service and National Park Service both manage lands designated as wilderness areas under the Wilderness Act of 1964 (16 U.S.C. 1131-1136). Within these areas, the Wilderness Act states the following: (1) New or temporary roads cannot be built; (2) there can be no use of motor vehicles, motorized equipment, or motorboats; (3) there can be no landing of aircraft; (4) there can be no other

form of mechanical transport; and (5) no structure or installation may be built. A large amount of suitable wolverine habitat, about 28 percent for the states of Montana, Idaho, and Wyoming, occurs within Federal wilderness areas in the United States (Inman personal communication 2007b). As such, a large proportion of existing wolverine habitat is protected from direct loss or degradation by the prohibitions of the Wilderness Act.

National Environmental Policy Act

All Federal agencies are required to adhere to the National Environmental Policy Act (NEPA) of 1970 (42 U.S.C. 4321 *et seq.*) for projects they fund, authorize, or carry out. The Council on Environmental Quality's regulations for implementing NEPA (40 CFR 1500–1518) state that agencies shall include a discussion on the environmental impacts of the various project alternatives (including the proposed action), any adverse environmental effects which cannot be avoided, and any irreversible or irretrievable commitments of resources involved (40 CFR 1502). The NEPA itself is a disclosure law, and does not require subsequent minimization or mitigation measures by the Federal agency involved. Although Federal agencies may include conservation measures for wolverines as a result of the NEPA process, any such measures are typically voluntary in nature and are not required by the statute. Additionally, activities on non-Federal lands are subject to NEPA if there is a Federal action.

For example, wolverines are designated as a sensitive species by the Forest Service, which requires that effects to wolverines be considered in documentation completed under NEPA. NEPA does not itself regulate activities that might affect wolverines, but it does require full evaluation and

disclosure of information regarding the effects of contemplated Federal actions on sensitive species and their habitats.

National Forest Management Act

Under the National Forest Management Act of 1976, as amended (16 U.S.C. 1600–1614), the Forest Service shall strive to provide for a diversity of plant and animal communities when managing national forest lands. Individual national forests may identify species of concern that are significant to each forest's biodiversity. Outside of designated wilderness but still on Forest Service-managed lands, wolverines occur mainly in alpine areas. Their habitat is generally offered more protections from timber harvest than would otherwise be the case in lowland areas due to the difficulty of accessing wolverine habitat, especially in areas where motorized access is limited or absent, such as most National Forest land and all designated wilderness areas.

National Park Service Organic Act

The NPS Organic Act of 1916 (16 U.S.C. 1 *et seq.*), as amended, states that the NPS ''shall promote and regulate the use of the Federal areas known as national parks, monuments, and reservations to conserve the scenery and the national and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations.'' Where wolverines occur in National Parks, they and their habitats are protected from large-scale loss or degradation due to the Park Service's mandate

to ‘‘...conserve scenery... and wildlife...[by leaving] them unimpaired.’’ Wolverine harvest and trapping of other furbearers is also prohibited in National Parks.

Clean Air Act of 1970

On December 15, 2009, the Environmental Protection Agency (EPA) published in the Federal Register (74 FR 66496) a rule titled, “Endangerment and Cause or Contribute Findings for Greenhouse Gases under Section 202(a) of the Clean Air Act.” In this rule, the EPA Administrator found that the current and projected concentrations of the six long-lived and directly emitted greenhouse gases (GHGs)—carbon dioxide, methane, nitrous oxide, hydrofluorocarbons, perfluorocarbons, and sulfur hexafluoride—in the atmosphere threaten the public health and welfare of current and future generations; and that the combined emissions of these GHGs from new motor vehicles and new motor vehicle engines contribute to the GHG pollution that threatens public health and welfare (74 FR 66496). In effect, the EPA has concluded that the GHGs linked to climate change are pollutants, whose emissions can now be subject to the Clean Air Act (42 U.S.C. 7401 *et seq.*) (see 74 FR 66496). However, specific regulations to limit GHG emissions were only proposed in 2010 and, therefore, cannot be considered an existing regulatory mechanism. At present, we have no basis to conclude that implementation of the Clean Air Act in the future (40 years, based on global climate projections) will substantially reduce the current rate of global climate change through regulation of GHG emissions. Thus, we conclude the Clean Air Act is not designed to address the primary threat to wolverine of the loss of snowpack due to the effects of climate change.

State Laws and Regulations

State Comprehensive Wildlife Conservation Strategies and State Environmental Policy and Protection Acts

The wolverine is listed as State Endangered in Washington, California, and Colorado. In Idaho and Wyoming it is designated as a protected nongame species (Idaho Department of Fish and Game 2010, p. 4; Wyoming Game and Fish 2005, p. 2). Oregon, while currently not considered to have any individuals other than possible unsuccessful dispersers, has a closed season on trapping of wolverines. These designations largely protect the wolverine from mortality due to hunting and trapping. In Montana, the wolverine is classified as a regulated furbearer (Montana Fish, Wildlife, and Parks 2010, p. 8). Montana is the only State in the contiguous United States where wolverine trapping is still legal.

Wolverines receive some protection under State laws in Washington, California, Idaho, Montana, Wyoming, and Colorado. Each State's fish and wildlife agency has some version of a State Comprehensive Wildlife Conservation Strategy (CWCS) in place. These strategies, while not State or Federal legislation, can help prioritize conservation actions within each State. Named species and habitats within each CWCS may receive focused attention during State Environmental Protection Act (SEPA) reviews as a result of being included in a State's CWCS. However, only Washington, California, and Montana appear to have SEPA-type regulations in place. In addition, each State's fish and wildlife agency often specifically names or implies protection of wolverines in its hunting and trapping regulations. Only the State of Montana currently allows wolverine harvest (see discussion under Factor B).

Before 2004, the Montana Department of Fish, Wildlife, and Parks regulated wolverine harvest through the licensing of trappers, a bag limit of one wolverine per year per trapper, and no statewide limit. Under this management, average wolverine harvest was 10.5 wolverines per year. Due to preliminary results of the study reported in Squires *et al*. (2007, pp. 2213-2220), Montana Department of Fish, Wildlife, and Parks adopted new regulations for the 2004–2005 trapping season that divided the State into three units with the goal of spreading the harvest more equitably among available habitat. In 2008, Montana Department of Fish, Wildlife, and Parks further refined their regulations to prohibit trapping in isolated mountain ranges, and reduced the overall statewide harvest to five wolverines with a statewide female harvest limit of three. Under factor B, above, we concluded that trapping, including known rates of incidental trapping in Montana, by itself, is not a threat to the wolverine DPS, but that by working in concert with the primary threat of climate change, the trapping program may contribute to population declines (see Synergistic Interactions Between Threat Factors, below).

Summary of Factor D

The existing regulatory mechanisms appear to protect wolverine from several of the factors described in Factors A and B above. Specifically, State regulations for wolverine harvest appear to be sufficient to prohibit range–wide overutilization from hunting and trapping in the absence of other threats. However, given that climate change impacts are expected to reduce wolverine populations and fragment habitat, the impact of harvest to wolverine would be expected to increase if harvest levels were maintained at current levels. Federal ownership of much of occupied wolverine habitat protects the species from direct losses of habitat and provides further protection from many of the forms of disturbance described above. Wolverines use habitats affected by human disturbance, and additional

protection is afforded wolverines by the large area of their range that occurs in designated wilderness and national parks. The current regulatory regime does not address the potential impacts of dispersed winter recreation outside of protected areas; however, at this time the available information does not suggest that dispersed winter recreation is a threat to the DPS.

Our review of the regulatory mechanisms in place at the national and State level demonstrates that the short-term, site-specific threats to wolverine from direct loss of habitat, disturbance by humans, and direct mortality from hunting and trapping are, for the most part, adequately addressed through State and Federal regulatory mechanisms. However, as described under Factor A, the primary threat with the greatest severity and magnitude of impact to the species is loss of habitat due to continuing climate warming. The existing regulatory mechanisms currently in place at the national level were not designed to address the threat to wolverine habitat from climate change.

**Commented [O154]:** See Attachment A

*Factor E. Other Natural or Manmade Factors Affecting its Continued Existence*

Small Population Size

Population ecologists use the concept of a population's "effective" size as a measure of the proportion of the actual population that contributes to future generations (for a review of effective population size, see Schwartz *et al*. 1998, entire). In a population where all of the individuals contribute offspring equally, effective population size would equal true population size, referred to as the population census size. For populations where contribution to the next generations is often unequal, effective population size will be smaller than the census size. The smaller the effective population size,

the more reproduction in each generation is dominated by a few individuals in each generation. For wolverines it is likely that high-quality home ranges are limited, and individuals occupying them are better able to reproduce. Therefore, mature males and females that are successful at acquiring and defending a territory may dominate reproduction. Another contributing factor that reduces effective population size is the tendency in wolverines for a few males to monopolize the reproduction of several females, reducing reproductive opportunities for other males. Although this monopolization is a natural feature of wolverine life history strategy, it can lead to lower effective population size and reduce population viability by reducing genetic diversity. The effective population is not static, members of the effective population in 1 year may lose this status in the following year and possibly regain it again later depending on their reproductive success. When members of the effective population are lost, it is likely that their territories are quickly filled by younger individuals who may not have been able to secure a productive territory previously.

Effective population size is important because it determines rates of loss of genetic variation and the rate of inbreeding. Populations with small effective population sizes show reductions in population growth rates and increases in extinction probabilities when genetic diversity is low enough to lead to inbreeding depression (Leberg 1990, p. 194; Jimenez *et al*. 1994, pp. 272-273; Newman and Pilson 1997, p. 360; Saccheri *et al*. 1998, p. 492; Reed and Bryant 2000, p. 11; Schwartz and Mills 2005, p. 419; Hogg *et al*. 2006, p. 1495, 1498; Allendorf and Luikart 2007, pp. 338-342). Franklin (1980, as cited in Allendorf and Luikart 2007, p. 359) proposed an empirically based rule suggesting that for short-term (a few generations) maintenance of genetic diversity, effective population size should not be less than 50. For long-term (hundreds of generations) maintenance of genetic diversity, effective population size should not be less than 500 (for appropriate use of this rule and its limitations

see Allendorf and Luikart 2007, pp. 359-360). Others suggest that even higher numbers are required to ensure that populations remain viable, suggesting that long-term connectivity to the reservoir of genetic resources in the Canadian population of wolverines will be required for the long-term genetic health of the DPS (Traill *et al.* 2010, p. 32). All evidence suggests that no habitat area within the contiguous United States is large enough to support a wolverine population with an effective population size of 500 animals. Given the life history of wolverines that includes high inequality of reproductive success and a metapopulation of semi-isolated subpopulations, effective population sizes would likely never reach even 100 individuals at full habitat occupancy as this would suggest a census population of over 1,000. In this case, population connectivity exchange with the larger Canadian/Alaskan population would likely be required for long-term viability.

Wolverine effective population size in the northern Rocky Mountains, which is the largest extant population in the contiguous United States, is exceptionally low and is below what is thought necessary for short-term maintenance of genetic diversity. Estimates for effective population size for wolverines in the northern Rocky Mountains averaged 35 (credible limits = 28–52) (Schwartz *et al*. 2009, p. 3226). This study excluded the small population from the Crazy and Belt Mountains (hereafter "CrazyBelts") as they may be an isolated population, which could bias the estimate using the methods of Tallmon *et al*. (2007, entire). Measures of the effective population sizes of the other populations in the contiguous United States have not been completed, but given their small census sizes, their effective sizes are expected to be smaller than for the northern Rocky Mountains population. Thus, wolverine effective population sizes are very low. For comparison, estimates of wolverine effective population size are bracketed by critically endangered species, such as the black-footed ferret (*Mustela nigripes*) (4.10) (Wisely *et al*. 2007, p. 3) and the ocelot (*Leopardus pardalis*) (2.9 to 13.9) (Janecka *et al*. 2007,

p. 1), but are substantially smaller than estimates for the Yellowstone grizzly bear (*Ursus arctos*) (greater than 100), which has reached the level of recovery under the Act (Miller and Waits 2003, p. 4338). Therefore, we conclude that effective population size estimates for wolverines do not suggest that populations are currently critically endangered, but they do suggest that populations are low enough that they could be vulnerable to loss of genetic diversity, and may require intervention in the future to remain viable. To date, no adverse effects of the lower genetic diversity of the contiguous United States wolverines have been documented.

Wolverines in the contiguous United States are thought to be derived from a recent recolonization event after they were extirpated from the area in the early 20th century (Aubry *et al.* 2007, Table 1). Consequently, wolverine populations in the contiguous United States have reduced genetic diversity relative to larger Canadian populations as a result of founder effects or inbreeding (Schwartz *et al.* 2009, pp. 3228-3230). Wolverine effective population size in the northern Rocky Mountains was estimated to be 35 (Schwartz et al. 2009, p. 3226) and is below what is thought to be adequate for short-term maintenance of genetic diversity. Loss of genetic diversity can lead to inbreeding depression and is associated with increased risk of extinction (Allendorf and Luikart 2007, pp. 338-343). Small effective population sizes are caused by small actual population size (census size), or by other factors that limit the genetic contribution of portions of the population, such as polygamous mating systems. Populations may increase their effective size by increasing census size or by the regular exchange of genetic material with other populations through interpopulation mating.

**Commented [O155]:** Aubry stated "extirpated, or nearly so" as did the references they cited; the genetics paper in review by McKelvey et al. may support extirpation but that is not published yet

The concern with the low effective population size was highlighted in a recent analysis that determined that, without immigration from other wolverine populations, at least 400 breeding pairs

would be necessary to sustain the long-term genetic viability of the northern Rocky Mountains wolverine population (Cegelski *et al*. 2006, p. 197). However, the entire population is likely only 250 to 300 (Inman 2010b, pers. comm.), with a substantial number of these being unsuccessful breeders or nonbreeding subadults (i.e., part of the census population, but not part of the effective population).

Genetic studies demonstrate the essential role that genetic exchange plays in maintaining genetic diversity in small wolverine populations. The concern that low effective population size would result in negative effects is already being realized for the contiguous United States population of wolverine. Genetic drift has already occurred in subpopulations of the contiguous United States: Wolverines here contained 3 of 13 haplotypes found in Canadian populations (Kyle and Strobeck 2001, p. 343; Cegelski *et al*. 2003, pp. 2914-2915; Cegelski *et al*. 2006, p. 208; Schwartz *et al*. 2007, p. 2176; Schwartz *et al*. 2009, p. 3229). The haplotypes found in these subpopulations were a subset of those in the larger Canadian population, indicating that genetic drift had caused a loss of genetic diversity. One study found that a single haplotype dominated the northern Rocky Mountain wolverine population, with 71 of 73 wolverines sampled expressing that haplotype (Schwartz *et al*. 2007, p. 2176). The reduced number of haplotypes indicates not only that genetic drift has occurred but also some level of genetic separation; if these populations were freely interbreeding, they would share more haplotypes (Schwartz *et al*. 2009, p. 3229). The reduction of haplotypes is likely a result of the fragmented nature of wolverine habitat in the United States and is consistent with an emerging pattern of reduced genetic variation at the southern edge of the range documented in a suite of boreal forest carnivores (Schwartz *et al*. 2007, p. 2177).

Immigration of wolverines from Canada is not likely to bolster the genetic diversity of wolverines in the contiguous United States. There is an apparent lack of connectivity between wolverine populations in Canada and the United States based on genetic data (Schwartz *et al.* 2009, pp. 3228-3230). The apparent loss of connectivity between wolverines in the northern Rocky Mountains and Canada prevents the influx of genetic material needed to maintain or increase the genetic diversity in the contiguous United States. The continued loss of genetic diversity may lead to inbreeding depression, potentially reducing the species' ability to persist through reduced reproductive output or reduced survival. Currently, the cause for this lack of connectivity is uncertain. Wolverine habitat appears to be well-connected across the border region (Copeland *et al.* 2010, Figure 2) and there are few manmade obstructions such as transportation corridors or alpine developments. However, this lack of genetically detectable connectivity may be related to harvest management in southern Canada.

**Commented [O156]:** In what way do you mean this? Are you suggesting that harvest is removing so many wolverines in Canada that there are none to disperse into the U.S.? or are you suggesting that trapping in Canada is opening up home ranges that then absorb the potential dispersers? Copeland and Yates 2008 study suggests wolverine habitat in Glacier National Park is saturated based on the home range maps; wolverines to the north of the park may disperse into trapped areas rather than into GNP; if this were the case, even a trapping closure immediately north of the border with Canada would not necessarily increase dispersal into GNP because a saturated population in GNP could still pose a "barrier" to dispersers if this sociobiological phenomenon exists; see dispersal route of Eowyn outside the home ranges of resident wolverines in Washington and the new male from this past field season. Both may have dispersed around the home ranges of resident wolverines, although Jens Persson has GPS data that shows dispersers going through resident home ranges (unpublished data) but there they may have no other option.

Summary of Factor E

Small population size and resulting inbreeding depression are potential, though as-yet undocumented, threats to wolverines in the contiguous United States. There is good evidence that genetic diversity is lower in wolverines in the DPS than it is in the more contiguous habitat in Canada and Alaska. The significance of this lower genetic diversity to wolverine conservation is unknown. We do not discount the possibility that loss of genetic diversity could be negatively affecting wolverines now and continue to do so in the future. It is important to point out, however, that wolverine populations in the DPS area are thought to be the result of colonization events that have occurred since the 1930s. Such recent colonizations by relatively few individuals and subsequent population growth are likely to have resulted in founder effects, which could contribute to low genetic diversity. The

effect of small population sizes and low genetic diversity may become more significant if populations become smaller and more isolated, as predicted due to climate changes.

Based on the best scientific and commercial information available we conclude that demographic stochasticity and loss of genetic diversity due to small effective population sizes, by itself, is not a threat to the wolverine DPS. However, by working in concert with the primary threat of habitat loss due to climate change, this may contribute to the cumulative effect of population declines. Therefore, we conclude that demographic stochasticity and loss of genetic diversity due to small effective population sizes is a threat to wolverines when considered cumulatively with habitat loss due to climate change (see discussion under Synergistic Interactions Between Threat Factors).

Synergistic Interactions Between Threat Factors

We have evaluated individual threats to the distinct population segment of the North American Wolverine throughout its range in the contiguous United States. The wolverine DPS faces one primary threat that is likely to drive its conservation status in the future: habitat change and loss due to climate change. This factor alone is enough to determine that the species should be proposed for listing under the Act. Other factors, though not as severe or geographically comprehensive as the potential habitat effects from climate change may, when considered in the context of changes likely to occur due to climate change, become threats due to the cumulative effects they have on wolverine populations. For wolverines, the only such threat factors found in our analysis to have a basis of support as threats to wolverines were the effects of small subpopulation sizes and subpopulation isolation on wolverine genetic and demographic health, and the subsequent potential future influence of trapping.

**Commented [O157]:** Not supported by the best available science; see Attachment A

**Commented [O158]:** If these are factors, then certainly an increasing human footprint (infrastructure, perhaps even increased recreation beyond the levels that now occur) at some threshold level must also be a threat, especially in the intervening areas between current wolverine habitat islands, which already threaten dispersal/survival to some unknown extent

As discussed in our analysis of the effects on wolverine habitat from climate change under Factor A, wolverine habitat in the contiguous United States is likely to become smaller overall, and remaining habitat is likely to be more fragmented and fragments more isolated from one another than they are today (McKelvey *et al*. 2011, Figure 8). Given that wolverine subpopulations in the DPS are already so small, and movement between subpopulations so restricted, inbreeding has become likely (Kyle and Strobeck 2001, p. 343; Cegelski *et al*. 2003, pp. 2914-2915; Cegelski *et al*. 2006, p. 208; Schwartz *et al*. 2007, p. 2176; Schwartz *et al*. 2009, p. 3229). The longterm maintenance of wolverines in the DPS will require continued connectivity between subpopulations within the DPS, and with populations to the north in Canada. To the extent that wolverine habitat becomes more fragmented, and fragments become more isolated due habitat loss resulting from climate change, these factors will become more significant to wolverine conservation. The risk factor of small population size, including measures of effective population size and their consequent effects on maintenance of genetic diversity, is a threat to the North American wolverine DPS when considered cumulatively with habitat loss resulting from climate change.

**Commented [O159]:** I disagree, at least as far as "the foreseeable future" is concerned; See Attachment A

**Commented [O160]:** And if habitat loss and fragmentation due to climate warming is not a factor in the foreseeable future, the increasing human footprint in areas where wolverines need to disperse would be the overriding conservation issue; i.e., the need for dispsersal corridors exists today

Wolverine populations have been expanding in the DPS area since the early 20th century, when they were likely at or near zero (Aubry *et al*. 2007, p. 2151). Most of this expansion has occurred under trapping regulations that allowed a higher level of trapping than currently occurs (see Montana Department of Fish, Wildlife, and Parks 2007, p. 1). Therefore, it might be argued that wolverine trapping is not occurring at levels that would significantly affect conservation of the DPS. However, future habitat changes due to climate change are predicted to reduce habitat connectivity and extent. As described above, these changes are likely to exacerbate the problem of loss of genetic diversity and

**Commented [O161]:** See Attacment A

demographic stability caused by low effective population size and insufficient movement between populations, leading to inbreeding. Given these likely secondary effects of climate change, human-caused mortality due to harvest is likely to become more significant to the wolverine population as connectivity needs increase and connectivity simultaneously becomes more difficult. As habitats become smaller and more isolated from one another, more wolverines will be needed to attempt to move between subpopulations to maintain population viability. Harvest currently removes up to five wolverines from the population every year, reducing the number of animals available for dispersal. In addition, incidental trapping of wolverines removes still more. For these reasons, we find that harvest and incidental trapping, when considered cumulatively with habitat loss resulting from climate change, are likely to become threats to the DPS due to the likely synergistic effects they may have on the population as habitat becomes smaller and more fragmented.

**Commented [O162]:** As will increasing human footprint in areas between wolverine habitat islands, perhaps more so than incidental take

**Commented [O163]:** And if habitat is not affected by climate warming in the foreseeable future, it could be argued that harvest and incidental trapping are less of a threat than increasing human developments in areas between wolverine habitat islands

**Proposed Determination**

We have carefully assessed the best scientific and commercial information available regarding the past, present, and future threats to the wolverine DPS. We have identified threats to the contiguous United States population of the North American wolverine attributable to Factors A, B, and E. The primary threat to the DPS is from habitat and range loss due to climate warming (Factor A). Wolverines require habitats with near-arctic conditions wherever they occur. In the contiguous United States, wolverine habitat is restricted to high-elevation areas in the West. Wolverines are dependent on deep persistent snow cover for successful denning, and they concentrate their year-round activities in areas that maintain deep snow into spring and cool temperatures throughout summer. Wolverines in the contiguous United States exist as small and semi-isolated subpopulations in a larger metapopulation

**Commented [O164]:** Define what this means

**Commented [O165]:** Define specifically so that it can be tested now and in the future

**Commented [O166]:** Define specifically here so that it can be tested now and in the future

that requires regular dispersal of wolverines between habitat patches to maintain itself. These dispersers achieve both genetic enrichment and demographic support of recipient populations. Climate changes are predicted to reduce wolverine habitat and range by 31 percent over the next 30 years and 63 percent over the next 75 years, rendering remaining wolverine habitat significantly smaller and more fragmented. We anticipate that, by 2045, maintenance of the contiguous United States wolverine population in the currently occupied area may require human intervention to facilitate genetic exchange and possibly also to facilitate metapopulation dynamics by moving individuals between habitat patches if they are no longer accessed regularly by dispersers, or risk loss of the population.

**Commented [O167]:** Not supported by the best available science; Appendix A

Other threats are minor in comparison to the driving primary threat of climate change; however, cumulatively, they could become significant when working in concert with climate change if they further suppress an already stressed population. These secondary threats include harvest (including incidental harvest) (Factor B) and demographic stochasticity and loss of genetic diversity due to small effective population sizes (Factor E). All of these factors affect wolverines across their current range in the contiguous United States.

**Commented [O168]:** Downplaying the significance of the effects of continued growth of the human population and expansion into areas between wolverine habitat islands seems counterproductive for wolverine conservations initiatives especially following the statement just above that states "Wolverines in the contiguous United States exist as small and semi-isolated subpopulations in a larger metapopulation that requires regular dispersal of wolverines between habitat patches to maintain itself."

The Act defines an endangered species as any species that is "in danger of extinction throughout all or a significant portion of its range" and a threatened species as any species "that is likely to become endangered throughout all or a significant portion of its range within the foreseeable future." We find that the contiguous United States wolverine DPS presently meets the definition of a threatened species due to the likelihood of habitat loss caused by climate change resulting in population decline leading to breakdown of metapopulation dynamics. Breakdown in metapopulation dynamics would make the DPS vulnerable to further loss of genetic diversity through inbreeding, and likely vulnerable to

demographic endangerment as small subpopulations could no longer rely on demographic rescue from nearby populations. At that point wolverine populations would meet the definition of an endangered species under the Act. We base this determination on the immediacy, severity, and scope of the threats described above. Therefore, on the basis of the best available scientific and commercial information, we propose listing the contiguous United State DPS of the North American wolverine as a threatened species in accordance with sections 3(6) and 4(a)(1) of the Act.

Under the Act and our implementing regulations, a species may warrant listing if it meets the definition of an endangered or threatened species throughout all or a significant portion of its range. The contiguous United States DPS of the North American wolverine proposed for listing in this rule is wide-ranging and the threats occur throughout its range. Therefore, we assessed the status of the DPS throughout its entire range. The threats to the survival of the species occur throughout the species' range and are not restricted to any particular significant portion of that range. Accordingly, our assessment and proposed determination applies to the DPS throughout its entire range.

**Available Conservation Measures**

Conservation measures provided to species listed as an endangered or threatened species under the Act include recognition, recovery actions, requirements for Federal protection, and prohibitions against certain practices. Recognition through listing results in public awareness and conservation by Federal, State, Tribal, and local agencies, private organizations, and individuals. The Act encourages cooperation with the States and requires that recovery actions be carried out for all listed species. The

protection required by Federal agencies and the prohibitions against certain activities are discussed, in part, below.

The primary purpose of the Act is the conservation of endangered and threatened species and the ecosystems upon which they depend. The ultimate goal of such conservation efforts is the recovery of these listed species, so that they no longer need the protective measures of the Act. Subsection 4(f) of the Act requires the Service to develop and implement recovery plans for the conservation of endangered and threatened species. The recovery planning process involves the identification of actions that are necessary to halt or reverse the species' decline by addressing the threats to its survival and recovery. The goal of this process is to restore listed species to a point where they are secure, self-sustaining, and functioning components of their ecosystems.

Recovery planning includes the development of a recovery outline shortly after a species is listed, preparation of a draft and final recovery plan, and revisions to the plan as significant new information becomes available. The recovery outline guides the immediate implementation of urgent recovery actions and describes the process to be used to develop a recovery plan. The recovery plan identifies site-specific management actions that will achieve recovery of the species, measurable criteria that determine when a species may be downlisted or delisted, and methods for monitoring recovery progress. Recovery plans also establish a framework for agencies to coordinate their recovery efforts and provide estimates of the cost of implementing recovery tasks. Recovery teams (composed of species experts, Federal and State agencies, nongovernmental organizations, and stakeholders) are often established to develop recovery plans. The recovery outline is available on our website at http://www.fws.gov/mountain-prairie/species/mammals/wolverine/ and

on http://www.regulations.gov concurrently with the publication of this proposed rule. When completed, the draft recovery plan and the final recovery plan will be available on our website or from our Montana Ecological Services Field Office (see **FOR FURTHER INFORMATION CONTACT**).

Implementation of recovery actions generally requires the participation of a broad range of partners, including other Federal agencies, States, Tribal, nongovernmental organizations, businesses, and private landowners. Examples of recovery actions include habitat restoration (e.g., restoration of native vegetation), research, captive propagation and reintroduction, and outreach and education. The recovery of many listed species cannot be accomplished solely on Federal lands because their range may occur primarily or solely on non-Federal lands. To achieve recovery of these species requires cooperative conservation efforts on private, State, and Tribal lands.

If this species is listed, funding for recovery actions will be available from a variety of sources, including Federal budgets, State programs, and cost share grants for nonfederal landowners, the academic community, and nongovernmental organizations. In addition, pursuant to section 6 of the Act, the States inhabited by wolverines or uninhabited states with suitable habitat would be eligible for Federal funds to implement management actions that promote the protection and recovery of wolverines. Information on our grant programs that are available to aid species recovery can be found at: *http://www.fws.gov/grants*.

Although the wolverine DPS is only proposed for listing under the Act at this time, please let us know if you are interested in participating in recovery efforts for this species. Additionally, we invite

you to submit any new information on this species whenever it becomes available and any information you may have for recovery planning purposes (see **FOR FURTHER INFORMATION CONTACT**).

Section 7(a) of the Act requires Federal agencies to evaluate their actions with respect to any species that is proposed or listed as endangered or threatened and with respect to its critical habitat, if any is designated. Regulations implementing this interagency cooperation provision of the Act are codified at 50 CFR part 402. Section 7(a)(4) of the Act requires Federal agencies to confer with the Service on any action that is likely to jeopardize the continued existence of a species proposed for listing or result in destruction or adverse modification of proposed critical habitat. If a species is listed subsequently, section 7(a)(2) of the Act requires Federal agencies to ensure that activities they authorize, fund, or carry out are not likely to jeopardize the continued existence of the species or destroy or adversely modify its critical habitat. If a Federal action may affect a listed species or its critical habitat, the responsible Federal agency must enter into formal consultation with the Service.

Federal agency actions within the species habitat that may require conference or consultation or both as described in the preceding paragraph include management and any other landscape altering activities on Federal lands in suitable wolverine habitat within the range of the species administered by the Department of Defense, U.S. Fish and Wildlife Service, Bureau of Land Management, National Park Service, and U.S. Forest Service; construction and management of gas pipeline and power line rights-of-way in suitable wolverine habitat by the Federal Energy Regulatory Commission; construction and maintenance of roads or highways by the Federal Highway Administration in suitable wolverine habitat; and permitting of infrastructure development in suitable wolverine habitat for recreation, oil

and gas development, or residential development by the U.S. Forest Service, National Park Service, Bureau of Land Management, U.S. Fish and Wildlife Service, or Department of Defense.

The Act and its implementing regulations set forth a series of general prohibitions and exceptions that apply to all endangered wildlife. The prohibitions of section 9(a)(2) of the Act, codified at 50 CFR 17.21 for endangered wildlife, in part, make it illegal for any person subject to the jurisdiction of the United States to take (includes harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect; or to attempt any of these), import, export, ship in interstate commerce in the course of commercial activity, or sell or offer for sale in interstate or foreign commerce any listed species. Under the Lacey Act (18 U.S.C. 42–43; 16 U.S.C. 3371–3378), it is also illegal to possess, sell, deliver, carry, transport, or ship any such wildlife that has been taken illegally. Certain exceptions apply to agents of the Service and State conservation agencies.

We may issue permits to carry out otherwise prohibited activities involving endangered and threatened wildlife species under certain circumstances. Regulations governing permits are codified at 50 CFR 17.22 for endangered species, and at 17.32 for threatened species. With regard to endangered wildlife, a permit must be issued for the following purposes: for scientific purposes, to enhance the propagation or survival of the species, and for incidental take in connection with otherwise lawful activities.

It is our policy, as published in the **Federal Register** on July 1, 1994 (59 FR 34272), to identify to the maximum extent practicable at the time a species is listed, those activities that would or would not constitute a violation of section 9 of the Act. The intent of this policy is to increase public

awareness of the effect of a proposed listing on proposed and ongoing activities within the range of species proposed for listing. The following activities could potentially result in a violation of section 9 of the Act; this list is not comprehensive:

Unauthorized collecting, handling, possessing, selling, delivering, carrying, or transporting of the species, including import or export across State lines and international boundaries, except for properly documented antique specimens of these taxa at least 100 years old, as defined by section 10(h)(1) of the Act.

Questions regarding whether specific activities would constitute a violation of section 9 of the Act should be directed to the Montana Ecological Services Field Office (see **FOR FURTHER INFORMATION CONTACT**). Requests for copies of the regulations concerning listed animals and general inquiries regarding prohibitions and permits may be addressed to the U.S. Fish and Wildlife Service, Endangered Species Permits, 134 Union Boulevard, Suite 650, Lakewood, CO 80228; Telephone 303-236-4265.

A determination to list the contiguous United States DPS of the North American wolverine as a threatened species under the Act, if we ultimately determine that listing is warranted, will not regulate greenhouse gas emissions. Rather, it will reflect a determination that the DPS meets the definition of a threatened species under the Act, thereby establishing certain protections for them under the ESA. While we acknowledge that listing will not have a direct impact on the loss of deep, persistent, late spring snowpack or the reduction of greenhouse gases, we expect that it will indirectly enhance national and international cooperation and coordination of conservation efforts, enhance research programs, and

encourage the development of mitigation measures that could help slow habitat loss and population declines. In addition, the development of a recovery plan will guide efforts intended to ensure the long-term survival and eventual recovery of the lower 48 states DPS of the wolverine.

*Special Rule Under Section 4(d) of the Act*

Whenever a species is listed as a threatened species under the Act, the Secretary may specify regulations that he deems necessary and advisable to provide for the conservation of that species under the authorization of section 4(d) of the Act. These rules, commonly referred to as ''special rules,'' are found in part 17 of title 50 of the Code of Federal Regulations (CFR) in §§ 17.40–17.48. This special rule for § 17.40 would prohibit take of any wolverine in the contiguous United States when associated with or related to trapping, hunting, shooting, collection, capturing, pursuing, wounding, killing, and trade. In this context, any activity where wolverines are attempted to be, or are intended to be, trapped, hunted, shot, captured, or collected, in the contiguous United States, will be prohibited. It will also be prohibited to incidentally trap, hunt, shoot, capture, pursue, or collect wolverines in the course of otherwise legal activities. All otherwise legal activities involving wolverines and their habitat that are conducted in accordance with applicable State, Federal, tribal, and local laws and regulations are not considered to be take under this regulation. This includes activities that occur in and may modify wolverine habitat such as those described below.

In this proposed listing rule, we identified several risk factors for the wolverine DPS that, in concert with climate change, may result in reduced habitat value for the species. These risk factors include human activities like dispersed recreation, land management activities by Federal agencies and

private landowners, and infrastructure development. However, the scale at which these activities occur is relatively small compared to the average size of wolverine's home range, between 300 and 500 $km^2$ (186 and 310 $mi^2$). For example, ski resorts constitute the largest developments in wolverine habitats. In Colorado, the state with the most ski resorts in the range of the wolverine, ski resort developments cover only 0.6 percent of available wolverine habitat (Colorado Division of Wildlife 2010, p. 16). Other developments are more localized still, such as mines and small infrastructure. It is possible that these forms of habitat alteration may affect individual wolverines, by causing the temporary movement of a few individuals within or outside of their home ranges during or shortly after construction. However, due to the small scale of the habitat alteration involved in these sorts of activities, we conclude that the overall impact of these activities is not significant to the conservation of the species. Dispersed recreation like snowmobiling and back country skiing, and warm season activities like backpacking and hunting, occur over larger scales; however, there is little evidence to suggest that these activities may affect wolverines significantly or have a significant effect on conservation of the DPS. Preliminary evidence suggests that wolverines can coexist amid high levels of dispersed motorized and nonmotorized use (Heinenmeyer *et al*. 2012, entire), possibly shifting activity to avoid the most heavily used areas within their home ranges.

Transportation corridors and urban development in valley bottoms between patches of wolverine habitat may inhibit individual wolverines' movement between habitat patches; however, wolverines have made several long-distance movements in the recent past that indicates they are able to navigate current landscapes as they search for new home ranges. As described above, we have no evidence to suggest that current levels of transportation infrastructure development or residential development are a threat to the DPS or will become one in the future.

**Commented [O169]:** May be better evidence that infrastructure development and residential development between habitat islands is more of a threat than an earlier spring melt of just 2 weeks over the remainder of the 21st century; there is no way to know how much transportation infrastructure etc. already has affected wolverines or will in the near and foreseeable future; "no evidence" does not guarantee "no effect"

Land management activities (principally timber harvest, wildland firefighting, prescribed fire, and silviculture) can modify wolverine habitat, but this generalist species appears to be little affected by changes to the vegetative characteristics of its habitat. In addition, most wolverine habitat occurs at high elevations in rugged terrain that is not conducive to intensive forms of silviculture and timber harvest. Therefore, we anticipate that habitat modifications resulting from these types of land management activities would not significantly affect the conservation of the DPS, as we described above.

The proposed special rule under section 4(d) of the Act will provide for the possession and take of wolverines that are (1) legally held at the time of listing (2) legally imported pursuant to applicable Federal and state statutes, or (3) captively bred without a permit. The special rule will also allow the continuation of the export of captive-bred wolverines provided applicable Federal and state laws are followed, and provide for the transportation of wolverine skins in commerce within the United States. The export skins from wolverines documented as captive-bred will be permitted. Legally possessed skins may be transported in interstate trade without permits.

**Commented [O170]:** I'm confused; does this affect possession and take of legally harvested wolverines in Alaska? Because it refers to wolverines "legally held at the time of listing"

In this proposed rule, we include a prohibition against incidental take of wolverine in the course of legal trapping activities directed at other species. However, documented take of wolverine from incidental trapping has been low. In the 2008–2009 trapping season, two wolverines were incidentally killed in traps set for other species in Beaverhead and Granite Counties, Montana (Montana Fish, Wildlife, and Parks 2010, p. 2). In Idaho, the U.S. Department of Agriculture Wildlife Services trapped three wolverines (one each in 2004, 2005, and 2010) incidental to trapping wolves involved in livestock

**Commented [O171]:** Where? In the DPS only?

depredations. One of these sustained severe injuries and was euthanized. We are requesting the public, Federal agencies, and the affected State fish and wildlife agencies to submit public comments on this issue, including any State management plans related to trapping regulations and any measures within those plans that may avoid or minimize the risk of wolverine mortality from incidental trapping for other species.

**Commented [O172]:** There are a number of methods that can be used to minimize incidental take while trapping other species

CRITICAL HABITAT

Section 3(5)(A) of the Act defines critical habitat as "(i) the specific areas within the geographical area occupied by the species, at the time it is listed...on which are found those physical or biological features (I) Essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species at the time it is listed...upon a determination by the Secretaries of Commerce and Interior that such areas are essential for the conservation of the species." Section 3(3) of the Act (16 U.S.C. 1532(3)) also defines the terms "conserve," "conserving," and "conservation" to mean "to use and the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this chapter are no longer necessary."

Section 4(a)(3) of the Act and implementing regulations (50 CFR 424.12) require that, to the maximum extent prudent and determinable, we designate critical habitat at the time a species is determined to be an endangered or threatened species. Critical habitat may only be designated within the jurisdiction of the United States, and may not be designated for jurisdictions outside of the United States (50 CFR 424(h)). Our regulations (50 CFR 424.12(a)(1)) state that designation of critical habitat

is not prudent when one or both of the following situations exist: (1) The species is threatened by taking or other activity and the identification of critical habitat can be expected to increase the degree of threat to the species; or (2) such designation of critical habitat would not be beneficial to the species. Our regulations (50 CFR 424.12(a)(2)) further state that critical habitat is not determinable when one or both of the following situations exists: (1) Information sufficient to perform required analysis of the impacts of the designation is lacking; or (2) the biological needs of the species are not sufficiently well known to permit identification of an area as critical habitat.

Delineation of critical habitat requires, within the geographical area occupied by the DPS of the North American wolverine in the contiguous United States, identification of the physical and biological features essential to the conservation of the species. In general terms, physical and biological features essential to the wolverine may include (1) Areas defined by persistent spring snowpack and (2) areas with avalanche debris (bottom of avalanche chutes where large trees, rocks, and other debris are swept) and talus slopes or boulder fields (debris piles of large rocks, trees, and branches) in which females can construct dens which provide security from large predators and buffer against wind and low temperatures.

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**Commented [O173]:** Include dispersal habitat that may have neither snowpack or avalanche debris and wildlife corridors outside of wolverine habitat

Information regarding the wolverine's life functions and habitats associated with these functions has expanded greatly in recent years. We need additional time to assess the potential impact of a critical habitat designation, including whether there will be any benefit to wolverine from such a designation. A careful assessment of the habitats that may qualify for designation as critical habitat will require a thorough assessment in light of projected climate change and other threats. At this time, we also need more time to analyze the comprehensive data to identify specific areas appropriate for critical

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habitat designation. Accordingly, we find designation of critical habitat to be "not determinable" at this time.

Commented [O174]: Particularly because the best science available indicates that erroneous assumptions about wolverine habitat requirements (deep snow until 15 May) led to incorrect evaluation of the threat of climate warming to wolverine habitat in the DPS (Attachment A)

**Peer Review**

In accordance with our joint policy on peer review published in the **Federal Register** on July 1, 1994 (59 FR 34270), we will seek the expert opinions of at least three appropriate and independent specialists regarding this proposed rule. The purpose of peer review is to ensure that our listing determination and critical habitat designation are based on scientifically sound data, assumptions, and analyses. We have invited these peer reviewers to comment during this public comment period.

We will consider all comments and information received during this comment period on this proposed rule during our preparation of a final determination. Accordingly, the final decision may differ from this proposal.

**Required Determinations**

*Clarity of the Rule*

Executive Order 12866 requires each agency to write regulations that are easy to understand. We invite your comments on how to make this rule easier to understand including answers to questions such as the following: (1) Are the requirements in the rule clearly stated? (2) Does the rule contain technical language or jargon that interferes with its clarity? (3) Does the format of the rule (grouping and order of sections, use of headings, paragraphing, etc.) aid or reduce its clarity? (4) Would the rule

be easier to understand if it were divided into more (but shorter) sections? (5) Is the description of the rule in the **SUPPLEMENTARY INFORMATION** section of the preamble helpful in understanding the rule? What else could we do to make the rule easier to understand?

Send a copy of any comments that concern how we could make this rule easier to understand to Office of Regulatory Affairs, Department of the Interior, Room 7229, 1849 C Street, NW., Washington, DC 20240. You also may e-mail the comments to this address: *Exsec@ios.goi.gov*.

*Paperwork Reduction Act of 1995 (44 U.S.C. 3501, et seq.)*

This rule does not contain any new collections of information that require approval by Office of Management and Budget (OMB) under the Paperwork Reduction Act. This rule will not impose recordkeeping or reporting requirements on State or local governments, individuals, businesses, or organizations. An agency may not conduct or sponsor, and a person is not required to respond to, a collection of information unless it displays a currently valid OMB control number.

*National Environmental Policy Act (42 U.S.C. 4321 et seq.)*

We have determined that environmental assessments and environmental impact statements, as defined under the authority of the National Environmental Policy Act of 1969, need not be prepared in connection with listing a species as an endangered or threatened species under the Endangered Species Act. We published a notice outlining our reasons for this determination in the **Federal Register** on October 25, 1983 (48 FR 49244).

**References Cited**

A complete list of all references cited in this proposed rule is available on the Internet at *http://www.regulations.gov* or upon request from the Field Supervisor, Montana Ecological Services Field Office (see **FOR FURTHER INFORMATION CONTACT** section).

**Authors**

The primary authors of this proposed rule are the staff members of the Montana Ecological Services Field Office (see **FOR FURTHER INFORMATION CONTACT**).

**List of Subjects in 50 CFR Part 17**

Endangered and threatened species, Exports, Imports, Reporting and recordkeeping requirements, and Transportation.

**Proposed Regulation Promulgation**

Accordingly, we propose to amend part 17, subchapter B of chapter I, title 50 of the Code of Federal Regulations, as set forth below:

**PART 17—[AMENDED]**

1. The authority citation for part 17 continues to read as follows:

Authority: 16 U.S.C. 1361-1407; 1531-1544; and 4201-4245, unless otherwise noted.

2. In § 17.11(h) add entries for "Wolverine, North American" to the List of Endangered and Threatened Wildlife in alphabetical order under Mammals to read as set forth below:

**§ 17.11 Endangered and threatened wildlife.**

* * * * *

(h) * * *

Species□Historic range□Vertebrate population where endangered or threatened□Status□When listed□Critical habitat□Special rules□□Common name□Scientific name□□□□□□□□□

Historic range□Vertebrate population where endangered or threatened□Status□When listed□Critical habitat□Special rules□□Common name□Scientific name□□□□□□□□□

Vertebrate population where endangered or threatened□Status□When listed□Critical habitat□Special rules□□Common name□Scientific name□□□□□□□□□

Status□When listed□Critical habitat□Special rules□□Common name□Scientific name□□□□□□□□□

When listed□Critical habitat□Special rules□□Common name□Scientific name□□□□□□□□□

Critical habitat□Special rules□□Common name□Scientific name□□□□□□□□□

Special rules□□Common name□Scientific name□□□□□□□□□

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Mammals

*  *  *  *  *  *  *

□□Wolverine, North American

□Wolverine, North American

Wolverine, North American

□*Gulo gulo luscus* □U.S.A. (Alaska and northern contiguous States); Canada□Where found within contiguous U.S.A., except where listed as an experimental population□T□□NA□17.40(a)

*Gulo gulo luscus* □U.S.A. (Alaska and northern contiguous States); Canada□Where found within contiguous U.S.A., except where listed as an experimental population□T□□NA□17.40(a)

U.S.A. (Alaska and northern contiguous States); Canada□Where found within contiguous U.S.A., except where listed as an experimental population□T□□NA□17.40(a)

Where found within contiguous U.S.A., except where listed as an experimental population□T□□NA□17.40(a)

T□□NA□17.40(a)

□NA□17.40(a)

NA□17.40(a)

17.40(a)

□□Wolverine, North American□*Gulo gulo luscus*□U.S.A. (Alaska and northern contiguous States); Canada□U.S.A. (specified portions of CO, NM, and WY; see 17.84(d))□XN□□NA□17.84(d)□□

□Wolverine, North American□*Gulo gulo luscus*□U.S.A. (Alaska and northern contiguous States); Canada□U.S.A. (specified portions of CO, NM, and WY; see 17.84(d))□XN□□NA□17.84(d)□□

Wolverine, North American□*Gulo gulo luscus*□U.S.A. (Alaska and northern contiguous States); Canada□U.S.A. (specified portions of CO, NM, and WY; see 17.84(d))□XN□□NA□17.84(d)□□

*Gulo gulo luscus*□U.S.A. (Alaska and northern contiguous States); Canada□U.S.A. (specified portions of CO, NM, and WY; see 17.84(d))□XN□□NA□17.84(d)□□

U.S.A. (Alaska and northern contiguous States); Canada□U.S.A. (specified portions of CO, NM, and WY; see 17.84(d))□XN□□NA□17.84(d)□□

U.S.A. (specified portions of CO, NM, and WY; see 17.84(d))□XN□□NA□17.84(d)□□

XN□□NA□17.84(d)□□

□NA□17.84(d)□□

NA□17.84(d)□□

17.84(d)□□

□

* * * * * * *□□

□

3. Amend § 17.40 by revising paragraph (a) to read as follows:

**§ 17.40 Special rules—mammals.**

(a) Wolverine, North American (*Gulo gulo luscus*).

(1) *Which populations of the North American wolverine are covered by this special rule?* This rule covers the distribution of this species in the contiguous United States.

(2) *What activities are prohibited?* Any activity where wolverines are attempted to be, or are intended to be, trapped, hunted, shot, captured, or collected, in the contiguous United States, will be prohibited. It will also be prohibited to incidentally trap, hunt, shoot, capture, pursue, or collect wolverines in the course of otherwise legal activities.

(3) *What activities are allowed?* Incidental take of wolverines will not be a violation of section 9 of the Act, if it occurs from any other otherwise legal activities involving wolverines and their habitat that are conducted in accordance with applicable State, Federal, tribal, and local laws and regulations. Such activities occurring in wolverine habitat include:

(i) Dispersed recreation such as snowmobiling, skiing, backpacking, and hunting for other species;

(ii) Management activities by Federal agencies and private landowners such as timber harvest, wildland firefighting, prescribed fire, and silviculture;

(iii) Transportation corridor and urban development;

(iv) Mining;

(v) Transportation and trade of legally possessed wolverine skins and skins from captive-bred wolverines within the United States.

* * * * *

Dated: 1/16/2013

/s/ Rowan W. Gould

Acting Director, U.S. Fish and Wildlife Service

Billing Code 4310–55–P

**From:** A J
**To:** Grizzle, Betty
**Subject:** Re: emails discussions
**Date:** Tuesday, April 18, 2017 5:11:48 PM

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My den site snow paper is now projected to be online in July. Final edits are in and awaiting proofs.

Sent from my iPhone

On Apr 18, 2017, at 2:40 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> I believe this is the one I have been reading, but thanks for sending. Having a hard time understanding why your comments weren't addressed.
>
> On Tue, Apr 18, 2017 at 3:32 PM, A J <222wsheridan@gmail.com> wrote:
> > Betty
> > Here are the comments I made on the status review that was sent to the 7 peer reviewers. Even some of these comments are probably out of date now. I assume you have this for all 7 reviewers, but just in case.....
> >
> > On Tue, Apr 18, 2017 at 2:23 PM, A J <222wsheridan@gmail.com> wrote:
> > > i'm not sure Frances ever completed that thesis; I got that draft from his advisor Dr. Cook
> > >
> > > On Tue, Apr 18, 2017 at 2:20 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > > > Thanks again. Also, just wanted to let you know that the photos in your "Associations and Movement Patterns of Reproductive Female Wolverines (*Gulo gulo luscus*) on the Southeast Alaska Mainland" (Final Report February 2010) were very interesting. But more importantly, I had been searching (without success) for the Frances 2008 MS Thesis that is included in that document as an Appendix (the UNM library said it was missing from their collection!).
> > > >
> > > > On Tue, Apr 18, 2017 at 3:15 PM, A J <222wsheridan@gmail.com> wrote:
> > > > > here it is
> > > > >
> > > > > On Tue, Apr 18, 2017 at 2:08 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > > > > > Looking for Attachment (appendix?) A right now.
> > > > > >
> > > > > > On Tue, Apr 18, 2017 at 3:05 PM, A J <222wsheridan@gmail.com> wrote:
> > > > > > > Here Attachment B; do you need any others?
> > > > > > >
> > > > > > > On Tue, Apr 18, 2017 at 1:33 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > > > > > > > Thanks Audrey. I found a few things, but not these (yet). I am looking at your peer review comments on previous proposed rule

and haven't found your "Attachment B" yet....will keep looking.

I apologize for having you search for and resend your earlier comments; I am trying to be thorough in this new assessment and have many questions about several analyses.
Betty

On Tue, Apr 18, 2017 at 2:20 PM, A J <222wsheridan@gmail.com> wrote:

> Betty
> I don't know if you have already seen these from Shawn's files, but these emails contain a discussion I had with Copeland and McKelvey after some reluctance on my part to get into such an exchange post-status review. I was pretty burned out by then on the whole subject. But you may find parts help answer some of the questions you recently sent. The McKelvey Email file is emails between Jeff and I until it became apparent that it was better to talk directly to Kevin and so his responses to me are in blue type in that email. The McKelvey Email Response file holds my answers back to him in black type. As you will see, there is little consensus on the matters under discussion. I had permission from both to share these emails and Shawn received copies. He had encouraged us to discuss these issues (and others) hoping to get some resolution of the differences of opinion, but as I suspected from the start, I don't think anyone changed their minds on anything.

--

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**From:** Malin Aronsson
**To:** A J
**Cc:** Grizzle, Betty
**Subject:** Re: Question re natal den abandonment (from 1998 publication)
**Date:** Wednesday, April 19, 2017 12:34:36 AM
**Attachments:** Paper 4_Malin Aronsson_2.pdf
Paper 5_Malin Aronsson_2[1].pdf
Kapitel 6 Malin Aronsson FINAL.pdf
Paper 7_Malin Aronsson_2.pdf

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Hi,

Here are all the 4 “wolverine chapters” from my PhD thesis.

/Malin

---

**From:** A J <222wsheridan@gmail.com>
**Date:** Tuesday, April 18, 2017 at 23:13
**To:** "Grizzle, Betty" <betty_grizzle@fws.gov>, Malin Aronsson <malin.aronsson@slu.se>
**Subject:** Re: Question re natal den abandonment (from 1998 publication)

It sounds like you have the doctoral thesis summary. The PhD doctoral thesis is actually 7 chapters; the first 3 on lynx and the last 4 on wolverine. I sent you #7.The sixth paper has already been published in Animal Conservation 2016 "Mismatch between goals and scale....You might ask Malin to send you #4 and #5---Malin, could you send those to Betty and to me?

On Tue, Apr 18, 2017 at 12:54 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> Oh, I see now. What I have is the Doctoral Thesis, about 63 pages. So, maybe I don't have this.
>
> On Tue, Apr 18, 2017 at 1:25 PM, A J <222wsheridan@gmail.com> wrote:
>
> > just wanted to be sure you mean Malin's PhD dissertation with 4 chapters on wolverines and not her Masters thesis???
> >
> > On Tue, Apr 18, 2017 at 12:15 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> >
> > > Yes, I have Malin Aronsson's thesis. I will need to do a little digging to find your previous comments/emails. I do see in my records your peer review comments from 2013; will take a look at those.
> > > Thank you.
> > >
> > > On Tue, Apr 18, 2017 at 12:59 PM, A J <222wsheridan@gmail.com> wrote:
> > >
> > > > Betty
> > > > Do you have my comments from the last status review regarding den abandonment relative to those dates? If I recall, I mention that none of the documented Rocky Mtns. den abandonments occurred after April. I did do a relatively in-depth analysis of SNOTEL data and sent comments to McKelvey when we discussing all this in

emails. I assume you have our email exchanges since I sent those to Shawn back then.

Den emergence will certainly have something to do with inherent growth rates. Kits born in late January will be much larger and more developed and may move to rendezvous sites even before snow melts at a natal den. Do you have Malin Aronsson's thesis with a paper on moves from natal dens? They were quite variable. We know much more now about dens and movements related to dens than we did back in 1998.

On Tue, Apr 18, 2017 at 11:01 AM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> Thanks Audrey. I might take a look through your dissertation (and Copeland's thesis) to see if there are some clues there, but, yes, it was quite some time ago! The temperature data relative to den abandonment might be interesting to evaluate relative to the dates that have been used in some of the snow models (e.g., May 15, May 1, mid- or late-April, etc.).
>
> I wonder if your observations on den emergence relate to inherent growth rates?
>
> I don't know much more about the Belgian sighting. I sent a similar news article to Bob hoping that he might have heard something more from your colleagues in Sweden.
>
> On Tue, Apr 18, 2017 at 11:33 AM, A J <222wsheridan@gmail.com> wrote:
>
> > Hi Betty
> > The Idaho den abandonment temperatures were taken from a SNOTEL site near where the den occurred (Banner Summit). The Alaska den abandonment occurred while I was in the field watching the dens and spring temperatures. I don't recall how many days; it was >20 years ago!!! In any event, it would probably be variable how many days would be required before den snow tunnels would begin to slump or dripping would occur in boulder/avalanche debris dens.
> >
> > I had not seen the Belgium birth article. Do you know when in February it was born? Born early or late would make a big difference in den emergence. Obviously, wolverines do not need snow to have young since many are born in captivity without snow, but it is interesting that it appears that kits beginning to explore outside the den still occurs around the same age. I can send you photos of kits of known age around den emergence time if that is relevant (from captive and wild with permission from the photographers).
> > Audrey
> >
> > On Tue, Apr 18, 2017 at 9:25 AM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> >
> > > Hi Audrey - In your 1998 paper, *Characteristics of Wolverine Reproductive Den Sites* (from The Journal of Wildlife Management), there is a section title "Den Abandonment" (p. 1316). There it says: "In both Alaska and Idaho, abandonment of natal dens coincided with a period when maximum daily temperatures rose above freezing for a number of days for the first time since

denning commenced."

Did you determine/estimate the actual number of days above freezing for abandonment of natal dens in these two areas?

Also, I am sure you heard about the wolverine (apparently born) in Belgium wildlife park (near Han-sur-Lesse).
Here is the Reuters article link:
http://www.reuters.com/article/us-belgium-wildlife-idUSKBN17G0TJ

Thanks for your time,
Betty
--

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# Female breeding dispersal in wolverines; a solitary carnivore with high territorial fidelity

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## Abstract

Individuals' fidelity to an area provides insight into the stability of the spatial and temporal organisation of animals, important for population structure and dynamics. Territorial fidelity is often influenced by reproductive success, age, the dispersion and predictability of resources, and intraspecific competition. We examined between-year territorial fidelity in wolverines (*Gulo gulo*), using location data from 47 individuals (42 females and 5 males) collected during 1993–2013 in northern Sweden, to assess the stability of the spatial organisation of this solitary carnivore. For females, we determined residency status from one year to the next in each territory. We found that our study population is characterized by a stable distribution of resident individuals, with both males and females showing higher fidelity at the total territory level compared to more intensively used core areas within their territory. In 86% of the yearly female residency status estimates (n = 122), the female remained stationary. The non-stationary females either vacated their territory (8% of residency statuses) or expanded into neighbouring territories (6% of residency statuses). We documented six cases of breeding dispersal (*i.e.* permanent movement of an individual between subsequent territories where it reproduced), representing one of the few known cases of breeding dispersal in long-lived large mammals. We suggest that the observed high territorial fidelity is enabled by wolverines' caching and scavenging behaviour, which buffer the unpredictable and large spatiotemporal variation in resource abundance in this low-productivity area. Female breeding dispersal may occur due to competition for high-quality territories in this saturated population, where females are forced to abandon their territory by competitors or bequeath territories to offspring. This study further highlights the complexity of the social and spatial dynamics in solitary carnivores.

*Keywords*: floater, social system, territoriality, space use, home range

## Introduction

Individuals' fidelity to an area reflects the stability of the spatial organisation of animals (Switzer 1993; Adams 2001), and interannual variation in space use patterns can influence both population structure and dynamics (Terraube *et al.* 2015; Uboni *et al.* 2015). Home range fidelity is generally associated to dispersion, predictability and depletion rate of resources, as well as reproductive success, age, and competition (Moorhouse & Macdonald 2005; Kirk *et al.* 2008; Edwards *et al.* 2009; Terraube *et al.* 2015). In solitary territorial species, space use is primarily driven by resource competition over access to food or the opposite sex (Sandell 1989; Aronsson *et al.* 2016). Territorial fidelity is beneficial because it allows individuals to become familiar with resources in an area, enhancing survival and reproductive success (Switzer 1993; Kirk *et al.* 2008). Furthermore, for species that aggressively defend territories, movement into unfamiliar areas increases mortality risk (Isbell *et al.* 1990; Stamps & Krishnan 2001). Despite this, some individuals may vacate an established territory and perform breeding dispersal (here defined as the movement of individuals, between subsequent breeding sites, following Greenwood 1980). Breeding dispersal has mostly been documented in birds (*e.g.* Greenwood and Harvey 1982; Terraube *et al.* 2015), and although it occurs in mammals (*e.g.* Berteaux & Boutin 2000; Jerina *et al.* 2014) it has rarely been documented in larger long-lived mammals (Jerina *et al.* 2014).

Breeding dispersal may be a consequence of reproductive failure, mate loss or an attempt to acquire a higher-quality territory (Wauters *et al.* 1995; Forero *et al.* 1999; Pasinelli *et al.* 2007). It can also result from intraspecific competition; both when resident individuals are evicted or disperse to take over a territory (Pasinelli *et al.* 2007; Mattisson *et al.* 2013). Breeding dispersal has also been considered as a form of parental investment when the territory is bequeathed to an offspring to enhance offspring survival and reproductive success (Lindström 1986; Berteaux & Boutin 2000). Moreover, some individuals that vacate a territory may become floaters (Smith 1978), forming a reservoir of individuals that can occupy vacant territories when they become available and thus influence population dynamics (Penteriani *et al.* 2011).

Long-term, individual-based ecological studies are essential to obtain information about between-year variation in space use and spatial organisation (Pelton & van Manen 1996; Clutton-Brock and Sheldon 2010). In this study, we use location data from 47 adult wolverines (*Gulo gulo*) monitored during 20 years (1993-2013) in northern Sweden. The wolverine is a solitary carnivore with a polygamous mating system (Hedmark *et al.* 2007), intrasexual territoriality (Persson *et al.* 2010; Inman *et al.* 2012*a*) and male-biased natal dispersal (Vangen *et al.* 2001; Flagstad *et al.* 2004). Wolverines occupy arctic tundra and boreal forest zones of North America and Eurasia (Copeland *et al.* 2010) and are adapted to harsh environmental conditions with low productivity by being an opportunistic generalist predator and scavenger that caches food for later use (Inman *et al.* 2012*b*; Mattisson *et al.* 2016). Wolverine female reproductive success is influenced by winter food availability as well as age-related reproductive costs, where the probability of successfully reproducing two years in a row decline with age (Persson 2005; Rauset *et al.* 2015). In northern Sweden, wolverines primarily feed on migratory, semi-domestic reindeer (*Rangifer tarandus*) (Mattisson *et al.* 2011; Mattisson *et al.* 2016) managed by indigenous Sámi reindeer herding communities (Persson *et al.* 2009).

The aim of this study was to assess the stability of wolverine spatial organisation by examining individual territorial fidelity from one year to the next. To account for the possibility that factors determining space use differ between intensively-used areas compared to the total territory (Aronsson *et al.* 2016), we measured site fidelity at two spatial scales; (i) total territory and (ii) core area. We also examined between-year changes in female residency status; *i.e.* did they remain resident or did they permanently leave an established territory. Breeding dispersal may occur to enhance future reproductive success (Wauters 1995; Pasinelli *et al.* 2007), or as a consequence of decreased reproductive potential with age (Berteaux & Boutin 2000). Therefore, we considered the influence of previous reproductive performance and age on fidelity in wolverine females. Territorial fidelity is generally predicted to be low in unpredictable environments with low and variable resource abundance (Switzer 1983; Maher & Lott 2000; Moorhouse & Macdonald 2005; Edwards *et al.* 2009). Still, we predict that wolverines exhibit high territorial fidelity because of their food caching behaviour that buffers temporal fluctuations in food availability, and thus promotes territoriality and site fidelity even when resources in the environment are unpredictable (Tye 1986; Maher & Lott 2000; Eide *et al.* 2004).

## Materials and Methods

The study was carried out in a 7000 $km^2$ area in and around Sarek National Park in northern Sweden (Kvikkjokk 67o00'N, 17o40'E). The climate is continental with cold winters (-13$^{o}$C in January) and medium warm summers (14$^{o}$C in July) and the ground is usually snow covered from November to May. The area is characterized by deep valleys, glaciers, and high alpine plateaus with peaks up to 2000 m a.s.l. Mountain birch (*Betula pubescens*) forms the tree line at 600-700 m a.s.l. (Rauset *et al.* 2015). The area consists of important spring and summer grazing pastures for semi-domestic reindeer. During winter, most reindeer are moved to winter grazing grounds to the east of the study area (Danell *et al.* 2006) resulting in a large temporal and spatial variation in reindeer density.

We used wolverine location and reproductive data collected from 1993-2013. Wolverines were captured and immobilized using ethics approved handling protocols (Persson *et al.* 2010). Animals were fitted with VHF-collars (1993-1995: MOD315, Telonics. USA), intraperitoneal VHF-transmitters (1996-2013: IMP/210/L, IMP/300/L, or IMP/400/L, Telonics. USA) or GPS-collars (2003-2006: Televilt PosrecTM C300, TVP positioning AB, Sweden; 2008-2013 GPS plus mini, Vectronics Aerospace, Germany). Female reproductive status and location of natal den sites (hereafter dens) was confirmed using a combination of radio tracking, snow tracking and visual observations (*see* Persson *et al.* 2006). Reproductions were classified as successful if the cubs survived to June (3–4 months old) and unsuccessful if the female showed denning behaviour but did not have cubs in June or did not reproduce. We aimed to capture and equip all cubs with intraperitoneal transmitters and monitor them throughout their life, consequently a large part of the individuals was of known age.

Only resident animals ≥ 3 years old were included in the analysis because wolverines in the study population rarely breed prior to 3 years (Rauset *et al.* 2015). We estimated annual space use for each individual as the annual utilization distribution (UD) using the fixed-kernel method with the reference bandwidth (Worton 1989) within the '*adehabitatHR*' package (Calenge 2013) for R (R Core Team 2014). Years were defined as calendar years. The number of locations acquired per individual and year varied extensively during the study period as telemetry technology developed. To reduce biases from different sampling frequencies (Börger *et al.* 2006) we randomly sampled 1 location/day for individuals with multiple daily locations. We only calculated UDs for individuals monitored for ≥ 6 months during ≥ 2 years with ≥ 20 yearly locations (Persson *et al.* 2010; Rauset *et al.* 2015), in this study mean (± SE) annual locations per individual was 146 ± 15. From the UD, a specific proportion (isopleth) of the animal's use of space can be

retained; we used the 90% isopleth as the annual territory and the 50% isopleth as the core area (Rauset *et al.* 2015). We quantified fidelity by estimating the overlap between annual UDs using the volume of intersection index (VI) for both the territory and core area level (Millspaugh *et al.* 2004). VI values ranges from 0 (no overlap) to 1 (identical UDs). We calculated VI for subsequent years, or year t and t+2 if location data from year t+1 was missing (5 out of 62 VI estimates). Because annual territory sizes do not differ for females with or without cubs (Persson *et al.* 2010), we calculated VI between years independent of female reproductive status. During part of the study period (*i.e.* 1999-2004) the focus of the project was to monitor yearly survival, reproductive success and denning behaviour of the resident females within the study area. Hence, females were intensively monitored during the denning period (Feb-May; Rauset *et al.* 2015) while there are relatively infrequent locations from ≥ 6 months/year for these females. Consequently, for females we also used distances between den sites as a measurement of fidelity, together with VI. We calculated distances between den sites in subsequent years or year t and t+2 if the female did not reproduce in year t+1 (22 out of 90 den distances). In total we obtained 129 interannual fidelity estimates for 5 males (7 VI) monitored for an average of 2.6 years ± 0.6 SE (range: 2–5) and 42 females (55 VI and 90 den distances) monitored for 4.5 ± 0.4 years (range: 2–11).

The closest distance between neighbouring females' den sites used in the same year was 4.6 km (Paper VII). Consequently, we considered females to have conducted breeding dispersal if the VI-estimate or locations showed that she moved from her territory, she reproduced again > 4.5 km from her previous den site and her previous territory was occupied by a new individual (Paper V). Furthermore, females that did not reproduce after moving were considered to have re-established when subsequent space use pattern showed that they became stationary in a new area. We used reproductive success to obtain a measurement of territory quality (Garshelis 2000; Stephens *et al.* 2015). For this we used the locations of all den sites for collared individuals and den sites from the national monitoring program (*i.e.* since 1996 wolverine den sites has been recorded in the Swedish national monitoring program for large carnivores; Aronsson & Persson 2016). For each female, we calculated the total number of den sites that had been documented within 2.1 km of her current den site (*i.e.* 2.1 km is the mean distance between consecutive den sites for stationary females in this study area; see results) or centre point of locations for females that did not reproduce (n = 2). We calculated local denning frequency for each area and year (LDF) as the total number of den sites divided by the time the area had been monitored (*i.e.* 18 years; 1996–2013). Because this measurement is based on successful reproductions, an important fitness component, within different territories, we argue that this is a good measurement of territory quality.

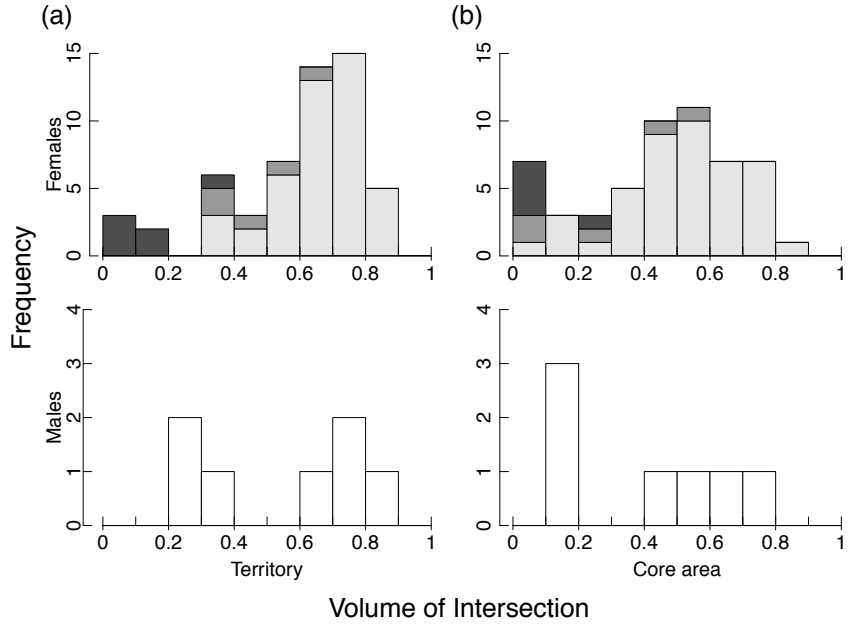


*Figure 1*. Frequency distributions of volume of intersection (VI) values showing: (a) territory and (b) core area fidelity for female and male wolverines in northern Sweden during 1993-2013. VI represents how similar space use was between years (*i.e.* VI value of 0 represents no overlap and VI represents identical space use). Females are divided into stationary (light grey), expanding (medium grey) and breeding dispersing or floating (dark grey).

We used Generalized Linear Mixed Models with a beta error distribution in the '*glmmADMB*' package (Skaug *et al.* 2012) in R with VI as the response variable. Individual identity was fitted as a random effect in all models to account for repeated measurements. We used isopleth level as a covariate to test if fidelity differed between territory and core area level. Due to the low sample size for males (n = 7) we did not conduct any statistical analysis for differences between sexes. For females, we included age, and reproductive success in year t (two-level factor; successful and unsuccessful reproduction) as covariates. Candidate models were compared using the sample-size corrected Akaike Information Criterion (AICc) and AIC weights (wi) from the '*MuMIn*' package (Bartoń 2013) in R. Means are presented with standard errors unless otherwise stated.

Table 1. *Individual females that moved from an established territory during the study period (1993–2013), total time they were monitored, age when moving, residency status (floater: F, breeding dispersal: BD, or re-established: R), reproductive performance before and after move and time from move to first reproduction in second territory. Relative local denning frequency (LDF) shows the difference in LDF for the first and second territory from the mean LDF for stationary females (0.21 ± 0.022).*

| ID | Years monitored | Age when moving | Residency status | Reproductive performance before moving | Reproduction in new territory | Time (years) | Relative LDF first territory | Relative LDF second territory |
|---|---|---|---|---|---|---|---|---|
| F9530* | 5 | 4 | *F** | Success | | 3* | 0.35 | |
| F9530 | " | 5 | *BD** | | Yes | | | -0.15 |
| F9530 | " | 6 | *BD* | Fail | Yes | 1 | -0.15 | -0.04 |
| F9646 | 2 | 7 | *BD* | Fail | Yes | 1 | -0.09 | 0.02 |
| F9870 | 5 | 6 | *BD* | Success | Yes | 1 | 0.02 | -0.15 |
| F03167 | 3 | ? | *BD* | Success | Yes | 2 | -0.15 | 0.02 |
| F05202 | 3 | ? | *BD* | Success | Yes | 2 | -0.15 | -0.15 |
| F9525 | 7 | 9 | *R* | Success | No | - | 0.02 | -0.21 |
| F9312 | 2 | 6 | *F* | Success | - | - | -0.15 | - |
| F9315 | 2 | 4 | *F* | Success | - | - | 0.35 | - |

* F9530 showed were classified as floater after more before establishing and reproducing in a new territory.

## Results

Female and male wolverines had similar overlap (volume of intersection; VI) patterns, and showed higher between-year fidelity for the annual territory compared to core areas (Fig. 1; 0.60 ± 0.03 vs. 0.44 ± 0.03 for females, and 0.55 ± 0.03 vs. 0.42 ± 0.1 for males, respectively; improvement in AICc for overlap model including isopleth level [*i.e.* 90% and 50%] compared to model without: females = 18 and males = 3.2). We determined female residency status from one year to the next in 122 territories, and in 105 (86%) of these the female remained stationary; hence, we considered that wolverine females showed high territorial fidelity. Eight of the 42 females vacated an established territory once (n = 7) or twice (n = 1), resulting in a total of 9 occasions when a resident female moved from her territory (Fig. 2, Table 1). These moving females re-established in a new territory in 7 of these 9 cases (Table 1). In all but one of these, the female reproduced in the new territory and thus conducted breeding dispersal (Figs. 2 and 3). Floating behaviour was exhibited by the 2 females that did not re-establish and 1 breeding dispersal female before she re-established (Table 1, Fig 2). Five additional females expanded their territory once (n = 3) or twice (n = 2) into a neighbouring territory after the neighbouring female died, resulting in reduced overlap. Thus, they subsequently occupied an area previously occupied by two or three females (hereafter called 'expanding'; Figs. 4a and 4c).

The mean distance between consecutive natal den sites for stationary females (excluding expanding females) was 2.1 ± 0.2 km (n = 79), for breeding dispersing females 9.8 ± 0.8 km (n = 6) and for expanding females 9.1 ± 2.3 (n = 5) (Fig. 5). Mean local denning frequency (LDF) for stationary females was 0.21 ± 0.02. To obtain a relative quality estimate for territories that were vacated in relation to where females re-established we used the difference in LDF for these sites from the mean for stationary females (Table 1). Of the 7 females that re-established there was no consistent pattern in how their LDF changed from before and after re-establishment; the LDF of 3 females improved, for 3 females it diminished and for the remaining female LDF did not change. However, only 2 females re-established in a territory with better quality than the mean for stationary females (Table 1). The mean territory and core area VI for stationary females was 0.66 ± 0.02 and 0.52 ± 0.03, respectively, and VI for moving and expanding females was 0.21 ± 0.05 and 0.09 ± 0.03, respectively (Fig. 1). By including all females in the analysis, we found that

both territory and core are fidelity was negatively affected by previous reproductive performance (*i.e.* females that successfully reproduced the first year included in the overlap measurement had lower VI values than females that did not reproduce the first year; Table 2a). However, by excluding females that dispersed or showed floating behaviour from the analysis removed the effect of reproductive success on fidelity (Table 2b). There was no effect of female age on territory or core area overlap (Table 2c).

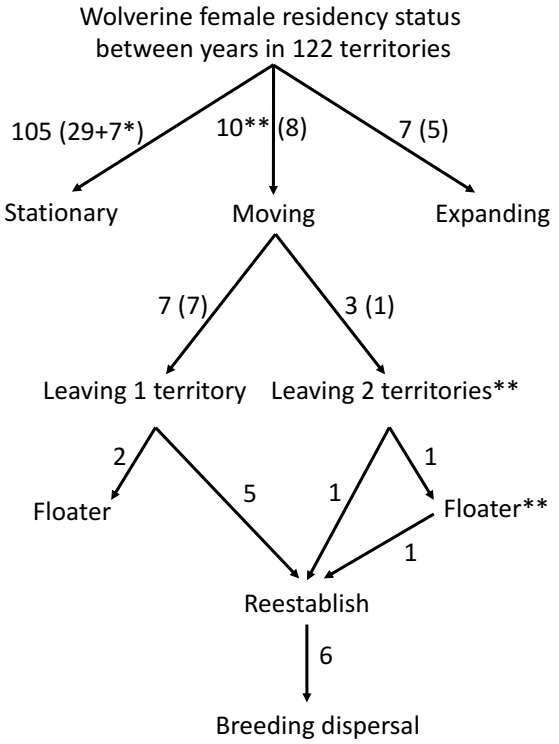


*Figure 2*. Summary of residency status from one year to the next in 122 territories for a total of 42 adult wolverine females monitored for ≥ 2 years during 1993–2013 in northern Sweden. Next to each arrow are indicated number of territories and (number of females). Seven females* were stationary before and/or after moving/expanding, hence these are included twice. One female moved from two territories** during the study period and before re-establishing the first time she was defined as floater during one year**. Consequently, although only 9 territories were vacated during the study period residency status were classified as moving in 10** occasions (floating followed by breeding dispersal in one territory).

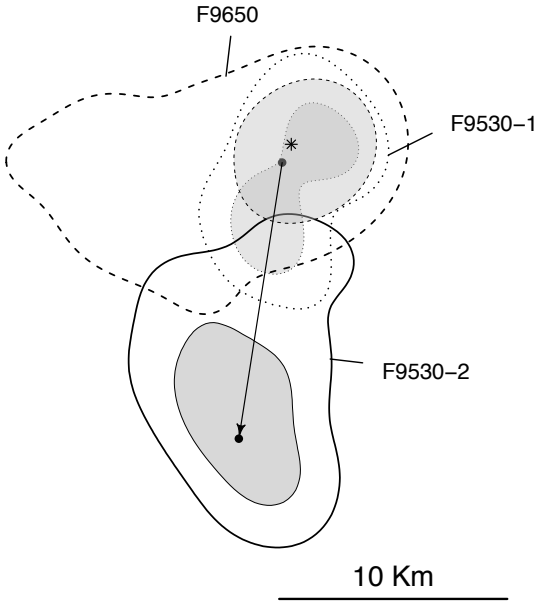


*Figure 3*. Breeding dispersal by wolverine female F9530. F9530 reproduced successfully in a territory (F9530–1; dotted line) in year 1. She subsequently left her first territory and re-established and reproduced in a new territory (F9530–2; solid line) in year 2. Den sites of F9530 are represented by filled circle (•), arrow show dispersal direction. Simultaneously, F9650 established a territory (dashed line) and reproduced (⁎) in the former area of F9530. Core areas are shown in grey with the same outline as corresponding territory

## Discussion

As predicted, wolverines showed high territorial fidelity, as females remained stationary in their territory between years in 86% of the residency status estimates (n = 122). This suggests that the population is characterized by a stable spatial distribution of resident individuals. However, we found six occasions of breeding dispersal, representing the first documentation of wolverine female breeding dispersal, and one of the few in long-lived, large mammals (Jerina *et al.* 2014). This behaviour creates infrequent exceptions to the stable spatial organisation and adds important knowledge regarding the complexity of spacing behaviour in large mammals in general and wolverines in particular.

Territorial fidelity is predicted to be low in habitats where food resources are low, variable, unpredictable and deplete fast (Wauters *et al.* 1995; Kirk *et al.* 2008; Edwards *et al.* 2009). This corresponds to the characterization of wolverine habitat in general (Persson 2005; Inman *et al.* 2012*b*), and particularly in northern Scandinavia where wolverines are highly dependent on migrating reindeer. Reindeer movements are influenced by seasonal snow conditions and Sámi reindeer herding practices (Persson 2005). Thus, prey availability is un-

predictable and varies both within and among years resulting in large territory sizes with high individual variation (Persson *et al.* 2010). However, food caching is an integral part of wolverine biology (Inman *et al.* 2012b; Mattisson *et al.* 2016), which buffers against depletion, unpredictability and variation in prey availability. As a consequence, food caching can be an important factor promoting the observed high territorial fidelity in wolverines despite the unpredictable environment (Tye 1986; Eide *et al.* 2004). In addition, occurrence of more efficient predators, such as the Eurasian lynx (*Lynx lynx*), provides wolverines with a relatively consistent availability of carcasses for direct consumption and caching (Mattisson *et al.* 2011). This decreases the variation and unpredictability in food availability and enhances wolverine reproductive success (Rauset *et al.* 2015; Mattisson *et al.* 2016). Our study area is largely saturated with wolverine territories, resulting in few available areas to settle (Persson *et al.* 2010; Paper V). Territories are maintained by patrolling in combination with marking and aggressive behaviour during encounters (Persson *et al.* 2003, 2009, 2010), and both subadult and adult wolverines are killed by conspecifics (Krebs *et al.* 2004; Persson *et al.* 2009). Consequently, the high potential cost associated with exploratory movements might contribute to the high territorial fidelity. Furthermore, the area is characterized by distinct features, such as mountains, deep valleys and rivers, which form natural territory borders that might facilitate territorial defence (Eason *et al.* 1999). This could confine individuals to established territories, and thus further promote territorial stability in time and space.

Fidelity was lower at the core area level than at the territory level for both males and females, suggesting that it is critical to maintain the outer territory boundary to secure long-term resources (Aronsson *et al.* 2016). In contrast, the extent of the most used area within the territory (*i.e.* core area) presumably varies among years because of spatial fluctuations in key resources. For instance, the spatial distribution of live reindeer and carcasses could greatly vary within and among years due to the nomadic behaviour of reindeer (Mattisson *et al.* 2016). In addition, female core areas could vary among years depending on their reproductive status and interannual variation in den site location. Male wolverines have territories that are several times larger than females (Persson *et al.* 2010). Larger areas are more difficult to defend from intrusion, which could decrease territorial fidelity (Jetz *et al.* 2004). However, both males and females in our study showed high mean overlap values between years. For males this could be a result of our low sample size (*i.e.* 5 individuals). Of the monitored males, 3 individuals showed lower overlap than the other 2 (Fig. 1). One male retreated from parts of his territory when a neighbouring male moved in, indicating that the former might have been actively pushed away by the latter (*i.e.* resulting in low overlap values for both males). The third male appeared to be abandoning his territory at the end of his monitoring period.

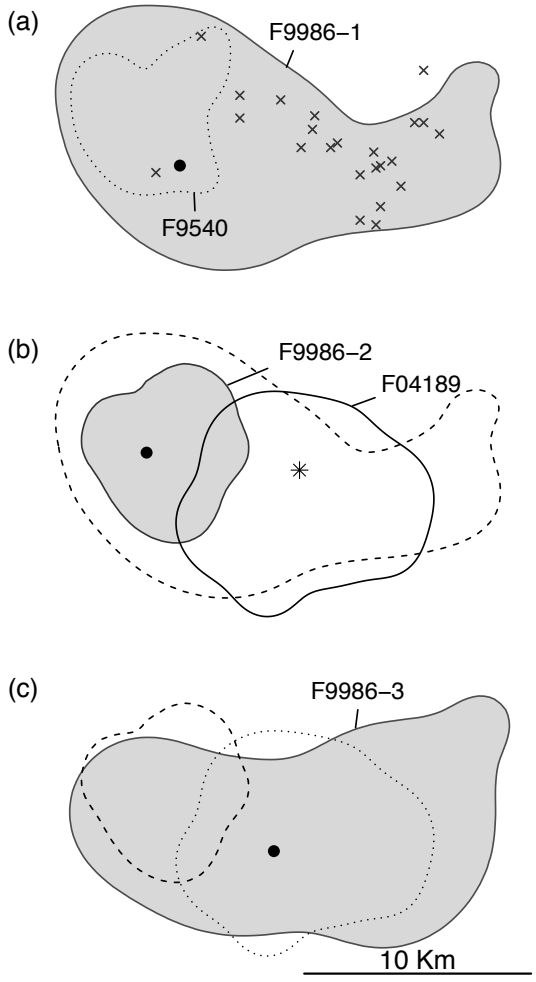


*Figure 4*. Territory expansion and split by wolverine female F9986. (a) F9986 expanded her territory after the death of the neighbouring female F04189 in 2003, telemetry locations for F9986 before expansion are represented by crosses (x). Consequently, the new territory of F9986 (F9986–1; grey) covers an area previously containing two female territories. Filled circle (•) represent the den site of F9986 in 2004 where she gets a female offspring (F04189). (b) In 2007 the area is split between mother (F9986–2; grey) and daughter (F04189), they are both reproducing in 2008, filled circle (•) represents den site of F9986 and star (∗) den site of F4189. (c) After the death of F04189 (lethal control June 2008) F9986 expands again (F9986–3; grey), filled circle (•) represent the den site of F9986 in 2009, she is poached later that same year.

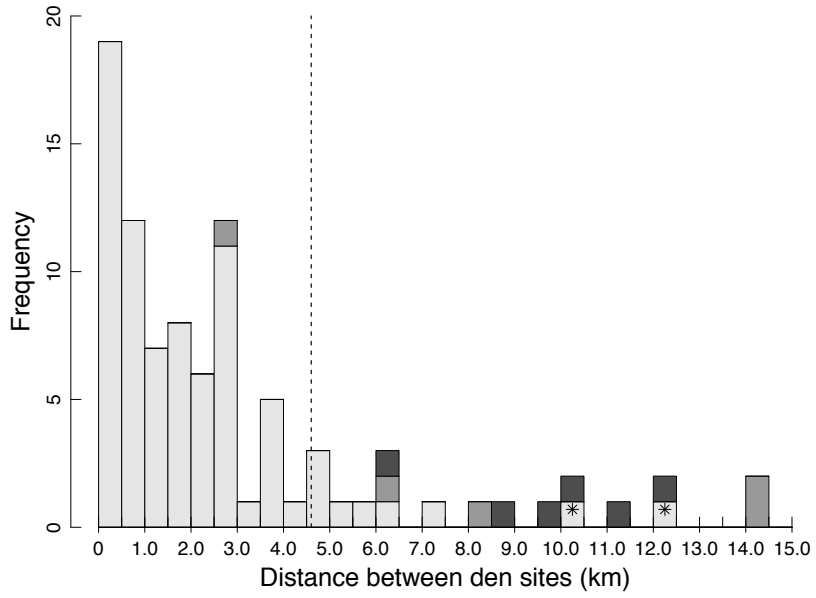


*Figure 5*. Frequency distribution of distances (km; n = 90) between yearly den sites for wolverine females in northern Sweden during 1993–2013. Females are divided into stationary (n = 79; light grey), expanding (n = 5; medium grey) and breeding dispersing (n = 6; dark grey). One female repeatedly used den sites at opposite ends of a large and elongated territory resulting in two large den distances (indicated by ∗).1 By removing these distances, the mean (± SE) distance between den sites for stationary females was reduced to 1.8 ± 0.2 km (n = 77), compared to 2.1 ± 0.2 km (n = 79). The dashed line indicates the closest distance between neighbouring females den sites used the same year within the study area during the study period (Paper VII).

Although wolverine females generally exhibit high territorial fidelity, we found that 8% of territories were vacated between years and 6% of territories were expanded (Fig. 2). If insufficient resources were the main reason for females to vacate a territory, we would expect them to have low reproductive success prior to moving (Pasinelli *et al.* 2007). Yet, on 7 of 9 occasions the moving females reproduced successfully the last year monitored before vacating her territory (Table 1), which suggests that reproductive failure is not the main factor causing established females to abandon a territory. That most females successfully reproduced before vacating their territory also explains the overall negative effect of reproductive success on both territory and core area fidelity (*i.e.* lower VI for females that successfully reproduced; Table 2a), as this effect was considerably diminished when dispersing, expanding and floating females were excluded (Table 2b). Five of the 7 females that reestablished reproduced the first year in the new territory. Considering the high reproductive frequency before and after dispersal (78% and 71%, respectively) compared to the average reproductive frequency in the population (53%; Persson *et al.* 2006) suggests that most females that moved were in prime condition (Table 1; see Rauset *et al.* 2015). Thus, possible reasons for their dispersal are to obtain a territory of higher quality (Wauters *et al.* 1995). Our measure of relative quality of territories that were vacated and re-established, respectively, showed an inconsistent pattern, contrary to what is expected if obtaining a higher quality territory would be the general driver of territory abandonment (Table 1). However, if territorial abandonment and reestablishments is the result of a takeover, the inconsistent pattern in LDF is expected, as the focal female could be either an intruding or evicted individual, which was unknown to us in most cases. The latter is supported by the fact that 3 females that abandoned a territory subsequently exhibited floating behaviour, suggesting that they did not leave because they had the opportunity to obtain a territory of higher quality. Instead, it is likely that they were forced to abandon their territory, possibly because their competitive ability had decreased (Smith 1978), especially considering that two of these females abandoned an area with very high LDF-value. Consequently, abandonment of established territories could be related a combination of searching for better territories and social interactions caused by competition for territories.

Another potential explanation for abandonment of territories by adult females is parental investment (Lindström 1986; Berteaux & Boutin 2000). Wolverine natal dispersal pattern is male-biased, where females tend to remain close their natal territory and age at natal dispersal varies more among females than males (Vangen *et al.* 2001). Young, inexperienced animals that have not settled are often subject to higher mortality than resident animals (Waser 1996; Blankenship *et al.* 2006). Juvenile wolverine females are sometimes killed when they explore areas outside their natal territory after independence, presumably by territorial neighbours (Persson *et al.* 2003), suggesting that territorial competition can be fierce for young inexperienced females in this saturated area. Hence, parental investment could explain why females vacate established territories after a successful reproduction, *i.e.* they bequeath their territory to a daughter. One of the moving females (F9525) was replaced by her young daughter (see Table 1, Paper V). Although we did not find any overall effect of age on female fidelity to territory or core area (Table 2c),

F9525 was older than all other moving females and although she was monitored for 3 years after re-establishment she did not reproduce again. Furthermore, females that expanded their territory subsequently covered an area that previously contained two reproducing females, indicating that there are resources for >1 female. This could be to secure an area that can later be bequeathed to a female offspring (see budding dispersal in social species; Gardner & West 2006; Nichols *et al.* 2012). One female (F9986) maintained her expanded territory for 4 years before her adult daughter (F04189) gained possession of half the area; she then regained the area after her daughter died (Fig. 4; Paper V). In another observation, one subadult daughter established in part of her mother's expanded territory although we could not determine her residency status because she died in an avalanche before first reproduction (27 months of age). The remaining 3 expanding females did not reproduce (n = 1) or only produced male offspring between the expansion and their death or end of the study period (n = 2, monitored for 2 and 5 years following territory expansion).

Table 2. *Candidate models relating wolverine female interannual territory and core area volume of intersection (VI) to reproductive success (Repro; difference of successful reproduction from unsuccessful reproduction) for (a) all VI (n = 55), (b) only VI for stationary females (i.e. excluding breeding dispersal, expanding and floating; n = 46), and (c) age for females with known age (n = 21). Models are ranked based on sample-size corrected AIC (AICc), difference in AICc relative to the highest-ranked model (ΔAICc) and AIC-weights (wi).*

| | VI territory level | | VI core area level | |
|---|---|---|---|---|
| Model | $\Delta AIC_c$ | $w_i$ | $AIC_c$ | $w_i$ |
| (a) | | | | |
| Repro* | 0.00 | 0.78 | 0.00 | 0.86 |
| Null model | 2.54 | 0.22 | 3.56 | 0.14 |
| (b) | | | | |
| Repro** | 0.00 | 0.5 | 0.98 | 0.38 |
| Null model | 0.01 | 0.5 | 0.00 | 0.62 |
| (c) | | | | |
| Null model | 0.0 | 0.82 | 0.00 | 0.82 |
| Age | 3.09 | 0.18 | 3.09 | 0.18 |

*Model predictions: VI = 0.53 for females that successfully reproduced the first year included in overlap estimate, VI = 0.64 for females that did not reproduce

** Model prediction: VI = 0.64 for females that successfully reproduced the first year included in overlap estimate, VI = 0.69 for females that did not reproduce.

To fully understand the causes and consequences of breeding dispersal in wolverine females requires detailed location data to determine the timing and interactions leading up to the dispersal event (*i.e.* if it is a result of an aggressive interaction). In addition, concurrent data are needed on habitat quality and the reproductive success of stationary versus dispersing adult females. However, due to the low reproductive rate of wolverines (Persson *et al.* 2006) and the rarity of this behaviour we could not fully disentangle the potential causes despite 20 years of individual-based data.

We suggest that the high territorial fidelity in wolverines in this study is a result of intrasexual territoriality in a saturated population with intense competition for high-quality territories. This is facilitated by scavenging and caching, which increase predictability in resource abundance, decrease depletion rate and create a valuable resource (cache sites) to defend. In addition, distinct terrain features may assist territorial defence, which promote territorial stability in time and space. Our results concur with the findings of Bischof *et al.* (2016) who investigated spatiotemporal patterns in wolverines using non-invasive genetic sampling to reveal that wolverines tended to stay in the same general area from year to year. We suggest that the ultimate driver of the observed breeding dispersal is high competition for territories, translated through social interactions between competitors (aggressive forcing) and mother-offspring (territory bequeathal). This demonstration of the complexity in carnivore spatial behaviour provides a stronger foundation for science-based management of wolverine populations that are subject to strong conservation and management concerns in many parts of its distribution (Saehter *et al.* 2005; Persson *et al.* 2009; McKelvey *et al.* 2011; Inman *et al.* 2013). Our results have implications for the design and interpretation of population monitoring schemes (Ellis *et al.* 2014; Aronsson & Persson, 2016), harvest strategies (Saether *et al.* 2005) and conflict mitigation (Persson *et al.* 2015; Aronsson & Persson 2016).

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# The link between local territorial dynamics and dispersal patterns for wolverine females

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## Abstract

Dispersal of individuals has direct consequences for population structure and dynamics; from individual fitness to species distribution and persistence. It is therefore vital to understand both causes and consequences of dispersal and settlement patterns for population conservation and management. The wolverine (*Gulo gulo*) is a solitary and territorial carnivore with male-biased dispersal, hence population distribution is presumably limited by female dispersal. A central issue in Scandinavian wolverine management is depredation conflicts, and removal of individuals is used as a conflict-mitigating tool. However, local territorial dynamics and dispersal patterns can have important impact on the effect of hunting on local and regional population density and distribution. We used long-term (1993-2014) spatial and demographic from an area where we monitored nearly all established females (n = 53) and their offspring (n = 71). We assessed causes of territory vacancy, time to replacement and origin of replacers, as well as how local territorial dynamics influences if young females dispersed from or established in the study area. We found that almost all vacated territories were reoccupied by individuals from the immediate surrounding, and that the mother's destiny was of fundamental importance for young females' decision to remain philopatric or disperse. Most dispersers left the population, although the probability to leave was influenced by the number of available territories in the area. Territory quality had limited effect on time to reoccupation of vacated territories. Altogether, this suggests that the population is highly saturated with limited room for dispersing individuals to establish, and that a surplus of young females leave the area. Thus, this population most likely acts as a source population, where the contribution to surrounding areas is related to survival of established females. Thus, local harvest may have limited effect on the local density of resident individuals while it is likely to reduce emigration. Consequently, we show how the link between territorial dynamics and dispersal patterns may affect both local and regional population density and distribution. This illustrates how understanding of mechanisms explaining territorial dynamics and dispersal provides vital information for management planning at different scales.

## Introduction

Dispersal of individuals has direct consequences for population structure and dynamics, from individual fitness to species distribution, colonization and persistence (Kokko & López-Sepulcre 2006; Ronce 2007; Clobert *et al.* 2009; Benton & Bowler 2012). Thus, it is vital to understand both determinants and consequences of dispersal for population conservation and management (Durant 2000; Bowler & Benton 2005, 2012; Robinson *et al.* 2008; Cooley *et al.* 2009).

The dispersal process is divided into three stages – departure, transience and settlement – with potentially different factors affecting these stages (Bowler & Benton 2005; Clobert *et al.* 2009; Bonte *et al.* 2012; Matthysen 2012). Although natal dispersal (*i.e.* the departure from the natal site to an individual's first breeding site) is a commonly studied aspect of animal dispersal, the causes and consequences of natal philopatry (*i.e.* an individual remains and breeds in its natal area, Greenwood 1980; Waser & Jones 1983) is an often-underestimated aspect, despite its importance for understanding the factors driving animal dispersal decisions (Clutton-Brock & Lucas 2012). Most polygamous species have a sex-biased dispersal pattern; consequently, population distribution is primarily limited by dispersal of the more philopatric sex. The benefit of natal area familiarity is a likely reason for natal philopatry (Waser & Jones 1983; Stamps 1987) in addition to individuals having only a limited knowledge of what is available. Thus, individuals within the vicinity of an area will generally be the

first to know if it becomes vacant and can take advantage of this knowledge to secure their occupancy (Sutherland 1996; Jacquot & Solomon 2004).

Dispersal can act as both a cause and effect of ecological patterns and processes (Starrfelt & Kokko 2012), and can hence be of great importance from a management perspective. Human-carnivore conflicts are globally widespread, especially due to predation on livestock and game species (Treves & Karanth 2003). As a consequence, removal of individuals (*i.e.* licensed hunting and/or lethal control) is used as a tool to decrease the damage caused by carnivores, often based on the general assumption that this will reduce local population density (Herfindal *et al.* 2005; Robinson *et al.* 2008; Minnie *et al.* 2016). However, the effect of harvest on local population density depends on species-specific factors such as life history, social structure and dispersal patterns, as well as general population density (Frank & Woodroffe 2001; Milner *et al.* 2007; Robinson *et al.* 2008; Cooley *et al.* 2009; Minnie *et al.* 2016). Density-dependent dispersal may maintain the number of established individuals in an area through movement between hunted (sink) and non-hunted (source) areas (Robinson *et al.* 2008; Turgeon & Kramer 2012; Gervasi *et al.* 2015; Minnie *et al.* 2016), or by the establishment of individuals from the local area that would have otherwise emigrated or remained as floaters (Newby *et al.* 2013; Fattebert *et al.* 2015). Removal of breeding individuals might enhance philopatry among remaining individuals, and thus influence longer-range dispersal patterns. Furthermore, territory quality might also influence dispersal as higher-quality territories should be occupied first (*e.g.* the despotic distribution hypothesis; Fretwell and Lucas 1970). Consequently, knowledge of territorial dynamics and factors influencing both the departure and settlement stages of dispersal will increase our understanding of the effect of hunting as a management tool on the abundance and distribution of carnivore populations at the local and regional scale.

In Scandinavia, large carnivores were almost hunted to extinction by the early 20th century, but due to subsequent legal protection carnivore populations have substantially increased (Chapron *et al.* 2014). The Scandinavian wolverine (*Gulo gulo*) population is a typical example of a carnivore conservation challenge, with the recovering population of this predator occurring in a multi-use landscape, mostly outside of protected areas. Important prey for wolverines in Scandinavia is semi-domestic reindeer (*Rangifer tarandus*), owned by the indigenous Sámi people, and free-ranging sheep (*Ovis aries*) during summer in Norway (Swenson & Andrén 2005; Persson *et al.* 2009; Hobbs *et al.* 2012). In Norway, wolverines are subject to intensive population regulation through licenced hunting and lethal control, while in Sweden wolverines are protected, fuelling a source-sink dynamic between the two countries (Gervasi *et al.* 2015). Still, in Sweden, lethal control (*e.g.* removal of females with dependent young) is implemented to reduce local wolverine density and predation pressure in high-conflict areas (*e.g.* reindeer calving grounds; SEPA 2014). This is in conjunction with the goal of increasing the wolverine distribution outside high-conflict areas in Sweden (SEPA 2014; Aronsson & Persson 2016). However, illegal killing is the main mortality cause for adult wolverines, both inside and outside of protected areas (Persson *et al.* 2009; Rauset *et al.* 2016). Wolverines are highly territorial and exhibit a polygynous mating system (Hedmark *et al.* 2007, Persson *et al.* 2010), and male-biased dispersal (dispersal from the natal area, males = 100% versus females = 69%; Vangen *et al.* 2001), and males disperse further than females (Flagstad et al. 2004). Thus, population distribution and colonization is primarily limited by female dispersal.

In this study, we used long-term (1993-2014) spatial and demographic data from individually monitored wolverine females. Through an intensive radio tracking effort, we have monitored nearly all established females and their offspring within the study area (Fig. 1). Thus, we use detailed data from a large carnivore to assess both female territorial dynamics and natal dispersal/philopatry in relation to detailed (monthly) information on: (1) territory availability, (2) territory quality, (3) individual age, (4) presence of kin, and (5) seasonal effects. First, we assess territorial dynamics by investigating: (i) the cause of territory vacancy (*e.g.* human-caused or natural mortality, and dispersal); (ii) the origin of the replacing individual, and (iii) how long it takes before the territory is reoccupied and the factors influencing the time to reoccupation. These analyses examine territorial dynamics and dispersal from the perspective of the territory, and provide a context for what happens when a territory is 'vacated' for management purposes. Second, we assess the departure and settlement stages of natal dispersal by investigating the factors that influence if young females: (i) establish in their natal territory, (ii) leave their natal territory to establish in a nearby territory (within the study population), or (iii) leave their natal territory to establish/disperse outside of the study population. These analyses examine territorial dynamics and dispersal from the perspective of young dispersing females, and evaluate the factors important for individual-level decisions. Our analyses of natal dispersal and territorial dynamics of wolverines help understand the dispersal process of a large carnivore, and this is of interest from both ecological and management perspectives. Taken together, this provide a clearer picture of how wolverine harvest might influence local recruitment, local and regional densities, and whether the harvest as a management tool achieves its desired aims.

## Material and methods

### Study area, animal capture and monitoring

We used location data from radio-collared wolverines captured in the Swedish Wolverine Research project during 1993-2014. One major goal for the project has been to equip all adult resident females within the study area with transmitters to monitor their survival and reproductive performance (Persson *et al.* 2003, 2005, 2006, 2009, 2015; Rauset *et al.* 2015; 2016). The study area is located in and around the Laponia UNESCO World Heritage Site in northern Sweden (Kvikkjokk 67o00'N, 17o40'E). The area is characterized by deep valleys at about 300 m a.s.l. and high mountainous plateaus of bare rock and glaciers with peaks up to 2000 m a.s.l. Tundra represents 57% of the study area and forest 36% (Mattisson *et al.* 2011). The vegetation at lower elevations mainly consists of mixed conifer forest (*Pinus sylvestris* and *Picea abies*) interspersed by bogs and lakes, followed by hillsides and high elevation valleys of mountain birch forest (*Betula pubescens*), which form the tree line at 600–700 m a.s.l. The climate is continental with distinct seasons, and the ground is snow-covered from November until May.

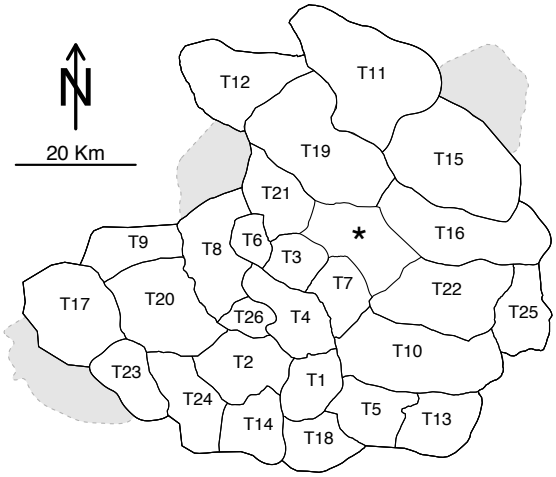
Presence of unmarked wolverines within the study area was assessed by snow tracking from the air by helicopter or on ground by snowmobile or skiing, and by searching for den sites during the spring (Paper VII). In addition, we used information from the national monitoring program. Since 1996, the main monitoring method for the Scandinavian wolverine population is yearly counts of den sites (see Aronsson & Persson 2016), as the number of reproductions are the main unit for national and regional management goals in both countries as well as the conservation performance payment system in Sweden (Persson *et al.* 2015). Coordinates for registered den sites are stored in the database Rovbase (rovbase30.miljodirektoratet.no). When presence of an unmarked female wolverine was identified within the study area, several attempts were made to capture that female. Consequently, nearly all resident females were marked within the core study area.

Wolverines were captured on the ground or darted from helicopter and immobilized using ethics-approved handling protocols (see Arnemo *et al.* 2012). At capture, a small tissue biopsy and a hair sample were taken for genetic analysis. In 1993-1995 wolverines were fitted with VHF-collars (MOD315, Telonics. USA); since 1996 all individuals were equipped with intraperitoneally implanted VHF-transmitters for long-term monitoring (IMP/210/L, IMP/300/L, or IMP/400/L, Telonics. USA). From 2003, individuals were additionally equipped with GPS collars (2003-2006: Televilt PosrecTM C300, TVP positioning AB, Sweden; 2008-2013 GPS plus mini, Vectronics Aerospace, Germany). Wolverines equipped with VHF-transmitters were radio-tracked on average every second week from the air (Persson *et al.* 2010), complemented by intensive radio-tracking during the denning season in spring. Due to different collar programming during the study period, GPS location frequency varied from 3 to 48 locations/day. Furthermore, we tried to capture all cubs born in the study area in late spring to equip them with intraperitoneally implanted VHF transmitters (Persson *et al.* 2006; 2009), thus the number of monitored individuals with known age increased along the study period. Approximate age for animals not monitored from birth was estimated based on tooth sectioning (Matson 1981), reproductive history (Rauset *et al.* 2015), and genetic relatedness to known age individuals (Hedmark *et al.* 2007).

### Study population and wolverine territories

The wolverine is a solitary carnivore with high intrasexual territoriality resulting in low home range overlap (Persson *et al.* 2010; Mattisson *et al.* 2011; Inman *et al.* 2012) and high territorial fidelity (Paper IV). We estimated home ranges for stationary females (Paper VI) as the 90% fixed-kernel density method with reference bandwidth (Worton 1989) in the 'adehabitatHR' package (Calenge 2013) for R (R Core Team 2014) for all females with ≥20 locations (the threshold was based on bootstrap simulations using >200 locations; Rauset *et al.* 2015). For females that were not stationary (*e.g.* conducted either breeding dispersal or territorial expansion, Paper IV), we estimated home ranges for the time before and after the dispersal or expansion event separately. For females with insufficient numbers of locations for home range analysis (n = 10) we assumed that they were resident when they reproduced, and used a 4.6 km buffer zone centred on their den sites to approximate their home range (*i.e.* the closest distance between neighbouring females' den sites; Paper VII).

For this study, we defined unique territories as the smallest spatial unit possessed for ≥1 year by one successfully reproducing female. During the study period, we monitored 53 wolverine females established within the core study area and based on their individual home ranges the core study area consisted of 26 territories (Fig. 1), monitored for a total of 321 territory years. Each territory was monitored for an average of 12.5 years ± 1.1 SE (range: 2-22) (Fig. 1), and was sequentially occupied by an average of 3 ± 0.2 females during the study period (range: 2-6). Each female was monitored in each territory for an average of 4 ± 0.4 years (range:1-15).




T1 1993–2014
T2 1993–2014
T3 1994–2014
T4 1994–2014
T5 1995–2014
T6 1995–2014
T7 1995–2014
T8 1995–2014
T9 1995–2013
T10 1996–2013
T11 1996–2011
T12 1996–2002
T13 1996–2001
T14 1997–2013
T15 1998–2013
T16 1998–2013
T17 1999–2014
T18 1999–2001
T19 2000–2012
T20 2001–2014
T21 2001–2014
T22 2004–2013
T23 2005–2014
T24 2005–2014
T25 2007–2013
T26 2008–2014

*Figure 1*. Approximate territorial boundaries within the core study area based on home ranges for resident females and the years monitored. Natal home ranges for females monitored from birth outside of the study area are shaded grey. The area marked with an asterisk in the middle of the study area where we never found a resident wolverine female and according to the monitoring program there has only been one den site within that area during 1996-2014.

## Territory quality

We used average reproductive output (*i.e.* reproductive events; quality1, and number of young; quality2) from each territory during the time it was monitored to assess territory quality (Garshelis 2000; Johnson 2007; Stephens *et al.* 2015). During the denning period (*i.e.* February-May, Paper VII) all adult females were intensively monitored to evaluate whether they displayed denning behaviour, which indicated a reproductive event (Persson *et al.* 2006; Paper VII). Because wolverines often den in deep snow (Magoun & Copeland 1998) we could not observe the number of cubs at parturition. In May-June we located females that had reproduced to count the number of cubs, ranging from 0 to 3, *i.e.*, approximately a third of the wolverine females lose their young during the denning season (Persson *et al.* 2006). Rauset *et al.* (2015) showed that both female age and reproductive cost influence wolverine reproduction in our study area. Females rarely reproduce before age 3 and the probability of breeding two years in a row decreases with age, hence the cost of previous reproduction is negatively influencing current reproduction for females ≥ 9 years of age (see Fig. 2 in Rauset *et al.* 2015). Consequently, to calculate the average number of reproductive events in each territory we only included years when the resident females were in prime age (*i.e.* 3–9 years of age); here we also included females that displayed denning behaviour, but had no cubs in early June.

To account for some females reproducing but losing their young during the denning period, we also used the average number of cubs produced in each territory during the same period. For periods when multiple territories were occupied by the same female (see below and Paper VI), her reproductive output was included in the quality estimates for all those territories. Between-year variation in environmental conditions can have strong effects on reproductive output and hence lessen its suitability as proxy for habitat quality (Stephens *et al.* 2015). Consequently, we did not estimate quality for territory T18 (only held by known individuals for 2 years). We also excluded three individuals during years when they were included in a supplementary feeding experiment (Persson 2005). Consequently, we used an important fitness component (reproductive output) to describe territory quality and only used territories monitored during ≥5 years and occupied by ≥2 females to reduce the influence of between-year environmental conditions and variation within and between individuals.

## Territorial dynamics

### Available territories and replacing females

A territory could become available by the following five causes; (i) *move* (*e.g.* breeding dispersal of an adult established female, Paper IV), (ii) *natural death* (non-human caused, *e.g.* intraspecific killing, disease, starvation), (iii) *illegal killing* (confirmed and assumed), (iv) *lethal control*, (v) *other causes* (*e.g.* capture-related or unknown causes). Mortality cause and time (month of

the year) for resident females were classified following Persson *et al.* (2009). For females that moved from an established territory we classified the territory as being available the last month the female was located within the territory before leaving. Censored individuals were included in the category "other causes" if they had an approximate time of disappearance and the territory was overtaken within the following winter (n = 3; see also Persson *et al.* 2009).

We found replacing females in the available territories using locations of collared individuals, or den site coordinates from the monitoring program. Replacing females were classified into one of the following six categories: (i) *moving*, marked females already established and reproducing within the study area that moved into the available territory; (ii) *expanding*, marked females already established and reproducing within the study area that expanded into a neighbouring available territory and hence subsequently occupied two or more territories (see also Paper IV); (iii) *natal dispersal*, females captured as juveniles and establishing as a first time breeder in the available territory after leaving the natal territory; (iv) *natal philopatry*, females establishing as a first time breeder in their natal territory instead of dispersing, hence replacing their mother; (v) *capture*, females captured for the first time after the territory became available; and (vi) *unknown*, if a den site was found within the monitoring program, but we did not manage to capture the female.

For replacers first captured in the available territory, we used genetic analysis to assess if they were born within the study area, by searching for their mother among all other resident individuals. Genomic DNA from tissue and hair samples were analysed using microsatellite markers, following Hedmark *et al.* (2004). We calculated the maximum likelihood estimates of relatedness between wolverines using the program ML-RELATE (Kalinowski *et al.* 2006). The existence of close genealogical relationships (*e.g.* mother-daughter) was tested by likelihood ratio tests using the maximum likelihood estimates of a pair being unrelated or having a relationship. The relationships with likelihood values within the 95% confidence interval were calculated in ML-RELATE, using 10000 randomizations to get the sample distributions for the null hypothesis. If mother-daughter was the most likely relationship between the replacing female and an older female that could have reproduced before first captured, the category for the replacing female changed to natal philopatry, if the mother was the previous territory holder; or natal dispersal, if the replacing female was young and the mother was established in another territory within the study area (Table 1).

Table 1. *Information regarding females whose territories became vacant during the study (original females) and the females that replaced them (replacing female). For the original females, columns show their ID number, age, the territory identity (see Fig. 1), the date the territory vacancy, the cause of the vacancy (M=move, IK=illegal killing, LC=lethal control, Nat=natural causes, O=other) and the occurrence of young individuals (≤3 years old) born in the available territory (Y, N or unknown (U)). For replacing females columns show their ID, the time in months from vacancy to replacement, the replacer category (NP=natal philopatry, E=expanding, M=move, ND=natal dispersal, C= Capture, U=unknown) and their kinship to the original female (Da=daughter, Mo=mother, Gd=granddaughter, O=other). Asterisks denote individuals whose origin was determined by DNA. For territories that was not reoccupied, time available is until the end of the study period (June 2014), included in italic.*

| Original female | | | | | | Replacing female | | | |
|---|---|---|---|---|---|---|---|---|---|
| ID 1 | Age | Territory | Date | Cause | Young | ID 2 | Time | Type | Kinship |
| 93012 | 5 | T1 | Nov-93 | M | U | 98070 | 55 | M | O |
| 93015 | 4 | T2 | Apr-94 | M | N | 95030 | 9 | C | O |
| 94024 | 9 | T3 | Jan-95 | IK | U | 99095 | 13 | ND | O |
| 95030 | 4 | T2 | Mar-96 | M | N | 96050 | 2 | C | O |
| 96048 | U | T10 | Jan-97 | IK | U | 95025 | 6 | M | O |
| 95033 | 5 | T5 | Apr-97 | LC | U | 98070 | 0 | NP* | Da |
| 96043 | 4 | T13 | Jun-97 | O | Y | 96046 | 0 | NP | Da |
| 95025 | 8 | T7 | Sep-97 | M | Y | 97062 | 0 | NP | Da |
| 95030 | 6 | T14 | May-98 | M | N | 10254 | 22 | C | O |
| 94019 | 7 | T4 | Jun-98 | O | U | 99083 | 0 | NP* | Da |
| 95038 | 6 | T8 | Dec-98 | Nat | N | Den | 13 | U | - |
| 95030 | 7 | T18 | May-99 | LC | N | 01130 | 20 | C | O |
| 96051 | 7 | T11 | Jan-00 | Nat | Y | 98079 | 0 | NP | Da |
| 96047 | 8 | T12 | Feb-00 | Nat | N | 01148 | 11 | U | O |
| 98070 | 6 | T5 | May-00 | M | U | 96046 | 11 | M | O |
| 99095 | 5 | T3 | Jun-00 | IK | Y | 99086 | 0 | NP | Da |

| Original female | | | | | | Replacing female | | | |
|---|---|---|---|---|---|---|---|---|---|
| 00112 | 5 | T19 | Jul-00 | O | U | 03174 | 44 | ND | O |
| 99093 | 5 | T9 | Aug-00 | Nat | U | 03171 | 0 | NP* | Da |
| 96046 | 5 | T13 | Apr-01 | M | N | - | 158 | - | - |
| 01130 | U | T18 | May-01 | IK | U | - | 157 | - | - |
| 95025 | 12 | T10 | Jun-01 | IK | N[1] | 97062 | 0 | E | Da |
| 98070 | 8 | T1 | Jul-02 | Nat | N | 96050 | 34 | E | O |
| 96046 | 6 | T5 | Sep-02 | O | Y | 02150 | 0 | NP | Da |
| 99087 | 6 | T17 | Dec-02 | IK | Y | 02156 | 0 | NP | Da |
| 01148 | 5 | T12 | Feb-03 | IK | N | - | 136 | - | - |
| 95040 | 11 | T6 | Apr-03 | IK | N | 99086 | 0 | E | Gd |
| 98073 | 11 | T15 | Dec-04 | O | N | 08241 | 59 | ND | O |
| 03171 | 5 | T9 | May-05 | LC | N | Den | 56 | U | - |
| 03167 | U | T24 | Jul-05 | Nat | N | 10254 | 56 | C | O |
| 05202 | 8 | T23 | May-06 | M | Y | 08234 | 37 | ND | Gd |
| 98069 | 15 | T16 | Mar-07 | Nat | Y | 05192 | 0 | NP | Da |
| 01142 | 8 | T21 | Mar-07 | IK | N | 02166 | 11 | E | O |
| 04190 | 3 | T25 | Mar-07 | IK | N | 01129 | 14 | E | Mo |
| 01125 | 9 | T20 | Jun-07 | O | N | 05202 | 0 | M | O |
| 05202 | 9 | T20 | Sep-07 | O | Y | 07225 | 0 | NP | Da |
| 04189 | 4 | T3 | Jun-08 | LC | N | 99086 | 0 | E | Mo |
| 08233 | 4 | T26 | Jun-08 | O | U | 99083 | 4 | E | Mo |
| 02150 | 6 | T5 | Jul-08 | LC | N | 09252 | 27 | ND* | O |
| 96050 | 14 | T1, 2 | Aug-08 | Nat | Y | 06215 | 0 | NP | Da |
| 99086 | 10 | T3, 6 | Apr-09 | IK | N | 02166 | 1 | E | O |
| 99083 | 11 | T4, 26 | Sep-09 | Nat | N | 11270 | 16 | ND* | O |
| 03174 | 7 | T19 | May-10 | IK | N | 10259 | 13 | ND | O |
| 09252 | 3 | T5 | Apr-11 | O | N | 06215 | 0 | E | Mo |
| 97062 | 15 | T7 | Apr-12 | Nat | N | 11270 | 0 | E | O |
| 01129 | 11 | T22, 25, 10 | Apr-12 | IK | N | 08241 | 12 | E | O |
| 10259 | 2 | T19 | Apr-12 | IK | N | Den | 21 | U | - |
| 05192 | 7 | T16 | May-12 | IK | N | 08241 | 1 | E | O |
| 12282 | U | T9 | Apr-13 | M | U | - | 14 | - | - |
| 07225 | 6 | T20 | May-13 | IK | Y | 11267 | 0 | NP | Da |
| 11270 | 5 | T4, 26, 7 | Oct-13 | O | Y | 13292 | 0 | NP | Da |
| 08241 | 5 | T15, 16, 22, 10, 25 | Dec-13 | IK | N | - | 6 | - | - |

[1] adult, established daughter to the dead females expanded into the vacant territory

### Time to replacement

We calculated time to replacement as the time (months) from when the territory became available until the replacing female was first recorded. For unknown replacers, we assumed that they were present in the available territory in January the year the den site was found (*i.e.*, the female was established ≥1 month before giving birth). Similarly, for females first found due to a den site within the monitoring program and then captured, we assumed that they were present from January the same year as the den site. Hence, time to replacement was likely overestimated for captured and unknown replacers. If an expanding female died when she still held ≥ 2 territories, we searched for replacers and calculated time to replacement in the territories separately; *e.g.*, there could be different replacers in the territories, but if both territories were re-occupied by the same female, we recorded the same time to replacement for both territories. If the available territory was not reoccupied, we calculated time as available from when it was available until the end of the study period (June 2014).

For all available territories, we assessed if there were any young females (≤3 years of age) born in that terri-

tory and still present in the study area. For females monitored from birth or monitored for ≥3 years we knew if and when they produced female offspring and if the offspring had already established elsewhere or left the study area (see natal dispersal philopatry below). For females not captured as juveniles and not monitored for ≥3 years, the occurrence of possible daughters in the study area was unknown.

### Statistical analysis: territorial dynamics

We used general linear mixed models with a Poisson error distribution using the *'lme4'* package (Bates *et al.* 2014) in R with time to replacement (months) as the response variable. Territory was fitted as random effect in all models to account for repeated measurements. Explanatory variables used were: replacer category, availability cause (*i.e.*, the reason explaining why the territory became vacant), territory quality (*i.e.* average number of reproductive events = quality1; and average number of young = quality2), and age of the first female. Candidate models were compared using the sample-size corrected Akaike information criterion (AICc) and AIC weights ($w_i$) (Burnham and Anderson 2002). We used a bootstrap method implemented in R using the *'ez'* package (Lawrence 2013) to calculate 95% confidence intervals for mixed models. Means are presented with standard errors unless otherwise stated.

## Natal dispersal and philopatry

### Dispersal and establishment

Between 1995 and 2013, we captured and radio marked juvenile wolverines in their natal territory during late spring/early summer. Previous studies have showed that juvenile wolverines start to move independent of their mother in late summer/early autumn (*i.e.* approximate time of independence; Vangen *et al.* 2001; May 2007). Hence only juveniles still alive in August were included in the dispersal study (n = 71, of which 67 were born within the core study area; Fig. 1). We defined natal dispersal as the permanent emigration of individuals with known origin from their natal territory (*i.e.* the home range of their mother as defined above). Animals were defined as established at the time of their first reproduction or when their subsequent space use pattern showed that they became stationary in an area (Paper IV). Consequently, females that established in their natal territory were defined as natal philopatric. Furthermore, for dispersing females we recorded if they established as a neighbour (*i.e.* adjacent to natal territory) or further away, and if they established inside or outside the core study area. Females that left and were monitored outside the core study area for ≥ 2 months before they died or were lost before establishing were classified as leaving; the remaining females were either classified as dead (within the core study area) or censored. The core study area was intensively monitored every year to capture all resident females. Five females that were lost as juvenile or subadults due to transmitter failure were recaptured again as resident adults and thus classified as established. Consequently, censored animals most likely left the study area or died and thus did not settle within the study area.

### Statistical analysis: dispersal

We used multistate mark–recapture models in program MARK (version 7.2; White and Burnham 1999) to estimate age-related state transition probabilities for the 67 female wolverines between 6 and 36 months old that were born in the core study area. They were followed every month until they transitioned to a new state or died. We focused on two state transition probabilities, *i.e.*, a young unestablished female present in the core study area in month $m$ (state P) would establish in a territory in the study area (state ES, state transition $\Psi_{P\rightarrow ES}$) or, leave (state L, transition $\Psi_{P\rightarrow L}$) in the following month ($m + 1$). We only included individuals born in the core study area and did not separate individuals that established in their natal territory from those who established in other parts of the core study area. We assumed that all individuals were born on February 15th (mean birth data in our study area; Paper VII), with monthly survey intervals being defined relative to this. The survival parameter for state P ($\Phi_P$, the probability that an unestablished individual present in the study area in month m was alive and still unestablished in month $m$ + 1) was estimated as a constant parameter, while survival in the other states was fixed at zero ($\Phi_{ES} = \Phi_L = 0$) to remove individuals from analyses once they settled or left the study area and did not return. Intraspecific predation is the main mortality cause for juvenile wolverines in our study area, mainly occurring in spring/early summer and early autumn (Persson *et al.* 2003; 2009). Human-caused mortality is the most important death cause for both adult and subadult wolverines in our study area (Persson *et al.* 2009) and the substantial spatial variation in poaching associated with human land use and activity likely has a large confounding effect on age-related patterns in survival (Rauset *et al.* 2016). Hence, we did not further model age-related survival patterns and used a single estimated value for $\Phi_P$ in all models (see Rauset *et al.* 2015). Because the analysis was based on radio-tracked individuals, the resighting parameter was fixed at 1 in all models. Censored animals have most likely left the study area; for this analysis, they were treated as dead because in many cases we could not assess the time when they disappeared and hence did not know what month they would have left the study area. The most general model (*i.e.* time effects in the $\Psi_{P\rightarrow ES}$ and $\Psi_{P\rightarrow L}$ transitions) was checked for goodness-of-fit using the median $\hat{c}$ variance inflation

measure in MARK, and this showed there was no extra-binomial variation ($\hat{c}$ = 1.2).

We fitted explanatory variables to each transition state (*i.e.* $\Psi_{P\rightarrow ES}$ and $\Psi_{P\rightarrow L}$). We first examined the influence of time since birth on the probability of transitioning by comparing a constant probability of transitioning versus a linear change in transition probability over time (*i.e.* age). Based on AICc support, the highest-ranked parameter structure for each transition state was used as the basis for fitting additional covariates (see also Low *et al.* 2010; Rauset *et al.* 2015). We considered the following time-varying covariates as potential factors influencing the probability of settling inside the study area: (1) number of vacant territories available each month within the study area (*vacant*); (2) distance from the natal den site to the central point of the closest available territory (*distance*), excluding the natal territory; and (3) a categorical variable representing if the natal territory was available or not (*natal*). In addition, we also considered the distance from the natal den site to the nearest border of the study area (*border*) and the following interactions: (1) natal x distance and natal x vacant to examine what is available in the surrounding area is only important when the natal territory is not available; (2) border x vacant and border x distance because animals born closer to the study area boundary are more likely to have closer, to us 'unknown' opportunities outside the study area; (3) age x vacant and age x distance, because their relation may change with time; and, (4) time x natal to see if they settled in the natal territory regardless of age. We modelled covariates on one transition state at a time with the other held constant with its time dependent structure (see Low *et al.* 2010). All model comparisons were based on Akaike's information criterion with a second-order correction for sample size (AICc). We relied on AICc weights for model support, variable relative importance weights (0.8–1.0 indicating strong support, 0.5-0.7 moderate support and <0.5 indicating weak or no support), and for deriving model-averaged estimates (Burnham and Anderson 2002). Uncertainties for prediction plots were generated using the MCMC module in MARK based on 50,000 iterations, using the posterior distributions of relevant parameters to generate predictions and associated uncertainties.

# Results

## Territorial dynamics

During the study, 51 territories became available within the core area; 33% due to illegal killing, 21% death from natural causes, 18 % because the resident female vacated her territory, 10% lethal control and 18% of causes were unknown (Table 1). There were no occasions when >1 female established in a vacant area, despite six of the available areas (12%) consisted of two or more potential territories, due to the death of an expanding female.

### Replacer category

Forty-six territories (90%) were reoccupied; 43 of the replacing females were known, and of these, 15 were daughters to the previous territory holding female (Table 1). Natal philopatric young females, expanding neighbouring adult females and young dispersers were the most common replacers (30%, 26% and 15%, respectively; Table 1). Four of the 12 expanding females were the mother to the previous female and one was a daughter (Table 1). Only 9 replacers were of unknown origin (6 captured and 3 unknown). The genetic analysis showed that each of the six unknown-origin captured replacers was related to several other females within the area, but we could not determine mother-offspring relationships. The four remaining replacers were already established in the study area but left their previous territory and moved to the vacated territory (*i.e.* breeding dispersal, Paper IV).

Table 2. *Highest ranked $AIC_c$-ranked candidate model set for the time to replacement of vacated territories. Replacer is the category of the newly established females (expanding, moving, natal dispersal and unknown origin (unknown and capture pooled)), Quality1 is territory quality based on reproductions per year, Quality2 is territory quality based on the number of young produced in the territory, and Cause1, 2 and 3 are different sets of categories based on what caused the territory to become available (1 – all causes, 2 – illegal killing vs. all other, 3 – death of resident female vs. resident females moved). Interactions are denoted by 'x'. For simplicity, only models with $w_i \geq 0.01$, univariate models, and intercept-only models are shown (see Table S1 for full candidate model set).*

| Model | $\Delta AIC_c$ | $w_i$ | df |
|---|---|---|---|
| Replacer + Cause 2 | 0 | 0.83 | 6 |
| Replacer | 4.93 | 0.07 | 5 |
| Replacer + Cause 3 | 6.91 | 0.03 | 6 |
| Replacer + Quality1 | 7.07 | 0.02 | 6 |
| Replacer + Quality2 + Replacer x Quality2 | 7.46 | 0.02 | 9 |
| Replacer + Quality2 | 7.90 | 0.02 | 6 |
| Replacer + Quality1+ Replacer x Quality1 | 9.00 | 0.01 | 9 |
| Replacer + Cause 1 | 9.61 | 0.01 | 9 |
| Cause1 | 53.2 | 0 | 6 |
| Cause2 | 58.4 | 0 | 3 |
| Cause3 | 65.3 | 0 | 3 |
| Quality1 | 65.7 | 0 | 3 |
| NULL | 66.2 | 0 | 2 |
| Quality2 | 67.6 | 0 | 3 |
| Age | 68.2 | 0 | 3 |

### Time to replacement

The average time until a territory was reoccupied was 12 ± 2.6 months (range 0-59); five territories were not reoccupied during the study period (Table 1). In all cases when replacement was natal philopatry the reoccupation of the available territory was instantaneous (Table 1). Thus, for assessing factors influencing the time to replacement, we excluded this group. Expanding neighbouring females occupied the available territories earlier than the other replacer categories (< moving females, < natal dispersers and females of unknown origin; Fig. 2; Table 2). The cause of vacancy also influenced time to replacement as territories vacated due to illegal killing (6.6 ± 1.9 months) were replaced faster than territories vacated by all other causes for all replacer categories (15 ± 3.6 months; Fig. 2; Table 2). There was no additional effect of territory quality or age of the replacer on the timing of territory replacement (Table 2). However, the three categories of female replacer that occupied territories the earliest (*i.e.* natal philopatry, expanding neighbour and moving females) moved into territories with higher-than-average quality in contrast to territories that were occupied by the two slowest categories (*i.e.* natal dispersers and unknown origin) or territories that remained unoccupied (Fig. 3). Territories became available and were replaced throughout the year (log-likelihood test; no effect of month on availability, G = 11.0, df = 11, p = 0.44; or replacement, G = 13.6, df = 11, p = 0.25).

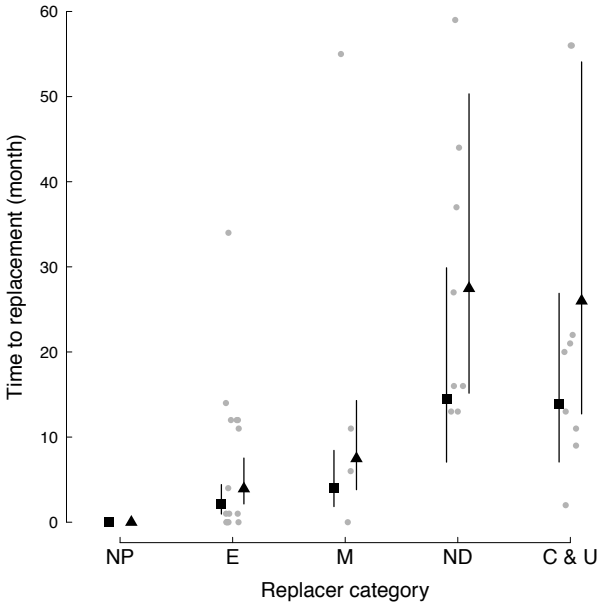



*Figure 2*. Time a territory remained vacant until it was reoccupied according to the category of the replacing female: natal philopatry (NP), expanding (E), moving (M), natal dispersal (ND) and unknown origin (capture: C, and unknown: U), and what caused the territory to become available: illegal killing (triangles) or other causes (squares). Predictions (means ± 95% CIs) are from the highest ranked model in Table 2, grey dots are raw data.

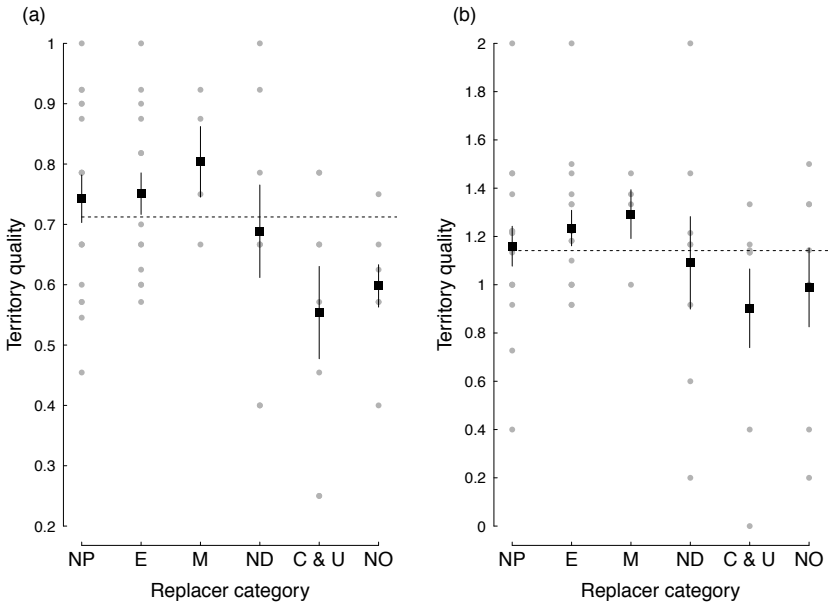



*Figure 3*. Territory quality (average number of reproductions per year [a] and average number of young per reproduction [b]) in available territories according to the category of the replacement female: natal philopatry (NP), expanding (E), moving (M), natal dispersal (ND), not replaced (NO), captured (C) and unknown (U) replacers are pooled because both have unknown origin (i.e. C&U). Means ± SE with raw data (grey) are shown. The horizontal dashed line is mean measure of quality for all reoccupied territories.

## Natal dispersal and philopatry

### Dispersal and establishment

We monitored 71 wolverine females from independence; of these 26 (37%) were monitored to establishment (21 to their first reproduction and 5 based on space use). The remaining females were censored (n = 28), left the study area but did not establish (n = 9) or died (n = 8). Of the 26 established females, 13 (50%) established in their natal territory, 10 (38%) in a neighbouring territory (7 inside and 3 outside core study area), and 3 (12%) established further away. In only two cases (13 %) when the natal territory was available did the young female not establish there (Fig. 4); in one case she established in the neighbouring territory and in the other case she died (1.5 months after her mother, both illegally killed). Mean distance from natal den site to first own den or centre point of home ranges for established females was 17 ± 6.4 km. For females establishing in their natal territory this distance was 4.1 ± 10 km, establishing in neighbouring territory 11 ± 1.5 km, and establishing further away 90 ± 35 km.

### Probability of establishing in or dispersing from the study population

The monthly probability of leaving the core study area ($\Psi_{P\rightarrow L}$), or establishing in the core study area ($\Psi_{P\rightarrow ES}$) increased with age (Table 3, Fig. 5). Furthermore, probability of leaving was negatively related to the number of vacant territories within the core study area, meaning that females were more likely to leave when there were fewer vacant territories (Table 3, Fig. 5b). The probability of establishing in the study area was dramatically increased if the natal territory became available, and there was a weak positive effect of the number of vacant territories (Table 3, Fig. 5a). When the natal territory was not available, there was no support for the number of vacant territories or the distance to closest vacant territory influencing the probability to establish or leave the study area. There was no support for the distance to the study area border influencing any of the transition states (Table S2 and S3, Supporting Information).

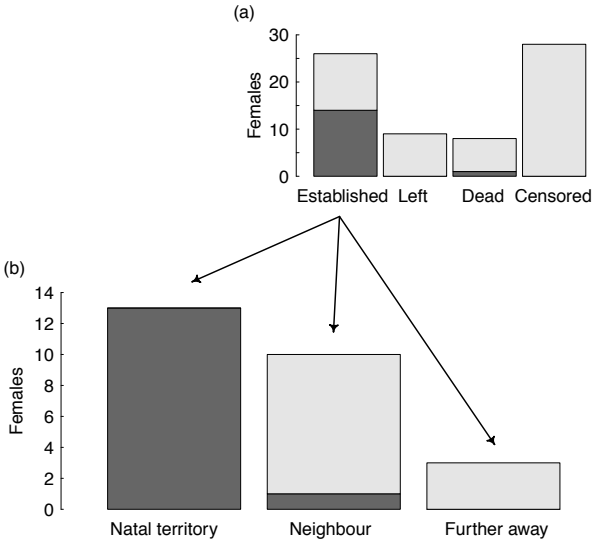



*Figure 4*. Fate of young females after independence: (a) shows all females, while (b) shows where settled females established relative to their natal territory. Light grey shading indicates the natal territory was unavailable (still occupied by their mother), while dark grey shading is when the natal territory was available (mother died or moved).

Table 3. *AIC-weighted model averaged parameter estimates (±SE) and relative importance weights (VRI) for transition probabilities from multi-state mark-recapture models (Binomial distribution with a logit link). Parameters are; age of the female (Age; months, starting at 6 months), a 2-level categorical variable representing if the natal territory is available (Natal; difference of not available from available), number of vacant territories available each month within the study area (Vacant), and interactions (x). Model averaged estimates were derived from candidate models in Table SX. For $\Psi_{P\rightarrow L}$ estimates, parameters were averaged across models where the $\Psi_{P\rightarrow ES}$ structure was fixed at Intercept + Age + Natal (Table S2). For $\Psi_{P\rightarrow ES}$ estimates, parameters were averaged across models where the $\Psi_{P\rightarrow L}$ structure was fixed at Intercept + Age + Vacant (Table S3).*

| | *Leaving study area ($\Psi_{P\rightarrow L}$)* | | *Establish in study area ($\Psi_{P\rightarrow ES}$)* | |
|---|---|---|---|---|
| Parameter | Estimate | VRI | Estimate | VRI |
| Intercept | -5.06 ± 0.05 | 1.0 | 1.26 ± 0.02 | 1.0 |
| Age | 0.09 ± 0.001 | 0.95 | 0.09 ± 0.001 | 1.0 |
| Natal | -0.02 ± 0.08 | 0.24 | -6.75 ± 0.39 | 1.0 |
| Vacant | -0.91 ± 0.27 | 0.98 | 0.33 ± 0.33 | 0.67 |
| Age x Vacant | - | - | 0.01 ± 0.06 | 0.16 |
| Natal x Vacant | - | - | -0.15 ± 0.15 | 0.17 |

## Discussion

In this long-term study of wolverine dispersal and territorial dynamics we showed that almost all vacant territories were reoccupied by females from the immediate surroundings – with 65% of replacers being philopatric daughters or neighbours. We also show that the availability of the natal territory is of fundamental importance for the probability of young females to remain and establish in the local area, rather than dispersing elsewhere. Indeed, an increased number of available territories in the local area decreased the probability that young individuals leave the local area. Our study population most likely acts as a source population, where the contribution to surrounding areas is related to survival of adult reproductive females; thus local harvest may have limited effect on the local density of resident individuals while it is likely to reduce emigration. Consequently, we show how the link between territorial dynamics and dispersal patterns in this solitary and territorial carnivore may affect both local and regional population density and distribution.

Philopatric daughters were the most common replacers (30%) and they occupied vacant territories instantaneously (Fig. 2, Table 1). Almost all young females established in their natal territory if possible (*i.e.* if their mother died or moved; Fig. 4). Consequently, whether the natal territory was available was the most important factor determining the probability that young females would establish within the study area (Fig. 5; Table 3). Young females probably benefit from being present when the territory becomes vacant (Sutherland 1996), as vacancies are otherwise rare (mean number of available territories per year within the study area was 2.4 (*i.e.* 9%)) The probability to establish in the study area increased with age, independent of whether the natal territory was available or not, and there was a weak positive effect of the number of vacant territories on this probability (Fig. 5). Hence, young and inexperienced females might be evicted by stronger and more competitive females when the availability of territories is low. Only two females did not establish in their natal territory when vacant: one died soon after the mother and one established as a neighbour (Fig. 4).

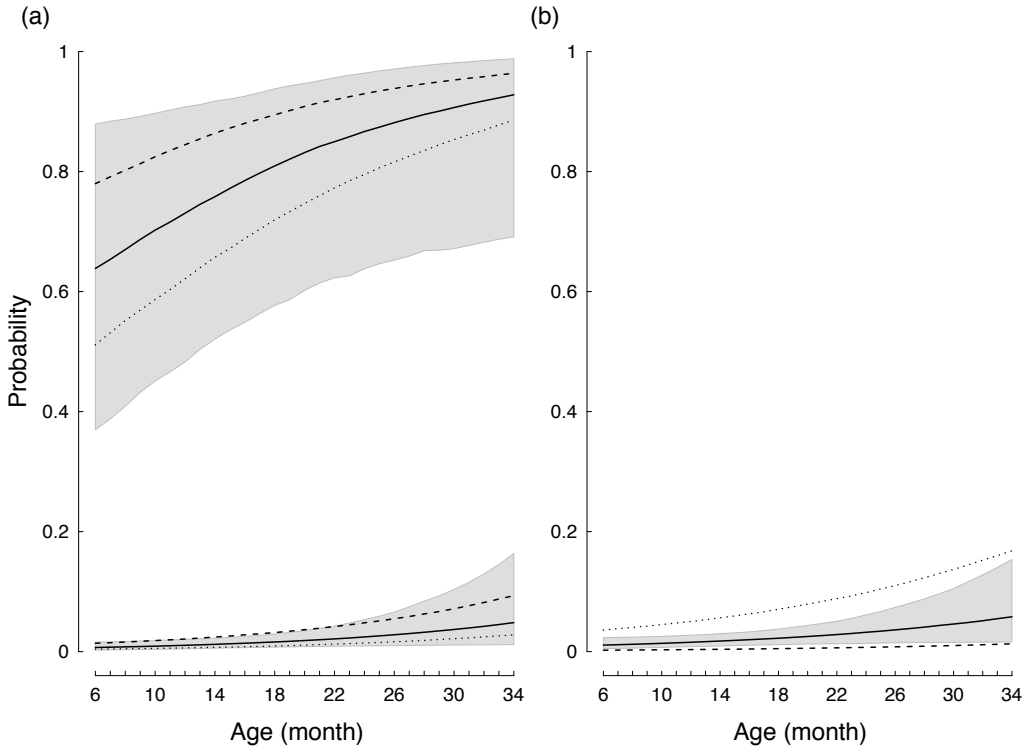



*Figure 5*. Monthly probability of a young female establishing in or leaving the core study area relative to her age. (a) shows the probability of establishing in the core area if the natal territory is available (upper curve) versus if the natal territory is not available (lower curve); (b) is the probability of leaving the core study area. Solid lines are mean model predictions (from Table 3, at mean number of available territories) and shaded areas 95% CIs. The dashed and dotted line shows how the mean model prediction changes when the number of available territories is reduced to the minimum (dotted) or increased to the maximum (dashed).

Natal philopatric females could be divided into two categories depending on the age when they inherited their natal territories. Eight of the known-age daughters (n = 11) were 7-16 months old when their mother died (n = 10) or moved (n = 1). Mean dispersal age for females in our study area is 13 ± 6 months (Vangen *et al.* 2001); consequently, if young dispersing females simply establish in the closest available area, for these females it would be their natal territory. However, the remaining philopatric females were > 2 years old (*i.e.* 23, 25 and 30 months) before their mother died. Although sample size is limited, this may indicate that some females delay dispersal to gain the advantage of inheriting their natal territory and avoid potential costs of dispersal (Kokko & Ekman 2002; Zedrosser *et al.* 2007; Gill *et al.* 2010; Paper IV). In two of these three cases the mothers were 14 and 15 years old when they died, twice as old as the average age when resident females died in the study area (*i.e.* 7 ± 0.5 years). If this pattern is real, some young females may delay dispersal because they know their mother is likely to soon die or because older mothers may be more tolerant of their daughters due to higher inclusive fitness benefits (*i.e.* their relatively low own future reproductive output).

The importance of being present in the vicinity of a vacant territory is further illustrated by our finding that neighbouring females that expanded into a vacant territory was relatively common and with a short time to replacement (Fig. 2; Table 2). Furthermore, the fact that many vacant territories without a daughter present were not occupied by an expanding neighbour, suggests that there is a cost associated with territorial expansion behaviour (*i.e.* defending a larger area than necessary for survival and reproduction). Hence, it might only be females in prime condition that show this behaviour, possibly to be able to bequeath an area to future female offspring (Berteaux & Boutin 2000; Paper IV). Consequently, even though time to replacement by young dispersers was longer, some vacant territories will be available for young dispersers. Furthermore, most dispersing females that established within the study area were born in a neighbouring territory (Fig. 4), again suggesting an advantage of fast detection.

We did not find any effect of territory quality on time to replacement (Table 2). This could be because: (1) the area is highly saturated, and so individuals have limited possibilities to be selective, (2) our measures of territory quality are too crude to detect this relationship, and/or (3) territory quality may be difficult to assess in systems where the cost of exploration is high (*e.g.* because of intraspecific killing). This is in contrast to systems where failed breeders can easily observe the reproductive output of surrounding territories and use this as a basis for their decisions to shift (*e.g.* in birds; Pärt *et al.* 2011). Still, females that shifted territories, moved to territories of higher-than-average quality (Fig. 3). This suggests that resident individuals will only voluntarily abandon a territory when they can occupy a higher quality territory (Wauters *et al.* 1995; Forero et al. 2004; Pasinelli *et al.* 2007), leading in some cases to breeding dispersal (Paper IV).

The observed pattern of territorial replacement in our study has several implications. The first is that there are very limited opportunities for immigrants to establish in saturated areas like our study site. The evidence for this comes from the origin of territorial replacers: a minimum of 43 of 46 replacers came from the local area, with the origin of the remaining 3 replacers unknown (not captured and so could not be determined). In addition, even young dispersers from the local area have few opportunities to establish unless their natal territory is available. This leads to the second implication of our study, being that dispersal decisions are largely driven by the availability of vacant sites in the neighbourhood of the natal territory. Only 28% of the young females born in the core study area (n = 67) also established within the core study area, and the probability of establishing was not influenced by the distance to closest available territory (excluding natal philopatry) or study area border. The probability for young females to leave the study area increased with age and decreased with the number of vacant territories (Fig. 5, Table 3). This suggests high competition for available territories and a surplus of young females that have to leave the area to establish their own territory. This suggests the third implication, which is the study population likely acts as a source population to surrounding areas *e.g.* Gervasi *et al.* 2015. This is further supported by an estimated closed population growth of 1.06 (λ) based on observed vital rates (Persson *et al.* 2015), while the number of resident wolverines within the area was relatively stable and the population growth was 0.99 (λ), based on 3-year average number of den sites documented within the study area (Landa *et al.* 1998; rovbase30.miljodirektoratet.no).

## Implications for conservation and management

Territories vacant due to illegal killing were reoccupied faster than territories vacant by other causes (Table 2; Fig. 2), suggesting that these are attractive territories for wolverines. One outcome of this is that where poaching is ongoing and focussed on specific areas or territories, this may create local ecological traps in the landscape (Delibes *et al.* 2001).

A population with relatively low adult female mortality can act as a source for other areas that are subject to higher levels of human-caused mortality, as shown for different species (*e.g.* Robinson *et al.* 2008; Turgeon & Kramer 2012; Gervasi *et al.* 2015; Gilroy *et al.* 2015). This can contribute to the persistence of threatened populations, but can also cause complications when management goals and regimes differ between areas. The

Scandinavian wolverine population is one such example. The population is subject to much lower harvest levels in Sweden compared to Norway, resulting in an increasing Swedish population during the last decades (Persson *et al.* 2015; Aronsson & Persson 2016). Consequently, at a large scale there is a net flow of individuals from Sweden (source) to Norway (sink; Gervasi *et al.* 2015), which may hinder both countries achieving their management goals (*i.e.* increase in Sweden, decrease in Norway). Furthermore, our findings suggest that the recent increase in wolverine density along the Swedish mountain range (Persson *et al.* 2015) has resulted in an increasing number of young females dispersing to surrounding areas. Consequently, this is presumably an important driver behind the recent recolonisation of the forest landscape east and south of the alpine areas (Aronsson & Persson 2016).

Hunting is frequently used to decrease damage caused by carnivores, often at a local scale, with the intent of decreasing conflicts (*e.g.* Robinson *et al.* 2008; Persson *et al.* 2009). However, our results suggest that this will likely have a limited effect on the local density of resident individuals in saturated populations of territorial species like the wolverine. The territorial dynamics and dispersal patterns reveal that females will not disperse when there are vacancies available in the immediate surroundings. This suggests that dispersal might be positively density dependent (Murray 1967; Matthysen 2005), and that wolverine females follow a saturated dispersal pattern (Sinclair 1992; Stenseth & Lidicker 1992; Fryxell *et al.* 2014). Consequently, the primary effect of harvest will be to decrease emigration to surrounding areas, while the proportion of young resident individuals in the local area will increase; thus, changing the age structure of the population. Furthermore, hunting might alter demographic and reproductive patterns by increasing per capita reproductive output due to more available resources (Fuller & Sievert 2001; Minnie *et al.* 2016). Lethal control of wolverines in both Sweden and Norway has for long focused on removing females with dependent young during the denning season (SEPA 2014). Female wolverines have an age-dependent reproductive pattern with very low reproductive output for females ≤2 years old and age-related reproductive costs where the probability of reproducing two years in a row decreases with age for old females (Rauset *et al.* 2015). Consequently, removal of denning females will target the segment of the population with the highest reproductive output, and increase the number of young and old females with lower reproductive potential. One consequence of this, in Sweden, is that it could reduce the economic compensation to reindeer herders in the area. This is because compensation for depredation losses is based on the number of documented wolverine reproductions in a reindeer-herding district (Persson *et al.* 2015). Thus, lethal management approaches may create a situation where the scale of the conflict remains relatively unchanged, but emigration from the area will decrease and potentially also the compensation.

Management of carnivores needs to consider the scale of management versus the scale of ecological processes (Cumming, Cumming & Redman, 2006; Guerrero *et al.*, 2013; Hermoso *et al.*, 2016). This is relevant for management from a very local scale (*e.g.* lethal control of single individuals; Linnell *et al.* 1999) to management across national borders (Bischof *et al.* 2015; Gervasi *et al.* 2015). Here, we show that a saturated source population will provide a surplus of individuals that are forced to disperse out of the area. However, this emigration will drastically decrease before the density of resident individuals decreases as a consequence of harvest. This illustrates how understanding of mechanisms behind patterns of territorial dynamics and dispersal provides vital information for management planning at different scales.

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# Mismatch between goals and the scale of actions constrains adaptive carnivore management: the case of the wolverine in Sweden

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**Keywords**
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## Abstract

Efficient conservation of wide-ranging carnivores requires that adaptive management consider the varying ecological and societal conditions within the entire range of a population. In northern Europe, large carnivore management has to balance carnivore conservation and maintaining the indigenous reindeer-herding culture. Wolverine *Gulo gulo* monitoring and management in Sweden is currently focused on alpine reindeer husbandry areas where wolverine abundance and associated depredation conflicts have been highest. However, this focus ignores a potential southwards population expansion because current monitoring relies on snow-based tracking methods that are not applicable outside northern alpine areas. Thus, in this study we: (1) used available monitoring data from 1996 to 2014 in Sweden to assess wolverine distribution trends in relation to national management goals, and (2) evaluate the current monitoring protocol against the use of camera stations as an alternative, snow-independent, method for detecting wolverine presence at the southern periphery of its distribution. We show that the wolverine population in Sweden has expanded considerably into the boreal forest landscape, and colonized areas without reindeer husbandry and persistent spring snow cover. The latter indicates a less strict relationship between wolverine distribution and snow cover than previously hypothesized. Current management continues to use a monitoring protocol that is only adapted to high-conflict alpine areas, and is not adapting to changing conditions in the population range, which creates a problematic scale mismatch. Consequently, national management decisions are currently based on incomplete population information, as roughly a third of wolverine's range is not included in official population estimates, which could have detrimental consequences for conflict mitigation and conservation efforts. This illustrates that an important key to successful carnivore conservation is flexible management that considers the entire range of conditions at the appropriate regional and temporal scales under which carnivores, environment and people interact.

## Introduction

A common challenge for conservation of natural resources is matching the scales at which actions are planned and implemented to the scale of ecological processes or conservation issues (Cumming, Cumming & Redman, 2006; Guerrero *et al.*, 2013; Hermoso *et al.*, 2016). Scale mismatches can have negative consequences for species' conservation and management of focal species' impacts on ecosystems and human interests (Cumming *et al.*, 2006; Delsink *et al.*, 2013; Creel *et al.*, 2015; Hermoso *et al.*, 2016). As many carnivores range over vast areas the same population could encompass a variety of habitats (Balme *et al.*, 2013; Linnell, 2015). Thus, management conditions may vary within populations because of variation in conflict levels, conflict mitigation systems and environmental conditions (Swenson & Andrén, 2005; Blanco & Cortés, 2011; Linnell & Boitani, 2012). Consequently, carnivore conservation is challenging and requires adaptive management at the appropriate scale in relation to actual conditions and conservation goals (Linnell & Boitani, 2012; Balme *et al.*, 2013; Linnell, 2015). Moreover, additional complexity is added to carnivore management and policy in areas where indigenous communities or traditional practices are affected by carnivores (Lundmark & Matti, 2015).

Because adaptive management requires reliable population estimates to interpret the effects of management actions, a clear link among population monitoring, management actions and population goals is crucial (Walters & Hilborn, 1978). Consequently, monitoring programmes need to be flexible to

account for changes in the population's range or environmental conditions to provide updated knowledge on population status. For example, where monitoring of large carnivores has traditionally relied on snow tracking (Landa *et al.*, 1998; Andrén *et al.*, 2002; Liberg *et al.*, 2012*a*), there is an urgent need to adapt monitoring methods to decreased snow cover resulting from global warming and/or population range expansions outside of areas with regular snow.

Due to intense persecution in the 1900s, the Swedish wolverine *Gulo gulo* population was diminished and restricted to northern alpine areas (Flagstad *et al.*, 2004). Today the wolverine distribution largely overlaps with the reindeer husbandry area where semi-domestic reindeer *Rangifer tarandus* are the predominant prey for wolverines (Mattisson *et al.*, 2011). Consequently, wolverines and other predators cause significant economic losses for indigenous Sámi reindeer-herding communities (Hobbs *et al.*, 2012), which necessitates balancing carnivore conservation and sustainability of an indigenous culture (United Nations Declaration on the Rights of Indigenous Peoples, 2008). In 1996, a conservation performance payment system (CPP) was implemented, where reindeer-herding districts are paid in relation to wolverine presence (Persson, Rauset & Chapron, 2015). The unit for payments is yearly number of wolverine reproductive events (hereafter reproductions) and, as wolverines give birth in February–March (Inman *et al.*, 2012), monitoring is mainly based on snow tracking to find den sites in the spring. The CPP has had a positive effect on wolverine female survival, which has contributed to a considerable population increase within the reindeer-husbandry area (Persson *et al.*, 2015). However, losses to predators must not exceed 10% of reindeer numbers in any reindeer-herding district [Swedish Environmental Protection Agency (SEPA), 2014] and lethal control is implemented within the reindeer husbandry area as a conflict mitigating measure to decrease predation pressure (Persson, Ericsson & Segerström, 2009). Consequently, the Swedish national management plan aims to increase wolverine distribution outside the reindeer husbandry area, to be able to reduce depredation conflicts while maintaining the national population goal of at least 600 wolverines (SEPA, 2014).

The political goal to promote a southwards population expansion presents challenges for wolverine conservation in Sweden. Wolverines are hypothesized to be dependent on persistent spring snow cover due to its importance for reproductive success (i.e. den site suitability) and food caching efficiency (Copeland *et al.*, 2010; Inman *et al.*, 2012). Furthermore, the current monitoring programme, and thus population estimates, primarily relies on snow tracking. Thus, snow conditions could limit both the desired southwards expansion of the wolverine population as well as the detection of any southwards expansion through snow-based monitoring methods.

In this study we assess the wolverine population trend in Sweden regarding both population size and distribution in relation to national management goals, as well as the potential need for modification of the current monitoring programme to adequately monitor the desired range expansion. First, we compare monitoring results from different parts of Sweden: (1) inside and outside the reindeer husbandry area and (2) in alpine areas, which have since long been perceived as the typical wolverine habitat in Sweden, relative to the boreal forest landscape both within and south of the reindeer husbandry area (Fig. 1). Second, we conducted a pilot study at the southernmost periphery of wolverine distribution (Fig. 1) where we evaluated if we could document wolverine presence using both the current monitoring methods (see Methods) and an alternative, snow-independent, monitoring method developed for wolverines (i.e. camera stations) following Magoun *et al.* (2011).

## Materials and methods

### Wolverine monitoring and population estimates

The monitoring programme for wolverines in Scandinavia started in 1996 and is based on annual minimum counts of reproductions (i.e. documentation of active den sites and females with offspring). The monitoring protocol is strictly regulated by the SEPA (www.swedishepa.se) and Norwegian Rovdata (www.rovdata.no; SEPA & Rovdata, 2013*a*,*b*, 2014). Authorized monitoring personnel register wolverine activity in the field from February to June each year (SEPA & Rovdata, 2014). Within the monitoring programme reproductions can be classified as either *documented* or *considered certain* (Anon 2015*a*). A reproduction is classified as *documented* if one of the following criteria is fulfilled: (1) monitoring personnel has photographed wolverine cub/-s or tracks of cub/-s; (2) a wolverine cub is euthanized (i.e. due to lethal control of females with dependent young) or found dead or (3) a lactating wolverine female is captured or found dead (SEPA & Rovdata, 2013*a*). A *considered certain* reproduction represents a lower level of certainty and the criteria are based on repeated wolverine activity and signs indicating that a reproduction has occurred at a suspected den site (see Supporting Information Appendix S1). Suspected den sites are found by snow tracking and most of the criteria for a *considered certain* reproduction are based on snow tracking, however, a suspected den site can also be inspected during early summer (i.e. bare ground investigation) in search for specific signs of repeated activity that can result in the site being classified as a *considered certain* reproduction (see Supporting Information Appendix S1).

For each registered reproduction, coordinates and dates for fulfilment of criteria are stored in the Scandinavian database Rovbase (rovbase30.miljodirektoratet.no) where it is subject to independent quality control by a central coordinator in each country (Anon 2015*a*). Since 2004, in addition to reproductions, validated opportunistic observations of wolverine presence (i.e. visual observations, observations of tracks and collection of DNA from scats) are stored in the database. Scat samples are genetically analysed, and information regarding individual identity and sex are recorded [SEPA & Rovdata, 2013*b*; see Hedmark *et al.* (2004) and Brøseth

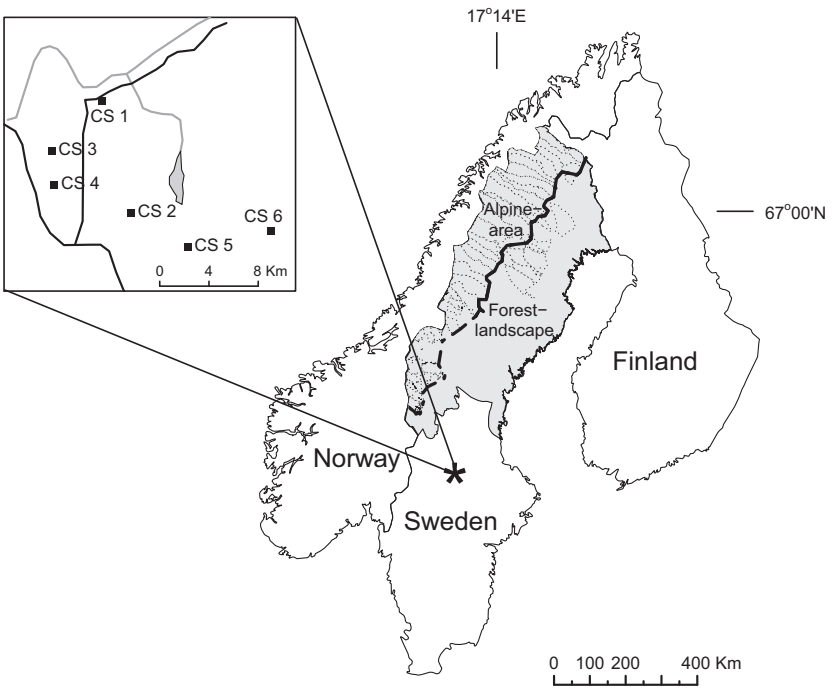


**Figure 1** The reindeer husbandry area of Sweden (shaded area) with year-round grazing areas (grey dotted lines). The 'cultivation limit' (black line; cf. Lundmark, 2006; Axelsson *et al.*, 2007) and year-round reindeer grazing areas (black dotted line) differentiate alpine areas and boreal forest landscape in this study. The pilot study of monitoring methods was conducted in the southern periphery of the wolverine distribution (*), placement of camera stations (CS) within the study area is showed in the upper left panel.

*et al.* (2010) for detailed description of the microsatellite genotyping for sex and individual identity used within the monitoring programme].

National population estimates (i.e. total number of >1-year-old individuals) are calculated each year, using a population model that includes the average number of registered reproductions the last 3 years, sex ratio, age structure and proportion of reproducing females for different age classes (Landa *et al.*, 1998; Brøseth *et al.*, 2010; Anon, 2015*a*). Consequently, annual estimates of population size are based solely on the number of reproductions, not other data (Anon, 2015*a*).

## Population trend

To assess changes in wolverine numbers and distribution in Sweden, we used Rovbase data from 1996 to 2014. These data include coordinates for all reproductions from 1996 to 2014 and all other registered wolverine observations from 2004 to 2014. We created a 10-km buffer zone around each location (i.e. to include an area slightly larger than the mean female territory to account for additional individuals; Persson, Wedholm & Segerström, 2010) and merged them to yearly polygons for reproductions and observations, respectively.

The reindeer husbandry area covers 230 000 km$^2$ of Sweden and is divided into 51 reindeer-herding districts (~50% of land area; Fig. 1) that consist of areas designated for winter-only and year-round reindeer grazing (Hobbs *et al.*, 2012); reindeers are absent south of the reindeer husbandry area. Northern alpine areas have long been perceived as typical wolverine habitat in Sweden (Aronsson & Persson, 2012). To differentiate alpine areas from the boreal forest landscape, we used the 'cultivation limit' (Swedish *odlingsgränsen*, a juridical border created in the late 1800s to limit agricultural settlements in alpine areas designated to Sámi reindeer-herding practices; Lundmark, 2006; Axelsson, Angelstam & Svensson, 2007). South of the cultivation limit we connected year-round reindeer grazing areas to differentiate boreal forest and alpine areas (Fig 1). Moreover, our eastern and southern border for alpine areas corresponds to the limit of areas with persistent spring snow cover correlated with worldwide wolverine distribution (cf. fig. 3 in Copeland *et al.*, 2010; Supporting Information Figs S1 and S2). Thus, we used habitat, land-use practices, bioclimatic conditions and prey availability (i.e. year-round reindeer presence, the only medium-sized ungulate prey for wolverines) to delineate 'typical' wolverine habitat in alpine areas from lower-altitude boreal forest landscape. We performed all spatial analysis in ArcGIS 10.1 and maps were available from the Swedish Mapping, Cadastral and Land Registration Agency (www.lantmateriet.se).

## Pilot study of monitoring methods

This part of the study was conducted in a 350-km$^2$ area in the southern part of Dalarna county (60°17′N 14°58′E) (Fig. 1) in 2013 and 2014. This area represents the extreme

south of present wolverine occurrence, based on recorded observations (Fig. 2c) and reports from local residents who have observed wolverine tracks in the area during the last 6–8 winters (Aronsson & Persson, 2012). The habitat is mainly managed boreal forest (Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*), interspersed with mires, lakes and smaller settlements. Elevation ranges from 150 to 500 m a.s.l, and mean temperature ranges from −6°C (January) to 17°C (July). Average dates for first and last day with snow cover ≥5 cm are November 17 and March 31, respectively. Daily snow depth for the study period was accessed from the closest weather station (Dala-Järna, 60°32′N 14°21′E), northwest of the study area (available at: www.smhi.se). Potential food sources for wolverines in the study area are moose *Alces alces*, roe deer *Capreolus capreolus*, tetraonids, beaver *Castor fiber*, mountain hare *Lepus timidus* and rodents. Wolves *Canis lupus*, brown bears *Ursus arctos*, lynx *Lynx lynx* and red fox *Vulpes vulpes* occur in the area.

Together with local volunteers, we opportunistically searched the study area by car or ski when snow conditions were favourable to find wolverine tracks in the snow to mimic the official monitoring protocol implemented in northern areas. When tracks were found we followed them to search for suspected den sites using the established monitoring protocol and collect samples (scats, hair or anal gland secretion) for DNA analysis. All samples were genetically analysed within the national monitoring programme for sex and individual identity (see Wolverine monitoring and population estimates). In addition, from 15 February 2013 to 2015 January 2015 we used six camera stations (Fig. 1) within a 200-km$^2$ area in the centre of the study area, corresponding to the size of one female home range (Persson *et al.*, 2010). Camera stations were constructed following Magoun *et al.* (2011) and consisted of a run pole where wolverines are supposed to stand and reach for overhanging bait, showing abdominal and chest area to enable individual and sex identification. We used two motion-detecting infrared cameras (PC800; RECONYX Inc., Holmen, WI, USA) at each camera station, one for frontal pictures and one on the ground to document wolverines visiting the site without climbing the run pole. The cameras took one picture per second when an animal moved in front of it. Sites for camera stations were selected based on information from locals about frequent observations of wolverine tracks to maximize the chance to be visited by a wolverine (cf. Magoun *et al.*, 2011). We used parts of moose, roe deer and beaver obtained from road kills or from hunters as bait and visited all camera stations at least once every second month (range: 2–8 weeks) to retrieve photos, check battery status and change bait. We defined all wolverine photos taken within a maximum of 30 min as belonging to a single visit.

## Results

### Population trend

Since the start of the monitoring programme, a total of 1477 reproductions have been registered in Sweden, of these only 13 (<1%) were registered outside the reindeer husbandry area (Fig. 3a). At the start of the monitoring programme,

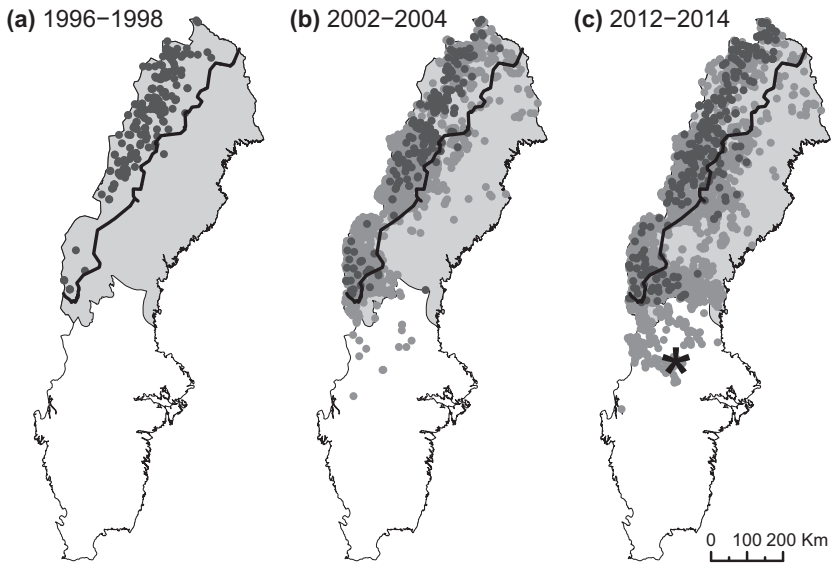


**Figure 2** Wolverine population distribution trend in Sweden based on reproductions (black dots) and observations (grey dots) registered within the national monitoring programme. Monitoring results are presented for 3-year periods; (a) start of the monitoring programme, (b) wolverine observations started to be registered and (c) current distribution range of reproductions and observations. The star (*) shows the location of the pilot study. Shaded area shows the reindeer husbandry area and black line shows the border used to differentiate alpine areas and boreal forest landscape. Snow depth and days with persistent spring snow cover increase to the northwest (Supporting Information Figs S1 and S2).

reproductions were almost exclusively registered in alpine areas (Fig. 2a). Thereafter, both the number and distribution of reproductions in the forest landscape has increased (Fig. 2b and c), and since 2002 there has been at least one reproduction registered within the forest landscape each year, although mostly within the reindeer husbandry area (Fig. 3a).

Similar to the reproductions, the number and distribution of wolverine observations has increased in the boreal forest landscape (Fig. 2b and c) from 303 in 2004 to 643 observations in 2014 (Fig. 3b).

Based on observations registered within the monitoring programme in 2012–2014 the wolverine distribution in Sweden covers ~171 000 km$^2$, reaching ~170 km south of the reindeer husbandry area and ~190 km south of the southernmost registered reproduction. Furthermore, in 30% (52 100 km$^2$) of this range there has never been any reproduction registered, and 49% (25 700 km$^2$) of the area without reproductions is south of the reindeer husbandry area.

## Pilot study of monitoring methods

In 2013–2014 we collected 32 scat samples for genetic analysis, of which 66% were successfully genotyped, and from these four individuals (one female and three males) were identified. Only one of the males had previously been documented in this area within the monitoring programme using DNA (one sample in 2008). From the camera stations we obtained 9784 photos in 3882 camera-days (Supporting Information Table S1 and S2). Wolverine was the most frequently photographed species (59% of photos) followed by red fox (10%) and pine marten *Martes martes* (8%), see Supporting Information Table S2 for a complete list of

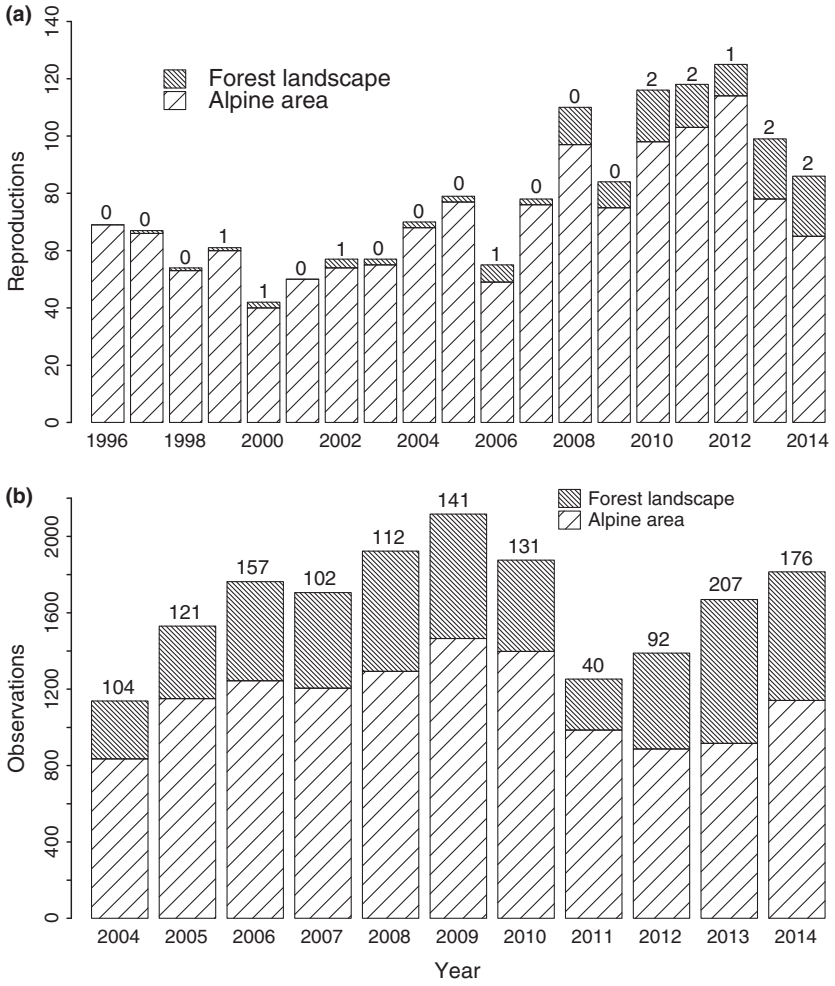


**Figure 3** Number of wolverine reproductions (a) and observations (b) registered within the monitoring programme in Sweden each year (monitoring of reproductions started in 1996 and registrations of observations started in 2004). Shading of the bars shows the proportion of reproductions and observations located in alpine areas versus the boreal forest landscape. Numbers above bars represent reproductions and observations registered south of the reindeer husbandry area each year.

photographed species. In 16% of the photos there were no visible animals, presumably because moving branches or intense sunlight triggered the camera. Wolverines were photographed at all 6 camera stations during a total of 66 visits, of which wolverines were photographed on the run pole during 39 visits (59%). Time from set up of the camera station to first wolverine visit varied greatly among camera stations (mean ± SE: 92 ± 41 days) (Supporting Information Table S1). We identified five different wolverine individuals based on chest patterns; two males, one female and two of unknown sex. We identified the individual in 82% ($n$ = 32) of the visits when the wolverine was photographed on the run pole, and identified the sex in 21% ($n$ = 8) of the visits.

## Discussion

Our assessment clearly shows that the Swedish wolverine population is expanding into the boreal forest landscape east and south of the alpine area, as well as outside both the reindeer husbandry area and areas with persistent spring snow cover. This implies that wolverines are now in the process of recolonizing what is believed to be their historical distribution (Persson & Brøseth, 2011), and that the political goal for the distribution of the species could be attained (SEPA 2014). We suggest several explanations for this range expansion. The wolverine population has increased considerably in alpine areas (Persson *et al.*, 2015), presumably leading to an increased number of dispersers colonizing forest landscapes. Moreover, from 1996 to 2015 the Scandinavian wolf population increased from 4 to 57 packs (Wabakken *et al.*, 2001; Anon, 2015*b*), and is now overlapping with most of the wolverine distribution south of the reindeer husbandry area. This has presumably increased year-round scavenging opportunities for wolverines on remains from wolf kills (van Dijk *et al.*, 2008). In addition, the annual moose hunt provides significant amounts of meat each autumn (Wikenros *et al.*, 2013) that can be cached and utilized for extended periods. These scavenging opportunities presumably facilitate wolverine establishment and reproduction (cf. Persson, 2005; Rauset, Low & Persson, 2015) south of the reindeer husbandry area, and thus buffer for potential negative effects of decreased snow cover. Hence, this expansion into areas without persistent spring snow cover suggests a less strict relationship between wolverine distribution and snow cover than previously hypothesized (cf. Copeland *et al.*, 2010). It remains unclear what will limit the southwards expansion of wolverines in Sweden, but we suggest that this limitation will be the result of interactions among availability of snow cover for denning and food caching (Copeland *et al.*, 2010; Inman *et al.*, 2012), competition from other predators and scavengers and food availability (Persson, 2005; Mattisson *et al.*, 2011; Rauset *et al.*, 2015).

While wolverines seem to cope better than expected with non-persistent spring snow cover in south-central Sweden, the monitoring protocol does not. Wolverine reproductions are only found in 70% of the wolverine range (as defined by recurrent wolverine observations). As population size estimates are based solely on reproductions, this strongly suggests that wolverines in about one-third of their range are not included in population size estimate. This is due to decreasing possibilities to fulfil the monitoring criteria for reproductions south and east of alpine areas, due to poor snow conditions at lower altitude and latitude (Anon, 2015*a*), as well as low monitoring effort. Consequently, there is a need for modification of the current monitoring programme to obtain relevant population estimates.

The current monitoring protocol was developed for northern alpine areas because it was only in those areas where wolverines were present at the onset of the monitoring programme in Scandinavia (Fig. 2). Our pilot study demonstrates a clear example of the need for survey methods that do not require persistent snow cover, as the snow cover was very poor for snow tracking shortly after wolverine females give birth and initiate denning (Fig. 4). The average date when a reproduction fulfilled the criteria to be registered as *documented* within the monitoring programme in 2013–2014 was April 17 ($n$ = 111; Rovbase). Hence, it would have been exceptionally hard to document a reproduction in our study area following the current monitoring protocol (Fig. 4). Furthermore, to conduct a bare ground investigation of a suspected den site in early summer (see Supporting Information Appendix S1), the suspected den site has to be located by snow tracking during the spring. Considering that the average date for the first detection of suspected den sites in 2013 and 2014 was March 24 ($n$ = 180; Rovbase) this alternative would also be hard to implement. However, using camera stations we documented the presence of at least five different individuals within a very limited part of the sampled area that is not supposed to contain wolverines according to national population estimates (Anon 2015*a*). The development of a camera-trapping protocol where camera stations specifically developed for wolverines are efficiently implemented over larger areas could provide a snow-independent method to record information on wolverine distribution, sex ratio, population density estimates (cf. Royle *et al.*, 2011) and most importantly the presence of resident females, which would help locate suspected den sites. Furthermore, because camera stations are suitable for identifying lactating females (Magoun *et al.*, 2011), they could be integrated as a snow-independent criterion for reproductions. As reproductions are the main unit for the conservation performance payment in Sweden, and the monitoring of reproductions provides indirect protection from poaching for wolverine females, and presence of reproductive females provides important information about population status (Persson *et al.*, 2015), it is important to continue using reproductions as the main monitoring unit. DNA collected from non-invasive samples can be used in retrospect to confirm reproductions (Flagstad *et al.*, 2004). However, DNA collection needs to be done in a less snow-dependent way than scat sampling, as wolverine scats are hard to find and to distinguish from other species without corresponding footprints in snow. One alternative is to collect DNA with hair snags at camera stations (cf. Magoun *et al.*, 2011).

Apart from the snow-dependent monitoring system, the southwards population expansion *per se* provides a challenge

for wolverine management in Sweden. South of the reindeer husbandry area in Sweden there is no documentation of wolverine depredation on livestock (Frank, Månsson & Zetterberg, 2016), hence wolverines are subject to low levels of human conflict. Therefore, these areas may be of critical importance for wolverine conservation. However, management efforts south of the reindeer husbandry area are mainly focused on wolf and lynx as these are more controversial species in this area (Andrén *et al.*, 2006; Liberg *et al.*, 2012*b*). Thus, in the southern part of wolverine distribution monitoring is limited to opportunistic documentation of snow tracks and scats from wolverines registered during wolf or lynx monitoring (Fig. 2; Aronsson & Persson, 2012). For example, within our pilot study area we identified five and four different individuals using camera stations and DNA from scat samples, respectively, and even though locals have reported wolverine presence the past 8–10 years, only DNA from one individual had been sampled once in this area within the monitoring programme before our study. Furthermore, although wolverines are regularly observed over vast areas up to 170 km south of the reindeer husbandry area (Fig. 2), only 2 of 86 reproductions in 2014 were registered south of the reindeer husbandry area (2.3%, Fig. 3a) and there is no population estimate available for this part of wolverine range (Anon 2015*a*).

The consequence of the current situation is that wolverine management decisions in Sweden are not based on the status of the entire population. Such a scale mismatch may have impact on conservation outcomes when management actions cannot be adapted to national population goals (Linnell, 2015). This clearly shows that systematic monitoring of the entire population is needed to conduct adequate, population-level adaptive management in relation to national goals. The observed range expansion is an important step towards the political goal of increasing the wolverine range to reduce depredation levels within the reindeer husbandry area (SEPA, 2014). In particular, this highlights the need for implementation of snow-independent, flexible monitoring techniques adapted to local conditions. Lethal control is currently the main management tool to decrease predation by wolverines because few preventive measures are applicable to modern, extensive reindeer herding (Persson *et al.*, 2009). However, harvest rates need to balance conflict mitigation, attainment of favourable conservation status (Council of the European Union, 1992) and national population goals. Consequently, it is important that harvest rates are set in relation to the total population size. The scale mismatch where official population estimates do not reflect reality may hinder conflict mitigation within the reindeer husbandry area, that is, the room for implementation of lethal control in high-conflict areas is influenced by the number of wolverines outside the reindeer husbandry area. If conflict mitigation is limited by known underestimation of population size, this could have detrimental consequences for stakeholders' trust in management (Young *et al.*, 2016), and thus decrease acceptance for wolverines and their conservation in the reindeer husbandry area.

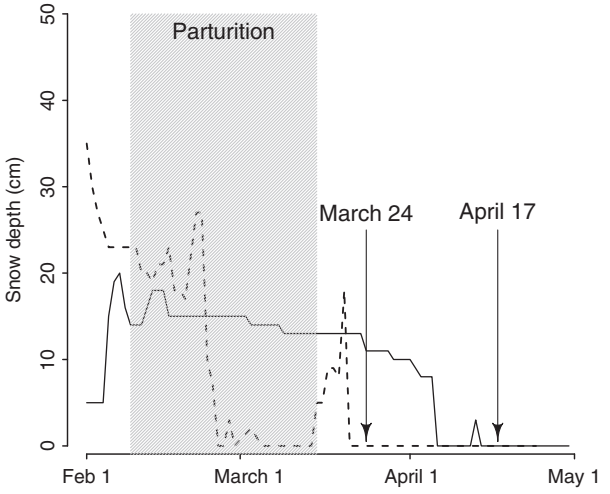


**Figure 4** Daily snow depths during the spring for the pilot study area in 2013 (solid line) and 2014 (dashed line). Shaded area shows peak parturition period for wolverines (Inman *et al.,* 2012). Arrows show average dates for the first detection of suspected den sites (March 24) based on snow tracking and when reproduction fulfilled the criteria to be considered *documented* (April 17) within the monitoring programme in 2013 and 2014, based on snow tracking.

In summary, we have illustrated how Swedish wolverine management neglects changing conditions by only focusing on high-conflict areas, and thereby misses an opportunity to adequately evaluate management goals and to efficiently manage human–carnivore conflicts for long-term carnivore conservation. This provides an important example of how carnivore management often concentrate actions to specific parts of populations, commonly in protected areas or high-conflict areas (Linnell, Swenson & Andersen, 2001; Balme *et al.*, 2013). Instead, the key to successful carnivore conservation requires flexible management policy adapted to biologically relevant scales and to ecological change, and thus considers the entire range of conditions under which carnivores, the environment and people interact because the solution may be found outside areas with high management focus.

## Acknowledgment

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## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Mean number of days per year with snow cover in Sweden from the measurement period 1961–1990.
**Figure S2.** Mean snow depth and proportion of years with snow cover in Sweden on the 15th of March from the measurement period 1961–1990.
**Table S1.** Information for each camera station regarding period activated, total number of wolverine visits and time from deployment to first wolverine visit.
**Table S2.** Complete list of mammal and bird species photographed at camera stations, total number of photos and number of visits for each species.
**Appendix S1.** Description of monitoring criteria for a wolverine reproduction to be classified as *considered certain* within the Scandinavian monitoring programme.

# Supporting information

Aronsson, M. & Persson, J

Mismatch between goals and the scale of actions constrain adaptive carnivore management: the case of the wolverine in Sweden

## Appendix S1

For a wolverine reproduction to be *considered certain* within the Scandinavian monitoring program requires that one of the following criteria are fulfilled (SEPA & Rovdata, 2013a): 1) Monitoring personnel has observed wolverine cub/-s or tracks of cubs but not obtained photo documentation, 2) monitoring personnel has documented wolverine tracks of different ages leading to and from a hole in the snow at a suspected den site during 3 visits over at least 21 days if a reproduction has been documented at the site previously, or 4 visits over at least 28 days if a reproduction has not been documented at the site previously, or, 3) monitoring personnel document wolverine tracks of different ages leading to and from a hole in the snow at a suspected den site during at least one visit, and the suspected den site is inspected after snow melt. At this inspection, at least 4 of the following 6 signs of activity must be documented at the site (SEPA & Rovdata, 2014); i) remains from >1 prey individual, ii) a substantial amount of scats at latrines, iii) ≥ 2 daybeds, iv) wool from wolverine cubs, v) bite marks on ground vegetation at ≥ 2 places, and vi) distinct tunnel system is seen on the ground, in the vegetation or in remaining snow.

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## Figures and tables

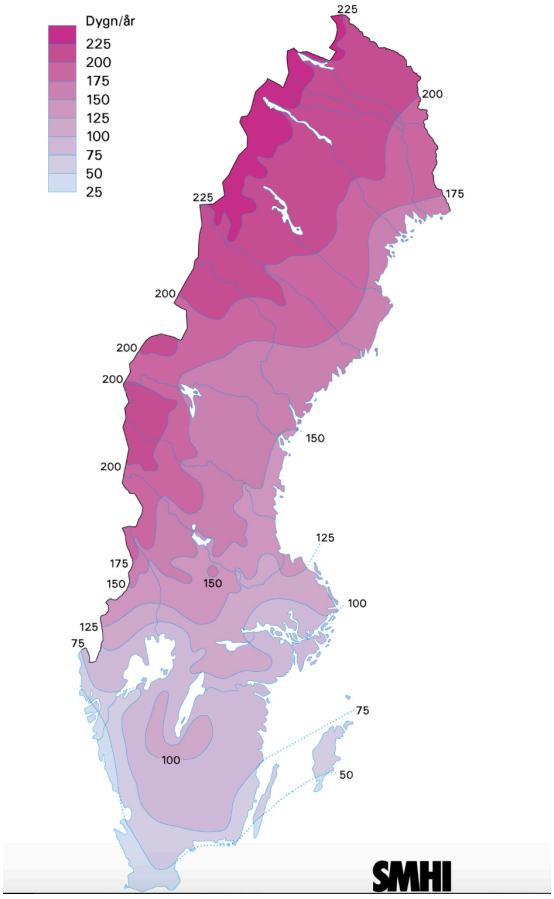
Table S1. *Period activated, total number of wolverine visits and time from deployment to first visit for each camera station.*

| Camera station | Period running | Camera days | Wolverine visits* | Days to first visit* |
|---|---|---|---|---|
| 1 | 15/2/2013 – 15/1/2015 | 699 | 12(5) | 8(100) |
| 2 | 6/3/2013 – 29/10/2014 | 602 | 4(0) | 2(-) |
| 3 | 26/2/2013 – 15/1/2015 | 688 | 29(21) | 219(225) |
| 4 | 6/3/2013 – 15/1/2015 | 680 | 6(5) | 67(351) |
| 5-1** | 4/3/2013 – 3/10/2013 | 213 | 0 | - |
| 5-2** | 3/3/2014 – 15/1/2015 | 318 | 10(4) | 7(40) |
| 6 | 4/3/2013 – 15/1/2015 | 682 | 5(4) | 34(58) |

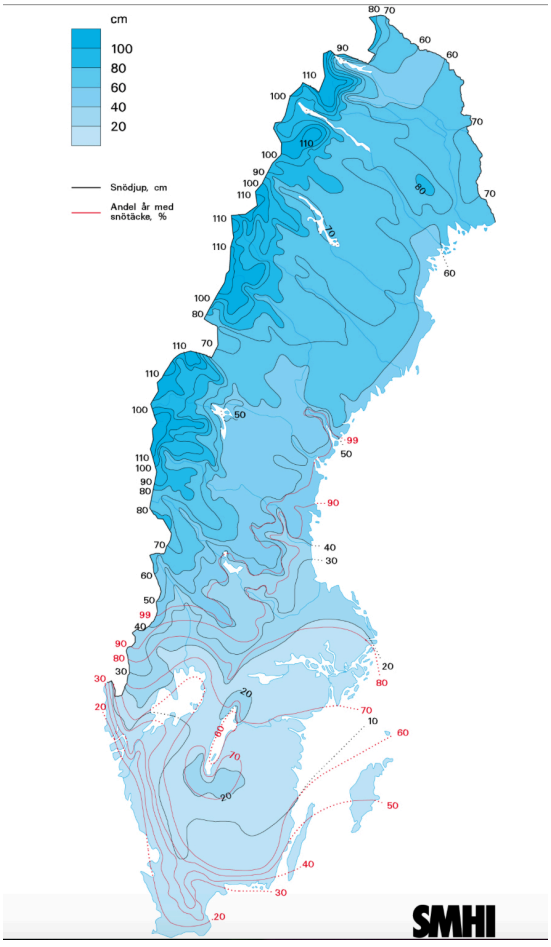
* Wolverine photographed on the ground (wolverine photographed on run pole)
** Cameras at camera station 5 was turned off 3rd October 2013 and started again 3rd March 2014.

Table S2. *List of mammal and bird species photographed at camera stations, total number of photos for each species and number of visits (i.e. photos taken within 30 minutes).*

| Species | Camera station | Photos | Visits |
|---|---|---|---|
| Wolverine *(Gulo gulo)* | 1,2,3,4,5,6 | 5791 | 66 |
| Red fox *(Vulpes vulpes)* | 1,3,4,5 | 1020 | 30 |
| European pine marten *(Martes martes)* | 1,2,3,4 | 821 | 30 |
| Moose *(Alces alces)* | 2,3,4,5,6 | 312 | 18 |
| Eurasian jay *(Garrulus glandarius)* | 1,3 | 119 | 12 |
| Roe deer *(Capreolus capreolus)* | 1,2,4,5 | 60 | 9 |
| Tit *(Paridae spp.)* | 1,2,3,4,5 | 29 | 16 |
| European badger *(Meles meles)* | 1,3,5 | 11 | 4 |
| Brown bear *(Ursus arctos)* | 3 | 9 | 1 |
| Capercaillie *(Tetrao urogallus)* | 5,6 | 8 | 2 |
| Eurasian lynx *(Lynx lynx)* | 1,5 | 6 | 2 |
| Woodpecker *(Dentrocopos major)* | 2 | 4 | 1 |
| Hare *(Lepus timidus)* | 5 | 3 | 1 |
| Wolf *(Canis lupus)* | 5 | 1 | 1 |
| Red squirrel *(Sciurus vulgaris)* | 5 | 1 | 1 |
| Unknown mammal | 1,4,5 | 13 | 10 |
| No visible animal | 1,2,3,4,5,6 | 1576 | - |




*Map S1.* Mean number of days per year (dygn/år) with snow cover in Sweden. From the measurement period 1961-1990, as defined by the World Meteorological Organization (WMO). The map is available from the Swedish Meteorological and Hydrological Institute (SMHI) at www.smhi.se




*Map S2.* Mean snow depth in cm (snödjup, cm; black lines) and proportion of years with snow cover (andel år med snötäcke, %; red lines) in Sweden the 15th of March. From the measurement period 1961-1990, as defined by the World Meteorological Organization (WMO). The map is available from the Swedish Meteorological and Hydrological Institute (SMHI) at www.smhi.se

# Reproductive timing and denning behaviour of female wolverines in relation to resource availability and population monitoring

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## Abstract

Reproduction is a key aspect of animal ecology, and important to understand in detail for management. Reproduction is costly and so timing of parturition and offspring rearing in relation to resource availability and climate is vital. Wolverines (*Gulo gulo*) are solitary carnivores adapted to low-productive habitats with large seasonal variation in resource availability, and they give birth earlier than other northern carnivores that do not hibernate. Scandinavian wolverine management focuses on mitigating depredation conflicts by compensating damage and killing wolverines. Wolverine reproductions are the main indicator for management goals and the conservation performance payment system in Sweden. Thus, appropriate monitoring of reproductive den sites is crucial for management. We used location data from 18 adult GPS-collared wolverine females to assess parturition time and den site use, *i.e.* how often and how far females move between consecutive reproductive den sites. We related this to offspring development, resource availability and wolverine foraging strategy. We also assessed how the knowledge can be used to improve population monitoring. Peak parturition time was mid-February (mean = February 15; range: January 29-March 9). Females generally used natal dens for an extended time (mean = 47 days), and then moved infrequently and short distances between subsequent dens the first 2-2.5 months. This corresponded to the lactation period when prey was rare and caching and scavenging important, and a persistent snow cover to provide secure den sites and efficient food caching. After weaning, frequency of den shifting over longer distances increased progressively, presumably reducing the need to bring food back to the den. This coincided with increased prey availability due to the return of migrating reindeer and their calving period. We suggest that the timing of reproduction and denning behaviour reflects wolverines' adaptation to match parturition and rearing to prevailing resources. Similar seasonal shifts in resource abundance are observed at multiple locations at different latitudes within the wolverine range, suggesting that the observed pattern is general within the distribution of this solitary carnivore. Timing of reproduction and denning behaviour also has implications for appropriate defining of harvest season and monitoring of reproductions. In particular, we suggest distance criteria to separate documented den sites that are dynamic over time during the denning season (*i.e.* the monitoring period).

## Introduction

Time of parturition and rearing of young in seasonal environments has evolved in response to resource availability. Therefore, at high latitudes, where climate and biotic interactions show strong seasonality, reproduction is often temporally synchronized (Ims 1990). Reproduction is also a key fitness component directly linked to population dynamics. Thus, factors influencing reproductive chronology are critical parts of species' life history. Consequently, timing of parturition and rearing of young have been intensively studied in relation to species responses to environmental variation or climate change (*e.g.* Bronson 1989; Bowyer & van Ballenbergh 1998; Post & Forschhammer 2008; Wolcott *et al.* 2015). Reproductive chronology is also important for conservation and management: for example, in population monitoring, harvest regulations and disturbance prevention (Shea *et al.* 1998; Knight *et al.* 1995; Linnell *et al.* 2007; Ordiz *et al.* 2007; Malmsten *et al.* 2014; Sidirovich *et al.* 2016).

Reproduction is associated with high costs (Stephens *et al.* 2009). Lactation is the most energy-consuming activity during offspring rearing for mammals (Bårdsen *et al.* 2009; Fletcher *et al.* 2013), but also provisioning of weaned offspring requires higher than the basal energy income (Sadleir 1969; Bronson 1989). Therefore, timing of parturition and offspring rearing in relation to external factors such as food availability, climate and predation risk, and the resulting energy balance, is important for reproductive output (Bronson 2009; Fletcher *et al.* 2013; Plard *et al.* 2014; Wolcott *et al.* 2015;

Rotella *et al.* 2016). Thus, timing of reproduction is expected to be adapted to resources available for both lactation and post-weaning rearing (Bronson 1989, 2009).

The wolverine (*Gulo gulo*) has a unique reproductive chronology as they give birth earlier (*i.e.* February through early March) than other northern carnivores that do not hibernate (Inman *et al.* 2012*a*). Wolverines are opportunistic predators and scavengers mainly occupying low-productive habitats with large seasonality in food availability (Copeland *et al.* 2010; Inman *et al.* 2012*a*). It is suggested that wolverine distribution is limited by the spatial extent of persistent spring snow cover during the denning period (Copeland *et al.* 2010) primarily to provide secure den sites (Magoun & Copeland 1998), and/or limited by cooler conditions in general that are favorable for caching, especially during the lactation period (Inman *et al.* 2012*a*). Existing data suggest that females keep their cubs in a den at least until weaning, although females sometimes shift den sites during the denning period (Inman *et al.* 2012*a*). Den sites are often located in steep and rugged terrain (May *et al.* 2012; Makkonen 2015), frequently linked to snowdrifts, boulders, cliffs or fallen trees (Magoun and Copeland 1998, May *et al.* 2012, Makkonen 2015). However, detailed knowledge about wolverine reproductive timing and denning behaviour is still limited.

In Scandinavia, the wolverine population occupies large parts of alpine tundra and boreal forests (Aronsson and Persson 2016), where free ranging, semi domestic reindeer (*Rangifer tarandus*), managed by the indigenous Sámi reindeer-herding communities are common prey (Mattisson *et al.* 2016). In Norway wolverines also prey upon free-ranging domestic sheep (*Ovis aries*) during the summer (Landa *et al.* 1997; Mattisson *et al.* 2016). Thus, depredation conflicts are a central management issue (Persson *et al.* 2009; Hobbs *et al.* 2012), and it is mitigated mainly through economic compensation, lethal control and licenced hunting (Norway only) to decrease wolverine numbers in high-conflict areas. In Sweden, a Conservation Performance Payment system (CPP) is implemented, where compensation is paid to reindeer herding districts in relation to the number of wolverine reproductive events within the district (200,000 SEK per reproduction; Persson *et al.* 2015). Thus, reproductions are the main indicator in the CPP, but also the main unit for national and regional management goals. Consequently, the accuracy of the monitoring system has socioeconomic consequences and influences the credibility of wolverine management in both countries (Aronsson & Persson 2016).

The numbers of reproductions are documented by annual counts of wolverine den sites by authorized personnel during February 1– July 31 following predefined criteria in the monitoring protocol (Aronsson & Persson 2016). A challenge within the monitoring system is to assess if multiple den sites belong to the same reproductive event or not (Persson *et al.* 2012). When two or more den sites are observed within the same area, one of three criteria are used to determine if they represent the same or different reproductions: (1) DNA samples from both sites reveal the identity of the breeding individuals, (2) snow tracking simultaneously documents separate activities at both sites, or (3) a pre-defined distance criteria classifying all den sites within 10 km as belonging to the same reproductive event independent of when during the denning period the den sites were observed (SEPA 2013).

In this study, our goal was to assess timing of reproduction and denning behaviour in wolverine females. We relate this to available knowledge about offspring development as well as the spatiotemporal resource availability and wolverine foraging strategy (see Fig. 1a. and *'study area'*). We used location data from 18 adult wolverine females equipped with GPS-collars to assess when wolverines give birth, and how often and how far females move between den sites during the same denning period. We then assess how this increased knowledge of wolverine parturition dates and detailed denning behaviour can be utilised in wolverine management, focusing on the Scandinavian monitoring program.

## Methods

### Study area

The study was carried out in and around Sarek National Park in northern Sweden (Kvikkjokk: 67°00´N, 17°45´E). The area consists of deep valleys from about 300 m a.s.l. to alpine mountains with peaks up to 2,000 m a.s.l., and encompass distinct vegetation gradients within short distances. The main vegetation at lower elevations consists of mixed conifer forest (Scots pine; *Pinus sylvestris*, Norway spruce; *Picea abies*) interspersed by numerous bogs and lakes, followed by hillsides and high elevation valleys of mountain birch forest (*Betula pubescens*) which form the tree line at 600-700 m a.s.l. The higher parts of the hillsides include low alpine tundra with dwarf birch (*Betula nana*) and willow shrubs (Salix spp.), succeeded by lower growing heaths, grass and meadows, and high plateaus of bare rock and glaciers. The climate is continental with average temperatures of -13°C in January and 5°C in May during the study period (www.smhi.se). The ground is usually snow covered from November until May, but altitudinal variation in time for spring snowmelt is large.

The study area includes important spring-autumn grazing pastures for semi-domestic reindeer. A large proportion of the reindeer herds are moved or migrate out from the study area in late autumn (November-December), although a very small but varying proportion

always remain in the area in winter (Bjärvall *et al.* 1990; Danell *et al.* 2006). The reindeer generally return in late April in time for the calving period that takes place in May with a peak from May 10-20 (Bjärvall *et al.* 1990). Consequently, there is a distinct and large spatiotemporal variation in reindeer density in the area (Bjärvall *et al.* 1990; Mattisson *et al.* 2011). Reindeer are the most important prey for wolverines in the area, and are frequently obtained as carrion from Eurasian lynx (*Lynx lynx*) kills (Mattisson *et al.* 2011; Mattisson *et al.* 2016). Occasional moose carrion can be locally important at times and rodents are presumably frequent prey after snowmelt (Landa *et al.* 1997). Other potential prey species are mountain hare (*Lepus timidus*), grouse (*Lagopus spp.*; *Tetrao spp.*), ptarmigan (*Lagopus spp.*) and rodents (*Rodentia*).

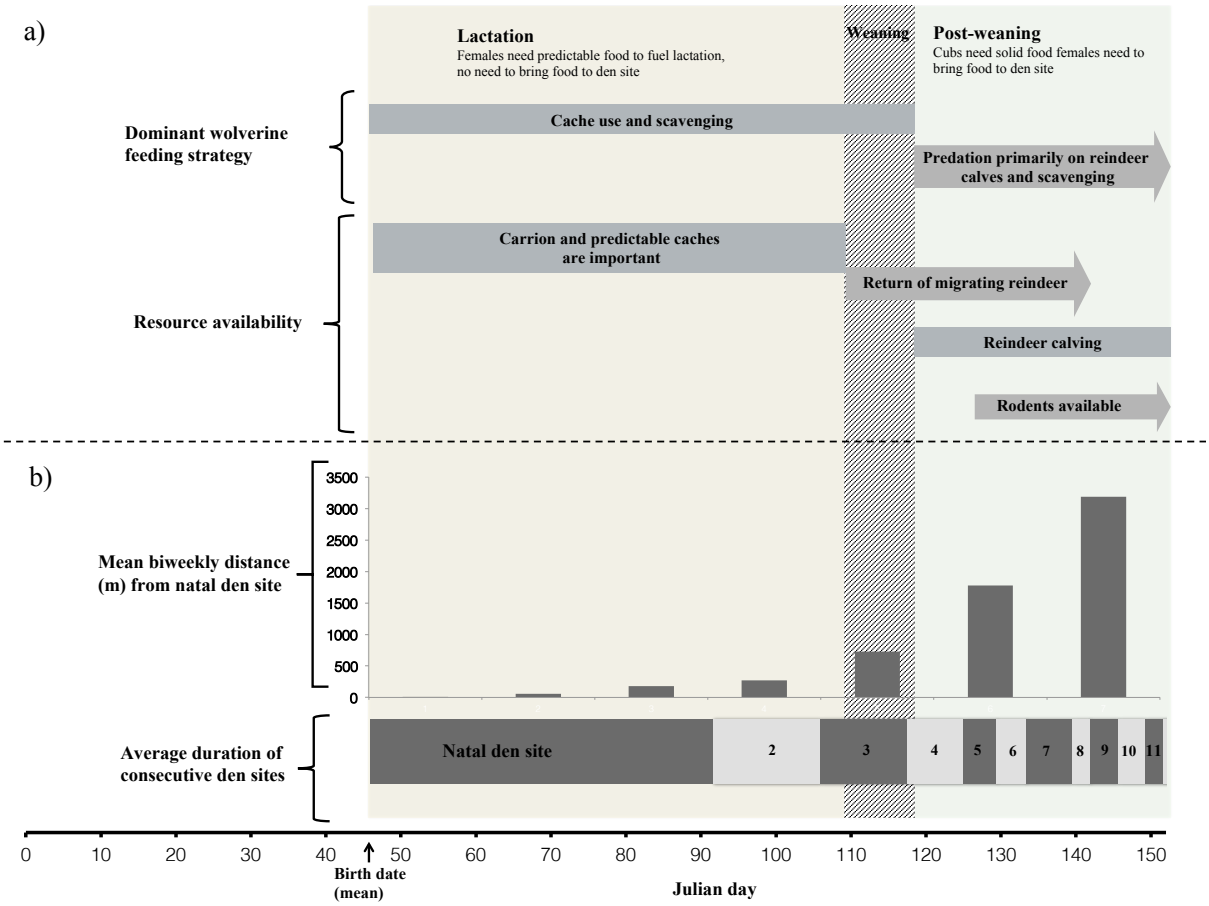


*Figure 1*. Schematic overview of (a) the most prevalent wolverine feeding strategies and corresponding resource availability (Bjärvall et al. 1990; Danell et al. 2006; Gustine et al. 2006; Inman et al. 2012; Mattisson et al. 2016) in relation to reproductive stages. (b) Temporal (biweekly) change in frequency of den site shifting and average duration for use of consecutive den sites, starting from the mean parturition date in this study (Feb 15). Time is denoted as Julian days from January 1.

## Wolverine capture, monitoring and identification of den sites

We captured wolverines by darting from helicopter or from the ground, and we immobilised them with a mixture of ketamine and medetomidine, following pre-established protocols (Arnemo *et al.* 2012) approved by the Animal Ethics Committee for northern Sweden and fulfil the ethical requirements for research on wild animals (protocol number A13-09). We equipped all females with GPS-collars (2004-2006: Televilt Posrec C300; TVP positioning, Lindesberg, Sweden, and 2008-2014: GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). We also equipped all individuals with intraperitoneally implanted VHF-transmitters (iMP/400/L, Telonics inc., Mesa, Arizona, USA).

We monitored all females intensively according to predefined programming to take 8-48 locations per day. We used location data from 18 adult wolverine females monitored during 54 denning seasons (February-May) to evaluate whether they displayed behaviours revealing that a reproductive event has occurred (Persson *et al.*

2006; Rauset *et al.* 2015). Of these 54 denning seasons, females exhibited intensive use of den sites during 31 denning seasons (1-4 reproductive events per female). Den sites were identified by detection of distinct clusters of GPS locations using GIS software (ArcMap 9.3, ESRI), complemented with VHF radio tracking from the ground or by helicopter. The natal den site (*i.e.* where the cubs were born), was defined as the first place where location data showed that a female remained within a very restricted area (≈ 50 m radius) for several (10-84) consecutive days, often in combination with an increase in unsuccessful fixes, which indicate that the female is at a place with obstructed contact with satellites (Mattisson *et al.* 2010). Furthermore, all natal den sites were preceded by roaming behaviour over large areas, typical of an average non-reproductive wolverine (Inman *et al.* 2012*b*). Reproduction was confirmed by observation of cubs (n = 27), or by cubs found dead at the den site (n = 2). In the remaining two cases we lost contact with the denning female due to collar failure (n = 1) or poaching (n = 1). We defined the date for parturition as the first day at the natal den site (as in Walsh *et al.* 2016).

We also identified 214 den sites used after the natal den. Females used these sites for 1-54 days. We thoroughly investigated all identified clusters to separate den sites from other activities, such as feeding sites or daybeds (Mattisson *et al.* 2011; Mattisson *et al.* 2016). We classified a cluster as a den site if it was characterized by concentrated consecutive locations predominantly during daytime (Mattisson *et al.* 2010). In most cases (n = 197) these clusters were used over several days. The identification of den sites was further supported by visual observations of female and cubs and/or the site being visited in the field after abandonment to confirm signs of use as a den (n >124). The combination of detailed investigation of high-resolution GPS data and field observations provides for reliable identification of den sites. However, it became increasingly difficult to confidently identify den sites, often from mid-May, because females moved frequently with the cubs, and we did not include any sites used after 1 June in this study.

We used general linear mixed models with a Poisson error distribution using the *'lme4'* package (Bates *et al.* 2014) in R to test the differences in duration of use of the first two den sites together with the combined use of all remaining den sites, as well as to describe the use of a den site in relation to den site sequence number. Female and year was included as a random factor, to be able to compare the same female's use of different den sites.

### Distances between den sites and female use of the denning area

We used two approaches to quantify the distance between consecutive den sites used by the same female during the denning season. First, we measured the daily distance (*i.e.* one measure each monitored day even if the females had not changed den sites) between natal den site and subsequent den sites throughout the denning period. Second, we measured the distance from the current den site to the most distant of the previous dens (*i.e.* maximum distance). The latter is a conservative approach based on the need within the monitoring program to separate den sites found at different time periods during the denning season and because it is hard to separate natal sites from subsequently used den sites for unmarked females in the field. Distances were measured from the centre point of each den site using the *'rgeos'* package (Bivand & Rundel 2016) in R (R Core Team 2014). We also calculated daily distances between simultaneous den sites for 19 neighbouring female pairs. Here we only included days during the denning season when we had coordinates for both females' den sites (n = 2650 daily distances).

To assess the amount of time a female spends at the den site and the immediate surrounding (*i.e.* denning area), we recorded the number of daily locations within 100 m from the central point of the den site. Because the locations frequency varied between females and years we calculated the daily proportion of total location attempts that resulted in a location inside or outside of the denning area, as well as the proportion of failed fix attempts, in relation to time from parturition. We excluded the first and last day at each den site to avoid including locations when the cubs were moved from one den site to the next. Therefore, the daily sample size decreased in the later part of the denning period when females spent shorter time at each den site and we therefore limited the analysis to the first 75 days after parturition.

### The probability that two den sites belong to the same female

One critical task within the monitoring program is to determine if two den sites found within the same area belong to the same or different wolverine females. We used the dataset with all daily maximum distances (see above) between den sites used by the same female during the same denning season to model the probability that a female has a new den site further away than several specific threshold distances (*i.e.* 0.5, 1, 2, 3, 4 and 5 km). We modelled each threshold distance separately and in each model the daily maximum distances for monitored females were classified as either 0 or 1 depending on whether the distance was below or above the threshold value (*i.e.* 0 for distances ≤ threshold distance, and 1 for distance > threshold distance). By including date as an explanatory variable in the models we estimated how the probability that a female has a new den site above a given distance over the monitoring period, using the following hierarchical Bayesian model:

$$\gamma_i = \alpha_{j[i]} + \alpha x_i$$

$$u_i \sim \text{Bernoulli}(\gamma_i)$$

where $\gamma_i$ is the model prediction of the probability that a female has a new den site above a given distance, $u$ is the binary classification of the distance in our dataset, $x$ is the date, and the subscript $i$ indexes the number of distances in our dataset. Because we used all daily distances, many distances are for the same female, thus we included female year as a group level effect on the intercept (α), indexed by the subscript $j$:

$$\alpha_j \sim \text{normal}(\mu_\alpha, \sigma_\alpha)$$

We did not include threshold distances >5 km because our dataset contained very few distances exceeding 5 km (n = 121).

We estimated final model parameters and generated predictions using a Bayesian Gibb's sampler (*i.e.* JAGS: Just Another Gibb's Sampler; Plummer 2003) called from R using the *'rjags'* package (Plummer 2014). For each model we ran two independent chains with different starting values and after discarding the first 100,000 iterations we accumulated 900,000 samples from each chain. Convergence was assessed by visual inspection of trace plots to assure stability and homogeneous mixing and by using the Gelman and Rubin diagnostic (<1.1; Gelman & Rubin 1992). We report posterior means and 95% CRI for estimated model parameters and predictions unless otherwise stated.

# Results

## Parturition date

We estimated 31 parturition dates for 18 different females (1-4 per female), and the mean parturition date was February 15 (SD = 7.4 days). The earliest birth was January 29 and the latest was March 9 (Fig. 2); 50% of all births had occurred by February 14 and 90% by February 21. After parturition, the mean time to the females' first location outside the denning area was 5.7 days (SD = 2.8, range: 2-11). Furthermore, the proportion of locations outside the denning area was low the first 11 days (mean = 6%; range = 1-12%) and increased progressively until one month after birth (*i.e.* mean = 21%; range = 7-35% for days 12-31), after which it stabilized between 30 and 40% (mean = 36%, range: 29-51% for days 32-75; Fig. 3).

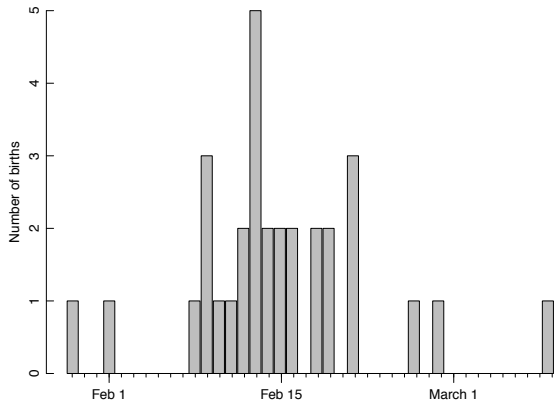


*Figure.* 2. Frequency distribution of birth dates (n = 31) in wolverine females (n = 18) monitored with GPS-collars in northern Sweden 2004-2014.

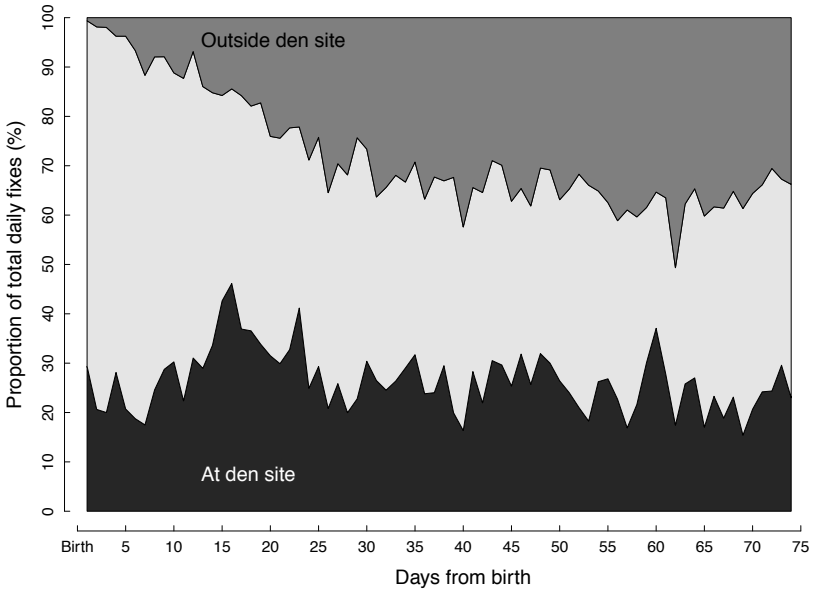


*Figure 3*. Locations at the den site (< 100 m from centre of den site; black field), outside the den site (> 100 m from centre of den site; dark grey field), and unsuccessful fixes (light grey field) as proportion of total number of fix attempts relative to the time from birth.

## Denning behaviour

Females spent on average 47 days (median = 52) at the natal den site, but this varied from 10-84 days (Table 1). Average date for abandonment of the natal den site was April 4 (median = April 8), with the earliest and latest abandonment at February 18 (10 days from birth) and May 4 (84 days from birth), respectively. In general, females spent more time at the natal den site than any of the consecutive den sites (Table 1; Fig. 4). The second den site was used for an average of 14 days (range = 1-54), and thereafter the use of a den site decreased with the den sites sequence number (compared to the null model: ΔAICc = 60.1).

We monitored 22 of the 31 denning periods until it was not possible to confidently identify den sites (mean 101 days after parturition, SD = 12; range: 74-118). The remaining nine denning periods were interrupted because two females lost the cubs early (6 and 11 days after parturition), two females were killed (minimum 28 and 70 days after parturition), and five seasons were interrupted due to transmitter failure (Fig. 3). On average, we documented 4.2 den sites (SD = 3.8; range = 1-16) during the first 70 days and 10 den sites (SD = 7; range = 3-24) in total for the entire denning season (n = 22). The use of the first two den sites together lasted longer (59.9 ± 22.3 SD days) than the combined use of all remaining den sites (41.5 ± 21.8 SD days; compared to the null model: ΔAICc = 71.2).

During the first month of the denning period (on average February 15-March 15), wolverine females rarely shifted den site (Table 1, Fig. 4), and females that did shift moved short distances from the natal den sites (Table 2, Fig. 5). After 2 months, the distance from the den site currently used to the natal den was still short (mean = 270 m; April 1-15). Thereafter, during late April and early May females change den site more often and moved longer distances between consecutive den sites (Table 2, Fig. 5). The variation among females also increased during the later part of the denning period. For instance, one female (giving birth on February 18) had only moved the cubs 280 m from the natal den in late May, while another (giving birth on February 1) moved 11 km with her cubs by the 29th of April (Fig. 5).

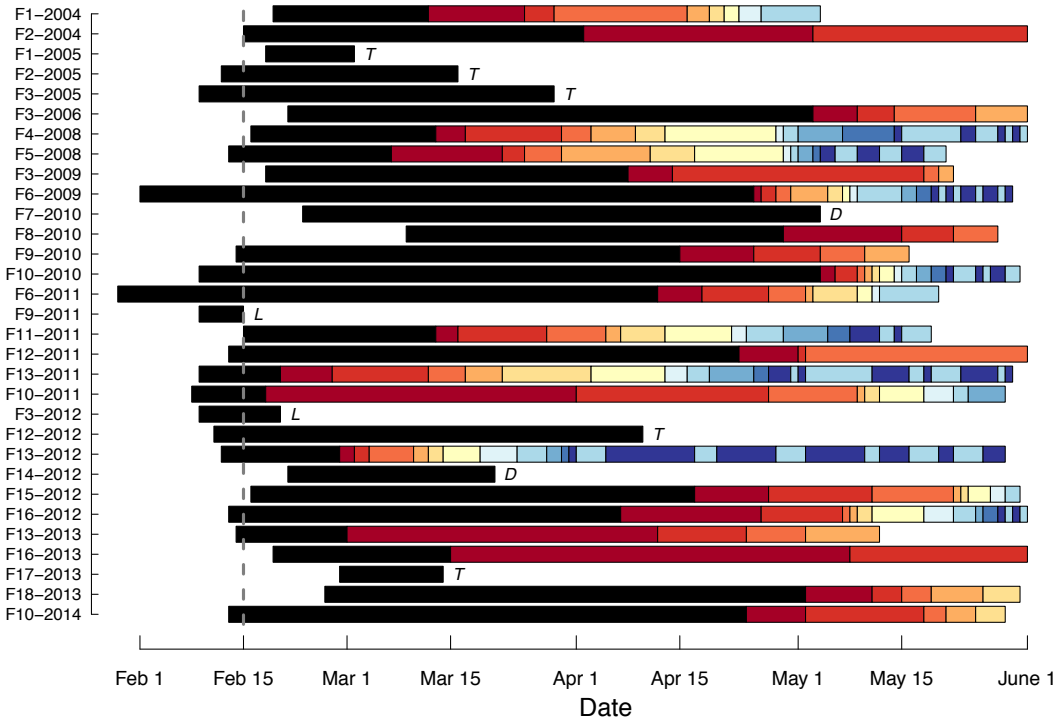


*Figure 4*. Monitored denning periods (n=31) for 18 GPS-collared wolverine females, in northern Sweden 2004-2014. Each bar represents a denning season with each used den site denoted with different colors in relation to date. Nine denning periods were interrupted because 2 females (L) lost their cubs early (6-11 days), 2 females were killed (D), or 5 periods were incomplete due to transmitter failure (T).

Table 1. *Number of days that consecutive den sites are used; from den site 1 (natal den) to den site 12.*

| | Mean | Min | Max | SD | N |
|---|---|---|---|---|---|
| Natal den* | 47 | 10 | 84 | 24 | 24 |
| Den 2 | 14 | 1 | 54 | 15 | 22 |
| Den 3 | 12 | 1 | 34 | 10 | 22 |
| Den 4 | 7 | 1 | 34 | 7 | 21 |
| Den 5 | 4 | 1 | 14 | 4 | 19 |
| Den 6 | 4 | 1 | 12 | 3 | 13 |
| Den 7 | 6 | 1 | 15 | 5 | 12 |
| Den 8 | 2 | 1 | 5 | 1 | 12 |
| Den 9 | 4 | 1 | 6 | 2 | 9 |
| Den 10 | 4 | 1 | 6 | 2 | 8 |
| Den 11 | 3 | 1 | 7 | 2 | 8 |
| Den 12 | 2 | 1 | 4 | 1 | 8 |

* Including 2 females that were killed before they abandoned the natal den (minimum 54 and 70 days after parturition, respectively).

## Denning behaviour in relation to population monitoring

The maximum distance between den sites for the same female and denning period followed the same pattern as the distance between current and natal den site (Figs 5 & 6, Table S1). No female moved her cubs further than 2.1 km before April 15 and thereafter both maximum distance and the variation increased (Fig. 6, Table S1). Accordingly, average distance to the most distant previous den in the first and second half of May was 2.1 km and 4.2 km, respectively, excluding two extreme distances of 14.2 and 22 km by one female. In contrast, the average distance between neighbouring females' den sites changed little from February to late May (mean distance ranging from 13 to 20 km; Fig. 6; Table S2). The shortest and longest distance between neighbouring females' den sites was 4.6 and 33.6 km, respectively.

The model predicted that the probability that a female has a new den site further away than 4 or 5 km from the previous den site was 0.3% at April 15 (Fig. 7). The probabilities increase over time, but was still less than 26% or 15% at May 15, whereas it had increased to 88% for 4 km and 66% for 5 km at June 1 (Fig. 7).

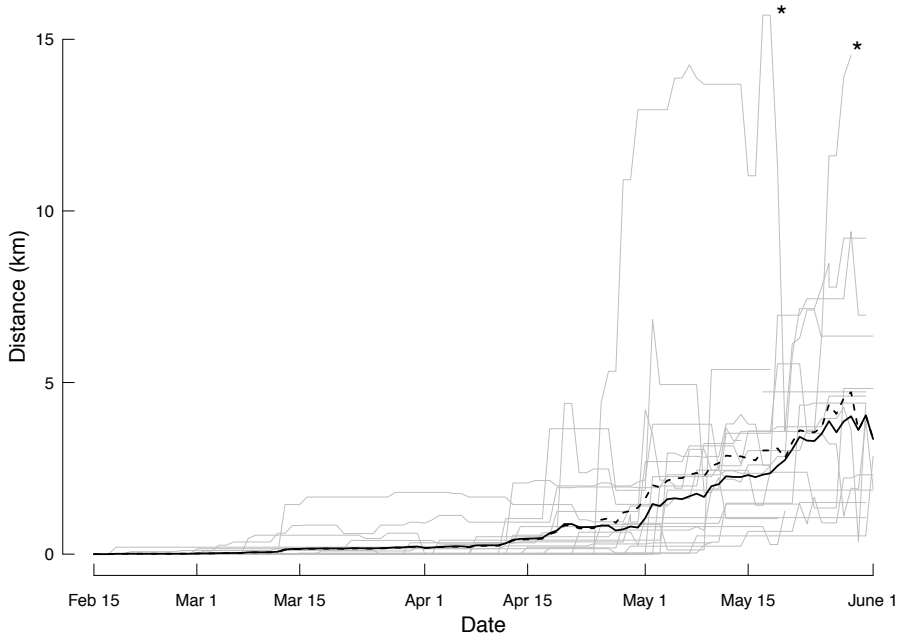


*Figure 5*. Daily distance from the natal den site to the current den site (i.e. where the female has the cubs that day) in relation to date. Mean value including all individuals (dashed line) and mean value excluding one female (*) that moved extreme distances from the den site (black line).

Table 2. *Distance (m) from the natal den to the current den site during different time periods during the denning season.*

| | Mean | *Median* | Min | Max | SD | Distances (n) | Denning periods (n) |
|---|---|---|---|---|---|---|---|
| 15 Feb.-28 Feb. | 10 | *0* | 0 | 200 | 40 | 302 | 27 |
| 1 March - 15 March | 60 | *0* | 0 | 1 450 | 180 | 360 | 25 |
| 16 March -31 March | 180 | *0* | 0 | 1 800 | 390 | 353 | 23 |
| 1 April - 15 April | 270 | *30* | 0 | 2 070 | 460 | 304 | 21 |
| 16 April-30 April* | 730 | *410* | 0 | 4 390 | 890 | 301 | 20 |
| 1 May-15 May* | 1 780 | *1 710* | 0 | 6 840 | 1 360 | 284 | 20 |
| 16 May-31 May* | 3 190 | *2 720* | 280 | 9 400 | 2 190 | 240 | 18 |

* One outlier was excluded (a female that moved extreme distances compared to all other females (see Fig. 5).

## Discussion

Wolverines generally gave birth in mid-February, with females spending an extended period at each den site and moving short distances between den sites for approximately 2.5 months after parturition. This corresponds to the lactation period when available prey are rare and females presumably rely on cached food, scavenging and opportunistic predation on reindeer (Fig. 1a-b). Moreover, early reproduction coincides with a persistent snow cover that provides for secure den sites and favourable conditions for food caching during the lactation period. In contrast, after weaning, den use is characterized by a progressive increase in frequency of den shifting over longer distances. This coincides with increased prey availability and presumably reduces the need to bring food back to the den from far away. We suggest that the documented timing of parturition and temporal change in denning behaviour reflects wolverines' adaptation to match birth time and offspring development to changes in resource availability and foraging strategies (Fig. 1). This denning behaviour also has implications for setting harvest season limits and how to separate different reproductions during monitoring.

### Parturition and denning behaviour

Our results show that wolverines give birth earlier than other non-hibernating carnivores in the northern hemisphere (see also Inman *et al.* 2012*a*). The parturition dates spanned a 40-day time window from January 29 to March 9. The peak period for parturition was mid-February, with 84% of births occurring between February 8 and 22, which is in the earlier part of the previously suggested range (*i.e.* February to mid-March; reviewed in Inman *et al.* 2012a). Hence, nidation primarily occurs in late December-early January, assuming a gestation period of 45-50 days (Mead *et al.* 1993; Inman *et al.* 2012*a*).

Our results also indicate that timing of parturition and the temporal pattern in wolverine denning behaviour reflects their adaptation to match birth time and offspring development to changes in resource availability and foraging strategies. Timing of births should be adapted to resources available for the energy-demanding period of lactation (Sadleir 1984; Oftedal & Gittleman 1989). The lactation period is about 10 weeks in wolverines (Iversen 1972; Inman *et al.* 2012a); thus, lactation usually lasts from mid-February until late April in our study area. During this period, prey availability is low as migrating reindeer have not yet returned (Bjärvall *et al.* 1990; Danell *et al.* 2006) and rodents are still hidden under snow cover (Hansson & Henttonen 1985). Furthermore, wolverine predation events are relatively rare during winter and scavenging is an important feeding strategy for wolverines (Haglund 1966, Mattisson *et al.* 2016). In addition, wolverines display extensive food-caching behaviour, which buffers against temporal fluctuations in prey availability (Inman *et al.* 2012; Mattisson *et al.* 2016) and it has been suggested that cub-rearing females rely more on cached food and less on predation during most of the denning period (Bjärvall 1982; Inman *et al.* 2012a). Additionally, in our study area the availability of reindeer carcasses during winter positively influences wolverine reproductive success during the spring (Persson 2005; Rauset *et al.* 2015). The early parturition dates in our study area and the low prey availability during a large part of the lactation period supports the suggestion that lactation is mainly sustained by scavenging and food caching of resources obtained earlier in winter (Persson 2005; Inman *et al.* 2012*a*). This could also be reflected by the denning behaviour. Females rarely leave the denning area during the first 11 days, and it is not until one month after parturition that the proportion of locations outside of the denning area stabilizes (Fig. 3). This indicates that females utilize predictable food resources in proximity to the den during this period. It is also rare that females change den site during the first month of the denning period, and if the young are moved then the distance from the natal den site to subsequent den sites is short until late April (Table 2; Figs 4-7). The use of the first two den sites lasted longer than the combined use of all remaining den sites. This pattern presumably reflects the cubs' relative immobility and dependency on the mother early during the denning period. Furthermore, the proportion of unsuccessful GPS fixes during the first weeks after parturition suggests that the female spends much time under objects obstructing the receiver (Mattisson *et al.* 2010); wolverine den sites are usually located under boulders or cliffs covered by snow drifts (Magoun and Copeland 1998, May *et al.* 2012, Makkonen 2015). Also, the early reproduction coincides with persistent and deep snow that provides for dens that protect cubs from cold temperatures and predators (Magoun & Copeland 1998; Persson *et al.* 2003) and favourable food caching conditions to sustain the mother during the lactation period (Inman *et al.* 2012*a*). As spring progresses, resource availability increases in our study area. The return of migrating reindeer in late April, and especially the start of their calving period in early May provides an abundance of small calves, representing easy prey for low cost (Mattisson *et al.* 2016), especially the first weeks after calving (Gustine *et al.* 2006). Also, beneficial snow conditions for predation, carcasses from winter deaths (Haglund 1966; Bjärvall *et al.* 1990; Inman *et al.* 2012a), and small mammals become increasingly available with snowmelt at lower altitudes (Hansson & Henttonen 1985). Coinciding with the increase in resource availability and weaning of cubs, wolverine females start to move their cubs more often, resulting in the distance between den sites increasing (Table 2; Figs 4-7). This behaviour probably reflects both the development of the cubs, and a shift in resource availability and

foraging strategy, when females increasingly prey upon reindeer calves (Mattisson *et al.* 2016). The cubs are more mobile and rely more on solid food brought by the mother, and it may be more efficient for females to move cubs closer to food sources, such as calving grounds and carcasses, to decrease costs of carrying food long distances to the den. Accordingly, the average distance of movements from the current den site is shorter in May compared to April (Myhr 2015). Habitats selected by reindeer remaining in winter and habitat selected during calving season is different (Pape & Löffler 2015), which might also influence where females move their cubs. Especially if food caches from the winter have become depleted nearby the natal den. Decreasing the time away from the cubs may also decrease the risk of infanticide (Persson *et al.* 2003). In May, the snow cover melts away sequentially from low to high altitudes, which changes conditions den site selection, which may also trigger frequent moves between den sites.

## Implications for management

### Timing of parturition and harvest

Time of birth has implications for defining an appropriate harvest season, especially for species with altricial young. Harvest seasons for wolverines vary among countries and regions. For instance, in Norway the licenced hunt is allowed from 10 September to February 15, while lethal control in Sweden is generally only allowed until January 15. In Alaska, the harvest season varies by units, but is often open until February 28, March 15 or March 31 (Alaska DFG 2016). In our study, most births occur from February 8 to 21 and females exhibit limited movements outside the denning area the first 10 days after parturition; consequently, these females start to move outside of the denning area again from February 18 – March 3. However, the earliest birth in our dataset occurred on January 29 and females giving birth that early are at risk of being harvested while altricial young are in the den, if harvest season extends into February.

### Denning behaviour and documentation of den sites

We found that wolverine females change den sites earlier and more often than previously suggested (Magoun & Copeland 1998; Inman *et al.* 2012*a*) and what was assumed when the Scandinavian monitoring system was originally designed and implemented (Aronsson & Persson 2012). For monitoring of wolverine den sites, our results show that searching for tracks of females moving back and forth to a den site should be initiated in early March, when most denning females have started to move outside of the denning area. The fact that few females change their den site during March and early April indicates that the chance to fulfil the criteria of 'long term activity' at a den site (*i.e.* 3-4 visits separated over at least 3-4 weeks; Aronsson & Persson 2016) will be highest during this period. In contrast, it will be increasingly difficult to document 'long term activity' at a den site later during the monitoring period. This is due to females starting to change den site more often and moving further between den sites beginning in the second half of April. Timing of snowmelt is another important factor to consider, hence the shorter time spent at den sites together with more unpredictable snow cover might decrease the possibility of documenting den sites from mid-April, especially at lower latitudes with earlier snowmelt than in our study area.

### Separation of documented reproductions

Females changing den sites make it difficult to correctly count the number of reproductions. If multiple observations within the monitoring systems of large carnivores in Scandinavia cannot be separated or merged by field observations or DNA-analysis, then the last resort is to use the distance between observations as a decision tool, *i.e.* distance-criteria (Ordiz *et al.* 2007; Linnell *et al.* 2007; SEPA 2013). For wolverines, 10 km is currently used as the distance-criteria to separate den sites. Consequently, if neighbouring den sites are located within 10 km these will be counted as one reproduction, whereas if the distance between the different den sites used by one female during the same denning period exceeds 10 km these will be counted as two. Apart from resulting in biased population estimates, even a few potential errors could negatively influence trust in management since one reproduction is compensated with 200,000 SEK to the reindeer herding district. Thus, the temporal relationship of distances between neighbouring den sites and distances between individual females' den sites is important in relation to separation of reproductions.

The frequency and distance of movements between an individual's den sites are low until about mid-April, while the average distance between neighbours' den sites is much larger and does not change with time. From February to mid-April, there is no overlap between the maximum distances between an individual's den sites (2.1 km) and the minimum distances between two neighbours' den sites (4.6 km). Therefore, the distance criterion drastically redused for the period from February to mid-April (Fig. 6). The model also predicted that at April 15 there is only 0.3% probability that two den sites separated by 5 km belong to the same female (Fig. 7). Furthermore, April 19 is the first date that the maximum distance moved from a previous den site (4.7 km) exceeds the shortest recorded distance between two neighbouring females' den sites (4.6 km). In addition, the first date that a female moved her cubs further away from the natal den site than the shortest distance between neighbouring den sites was April 30. During

the second part of April there is still minimal overlap between these distances.

Consequently, we suggest using a distance criterion that is dynamic with time. From February to mid-April a distance criterion between 2.5 and 4 km would minimize erroneous conclusions. Thereafter, in the first part of May and particularly during the latter part of May, distance criterion should be larger (*i.e.* ≥ 5 km) when the difference between individual females' den site movements and neighbouring den sites decreases and the overlap between these distances increases. Therefore, the later in the denning season, the harder it is to define robust distance criterion that minimize erroneous conclusions.

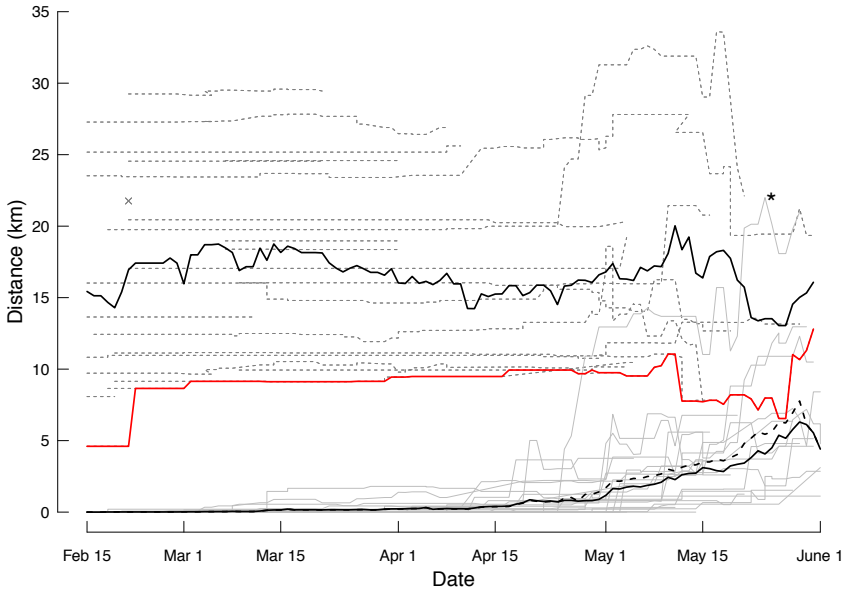


*Figure 6*. Daily distance between den sites of neighbouring females in relation to date (dotted grey lines = distance between individual neighbour-pairs, upper bold line = mean distance, red line = minimum distance), and daily distance from the current den site to the most distant of the previous den sites used for individual females (thin grey lines = individual distances, lower bold line = mean distance, bold dashed line = mean including a female that moved extreme distances [*]).

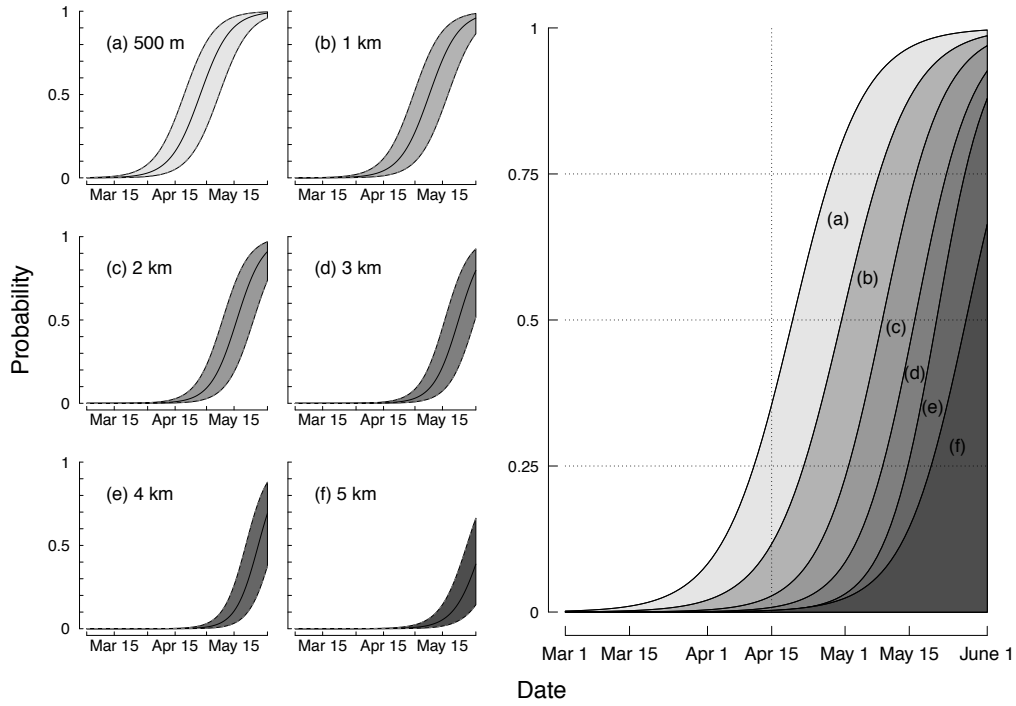


*Figure 7*. Left section - Probability and 95 % credible intervals that a female has a new den site more than 0.5, 1, 2, 3, 4 and 5 km from the most distant previous den site in relation to date. Right section - The upper 95 % credible interval of the probability that a female has a new den site more than a: 0.5, b: 1, c: 2, d: 3, e: 4 and f: 5 km from previous den site in relation to date (i.e. there is a 97.5% certainty that the probability will equal to or less than the line).

## Conclusion

We studied wolverine denning behaviour in the reindeer husbandry area mainly consisting of alpine tundra and high-altitude taiga, where snow cover normally persists until late spring. Although these results are likely representative of significant portions of the mountainous parts of the Scandinavian reindeer husbandry area, it is important to consider that the timing of births and denning behaviour could differ in areas with different conditions in terms of snow cover, resource availability and disturbance. Resource availability in our study area is strongly influenced by migrating reindeer, with strong seasonality. Where wolverines rely on resources that are less seasonal, timing of birth and denning behaviour may be different.

Still, similar temporal patterns in resource use and abundance seem prevalent in other areas, such as North America. In general, scavenging appears to be the main strategy in winter and predation more important in summer (Magoun 1987; Lofroth *et al.* 2007; Inman *et al.* 2012*a*, 2015). Moreover, resource availability in many areas increases in late winter and spring with an increase in neonatal ungulates such as caribou, elk (*Cervus elaphus*) and deer (*Odocileus spp*.), as well as the emergence of other small prey, such as marmots (*Marmota spp*.), ground squirrels (*Spermophilus spp*.) and small rodents (Magoun 1987; Gustine *et al.* 2006; Lofroth *et al.* 2007; Inman *et al.* 2015).

Furthermore, snow cover facilitates secure denning sites (Magoun & Copeland 1998) and caching efficiency (Inman *et al.* 2012*a*). Hence, timing of reproductive events could be different at lower altitudes and latitudes with less snow available for secure den sites. It is also important to consider that in areas at lower latitude and altitude, where snowmelt occurs earlier, documentation of reproductions needs to be conducted earlier or may be nearly impossible without snow-independent monitoring methods (Aronsson & Persson 2016).

Our study of female wolverine movements during denning indicate that their reproductive chronology and denning behaviour are adapted to offspring development in relation to changes in resource availability and foraging behaviour. During lactation, reproducing females are stationary and rarely move between den sites, supporting the possibility that when cubs are vulnerable and immobile females are likely sustained by cached carcasses After weaning, when cubs require solid food delivered by the female and availability of prey increases, frequency of den site switching and distance increases progressively. In addition, the observed denning behaviour has implications for the monitoring of wolverine reproductions. Monitoring of reproductions is presumably most efficient and reliable from early March until mid-April. Comparing distances between neighbouring females and sequential dens of individual females suggest that there should be a dynamic distance criterion to separate between different females' den sites. However, from February to mid-April there is a very robust distance criterion as there is no overlap between the maximum distances between an individual's den sites (2.1 km) and the minimum distances between two neighbours' den sites (4.6 km).

## Acknowledgements

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# Supporting information

Jens Persson, Malin Aronsson, Henrik Andrén & Matthew Low

## Reproductive timing and denning behaviour of female wolverines in relation to resource availability and population monitoring

### Figures and tables

Table S1. *Distance (m) between the same females' den sites during different time periods (ca. 15 days) during the denning season. The distances are the distance to the most distant previous den sites during the entire denning period.*

| | Mean | Median | Min | Max | SD | Distances (n) | Denning periods (n) |
|---|---|---|---|---|---|---|---|
| 15 Feb. - 28 Feb. | 10 | 0 | 0 | 200 | 40 | 298 | 16 |
| 1 March - 15 March | 60 | 0 | 0 | 1 450 | 180 | 363 | 18 |
| 16 March - 31 March | 180 | 0 | 0 | 1 800 | 390 | 371 | 18 |
| 1 April - 15 April | 270 | 0 | 0 | 2 130 | 460 | 324 | 17 |
| 16 April - 30 April* | 720 | 240 | 0 | 5 010 | 1 010 | 316 | 17 |
| 1 May - 15 May * | 2 080 | 1 620 | 0 | 6 880 | 1 820 | 293 | 17 |
| 16 May - 31 May * | 4 170 | 3 710 | 520 | 12 960 | 3 250 | 189 | 12 |

* Excluding one outlier (a female that moved extreme distances compared to other females; she moved 12,950 m 30 April, 14,250 m the first part of May and 22,000 m second part of May (see also Fig. 6 in main text).

Table S2. *Distance (m) between den sites of GPS-collared neighbouring females at different time periods during the denning season.*

| | Mean | *Median* | Min | Max | SD | Distances (n) | Pairs (n) |
|---|---|---|---|---|---|---|---|
| 15 Feb.-28 Feb. | 16 550 | *16 020* | 4 600 | 29 250 | 7 010 | 402 | 16 |
| 1 March - 15 March | 17 980 | *17 050* | 8 650 | 29 590 | 6 350 | 539 | 16 |
| 16 March -31 March | 17 510 | *17 050* | 9 120 | 29 590 | 6 010 | 580 | 15 |
| 1 April - 15 April | 15 800 | *14 800* | 9 440 | 26 900 | 5 390 | 402 | 13 |
| 16 April-30 April | 15 750 | *15 540* | 9 490 | 31 280 | 5 270 | 348 | 11 |
| 1 May-15 May | 16 820 | *13 940* | 7 720 | 33 600 | 7 300 | 264 | 11 |
| 16 May-31 May | 15 270 | *13 270* | 6 550 | 29 030 | 5 880 | 116 | 6 |

**From:** Grizzle, Betty
**To:** John Guinotte
**Subject:** Fwd: emails discussions
**Date:** Wednesday, April 19, 2017 9:51:12 AM
**Attachments:** Attachment A.pdf

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---------- Forwarded message ----------
From: **A J** <222wsheridan@gmail.com>
Date: Tue, Apr 18, 2017 at 3:15 PM
Subject: Re: emails discussions
To: "Grizzle, Betty" <betty_grizzle@fws.gov>

here it is

On Tue, Apr 18, 2017 at 2:08 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> Looking for Attachment (appendix?) A right now.
>
> On Tue, Apr 18, 2017 at 3:05 PM, A J <222wsheridan@gmail.com> wrote:
>
> > Here Attachment B; do you need any others?
> >
> > On Tue, Apr 18, 2017 at 1:33 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> >
> > > Thanks Audrey. I found a few things, but not these (yet). I am looking at your peer review comments on previous proposed rule and haven't found your "Attachment B" yet....will keep looking.
> > >
> > > I apologize for having you search for and resend your earlier comments; I am trying to be thorough in this new assessment and have many questions about several analyses. Betty
> > >
> > > On Tue, Apr 18, 2017 at 2:20 PM, A J <222wsheridan@gmail.com> wrote:
> > >
> > > > Betty
> > > > I don't know if you have already seen these from Shawn's files, but these emails contain a discussion I had with Copeland and McKelvey after some reluctance on my part to get into such an exchange post-status review. I was pretty burned out by then on the whole subject. But you may find parts help answer some of the questions you recently sent. The McKelvey Email file is emails between Jeff and I until it became apparent that it was better to talk directly to Kevin and so his responses to me are in blue type in that email. The McKelvey Email Response file holds my answers back to him in black type. As you will see, there is little consensus on the matters under discussion. I had permission from both to share these emails and Shawn received copies. He had encouraged us to discuss these issues (and others) hoping to get some resolution of the differences of opinion, but as I suspected from the start, I don't think anyone changed their minds on anything.
> > > >
> > > >
> > > >
> > > > --
> > > >
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ATTACHMENT A

Supplementary Documentation for Peer Review of the USFWS Proposed Listing Determination for the Wolverine in the Contiguous United States

Date: 30 April 2013

Reviewer: Dr. Audrey J. Magoun

Email: amagoun@ptialaska.net

Document Reviewed: USFWS proposal to list the distinct population segment of the North American wolverine occurring in the contiguous United States as a threatened species under the Endangered Species Act

Purpose of Peer Review: "to ensure our listing determination and critical habitat designation are based on scientifically sound data, assumptions, and analyses" (p. 114).

BACKGROUND

Proposed Listing Determination:

1) "the primary threat to the DPS is from habitat and range loss due to climate warming" (p. 100)
2) "the contiguous United States wolverine DPS presently meets the definition of a threatened species due to the likelihood of habitat loss caused by climate change resulting in population decline leading to breakdown of metapopulation dynamics" (p. 101)
3) "we base this determination on the immediacy, severity, and scope of the threats" (p. 101)
4) "other minor threats that could become significant when working in concert with climate change if they further suppress an already stressed population include
    a) harvest including incidental harvest
    b) demographic stochasticity and genetic diversity due to small effective population sizes " (p. 101)

Premise for the Proposed Listing Determination:

"We find that McKelvey et al. (2011, entire) represents the best available science for projecting the future impacts of climate change on wolverine habitat for four primary reasons:

1) their habitat projections are based on global climate models that are thought to be the most reliable predictors of future climate available (IPCC 2007a, p. 12)
2) they conducted downscaling analyses to infer geographic climate variation at a scale relevant to wolverine habitat
3) they used a hydrologic model to predict snow coverage during the spring denning period (the strongest correlate with wolverine reproductive success)
4) they used the habitat model developed by Copeland et al. (2010, entire) to relate projected climate changes to wolverine habitat" (p. 59)

REVIEW

Most responses in my review of the proposed listing determination are in the form of edits and comments directly on the Word version of the document provided by Shawn Sartorius. However, I have added this separate document (Attachment A) to provide detailed explanations of why I believe that the proposed listing determination is not based on the "best available science" because 1) there is consequential information that was not considered in the proposed listing determination and 2) there are errors in the data analyses relative to "persistent spring snow," which was integral to projecting future wolverine habitat under climate warming in the McKelvey et al. (2011) paper. McKelvey et al. (2011) cited Aubry et al. (2007), Schwartz et al. (2009), and Copeland et al. (2010) as their sources of information on wolverine habitat use and movements in relation to persistent spring snow cover (p. 2884, *Modeling snow*). McKelvey et al. (2011) used the 15 May MODIS-based snow cover data from Copeland et al. (2010) to analyze the effects of climate warming on future wolverine habitat in the western states. The dates chosen for modeling "persistent spring snow" are the primary basis for the climate models developed by McKelvey et al. (2011). In this supplementary documentation (Attachment A), I point out erroneous assumptions about wolverine habitat requirements in Copeland et al. (2010) associated with the 15 May MODIS-based snow cover, then discuss how climate models in McKelvey et al. (2011) were affected by these errors, and add a few comments regarding Schwartz et al. (2009) on dispersal and connectivity in relation to projected wolverine habitat under climate warming. I summarize my conclusions at the end of this document. Many of the points made below

are referred to in my comments on the Word document of the proposed listing determination. It is important to note that I am listed as an author on the Copeland et al. (2010) paper, which I had the opportunity to review before it was submitted for publication. At that time, I mentioned my concerns regarding the 15 May MODIS dates, as did one of the official reviewers for the Canadian Journal of Zoology during the review process (Attachment B). The ramifications of failing to consider problems with the 15 May MODIS data would not be fully apparent until the publication of McKelvey et al. (2011) and the subsequent use of this paper as the basis for this proposed determination. I feel it is important to bring my concerns forward here to ensure the listing determination is based on scientifically sound data, assumptions, and analyses. In addition, some information presented below was published subsequent to Copeland et al. (2010) and McKelvey et al. (2011) so the authors may not have had access to or known of the existence of this information prior to publishing their paper. This more recent research is cited in my discussion below where relevant.

1. Review of Copeland et al. (2010):

The failure of the bioclimatic envelope developed by Copeland et al. (2010) to encompass wolverine distribution and den sites across the species' entire range invalidates assumptions about the *obligatory* nature of spring snow cover (i.e., 15 May MODIS) for defining wolverine habitat. In this section, I present arguments why dates used by Copeland et al. (2010) for developing the bioclimatic envelope of the wolverine are in error and do not provide the best scientific data on wolverine denning and year-round habitat.

1a. *The Bioclimatic Envelope and Relevance to the 15 May MODIS Snow Model*

Copeland et al. (2010, p. 234), in their introductory remarks, stated that:

> "bioclimatic models consider climatic variables as correlates of a species' current distribution and are often used to predict range shifts that may result from different climate change scenarios [reference cited here]. These correlative approaches are sometimes criticized because they fail to account for interactions with biotic factors [references cited here] and may not accurately reflect the ecology, behavior, or physiology of the target species [references cited here]. *Consequently, evaluating an organism's*

> *climatic requirements by correlating current range with climatic factors is problematic* [italics mine]. However, if researchers possess reliable understandings of both an organism's geographic range and its climatically linked biological requirements, they can evaluate whether current range is consistent with the climatic conditions needed to fulfil those requirements [no reference cited]. This approach is taken here".

In other words, the authors are stating that they have a reliable understanding of the wolverine's geographic range and its "climatically linked biological requirements," which in this case refers to "persistent spring snow" for denning and the "upper thermal limits" for the species (p. 235-236). They conclude on p. 244 that "the strong concordance of wolverine den sites with the spring snow coverage clearly reflects an obligatory relationship with snow cover for reproductive dens."

To be clear, the term "spring snow coverage" and "persistent spring snow" in Copeland et al (2010) refers to snow cover that lasts to 15 May in at least 1 of 7 years in the period 2000–2006 as measured by MODIS at a 500-m resolution (p. 235). Any 500-m pixel determined to be bare of snow in the period 24 April–15 May was removed from the snow cover layer for that year. These data were used to produce a map referred to as the "spring snow coverage" (p. 235), which was subsequently used as the basis for the 15 May MODIS map in McKelvey et al. (2011, Fig. 2B, p.2887). No biological reasons were stated in either Copeland et al. (2010) or McKelvey et al. (2011) for why "persistent spring snow" would be required *in as few as 1 of 7 years* for wolverine habitat or why they excluded arctic regions that consistently have "persistent spring snow" every year.

What is the scientific basis for stating that wolverines require "persistent spring snow" to 15 May? Copeland et al. (2010) stated "it has been hypothesized that deep, persistent snow cover is an obligate component of wolverine reproductive denning habitat (Magoun and Copeland 1998)" (p. 234). Copeland et al. (2010) do not define "deep" in their paper nor do they refer to snow depth from the Magoun and Copeland (1998) paper. A careful reading of the Magoun and Copeland (1998) paper does not reveal a hypothesis that wolverines require deep snow until 15 May. That paper reports on a combined 10 natal dens and 8 maternal dens from Alaska and Idaho and reviews information about dens from earlier publications. Although the Alaska dens were in "deep snowdrifts" (p. 1315), the depth to the deepest point in one den was reported as

>1m, with the maximum depth in snow tunnels measured at 2.5 m. No depth measurements were provided for Idaho. From their study and their review of the literature on wolverine dens, Magoun and Copeland (1998) stated that "*almost all* verified wolverine reproductive dens were under 1–5 m of snow" (p. 1317) [italics mine]. One den was found in <1m of snow (i.e., ≤80 cm in Pulliainen 1968). Subsequently, Inman et al. (2007c) reported an occupied wolverine den that had <25 cm of snow covering a portion of the den (p. 71).

Date of den abandonment was variable for the Alaska and Idaho dens. Of the 18 dens that made up the sample in Magoun and Copeland (1998), only 2 in Alaska were known to be abandoned in May (p. 1316). These maternal dens were in 1) a remnant snowdrift (i.e., spring snowmelt had progressed to such an extent that the only snow left in the area occurred as lingering snowdrifts) and 2) a rock cave (not snow-covered; Magoun, personal observation). All other dens were abandoned (or could have been abandoned) before May (den abandonment date for one den in Alaska fell somewhere between 18 April and 5 May; Table 1, p. 1315). None of the dens in Idaho were used after 30 April. Magoun and Copeland (1998) concluded that "we believe a critical feature of wolverine denning habitat is dependability of deep snow throughout the denning period. *At least 1 m of snow, distributed uniformly or accumulated in drifted areas, should be present by February and persist until May"*(p. 1318) [italics mine]. It should be evident from this statement that "deep" refers to ≥1m, that snow need not be covering the entire area but could be in the form of remnant snowdrifts, and snow should persist *until* May (not 15 May). The "denning period" was defined in that paper as February–April (p. 1314).

At the time Magoun and Copeland (1998) was published, most wolverine reproductive dens had been "located in alpine, subalpine, taiga, or tundra habitat" and rarely "reported in low-elevation, densely forested habitats, although wolverines occupy these habitats" (p. 1317). Banci (1994, p. 10) speculated that the reason most dens were reported in tundra habitats [alpine and subalpine should be included here] was an artifact of where researchers searched for dens. The first detailed published account of a den site in lowland boreal forest in North America (or perhaps anywhere) was Dawson et al. (2010) for a den in Ontario, Canada [other than the mention of an unusual den in an

abandoned beaver lodge in Alaska reported by Rausch and Pearson (1972) that could have been in a lowland forested area]. The Ontario den was located in snow-covered boulders, and kits were later moved under a snow-covered fallen tree nearby and to another site in a dense stand of trees. Snow depth at these sites was not measured, however, snow depth was likely <1m at the time the den was established because snow depth in Red Lake, Ontario (the nearest weather station; located 40 miles SW of the den site) was 59 cm on 23 March 2004, the day the lactating female was captured. This was the deepest snow measured at this station during the denning season (February–April; Attachments D–F). Snow depth had fallen to 37 cm on 1 April, 19 cm on 8 April, and only 4 cm on 18 April, the last day with measurable snow at the Red Lake weather station (Environment Canada National Climate Data and Information Archive (Attachment F), except for a snowstorm on 12 May that produced 7 cm of ephemeral snow that disappeared by 16 May. Snow depths were similar in other areas of the region, with maximum snow depth during February–April at the Pickle Lake weather station 120 miles ENE of the den site measured at 69 cm (Attachments G–I). As mentioned above, wolverine dens sometimes occur under <1m of snow, with Pulliainen (1968) reporting a den with 3 kits in March in Finland that was located beneath 70–80 cm of snow (Den No. 20, p. 340).

Copeland et al. (2010) stated that this Ontario den "and all other dens that occurred outside the spring snow coverage [i.e., the 15 May MODIS snow cover] were located at sites containing adequate snow cover for establishing a reproductive den" (p. 242). To explain the position of the Ontario den outside the "spring snow coverage," Copeland et al. (2010) concluded that "there may be areas classified as snow-free at the southern extent of the spring snow coverage (at 500-m resolution) that contain enough drifted snow for reproductive dens" (p. 242). However, the Ontario den was not in drifted snow (A. Magoun, personal observation; Attachment J) but rather in a large pile of snow-covered boulders, and subsequently the kits were moved to a site under a snow-covered fallen tree (Dawson et al. 2010). This reproductive female was not an outlier in the region. At least 3 other resident female wolverines were captured in the Ontario study where this den site was found (Dawson et al. 2010), none of which had home ranges within the "spring snow coverage" (Neil Dawson, Ontario Ministry of Natural Resources,

unpublished data) and another lactating female was photographed in March in the area after the study was completed (Kim Austen, Ontario Ministry of Natural Resources, personal communication). Therefore, a resident breeding population of wolverines occurred in this region of Ontario and denned outside of the "spring snow coverage." Clearly, there was no deep snow persisting until 15 May in the area where these females lived (if deep is defined as ≥1m; e.g., Magoun and Copeland 1998, Pulliainen 1968).

Why then was 15 May MODIS data selected as the basis for determining the "spring snow coverage" that is necessary for wolverine denning? Copeland et al. (2010) did not offer an ecological explanation for the choice of 15 May but stated:

> "A portion of each daily MODIS image was typically obscured by clouds or, occasionally, by night. Generating cloud- and night-free images required compositing 21 consecutive daily images from 24 April to 15 May, which generally corresponds to the period of wolverine den abandonment (Magoun and Copeland 1998) and is consistent with the time period used by Aubry et al. (2007) to correlate historical occurrence records with spring snow cover." (p. 235) [see also Attachment C].

Is 15 May a realistic date for designating *obligate* snow cover for wolverine distribution and dens? Although wolverines use snow dens in May in many areas of their distribution, one cannot conclude that they *must* have snow for dens in May, and certainly there need not be "persistent spring snow" as measured by 15 May MODIS because, as stated above, wolverines live and den outside this spring snow coverage (also, see Section 1c below). Spring snowmelt and den abandonment is variable, with wolverines having some flexibility in when they abandon dens. Spring snowmelt and abandonment of snow dens has occurred by the end of April in as varied habitats as northwestern Alaska (Magoun 1985), Siberia (Zyranov 1989), Idaho (Magoun and Copeland 1998), and certainly in Ontario where snow had disappeared by the end of April at the Red Lake weather station (Attachment F). At high elevation and at high latitudes, wolverines may keep kits at snow dens into May (at least at maternal dens; Magoun and Copeland 1998) if spring snowmelt is relatively late [e.g., under a remnant snowdrift to 9 May in northwestern Alaska; Magoun and Copeland (2010); Table 1, p. 1315]. Use of snow dens into May, and especially to 15 May, is clearly not *obligatory*, especially where boulders, blowdown, and avalanche debris provide alternate sites for protecting kits.

Copeland et al. (2010) recognized that the range of wolverines extends "slightly beyond the spring snow coverage, particularly in areas with low topographic relief" (p. 239) and stated that "their presence outside the spring snow coverage probably reflects accelerated spring snow melt characteristic[s] of a topographically flat landscape." However, these observations offer no explanation of how the "extralimital" wolverines fit into the theory of a bioclimatic envelope that requires "spring snow coverage" to 15 May, or how wolverines biologically exist outside the bioclimatic envelope. Rather, the authors concluded that "the spring snow coverage should be viewed as an approximation of underlying bioclimatic requirements" (p. 244). They also concluded there is a "strong concordance of wolverine den sites with the spring snow coverage" and likely "an *obligatory relationship* with snow cover for reproductive dens" (p. 244, italics mine). Yet, the question is not whether wolverines require snow cover for reproductive dens, but how much snow cover, in what form, and f*or what portion of the denning season*. Given that wolverines sometimes abandon dens before the end of April, the best scientific data indicate that use of snow-covered dens at the *end* of the denning season is *optional* rather than *obligate*.

Copeland et al. (2010) stated that, for their sample of dens in North America, "most dens (45/65; 69%) were located in areas that were snow-covered for 6–7 years" of the 7 years in their dataset (p. 239). Viewed from a different perspective, this means that the locations of many dens, nearly one-third (20/65; 31%), were either in areas that were snow-covered in only 1–5 years out of 7 in 2000–2006 or in areas not snow-covered in any of the 7 years. In fact, as noted by the authors themselves (p. 239), most dens were not actually located in the years used for the MODIS analyses. Twelve dens were located outside the "spring snow coverage" (i.e., "occurred in areas where snow cover was insufficient to classify the 500 m X 500 m area as persistently snow-covered through 15 May") (p. 239). When positing a bioclimatic envelope for wolverines that is based on "an obligatory relationship with snow cover for reproductive dens", and this relationship is defined as the "spring snow coverage" map (Figs, 2, 3, and 8 in Copeland et al. 2010), the best test of an *obligatory relationship* would be to look for evidence of dens that do not adhere to the criteria for this relationship. Reasons provided for why 12 dens fell outside the "spring snow coverage" included the explanation that a subpopulation in Sweden had

"recently colonized lowland forests, but the viability of this population is unknown" (p. 240) and that populations in Alberta, Saskatchewan, and Manitoba in Canada are "at the southern extent of the spring snow coverage" and populations in Ontario and Finland are at the "extreme southern extent of current wolverine range" in these regions (p. 242). In other words, dens in areas where wolverines were recently established or occurred at the southern extent of their range were excluded from the bioclimatic envelope but no biological reasons were given for this exclusion. Nevertheless, large areas of lowland boreal forest in North America are occupied by wolverines outside the "spring snow coverage" (see Section 1c below).

An explanation for why 15 May worked reasonably well for the analysis of wolverine habitat requirements in Copeland et al. (2010) rests at least in part on den locations used in the analysis that were skewed toward dens located in mountain habitats, with 87% from Norway and Sweden alone. Other den sites in mountains were from British Columbia and the Rocky Mountains in the western United States. Therefore, it is not surprising that 97.9% of 562 dens were located in areas that were snow-covered until 15 May (i.e., in the "spring snow coverage"). By using 15 May as the target date for the "spring snow coverage", it is much more likely that mountain dens will fall within the "spring snow coverage," while low elevation dens in the southern boreal forests will fall outside the "spring snow coverage" due to the lower winter snow depth and earlier spring melt that occurs in the boreal compared to mountain regions. For example, see Attachment K for a comparison of temperature and snow depth data in April 2004 (the year the Ontario wolverine den was located) for Red Lake, Ontario and Banner Summit, Idaho; Banner Summit was the nearest SNOTEL station to a wolverine den found in the Idaho study area referred to in Magoun and Copeland (1998).

The large percentage of dens located in the "spring snow coverage" in Copeland et al. (2010), mainly in mountain and tundra habitats (i.e., high elevation or high latitude), is an artifact of where most dens have been found to date and bias of research toward mountain habitats within wolverine range. The location of these dens does not constitute a scientific argument for an *obligatory* relationship of wolverine dens to snow cover through 15 May. In fact, it speaks to criticisms of correlative approaches to bioclimatic models mentioned by Copeland et al. (2010, p. 234), i.e., that bioclimatic models may

"fail to account for interactions with biotic factors" and "may not accurately reflect the ecology, behavior, or physiology of the target species." Researchers need to take a closer look at the bioclimatic niche of the wolverine and obtain better information on the ecology, behavior, and physiology of wolverines to understand the habitat requirements of wolverines at the global scale of the bioclimatic envelope. A theory of an obligatory relationship between wolverine dens and snow cover must apply to all wolverine dens, or the relationship simply cannot be considered obligatory.

1b. *Snow Patches and Thermal Cover*

Without knowing the extent, distribution, and quality of snow patches near the end of the denning season, it may not be possible to delineate wolverine habitat using remotely-sensed snow metrics, at least not at the scale of a wolverine den site. Wolverines continue to use snow for cover even after the end of the denning period and into the summer months in some regions (e.g., northwestern Alaska, Magoun 1985, p. 73, Attachment L; Montana, Inman et al. 2007, Ch. 4, p. 84, Photo 11). Snow cover in the form of remnant snowdrifts is thought to be important to wolverines for kit-rearing habitat and food storage (Magoun and Copeland 1998, p. 1318; Inman et al. 2012, J. Mamm.). The MODIS snow cover data used in Copeland et al. (2010) [MODIS/Terra snow cover daily L3 global 500m grid, Version 4, 24 April – 21 May 2000–2006, National Snow and Ice Data Center, Boulder, Colorado; Copeland et al. 2010, p. 234 and 245] does not take into consideration the presence of fractional snow (i.e., discontinous snow within the 500-m pixels), which later versions of the MODIS products incorporate (Salomonson and Appel 2004; Painter et al. 2009; Raleigh et al. 2013). Even with versions that measure fractional snow, MODIS is unreliable in detecting snow cover if it covers <20% of a pixel (i.e., up to 12 acres of the pixel could be covered in snow and the pixel could be classified as bare ground) (Dorothy Hall, NASA Goddard Space Flight Center, Greenbelt, Maryland, personal communication; Attachment M).

The existence, size, distribution, and longevity of remnant snow patches in mountain habitats in the western states may be key to the way wolverines adapt to climate warming in the region. Remnant snow patches were used by wolverines as maternal dens and rendezvous sites on the tundra of northwestern Alaska from late April

to at least the end of June (Magoun 1985, p. 73) and were one of the few structures available in the home ranges of some females to protect kits (personal observation). Snow patches (remnant snowdrifts and snow beds) are much more numerous and last much longer in mountain terrain in the western United States than in the tundra environment of northwestern Alaska (A. Magoun, personal observation, Attachment N). In an experiment on melt patterns of snowdrifts in arctic Alaska and alpine Colorado, arctic drifts in Alaska melted out over 1.5 months before the alpine drifts in Colorado, despite identical drift size and nearly identical snow water equivalent, "a consequence of the different solar insolation regimes in the two regions. In a growing season of only about 90–100 days, this is a major difference indicating that increased snowfall could have more significant ecosystem consequences in the alpine than in the Arctic" (Walker et al. 1999, p. 2327-2328). In the context of wolverine habitat, alpine areas that have increased snowfall (as projected for some mountain habitat in the western states with climate warming; McKelvey et al. 2011, p. 2887) could even see positive benefits in the foreseeable future for wolverines, especially if deeper snow produces snow patches that linger in the mountains for longer periods.

There may be a number of reasons why snow patches may be beneficial for wolverines (Inman et al. 2012, J. Mamm., entire) but, at the *end* of the denning period, thermal cover would not be one of them. The need for snow as thermal cover (Magoun and Copeland 1998, p. 1318) would only apply during the coldest part of the denning period, when kits are small and not thickly furred (Attachment O). Pulliainen (1968) wrote "hunters reported that the female may leave the cubs alone in the den for a day or two. Thus the cubs must be well protected against cold. Besides the snow cover, the very dense pelage and huddling behaviour of the cubs form a good protection" (p. 342). Just after parturition, reproductive female wolverines remain in the dens with their kits for an average of 5.7 days; range 2–11 days (Jens Persson, unpublished data based on GPS collars) and a reproductive female with a GPS collar in Montana remained in her den for 10 days (Bob Inman, unpublished data). When the mother leaves the den, kits huddle together (Dale Pedersen, personal observation), presumably because of the energetic advantages of huddling (Marchand 1996, p. 101). Under most snow conditions, the "hiemal threshold" [i.e., "snow cover thickness at which the subnivean environment is

insulated from diel fluctuations of the ambient temperature" (Pruitt 1957, Pruitt 1970 as cited in Aitchison 2001, p. 229)] is generally reached when snow depth is ~20 cm (Aitchison 2001, p. 230), and even under the densest snow (i.e., snow with less insulative properties), the "hiemal threshold" is reached by 50 cm (Marchand 1996, p. 22).

The advantage of snow cover on thermoregulation is greatest in areas with very cold temperatures. Subnivean temperatures generally vary between 0°C and –10°C, depending on snow depth and density, but in hard tundra snow conditions, the subnivean temperature may drop to less than –20°C (Aitchison 2001, p. 230). These temperatures do not consider presence of 2 or 3 wolverine kits in a snow den, which would warm the den space to some degree (A. Magoun, personal observation from tests with a 30-kg dog in a snow den at -25°F air temperature; snow den temperature +10°F). Intranivean temperatures (i.e., within the snow column where some wolverine dens occur) are usually colder than subnivean temperatures. For example, where an extreme subnivean temperature of –18°C was recorded under at least 20 cm of snow in Siberia, intranivean temperature was –26°C while the ambient temperature was –48°C. However, in a warm maritime climate, the intranivean temperature may not be so different from the subnivean or ambient temperature (Aitchison 2001, p. 230).

In conclusion, there is no biological reason that kits need thermal cover once air temperatures are warming above freezing (or even approaching the freezing point). Snow cover in the form of remnant snow patches may still be useful for protection from wind or predators and are used by wolverines after the denning period and into summer (Magoun 1985; p. 73, Attachment L). Remnant snowdrifts are likely to be most critical for thermal cover in tundra habitats, where very cold temperatures can occur even in May (e.g., *minus* 30°F; personal observation), and where, for some reproductive female home ranges, few other structures such as boulders might be available for protection from predators (e.g., Attachment P). Before we can adequately define wolverine habitat in mountain habitats, more information is needed on wolverine use of snow patches and the effects of climate warming on decreasing or increasing the availability of snow patches at the end of the denning season.

1c. *Wolverines Distribution Outside the Spring Snow Coverage*

Despite lack of descriptions of wolverine dens in lowland boreal forest (Magoun and Copeland 1998), there is ample evidence that wolverines occupy and reproduce in areas outside the 15 May MODIS "spring snow coverage," especially where wolverines occur in lowland boreal forest:

*Alberta*

In a report on wolverine harvest in Alberta from 1985–2011, the distribution of female wolverines (based on harvested individuals) is mapped relative to the "spring snow coverage" (Webb et al. 2013, Fig. 6, p. 21). From this map, it is apparent that female wolverines are distributed largely throughout the Boreal Forest regions of northern Alberta (Attachment Q). In this report, the authors stated

> "the snow cover map indicates more consistent spring snowpack in the Rocky Mountains and a patchy distribution, with large areas devoid of spring snow cover, throughout most of northern Alberta (north of 56 degrees latitude; Figure 6). And yet, we have evidence of fairly consistent long term wolverine harvest from many areas that appear to lack large areas of spring snow cover (WMU 524, 527, 530, 541; Figure 6; Appendix 1)."

The authors also stated

> "we were surprised to find that large areas of the Boreal Forest lacked persistent spring snow cover, yet had consistent wolverine harvests through time (1985-2011). Studies have suggested that wolverines have an obligate need for persistent spring snowpack which is linked to successful denning recruitment (Copeland et al. 2010). Exploring other metrics, such as distance to the nearest spring snow cover, would help in determining whether wolverines tend to occur closer to places with spring snowpack."

In an email on 13 February 2013 (Attachment R), the lead author of the report wrote that lactating and pregnant females have been documented outside the spring snow cover.

*Saskatchewan*

The locations of female wolverines harvested in Saskatchewan has not been documented, but I reviewed the locations of harvested wolverines (by Fur Harvest Block), both sexes combined, from 1999-2000 to 2011-2012 and constructed a map of wolverine distribution based on trapper harvest for this period (Attachment S, Map A; Map A and harvest database provided by Saskatchewan Ministry of Environment, Fish

and Wildlife Branch, Saskatoon). I drew the approximate southern edge (dashed line) of contiguous Fur Conservation Blocks that contained harvested wolverines during the 13-year sampling period on the "spring snow coverage map" from Copeland et al. (2010) (Attachment S, Map B). The southern edge of contiguous Fur Conservation Blocks with harvested wolverines occurred at least 100 km south of the "snow cover layer," with >50 wolverines harvested outside the "spring snow coverage" during the 13-year period. Some wolverines were harvested even south of the dashed line on Map A. Most of the "spring snow cover" in Saskatchewan comprised areas with "spring snow cover" in ≤3 years out of 7 (Map B provided by Neil Dawson, Ontario Ministry of Natural Resources).

*Manitoba*

Wolverine harvest from Manitoba from 2000-2001 through 2011-2012 ranged from 24 to 72 per season. Most have been taken in the area above the dashed line in Attachment T, which includes area outside the "spring snow coverage" of Copeland et al. (2010). For example, the wolverine harvest from the Snow Lake trapping area averaged 6–8 wolverines annually (Attachment T). Some wolverines are also taken south of the dashed line, well outside the "spring snow coverage," including at least one female in 2012-2013 that was taken in southern Manitoba outside the species' current range in that province (Dean Berezanski, Manitoba Conservation and Water Stewardship, personal communication). The trapping area with the highest annual harvest (Pikwitonei) occurs at the southern edge of the "spring snow coverage" in an area where snow lasted until 15 May in only 1 year out of 7 analyzed by Copeland et al. (2010). Most of

*Ontario*

Wolverines appear to be expanding their range in Ontario, with detections during aerial track surveys becoming more common in the Hudson Bay Ecozone since 2004, coincident with expansion of the range of woodland caribou in this ecozone (Ontario Wolverine Recovery Team 2011; Ray et al. 2011). Aerial surveys for wolverine tracks since 2004 also indicate that wolverines may be more common now in areas that were considered peripheral habitat in 2004 (Attachment U). While some of the apparent wolverine range expansion is occurring within the "spring snow coverage," wolverines are also expanding outside the "spring snow coverage." Within the Copeland et al. (2010) snow cover layer in Attachment U, the majority of wolverine track detections are from

areas that had 15 May MODIS snow cover for ≤2 years. [Note that the density of detection locations in Attachment U is influenced by the number of aerial track surveys carried out in different portions of wolverine range in Ontario and do not represent relative densities of wolverines]. The core wolverine habitat in the western portion of Ontario near the Manitoba border extends south to about 51° N, outside the snow cover layer and somewhat south of where the den site was located in Ontario in 2004. Below this latitude, significant anthropogenic changes to landscapes and ecoystems have occurred and may limit wolverine distribution further south (Bowman et al. 2010, entire).

*Sweden*

In recent years wolverines have been expanding their range into the forested areas of southern Sweden and reproduction is occurring there (Persson and Brøseth 2011, Figs. 1a-e; Aronsson and Persson 2012, entire). Copeland et al. (2010) explained the occurrence of an "extralimital den" in Sweden as one "believed to be associated with a subpopulation that recently colonized lowland forests, but the viability of this population is unknown" (p. 240). Copeland et al. (2010) did not have the most up-to-date information on this range expansion in Sweden at the time their paper was published. In a 25 March 2013 email (Attachment V), Malin Aronsson, referring to the Aronsson and Persson (2012) paper, wrote:

> "we try to [summarize] the information we have about wolverines in the "forest areas" outside of "traditional wolverine area[s]" (mountains and forest close to the mountains). Figure 2 shows the documented den sites (from the national inventory) with a 20 km buffer zone (blue). The red line is our definition of the limit for "traditional wolverine areas" based on land use, vegetation, the mountain range and reindeer herding practices. We classify the den sites found to the east of that line as being outside of traditional wolverine areas. Our red line matches "the snow model" [i.e., Copeland et al. 2010] pretty well in the southern half of the Swedish wolverine distribution and if you compare Copelands paper with the maps in the two reports you can see that [the] area [has] quite a few den sites outside of the snow model in [recent] years. The blue triangles in figure 3 shows the number of documented den sites east of our red line, most of these den sites are found [in] the southern half of the wolverine distribution and hence outside of the snow model. From 2008 and to today 12-15% of the den sites have been found east of the red line (10-18/year and it looks like a majority of those are outside of the snow model, in the area where it says "Sweden" in figure 4 in Copelands paper). But still a majority of the total den sites (90-110/year) are found inside the snow

> model. As for distances den sites are found from just outside the snow model to approximately 140 km outside of the snow model (rough estimates because I don´t have a GIS layer of the snow model)."

*Finland*

Copeland et al. (2010) document the locations of 8 wolverine dens outside the "spring snow coverage" in Finland and simply stated that the Finland dens "represent populations at the extreme southern extent of current range." No other information on snow depth at the dens or dates of den abandonment was provided. The authors add that the presence of the dens "outside the spring snow coverage probably reflects accelerated spring snow melt characteristic of a topographically flat landscape" (p. 242). However, one would expect that dens falling outside the "spring snow coverage" would most likely be found at the southern extent of the distribution of the species and in areas with accelerated spring snow melt. Such dens would provide the best test of the "spring snow coverage" model, and the bioclimatic envelope for wolverine, and therefore should not be dismissed when searching for biologically-meaningful explanations of wolverine distribution.

1d. *15 May MODIS Snow Model Compared to Other Models of Wolverine Occurrence*

The proposed listing determination does not adequately address alternative models for distribution and habitat requirements of wolverines, choosing instead to emphasize the simplistic snow cover model of Copeland et al. (2010) (p. 59). However, as stated by the authors, the 15 May MODIS "spring snow coverage should be viewed as an *approximation* of underlying bioclimatic requirements" for the wolverine (Copeland et al. 2010; p. 244) [italics mine]. This paper does not explain all known den site locations or distribution of wolverines across the species' global range. Furthermore, other models of wolverine habitat have not found the "15 May MODIS spring snow coverage" to be one of the "explanatory variables for reproductive den site selection and year-round habitat use" or that "the strong concordance of wolverine den sites with the spring snow coverage clearly reflects an obligatory relationship with snow cover [i.e., snow cover to 15 May for at least 1 year out of 7 from 2000-2006] for reproductive dens" (Copeland et al. 2010; p. 244). For example, the location of primary and maternal wolverine habitat in the western United States determined by Inman et al. (2013, Paper III, Fig. 2 ) using a

resource selection function (RSF) model is very similar to the 15 May MODIS snow cover in Copeland et al. (2010) (with the exception of the California Sierras and Oregon Cascades for maternal habitat), but the RSF model did not use snow cover on 15 May, but rather snow depth on 1 April, distance to snow, and other variables (e.g., latitude-adjusted elevation, ruggedness, forest edge, high-elevation talus, and human density) for predicting wolverine primary and reproductive habitat (Table 2).

In Scandinavia, Rauset et al. (2013, Paper IV) did not find that the "spring snow cover" of Copeland et al. (2010) was a strong predictor of the distribution and frequency of wolverine reproductions. In their study, Rauset et al. (2013) examined the following parameters: three continuous topographical raster maps (elevation, terrain ruggedness, and slope), one categorical vegetation raster, one raster representing a proxy for primary production (integrated normalized difference vegetation index, NDVI), a spring snow cover index raster (Copeland et al. 2010), one vector map of roads, and five binary maps representing human land use and management policies: country (Norway or Sweden), management zones (wolverine reproductions allowed or not), national parks, designated reindeer areas (semi-domesticated and wild reindeer), and calving grounds of semi-domesticated reindeer. Because elevation and the 15 May MODIS spring snow coverage are correlated environmental variables, they were modeled separately. The "spring snow coverage" was not among the variables that best predicted where wolverine reproductions occurred in Scandinavia, but elevation and NDVI were strong predictive variables (Rauset et al. 2013, Paper IV, Tables 1–3). Moreover, predictors of wolverine distribution and denning in Scandinavia were complex and interactive, and some were specific to the Scandinavian situation.

1e. *Defining Dens, Denning Period, and Period of Den Abandonment*

Central to acceptance of the Copeland et al. (2010) snow model and the subsequent use of the snow model in McKelvey et al. (2011) for predicting future wolverine habitat in the western states, one must accept that wolverine denning extends to 15 May and continuous snow cover is required until then in the western states. As stated above, Copeland et al. (2010) provided no definitive biological or ecological rationale for choosing 15 May or assuming obligatory "spring snow cover." Indeed, available empirical evidence related to the timing of wolverine denning and 15 May MODIS "spring snow cover" does not support an obligatory relationship. The analysis of birth dates for wolverines in the western United States and information about den abandonment over the global range of the wolverine (see Section 1a above) suggest flexibility in the timing of wolverine den abandonment, including dates in April (e.g., 23 April). However, there is some confusion over the definition of the "wolverine denning period" because few studies have documented parturition dates or dates of den abandonment. For example, Myrberget (1968) reported dens found by hunters from 7 March to 12 May in Norway, and Myrberget and Sørumgård (1979) stated no kits seem to be born as late as April. Pulliainen (1968) concluded young are born in February and March and leave the den in April and May, with the latest 14 May in the Finnish fells. Zyranov (1989) reported finding a wolverine den in Russia on 28 March beneath 1 m of snow with 3 kits no more than 4 weeks old. When he returned to the den on 23 April, the den was abandoned, most of the snow had melted, and there was standing water all around. On 26 April they relocated the kits under windthrown trees that were not under snow. Serebryakov (1983) reported finding wolverine dens on 14 April and as late as 17 May in the tundra of Siberia. Rauset et al. (2013) stated that the ground in their Scandinavia study area is usually snow-covered from October *until* May (Paper III, p. 5) and the denning period was January–May and *den abandonment* May–June (Paper III, p. 6). Magoun and Copeland (1998) defined wolverine dens based on timing of parturition (natal dens), movement of kits to new locations (maternal dens), and age of kits to weaning (after which, the term rendezvous site was used instead of den). They defined the denning period as February–April (p. 1314) for dens located in northwestern Alaska and Idaho (p. 1314), although two maternal dens were abandoned as late as 9 May (Table 1). After maternal dens were abandoned, wolverines used rendezvous sites, which may or

may not have been under remnant snowdrifts (Magoun 1985, p. 73). Therefore, the definition of the "denning period" in the literature consulted by Magoun and Copeland (1998) depended not only on when kits were found in dens but also on whether authors discriminated between reproductive dens (natal or maternal) and rendezvous sites. Some of the reports of "dens" in May (or even April) in the early literature could have been rendezvous sites, but without knowing the date of den initiation or the age of the kits, it would not be possible to separate dens from rendezvous sites. Any place kits were found in snow, under trees, or in boulders or caves were referred to as dens before Magoun (1985; p. 73) began to differentiate between dens and rendezvous sites and Magoun and Copeland 1998 differentiated between natal and maternal dens.

Copeland et al. (2010) did not define a specific denning period, rather they stated that reproductive denning begins in early February to mid-March, post-weaning den abandonment occurs in late April and May (p. 2340), and the period 24 April–15 May "generally corresponds to the period of wolverine den abandonment" (p. 235). From the literature cited in the paragraph above, the reported period of den abandonment, regardless of the definition of a den, fell within the period 23 April–17 May on a global scale. These dates indicate flexibility of at least 23 days in the seasonal occurrence of den abandonment across the wolverine's range. The selection of 15 May for the "spring snow coverage" map in Copeland et al. (2010) falls near the end of this den abandonment period. As Copeland et al. (2010, p. 244) pointed out, "although 15 May represents the approximate end of denning, the actual date likely varies geographically. We made no attempt to fit the snow coverage to either the collected data or the heuristically derived range map, but recognize that slight shifts in the analysis period result in *significant* changes in the areal snow cover" [italics mine]. In other words, shifting the dates used for analysis of MODIS snow cover by small amounts in the den abandonment period has a significant effect on whether MODIS will classify a pixel as snow-covered or not, and consequently, on the strength of the correlation between areas with "persistent spring snow" and wolverine den locations.

The exact dates of snow den abandonment on a regional scale are probably determined by all of the following: wolverine birth dates; depth and density of snow; snow distribution; snow temperature at different depths at the time spring snowmelt

begins; range and duration of spring ambient temperatures (thawing degree days); structures within dens; and availability of alternate den sites in the latter part of the denning season that do not include snow. Together, these factors will determine how far into the spring months kits will use snow for dens and rendezvous sites, *whether or not this use is obligatory*.

There is no evidence that use of snow dens after April in the mountains of the western United States is obligatory. From the available data on known birth dates of wolverines in the western United States, wolverines give birth in February. For Idaho, estimated parturition dates were 16–23 February (n=3) (Magoun and Copeland 1998; Table 1); and also for Idaho 16–23 February (n=3) (Heinemeyer et al. 2010, p. 16-17). Copeland and Yates (2008) reported that wolverines in Glacier National Park occupied dens by late February (p. 7, no dates provided). For Greater Yellowstone, estimated latest possible parturition dates, excluding one based on tooth eruption, were 10–23 February (n=6) in Inman et al. (2007, Ch. 4, p. 69). Only one parturition date in March was reported in this study (8 March; Inman et al. 2007, Ch. 4, p. 69). However, this parturition date was based on tooth eruption pattern for a kit captured on 17 May (Bob Inman, personal communication; Attachment W) and this estimated date was recently revised and falls in the period 22 February–1 March, with the most likely date closer to 22 February than 1 March (Clint Long, information from hand-reared wolverines, personal communication, Attachment X). I could find evidence of only one possible birth occurring in March in the western states (Northern Cascades in Washington), but this date was an estimate based on Sirtrack satellite collar locations and the birth could have occurred from the end of February until sometime in the first week of March (Cathy Raley, USFS, personal communication).

In summary, the sample size of wolverine parturition dates for the western United States is still small and future investigations may reveal births in March, but the best scientific data at this time show births occurring largely, if not entirely, in February in the western states. The lack of verified birth dates after February 23 indicates that wolverine kits in the western states are likely to be at least 8–10 weeks old (and most at least 9 weeks old) by the end of April. Therefore, the use of a 15 May date for *obligatory* snow cover for denning wolverines in the western states is not supported by current scientific

data, even if we assume kits need snow cover to 9 weeks of age. Therefore, the use of a 15 May date for obligatory snow cover for denning wolverines in the western states is not supported by current scientific data. For analyzing effects of climate warming on wolverine denning habitat and distribution in general in the western United States, the best scientific data indicate that an assumption of an obligatory requirement for snow cover should not extend past 30 April, and could possibly be even earlier, based on data on birth dates and kit development.

2. Review of McKelvey et al. (2010):

As mentioned in the proposed listing determination (p. 59), McKelvey et al (2011) is considered "the best available science for projecting the future impacts of climate change on wolverine habitat" in the western United States in part because their analysis "used the habitat model developed by Copeland et al. (2010, entire) to relate projected climate changes to wolverine habitat." As argued above, however, the 15 May date used for developing the "spring snow coverage" in Copeland et al. (2010) and used subsequently by McKelvey et al. (2011) for developing climate change models [and by Schwartz et al. 2009 for analyzing dispersal habitat and connectivity] is not based on "the best available science." Despite the fact that McKelvey et al. (2011) is considered "the most sophisticated analysis regarding climate change effects to wolverines" (proposed listing determination, p. 50), the key assumption on which the analysis is based is in error and therefore invalidates the conclusions about the effect of climate warming on wolverine habitat in the western United States. Without further analysis using scientifically defensible information on denning requirements for wolverines in the western United States, McKelvey et al. (2011) cannot be considered "the best available science" for projecting the future impacts of climate change on wolverine habitat.

2a. *Projected Future Wolverine Habitat in the Western United States*

As stated in the proposed listing determination (p. 56), McKelvey et al. (2011) used two approaches to project the impacts of climate change on wolverine habitat in the western United States: 1) downscaling global climate models and 2) projecting the onset of spring snowmelt to occur 2 weeks earlier than it currently does. Both of these methods

were directly tied to the MODIS-derived "spring snow coverage" in Copeland et al. (2010), which has been shown to be problematic (see Section 1 above). In the first instance, the authors compared (cross-walked) the MODIS-based 15 May snow cover and a hydrologic model of snowpack that was based on an interpolation of historical temperature and precipitation data. This simply means that they found the best fit between their hydrologic model of snow depths and the "spring snow coverage" of Copeland et al. (2010) for 15 May. [The best fit occurred "when 1/16-degree pixels with average snow depth values >13 cm were considered snow covered and those with <13 cm were not" (p. 2887). The 13-cm cut-off may have been influenced by the fact that they chose snow depth on 1 May (not 15 May) "as the metric to match to MODIS-derived persistent spring snow cover" (p. 2885), presumably because temperature and precipitation used in the hydrologic model were input on the 1st of each month (McKelvey et al. 2011, p. 2885).]

McKelvey et al. (2011) took a more direct approach in the second method they used to model the effects of climate warming on wolverine habitat. McKelvey et al. (2011)'s first approach involved "localizing and downscaling GCMs, transforming temperature and precipitation data in snow cover through VIC [see cited references for details on methods], and cross-walking GCM-based snow depth to MODIS-based snow cover", with all the attendant errors that this approach necessarily involves and that were recognized by the authors (McKelvey et al. 2011, p. 2886). In part to avoid these errors and as a validation of their GCM analysis (see Methods, p. 2885-2886), the authors simply reanalyzed the MODIS snow cover data "based on persistent snow cover through 29 May rather than 15 May, thereby forcing spring snow melt two weeks earlier" (p. 2886). Unfortunately, McKelvey et al (2011) did not attempt to do the same analysis on different possible dates for the "den abandonment period" so we do not know how the GCMs might have looked under a 30 April MODIS analysis, for example, which would have been a more accurate estimate of the end of the wolverine denning period in the mountains of the western states (as examined in Section 1 above). However, one could take the same approach the authors used to model future climate when they projected the snow melt period 2 weeks earlier (i.e., 29 May). With this 29 May approach, McKelvey et al. (2011) determined that "spring snow cover in 29 May MODIS is most similar to

Ensemble 2085 projections (Table 2, compare Fig. 4A with Fig. 4 D)" (p. 2890). That is, the 29 May MODIS-projected snow cover is similar to that projected for the period 2070-2099 by the Ensemble 2085 GCM. By the same logic and using the more realistic date of 30 April as the end of the wolverine denning season in the western United States (see Section 1 above), one can project a more realistic future snow cover during the denning period in 2070-2099 by again projecting snow melt 2 weeks earlier, which would be 15 May. Because McKelvey et al. (2011) already presented the 15 May MODIS projection in Fig. 2A (p. 2887), the MODIS data need not be reanalyzed and it is therefore apparent that the "spring snow coverage" for 30 April ~2085 is the present-day spring snow coverage on 15 May.

2b. *Dispersal and Connectivity*

McKelvey et al. (2011) repeated the analyses of Schwartz et al. (2009) to investigate the effects of climate warming on wolverine dispersal and connectivity of wolverine habitat in the western states. The analysis by McKelvey et al. (2011) may have underestimated the area occupied by reproductive females. McKelvey et al. (2011, p. 2891) stated that "each point where a wolverine could originate requires a contiguous snow area larger than 15 X 15 km (225 $km^2$), which is the approximate home range size for female wolverines (Schwartz et al. 2009)". This statement indicates that the authors assumed that female wolverines only occupy home ranges that are 225-$km^2$ in size with continuous snow cover on 15 May (in at least 1 year out of 7; 2000-2006). They concluded that "the number of potential start locations [for dispersal] decreases from 558 in the Historical Reconstruction [present day] to 194 in Ensemble 2085 [under climate warming] and this decrease, in turn, leads to an order-of-magnitude reduction in the number of pairwise least-cost paths" [i.e., a large reduction in the number of corridors for dispersal]. However, Schwartz et al. (2009) stated that

> "we overlaid a 15 X 15 km grid of locations across the study area, eliminating those grid nodes that were not in areas characterized by spring snow to model corridors connecting spring snow areas large enough to support wolverine reproduction. This density of nodes was based on minimum female home range size (Banci 1994) and guaranteed that at least one grid node would occur in each snow-covered area large enough to support at least one resident female wolverine (Krebs et al. 2007)."

This appears to mean that each grid point used in the analysis of dispersal corridors fell within a MODIS pixel (500-m resolution; 0.25 $km^2$) that was classified as snow-covered in the 15 May MODIS snow cover map. If my interpretation is correct, for areas where snow melt had advanced far enough by 15 May to create patchy snow cover across the area (including areas that might have been entirely snow-covered in February–April), some grid nodes were eliminated that could have occurred in home ranges of reproductive females.

However, a more important point is that neither Schwartz et al. (2009) nor McKelvey et al. (2011) were claiming that wolverines need snow for dispersal, rather, the argument presented was that, with fewer areas capable of supporting female wolverines as a result of climate warming (i.e., habitat defined by snow cover on 15 May ~2085), wolverines in the future will have to disperse further to reach areas of wolverine habitat (as predicted by McKelvey et al. 2011 using present-day 29 May MODIS spring snow cover, Fig. 4D, p. 2889). In other words, in the future, wolverines will have to travel through areas that are classified as snow-covered on 15 May today but will not be classified as snow-covered on 15 May in the future [as measured by MODIS]. In the context of the climate models in McKelvey et al. (2011), the 15 May MODIS snow cover "acts as a surrogate for wolverine's within-home range movements and dispersals year-round" (Schwartz et al. 2009, p. 3230). In other words, Schwartz et al. (2009) and McKelvey et al. (2011) recognized that wolverine habitat is not just snow cover on 15 May but the underlying year-round landscape and ecology of areas that fall within the boundaries of the 15 May MODIS snow cover map. However, as I argued above, the best available science does not support a 15 May date for obligatory snow cover for wolverine denning and consequently for defining the area of year-round wolverine habitat. Regardless, it is undisputed that wolverines disperse outside the 15 May MODIS spring snow cover map, sometimes over long distances (Inman et al. 2009, entire; Packila et al. 2007, Ch. 7, Photo 5, p. 119), including females (Aubry et al. 2012, Fig. 5, p. 23).

Although the data on the timing, duration, and characteristics of dispersal in wolverines are still limited, the best available science indicates that dispersal (or initiation of dispersal) peaks in the period late January–early April but can occur over a much broader period (November–June, at least) (Inman et al. 2012, Fig. 2, p. 637). There have been few detailed accounts of wolverine behavior or habitat use during dispersal movements. However, the detailed movements of a male wolverine (M56) dispersing from Wyoming to Colorado, and documented by researchers in the Greater Yellowstone study (Inman et al. 2009, p. 22–25), illustrate the dispersal capabilities of the species (Attachment Y). This wolverine may have been making exploratory movements as early as March, when snow was widespread, because his signal was not heard after 13 March until he was located on 6 April (Mark Packila, personal communication). Between 6 April and 5 June, when he arrived in the Rocky Mountain National Park in Colorado, this wolverine traveled through atypical wolverine habitat, much of which was not snow-covered or even tree-covered during the time he was passing through, although at the time he initiated dispersal movements, snow cover would have been widespread. However, he did appear to select areas of topographic relief outside of snow-covered habitat (small isolated mountain ranges like Granite Mountains, Green Mountains, Shirley Mountains, and Elk Mountain; Mark Packila, unpublished data) when available (Attachment Z).

The point here is that wolverines will disperse through atypical habitat when necessary, but their movements may be influenced by landscape features with which they are familiar or which offer some sense of security. Consequently, in the western United States, one can logically expect wolverines to select for high elevation topography when dispersing, if this habitat is available, because they occupy mountain habitats in the western United States (Aubry et al. 2007, entire) and appear to select high elevation habitat there (Copeland et al. 2007, entire; Inman et al. 2013, Paper III, entire). Because the 15 May MODIS spring snow cover strongly correlates with elevation (or latitude-adjusted elevation) in the western states, a correlation of wolverine locations with 15 May MODIS snow cover is not surprising. Logically, this correlation would support the least-cost path analysis of gene flow in the Rocky Mountains used by Schwartz et al. (2009), but it does not prove a causal relationship between 15 May MODIS snow cover and wolverine gene flow and dispersal pathways. Schwartz et al. (2009) did not do similar analyses using any alternative variables that might explain wolverine habitat, dispersal corridors, or gene flow. For instance, the proposed wolverine habitat map in Copeland et al. (2010) and the one proposed by Inman et al. (2013, Paper III) are so similar that logic suggests that the least-cost path analysis used by Schwartz et al. (2009) with the 15 May MODIS snow cover would provide similar results using the habitat map of Inman et al. (2013, Paper III), which does not use 15 May MODIS snow cover but rather latitude-adjusted elevation, snow depth on 1 April, ruggedness, and other variables that may be strongly correlated with where snow cover is broadly distributed on 15 May in the mountains of the western states. In fact, the circuitscape analysis of wolverine habitat in Inman et al. (2013, Paper IV) better predicted the movement path of M56 than did the least-cost path analysis of Schwartz et al. (2009) (Attachment Y).

The problem with the Schwartz et al. (2009) analysis of dispersal corridors and gene flow is not with the use of the 15 May MODIS spring snow cover to examine gene flow, but with the assumption that the 15 May MODIS snow cover *defines* wolverine habitat and therefore can be used to support the proposed loss of habitat in the future due to climate warming (McKelvey et al. 2011). Copeland et al. (2010) acknowledges that the 15 May MODIS snow coverage should be viewed as an "*approximation of underlying bioclimatic requirements*" (p. 244). McKelvey et al. (2011) argued that the decline in the area of 15 May MODIS snow cover by ~2085 (based on the present day 29 May MODIS snow cover), and the least-cost path analysis that they did based on 29 May MODIS snow cover, can be interpreted to mean that there will be a loss in connectivity and greater genetic isolation by the end of the 21st century. However, this assumption fails to take into account that neither the 15 May MODIS snow cover nor the 29 May MODIS snow cover *defines* wolverine habitat or future wolverine habitat in the western states, but rather they are correlates of other variables that together define wolverine habitat year round (e.g., boulder scree, elevation, snow cover in February–April, avalanche debris, etc.) and there is no evidence that these variables will change *on a scale that will affect wolverine distribution and habitat use within the foreseeable future*. The majority of wolverine year-round habitat (>90%) in the area of the proposed listing occurs within U.S. Forest Service or National Park Service lands that are not subject to direct loss of wolverine habitat due to infrastructure development according to the proposed listing determination (p. 74 and p. 83). In addition, activities such as logging, road-building, and recreation on these lands can be managed by these agencies to mitigate detrimental effects on wolverines. Therefore, we can expect that ecosystems that support wolverines will remain relatively intact *for the foreseeable future* on these federal lands even under climate warming. In other words, because wolverines do not need snow as a prerequisite for dispersal movements, their movements through habitats where they currently occur should not be affected by a 2-week-earlier spring snow melt in ~2085. An earlier spring snow melt over the 21st century will not adversely affect wolverine movements through landscapes characterized by relatively high elevation, ruggedness, boulder scree, or many other habitat variables that together comprise wolverine habitat in mountain terrain (Inman et al. 2013, Rauset et al. 2013). References cited in the proposed determination

(p. 54) supporting the hypothesis that advances in tree line will have adverse effects on wolverine habitat in the western states in the foreseeable future are unconvincing (see comments on the proposed listing document). The only variables that will change current dispersal habitat to the point that wolverines will be impeded or stopped from dispersing occur on the lands that fall *outside* the federal lands mentioned above. Over the rest of this century, the growth of housing developments, industrial complexes, roads, traffic volumes, other infrastructure, etc. in the interstices of current or potential wolverine habitat in the western states, without regard for establishing wildlife dispersal corridors, is of much greater significance to isolation and loss of connectivity for the wolverine metapopulation in the western states than is the predicted climate warming effects on *snow cover on 15 May* in the mountains.

2c. *Limitations of the MODIS Data*

The limitations of MODIS-based snow cover models should be recognized and taken into consideration when evaluating the accuracy of snow model predictions. For example, McKelvey et al. (2011) recognized that there are issues with the scale at which the MODIS data can be applied:

> "in areas where snow is highly fragmented or limited to linear areas along ridgelines, the best fit [referring to "statistically fitting the MODIS snow coverage to VIC-derived snow depth" p. 2895] will produce larger pixels that are consistently classified as snow free. The excess (when compared to MODIS) snow cover in the Historical Construction [referring to "the optimal fit between snow depth and MODIS snow cover" p. 2885] in areas such as northern Washington and British Columbia, and the lack of snow in areas such as Idaho, is at least partially due to these scaling issues and is unavoidable" (p. 2896).

In addition, Version 4 of MODIS that was used to derive the spring snow cover map in Copeland et al. (2010) is considered problematic (Dorothy Hall, personal communication, Attachment M), however, this version may have been the only data set available at the time the lead authors analyzed global snow cover. Moreover, MODIS measures "snow cover" not "snow depth" and the 500-m resolution will not accommodate analyses of the distribution and size of snow patches that linger into the summer months in mountain and tundra habitats in wolverine range, unless methods for estimating fractional snow (Salomonson and Appel 2004, Painter et al. 2009) are used, although fractional snow models are not without problems (Raleigh et al. 2013). Version 4 of MODIS did not measure fractional snow. Measuring the size, distribution, and persistence of snow beds and incorporating this information into models of wolverine habitat is important for understanding how climate warming will impact wolverine habitat in the future.

Moreover, MODIS data will not differentiate between snow cover produced by late spring snowstorms (referred to as ephemeral snow on p. 25 in Copeland et al. 2010) and snow that has persisted throughout the entire denning period. Eliminating ephemeral snow in the "spring snow coverage" in the Copeland et al. (2010) analysis required a 21-day period over which MODIS was queried for pixels bare of snow. Consequently, the earlier the dates used for MODIS analyses, the more difficult it is to eliminate areas of ephemeral spring snow from regions that are not considered wolverine habitat (e.g., lower elevations in the Rocky Mountains and the northern prairies). A combination of methods used to detect snow cover, snow depth, snow beds, and spring snowstorms would be the most appropriate approach to measuring snow features important to wolverine habitat.

Finally, predictions of the effects of climate warming on wolverine habitat should also consider the possible beneficial effects in some areas of the wolverine's distribution. McKelvey et al. (2011, p. 2893) concluded that "given a warming trend, spring snow cover is expected to decline and snow-covered areas are expected to become more fragmented and isolated" but this statement derives from their analysis of spring snow cover on 15 May. If one considers that snow cover is important for denning wolverines during the period when temperatures are relatively cold and kits are relatively young (e.g., before 30 April or even earlier), then a warming trend that accelerates the spring

snow melt by only 2 weeks by ~2085 could actually have beneficial effects on wolverines, particularly if the same climate processes that cause earlier spring melting simultaneously increase early winter precipitation in the form of snow, i.e., in December/January/February (McKelvey et al. 2011, p. 2887). More snow earlier in the winter in the mountains may increase snow depths by the time denning is initiated, while an earlier onset of spring green-up will lengthen the period of primary production. In their analysis of factors affecting reproduction in female wolverines, Rauset et al. (2013, Paper II, entire) found that summer primary production as measured by NDVI positively influenced reproductive output of wolverines in Scandinavia. NDVI refers to the normalized difference vegetation index, which is a remotely-sensed measure of vegetation greenness (Pettorelli et al. 2005). “Increased primary production is assumed to positively influence the abundance of various small prey, and the limited information on summer diet in wolverines indicates that small prey constitute the major summer food items” (Rauset et al. (2013, Paper III, p. 15).

## SUMMARY AND CONCLUSIONS

Errors in defining wolverine habitat have significant repercussions for projections of future wolverine habitat in the western United States under climate warming. The proposed listing determination relies heavily on a few research studies as the "best available science" relative to wolverine habitat in the western states. As a consequence, I have focused my review in Attachment A on these particular studies: Aubry et al. (2007), Schwartz et al. (2009), Copeland et al. (2010), and McKelvey et al. (2011). In each of these studies, the assumption of obligate snow cover extending to 15 May [14 May in Aubry et al. 2007] was a critical component of the authors' conclusions regarding denning and year-round habitat for wolverines. Copeland et al. (2010) assumed that a suitable surrogate for where wolverine habitat occurs on a global scale is obligate snow cover on 15 May as determined by MODIS snow cover data. Even though the authors cautioned that the spring snow cover was an approximation of underlying bioclimatic requirements and that slight shifts in the analysis period could result in significant changes in areal snow cover, the 15 May MODIS snow cover was used to project future wolverine habitat under climate warming in McKelvey et al. (2011). However, the best available science does not support the assumption that the 15 May MODIS snow cover defines wolverine habitat for reasons detailed above in this Attachment. Consequently, conclusions regarding the effect of climate warming on future wolverine habitat in McKelvey et al. (2011) are invalid. The best available science indicates that snow cover as a requisite for wolverine denning in the western states is not obligatory after 30 April, possibly even earlier in April. Following the same approach as McKelvey et al. (2011, p. 2885–2886) to project future wolverine habitat in 2070–2099 (~2085) based on 29 May MODIS data and using a 30 April date for obligatory snow cover rather than a 15 May date, one must conclude that spring snow cover in ~2085 on 30 April will be similar to present-day 15 May snow coverage. Therefore, the projected loss of critical habitat for wolverines in the foreseeable future (i.e., over the 21st century) in the western United States is not supported by the science presented in the proposed listing determination.

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**From:** Grizzle, Betty
**To:** John Guinotte
**Subject:** Fwd: Attachment K
**Date:** Wednesday, April 19, 2017 10:03:29 AM
**Attachments:** Banner Summit_Idaho_Daily Temp_Apr 2004.pdf
Banner Summit_Idaho_Snow Depth_Apr 2004.pdf
Red Lake_Ontario_Daily Temp_April 2004.pdf
Red Lake_Ontario_Snow on Ground_April 2004.pdf

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---------- Forwarded message ----------
From: **A J** <222wsheridan@gmail.com>
Date: Tue, Apr 18, 2017 at 3:40 PM
Subject: Attachment K
To: "Grizzle, Betty" <betty_grizzle@fws.gov>

Files in attachment K
You should have them all now

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Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service
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Carlsbad, CA 92008
760-431-9440, ext. 215
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United States Department of Agriculture NRCS Natural Resources Conservation Service

National Water and Climate Center

**Idaho (PST) SNOTEL Site BANNER SUMMIT (312) (15E11S ) Daily series for month=2004-04-01**

2013-April-12 NRCS National Water and Climate Center - Provisional Data - subject to revision

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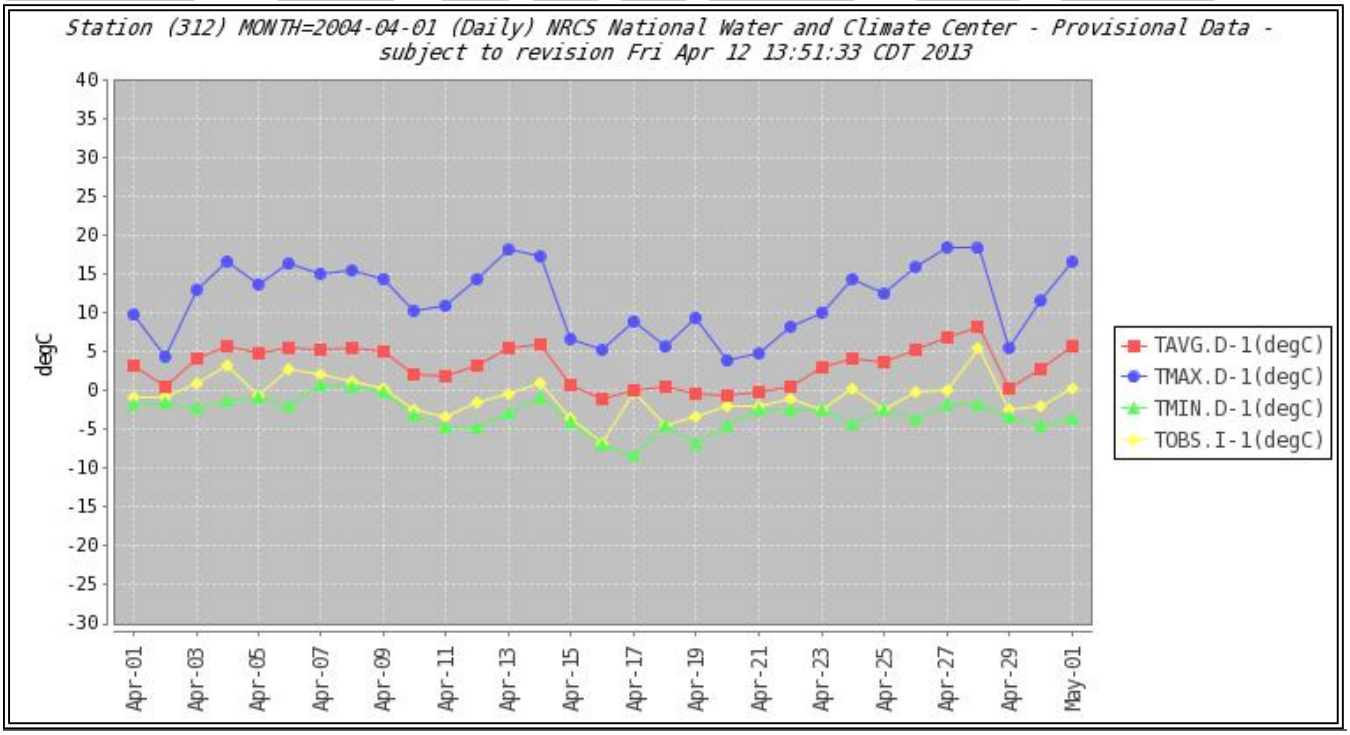


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2013-April-12 NRCS National Water and Climate Center - Provisional Data - subject to revision

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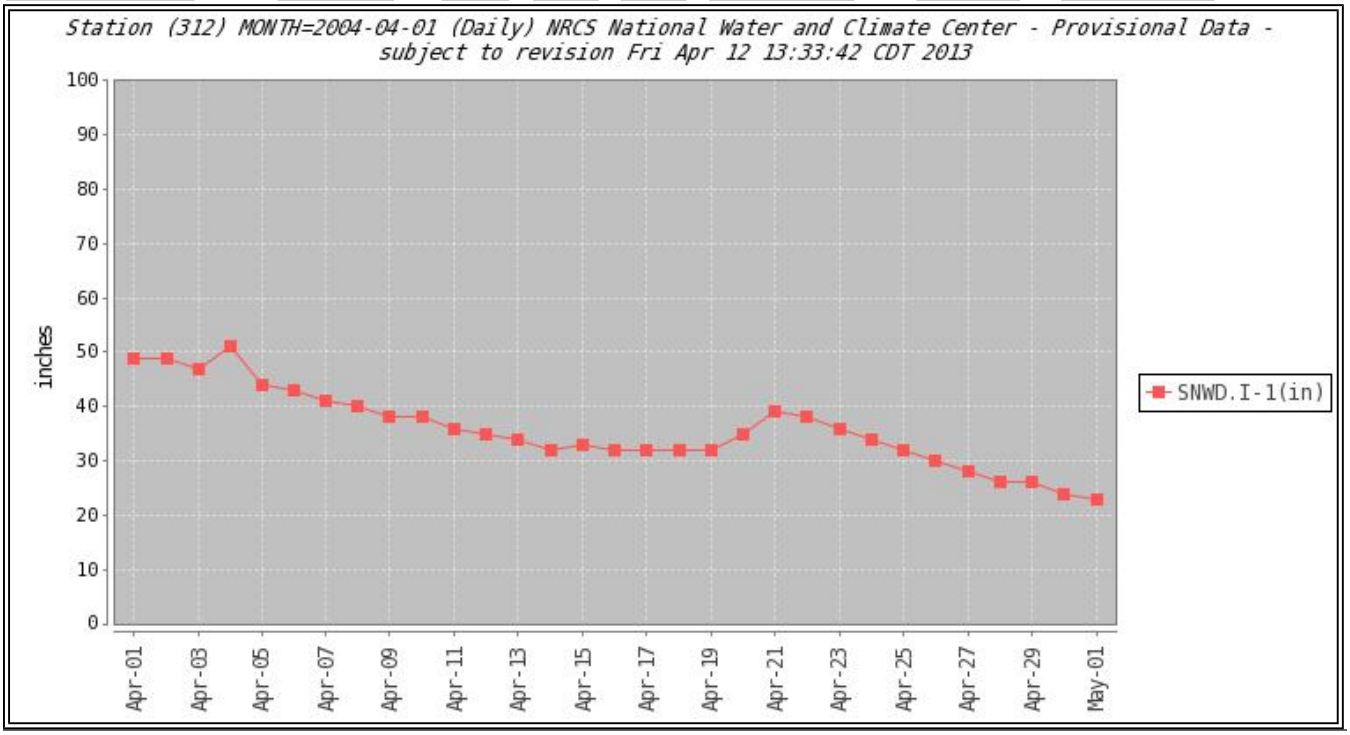


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Environment Canada Environnement Canada

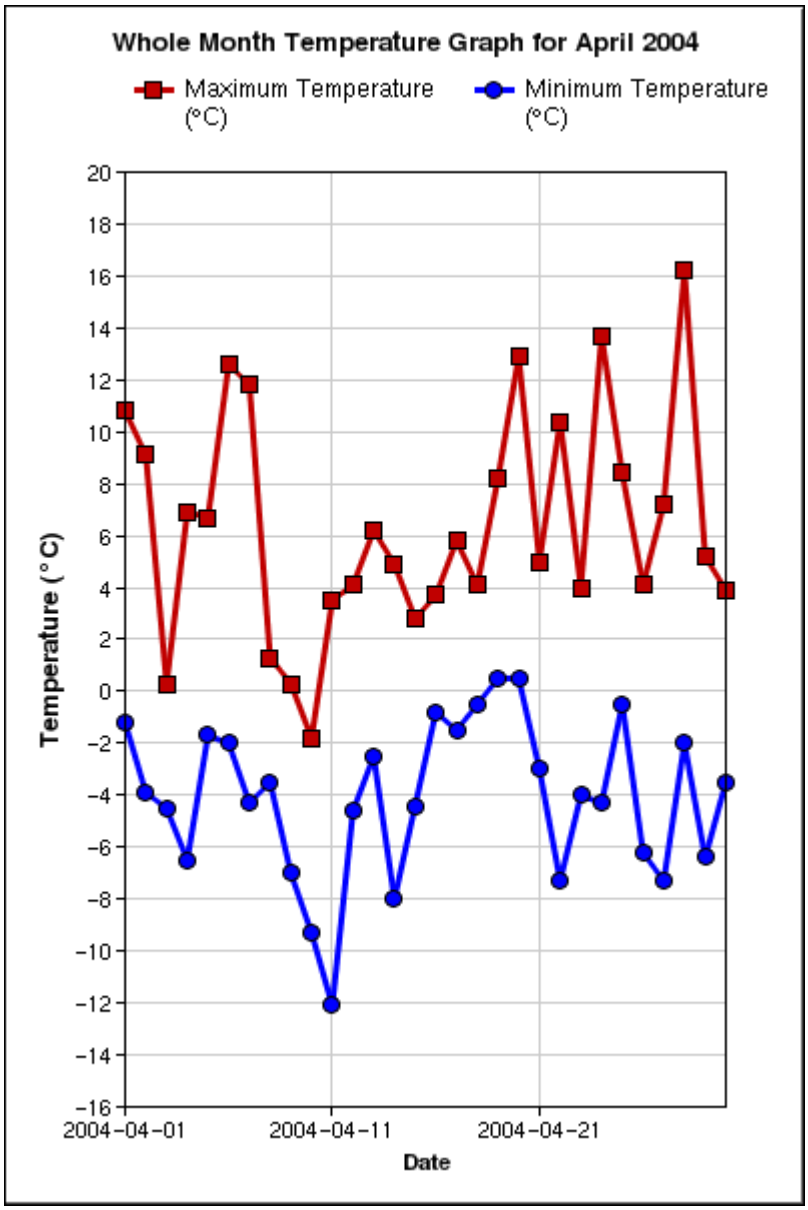
Canada

# Whole Month Temperature Graph for April 2004

RED LAKE A
ONTARIO

**Latitude**: 51°04'01.000" N **Longitude**: 93°47'35.000" W **Elevation**: 385.90 m

**Climate ID**: 6016975 **WMO ID**: 71854 **TC ID**: YRL




| Display Items |
|---|
| ☑ Maximum Temperature (°C) |
| ☑ Minimum Temperature (°C) |
| ☐ Extreme Maximum Temperature (°C) (1930-2012) |

- [ ] Extreme Minimum Temperature (°C) (1930-2012)
- [ ] Normal Maximum Temperature (°C)
- [ ] Normal Minimum Temperature (°C)

We'd like to hear from you! Please click "Contact Us" to share your comments and suggestions.

Date Modified: 2013-02-04

Environment Canada Environnement Canada

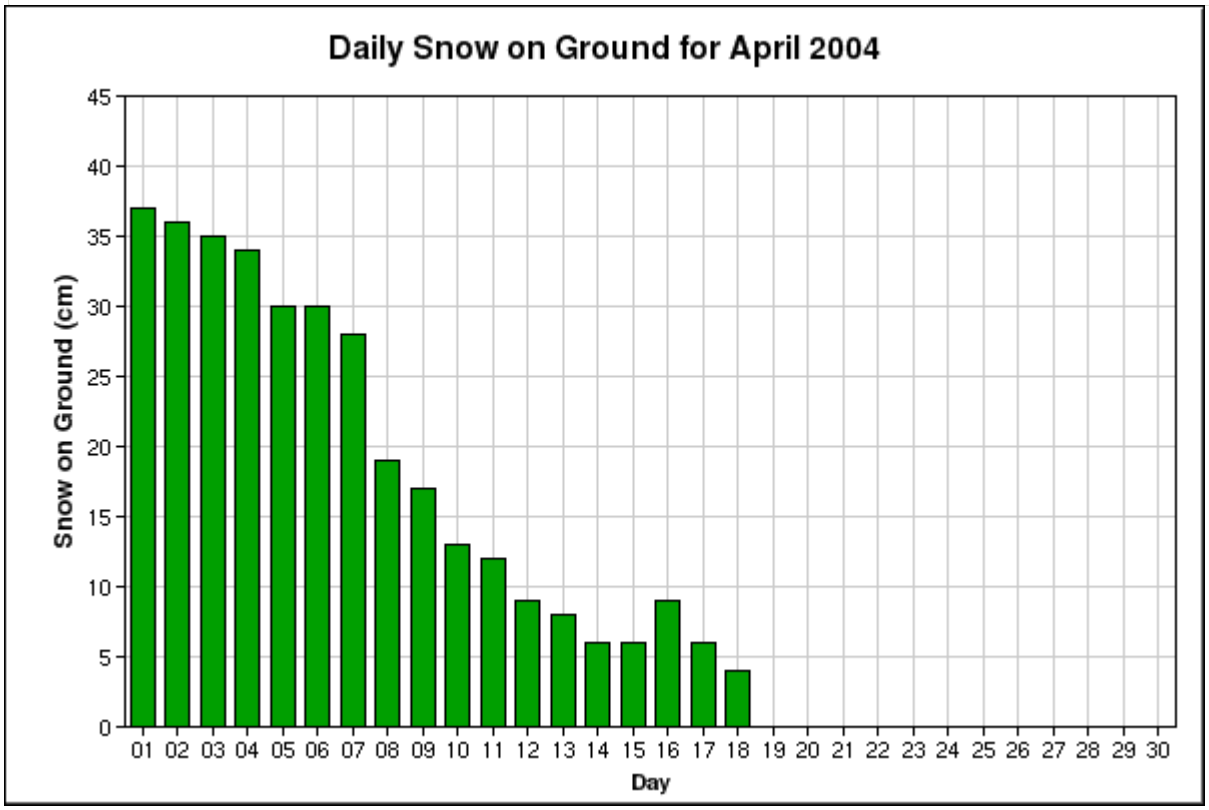
Canada

# Daily Snow on Ground for April 2004

RED LAKE A
ONTARIO

**Latitude**: 51°04'01.000" N **Longitude**: 93°47'35.000" W **Elevation**: 385.90 m

**Climate ID**: 6016975 **WMO ID**: 71854 **TC ID**: YRL

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| [empty] = No data available |
| M = Missing |
| E = Estimated |
| A = Accumulated |
| C = Precipitation occurred, amount uncertain |
| L = Precipitation may or may not have occurred |
| F = Accumulated and estimated |
| N = Temperature missing but known to be > 0 |
| Y = Temperature missing but known to be < 0 |
| S = More than one occurrence |
| T = Trace |
| * = The value displayed is based on incomplete data |
| † = Data for this day has undergone only preliminary quality checking |

We'd like to hear from you! Please click "Contact Us" to share your comments and suggestions.

Date Modified: 2013-02-04

**From:** Grizzle, Betty
**To:** John Guinotte
**Subject:** Fwd: Snow in Swedish denning site
**Date:** Wednesday, April 19, 2017 10:11:12 AM
**Attachments:** IMG_4711.JPG

---

---------- Forwarded message ----------
From: **A J** <222wsheridan@gmail.com>
Date: Tue, Apr 18, 2017 at 3:58 PM
Subject: Snow in Swedish denning site
To: betty_grizzle@fws.gov

Jens is standing just above an occupied wolverine den under boulders; note how little snow is on the ground and boulders; kits verified on camera; this is in Early March

Sent from my iPhone

--

Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

**From:** Grizzle, Betty
**To:** John Guinotte
**Subject:** Fwd: Mar 2 den
**Date:** Wednesday, April 19, 2017 10:11:44 AM
**Attachments:** IMG_4712.JPG

---

---------- Forwarded message ----------
From: **A J** <222wsheridan@gmail.com>
Date: Tue, Apr 18, 2017 at 3:57 PM
Subject: Mar 2 den
To: betty_grizzle@fws.gov

My husband in foreground is photographing the den entrance under the boulder in lower left

Sent from my iPhone

--

Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
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Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

**From:** Grizzle, Betty
**To:** John Guinotte
**Subject:** Fwd: original cover letter
**Date:** Wednesday, April 19, 2017 10:13:20 AM
**Attachments:** Cover Letter_Shawn Sartorius.pdf

---

---------- Forwarded message ----------
From: **A J** <222wsheridan@gmail.com>
Date: Tue, Apr 18, 2017 at 3:28 PM
Subject: original cover letter
To: "Grizzle, Betty" <betty_grizzle@fws.gov>

another file

--

Betty J. Grizzle, D.Env.
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U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

Shawn Sartorius
"WOLVERINE", U.S. Fish and Wildlife Service
585 Shepard Way, Suite 1
Helena, Montana 59601
30 April 2013

Dear Shawn:

I have completed my review of the proposed rules regarding the *Notice of the Proposed Listing of a Distinct Population Segment of the North American Wolverine Occurring in the Contiguous United States* and the *Establishment of a Nonessential Experimental Population of the North American Wolverine in Colorado, Wyoming, and New Mexico*. I made comments directly on the Word document for each rule and have included 26 attachments (Attachments A–Z) that supplement my comments on the Proposed Listing Rule. These documents are in a folder titled "Attachments." There is also a folder titled "Additional References" that contains 15 new references cited in Attachment A. Attachment A is a 30-page document that details reasons why I concluded that the determination to list the wolverine is not based on the best available science, so you may want to look at Attachment A first. A summary of this finding is on page 29 of Attachment A but I include it here so that you know beforehand what will be in this Attachment:

> Errors in defining wolverine habitat have significant repercussions for projections of future wolverine habitat in the western United States under climate warming. The proposed listing determination relies heavily on a few research studies as the "best available science" relative to wolverine habitat in the western states. As a consequence, I have focused my review in Attachment A on these particular studies: Aubry et al. (2007), Schwartz et al. (2009), Copeland et al. (2010), and McKelvey et al. (2011), particularly the latter two. In each of these studies, the assumption of obligate snow cover extending to 15 May [14 May in Aubry et al. 2007] was a critical component of the authors' conclusions regarding denning and year-round habitat for wolverines. Copeland et al. (2010) assumed that a suitable surrogate for where wolverine habitat occurs on a global scale is obligate snow cover on 15 May as determined by MODIS snow cover data. Even though the authors cautioned that the spring snow cover was an approximation of underlying bioclimatic requirements and that slight shifts in the analysis period could result in significant changes in areal snow cover, the 15 May MODIS snow cover was used to project future wolverine habitat under climate warming in McKelvey et al. (2011). However, the best available science does not support the assumption that the 15 May MODIS snow cover defines wolverine habitat for reasons detailed in Attachment A. Consequently, conclusions regarding the effect of climate warming on future wolverine habitat in McKelvey et al. (2011) are invalid. The best available science indicates that snow cover as a requisite for wolverine denning in the western states is not obligatory after 30 April, possibly even earlier in April. Following the same approach as McKelvey et al. (2011, p. 2885–2886) to project future wolverine habitat in 2070–2099 (~2085) based on 29 May MODIS data and using a 30 April date for obligatory snow cover rather than a 15 May date, one must conclude that spring snow cover in ~2085 on 30 April will be similar to present-day 15 May snow coverage. Therefore, the projected loss of critical habitat for wolverines in the foreseeable future (i.e., over the 21st century) in the western United States is not supported by the science presented in the proposed listing determination.

In addition, in my review I found 1) some inaccuracies in description and analysis of the biology, habitat, and historic distribution of the wolverine, as well as 2) some inaccuracies and inadequacies in the review and analysis of factors affecting the wolverine. I do not believe the conclusions reached are supported by the evidence that was provided and I found that, although literature was cited to support the assumptions, arguments, and conclusions, the literature was at times incorrectly cited and at times did not support the arguments being put forward. The specific places where this occurred are pointed out in the individual comments on the Word documents you provided.

I also found there was a lack of specificity for certain terms used in the document that led to uncertainty on my part on how to interpret what was being stated. I suggest specific definitions for terms that are used repeatedly throughout the documents such as deep persistent spring snow cover. I have pointed out where these terms occur in my review of the listing rule. These terms should be defined at the beginning of the document and used with quotes wherever you are referring to them in the document. Without specific definitions of terms, one does not know how to gauge the accuracy of the statement or how to test the stated fact either now or in the future. For example "spring snow cover" can be used either as a general reference to snow cover anytime in the spring or it could refer specifically to the "spring snow coverage" as defined by Copeland et al. 2010 or McKelvey et al. 2011.

Finally, my overall impression after a careful review of the proposed listing determination is that the document was intended as a justification for listing the wolverine rather than an unbiased scientific review of why the wolverine should be listed, and there is a difference. A review of the scientific basis for listing should be unbiased and thorough, and I feel that the proposed listing is weak on these two points. Biases in scientific reviews are often unintentional, even among scientists trained to avoid bias, so my intent is not to point fingers here but to suggest that any revision of the proposed listing determination should take special precautions to avoid bias in the scientific review process. A peer review of the scientific facts used to justify the listing should comprise *primarily* reviewers outside the community of researchers invested in wolverine research in the DPS (and that would include me) in order to avoid bias.

I thank you for the opportunity to review the listing proposal and 10j rule and will be happy to answer any questions regarding my review. I will be traveling over the next few weeks and may not have access to email so feel free to call if you have questions. I believe you have my cell phone number and my email is listed below. Please note that I am no longer with The Wolverine Foundation, Inc. so any mailings should be sent to me at the address below. Also, as requested, I have attached my current curriculum vitae.

Best regards,

Dr. Audrey J. Magoun
Wildlife Research and Management
3680 Non Road
Fairbanks, AK 99709
Email: amagoun@ptialaska.net

**From:** A J
**To:** Grizzle, Betty
**Subject:** Re: Makkonen thesis?
**Date:** Wednesday, April 19, 2017 5:23:18 PM

---

It is a relief to me to know that someone is even reading all that stuff, let alone is familiar with it (after spending every day for 3 months working on my review of the last status report and a week of sleepness nights trying to respond to Jeff and Kevin in those emails). If you have any references on niche modeling that you think I might be interested in, please forward.
All the best

On Wed, Apr 19, 2017 at 3:12 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

> Audrey - After reading through those email messages, I have to let you know about one very interesting coincidence. You cite the Araujo and Peterson 2012 paper at the end of the last email message. I had already cited that section of the paper in my current draft assessment. [I have dabbled a bit in niche modeling (i.e., using Maxent software program for predicting hantavirus distribution).]
> Betty
>
> On Wed, Apr 19, 2017 at 12:52 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
>
> > Thanks Audrey! I did get a short email reply back from Jens in March. He attached his 2016 paper, which I was already aware of, and the 2015 Rauset et al paper, which I was not aware of. I will reach out to him again; need to collect my thoughts and create logical questions, and I would like to digest the papers from Malin.
> >
> > On Wed, Apr 19, 2017 at 12:40 PM, A J <222wsheridan@gmail.com> wrote:
> >
> > > Here it is, Betty. By the way, I asked Jens Persson if he could estimate how many dens they have now found in southern Sweden that probably do not have snow after April (some even after March) and he said that the number is probably between 35 and 55. Have you heard from Jens? He has received a large grant to study the southern wolverine population. I would not be surprised if in a few years they have more dens located outside the snow model than all the dens found in the western states!! Hopefully he will be able to gather information on the survival of kits from these dens, but since the southern population apparently continues to expand, some of them must be surviving.
> > >
> > > On Wed, Apr 19, 2017 at 11:20 AM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> > >
> > > > Audrey - Do you have a copy of a thesis by T. Makkonen, University of Oulo, Finland? The title is "Den site characteristics of female wolverine (*Gulo gulo*) in Scandinavian forested landscape" dated 2015.
> > > > I have been unable to obtain this. It appears to have restricted access and is only available at the University.
> > > > Thanks.
> > > >
> > > > --
> > > >
> > > > Betty J. Grizzle, D.Env.
> > > > Fish and Wildlife Biologist
> > > > U.S. Fish and Wildlife Service
> > > > Carlsbad Fish and Wildlife Office
> > > > 2177 Salk Ave, Suite 250
> > > > Carlsbad, CA 92008
> > > > 760-431-9440, ext. 215

> > 760-431-5901 fax
>
> --
>
> Betty J. Grizzle, D.Env.
> Fish and Wildlife Biologist
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> Carlsbad, CA  92008
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--

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| | |
|---|---|
| **From:** | Joe Barsugli |
| **To:** | Guinotte, John; Kevin Doherty |
| **Cc:** | Andrea Ray |
| **Subject:** | Wolverine Climate Report: Figures Addendum 19APRIL2017 |
| **Date:** | Wednesday, April 19, 2017 7:51:13 PM |
| **Attachments:** | Wolverine Report Figures Addendum 19apr2017.docx |

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John, Kevin:

Please find attached the addendum for the FIGURES section. One missing figure has been added since the last installment, several figures have been relabeled for consistency, and the MODIS figures have been adjusted to include "2002" as the dry year for ROMO. Elevations of wolverine dens were added to the snow change vs. elevation figure for the DHSVM modeling. These changes are included in the latest version of the FIGURES that will be posted for the next distribution.

Yours,

Joe

--
Joseph Barsugli, Research Scientist III
CIRES, UCB216
University of Colorado Boulder
Boulder CO 80309
303-497-6042
PSD Science Board and
Attribution and Predictability Assessments Team Member

ADDENDUM: Added year 2002 to figure because it is the new representative dry year for ROMO due to DHSVM modeling issues. We kept 2012 because the MODIS analysis is not affected by the hydrologic modeling issue.

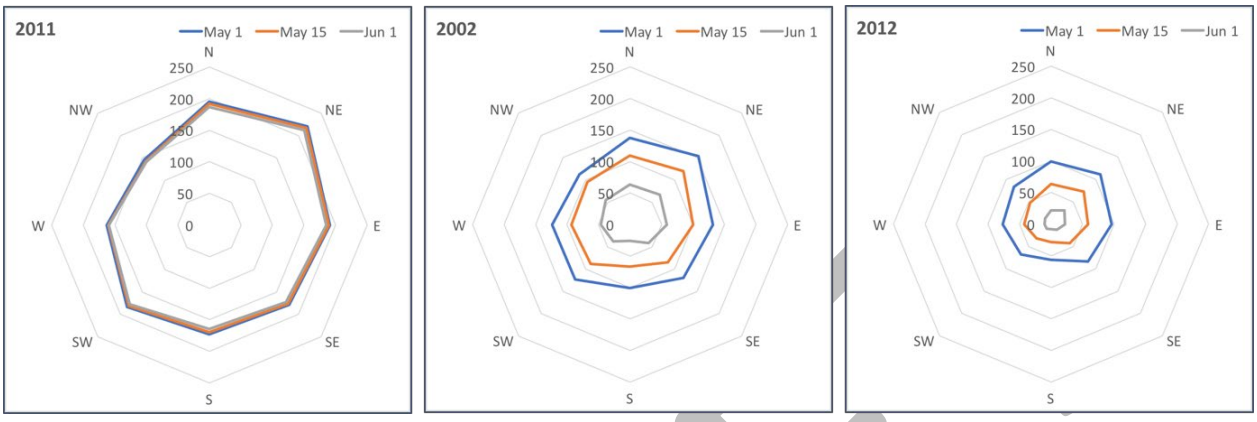


**Figure 4-15: Total snow covered area (km$^2$) as a function of aspect for "wet" (2011) and "dry" (2002) representative years for the ROMO study area.** For each year the snow covered area is shown for May 1 (blue), May 15 (red) , and June 1 (thick gray) Concentric octagons (thin gray) denote the magnitude scale ranging from 0 to 500 km$^2$. Note that while 2012 had the least snow cover in late Spring, 2002 was adopted as a representative dry year due to modeling considerations in Section 5. We show both dry years here which exhibit similar features.

DRAFT

ADDENDUM: Added year 2002 to figure because it is the new representative dry year for ROMO due to DHSVM modeling issues. We kept 2012 because the MODIS analysis is not affected by the hydrologic modeling issue.

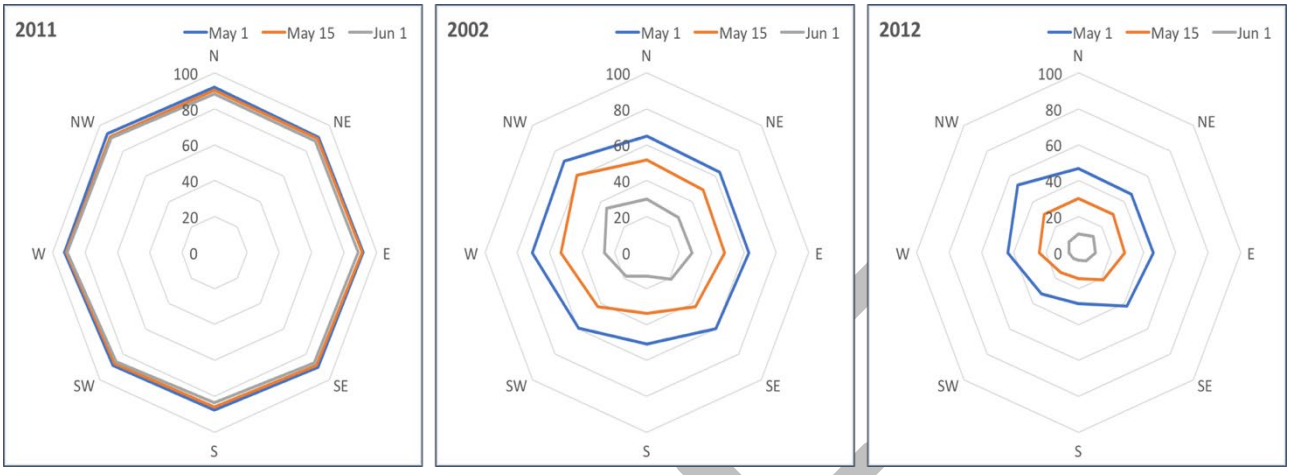


**Figure 4-17: Snow covered area fraction (%) as a function of aspect for 2011 ("wet") and 2002 ('dry") representative years in the ROMO study area.** May 1 (blue), May 15 (red), and June 1 (green) are shown for each year. The total snow covered area has been normalized by the total land area in each aspect octant. Concentric octagons (gray) denote the magnitude scale ranging from 0 to 100%. Note that while 2012 had the least snow cover in late Spring, 2002 was adopted as a representative dry year due to modeling considerations in Section 5. We show both dry years here which exhibit similar dependence of fractional snow cover on aspect.

DRAFT

ADDENDUM: Replaced 2012 with 2002. We did not keep 2012 because it would lead to too many lines on the graphic, but the structure, with the greater decline at high elevations is similar to 2012.

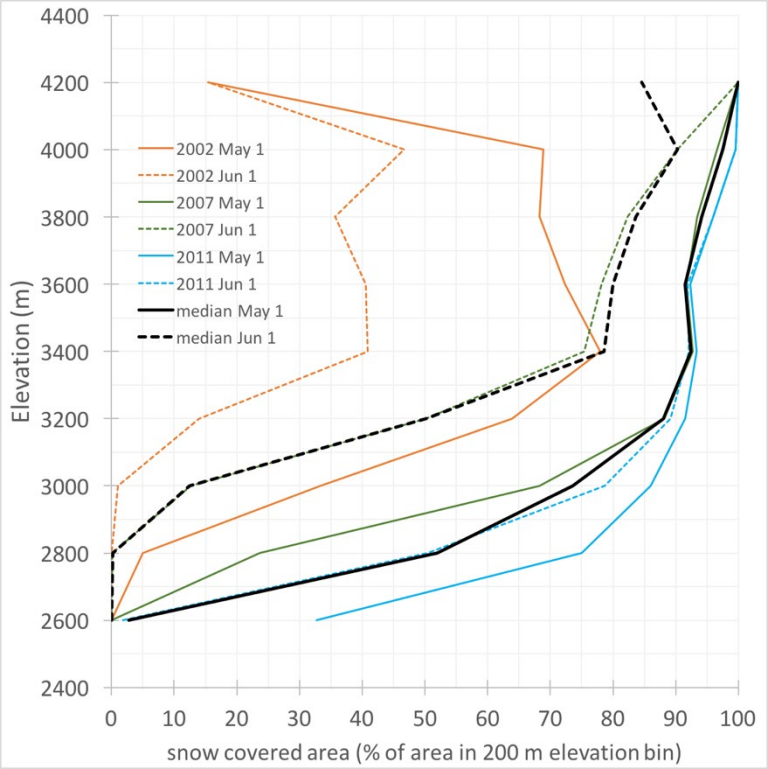


**Figure 4-18: Snow covered area fraction as a function of elevation for the ROMO study area for representative wet (2011; blue lines), near normal (2007; green lines), and dry years (2002; red lines).** MODIS pixels were classified into 200-meter elevation bands. Snow covered area is shown as the percentage of area within each elevation band with snow cover on May 1 and June 1. The median snow cover fraction for the given dates for the period 2000-2017 is shown in thick black lines. 2002 only is shown because it was ultimately used as a representative year in the scenarios analysis, not 2012. Note that 2012 also shows a decrease in snow covered area at the highest elevations.

DRAFT

ADDENDUM: Relabeled figure with “nicknames” for the scenarios rather than numbers. Caption has been expanded.

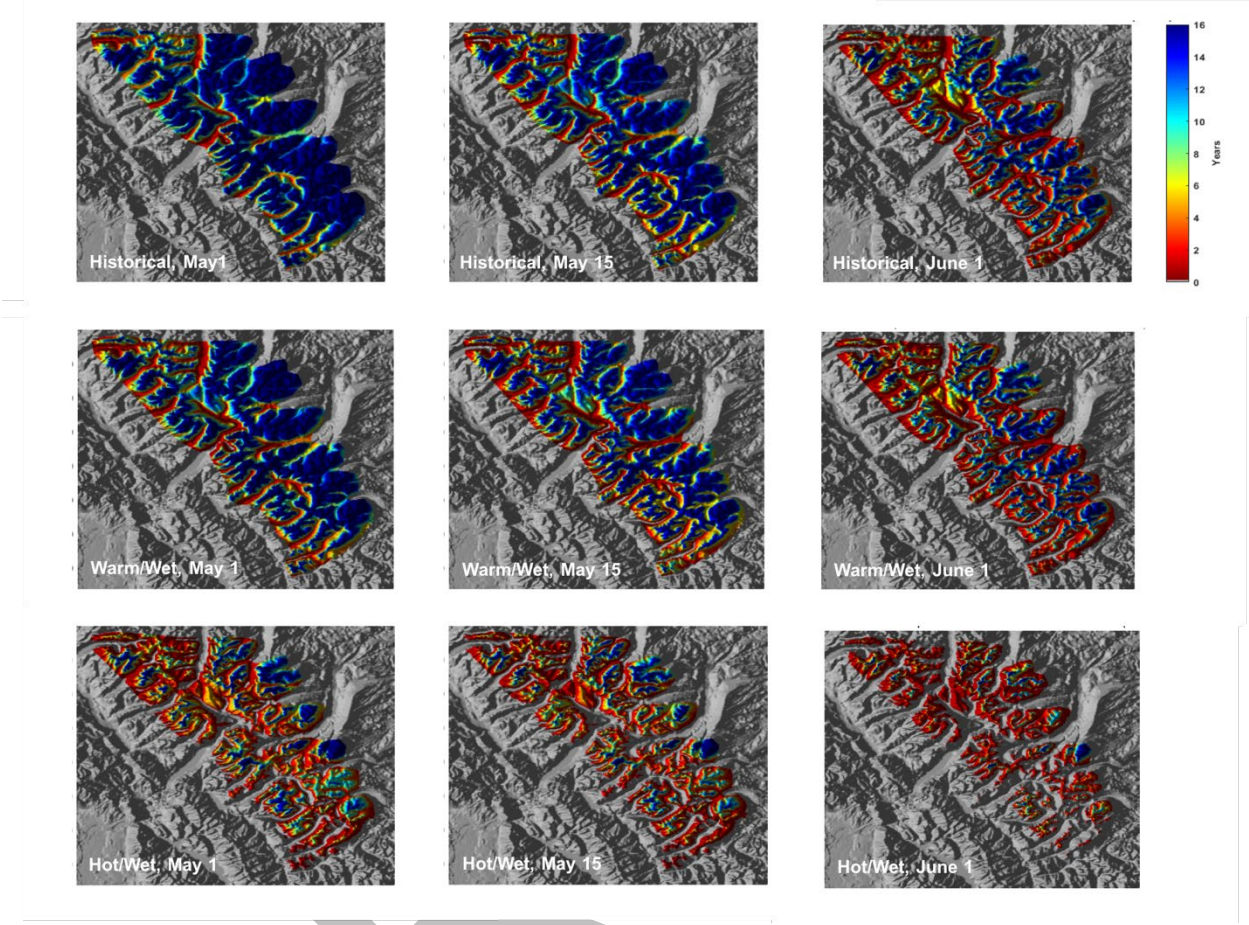


**Figure 5-14: Number of years (out of 1998-2013) with Snow Depth > 0.5 m for historic and two future climate scenarios**. The “number of years” indicates the yearly availability of deep snow at each model gridcell across all years in the DHSVM simulations, including wet, dry, and near normal years. Top Row: Historical Simulations on May 1st, May 15th and June 1st. Middle Row: Warm/Wet future scenario (GISS model, “Least Change”) at the same dates, Bottom Row: Hot/Wet future scenario (MIROC model, “Greatest Change”) at the same dates. The reduction in the number of years on May 1 for each future scenario can be compared to the historical simulation at a later calendar date, showing a < 2 week shift for the Warm/Wet scenario and a > 1 month shift for the Hot/Wet scenario. Scenarios are listed in Table 5-3.

DRAFT

ADDENDUM: This figure was missing from 14APRIL2017 Draft due to late arrival of figures from the modeling group. This is the ROMO version of figure 5-14 for GLAC. Caption has been expanded.

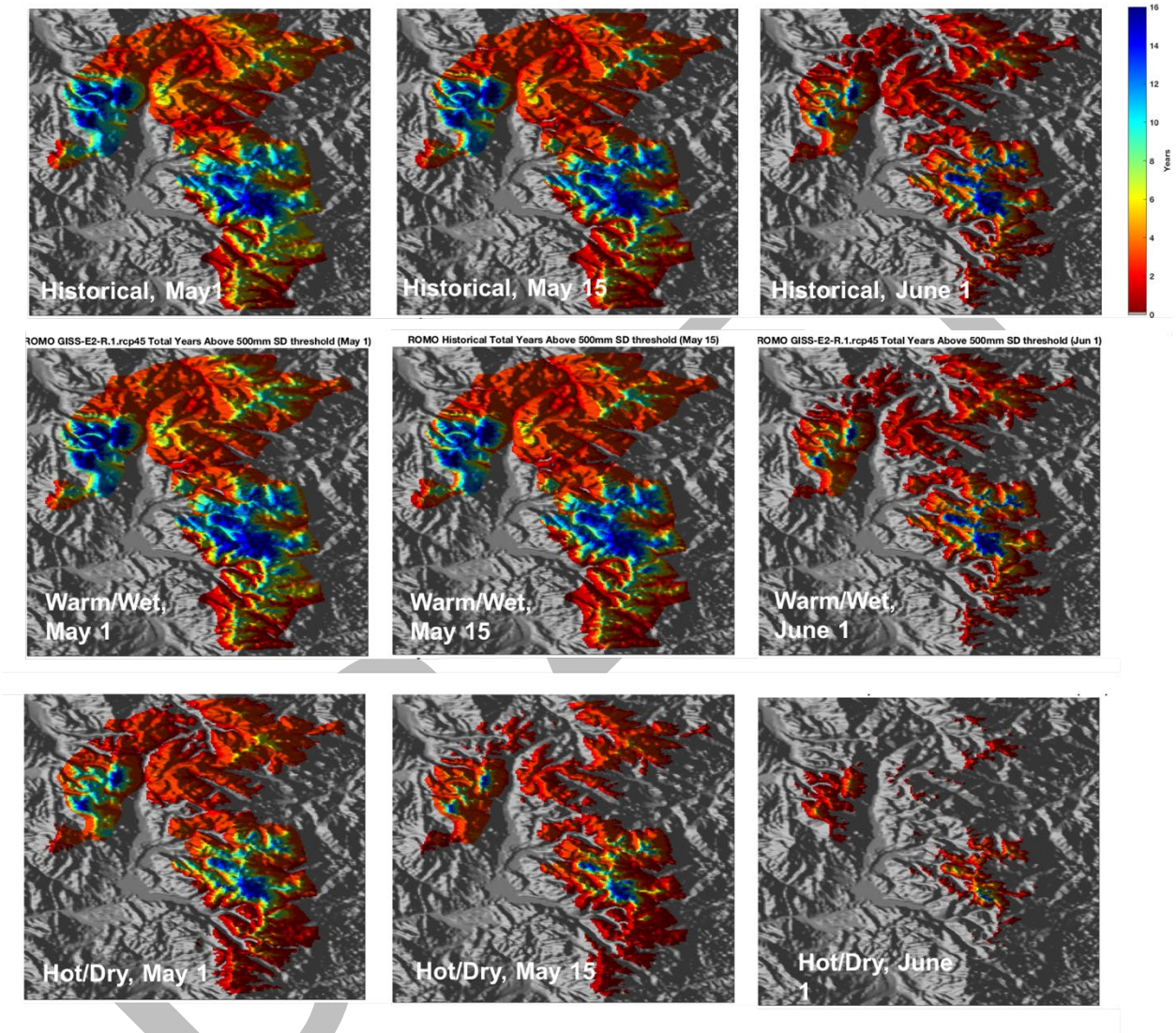


**Figure 5-21: Number of years (out of 1998-2013) with Snow Depth > 0.5 m for historic and two future climate scenarios**. The "number of years" indicates the yearly availability of deep snow at each model gridcell across all years in the DHSVM simulations, including wet, dry, and near normal years. Top Row: Historical Simulations on May 1st, May 15th and June 1st. Middle Row: Warm/Wet future scenario (GISS model, "Least Change") at the same dates, Bottom Row: Hot/Dry future scenario (Hadgem2 model, "Greatest Change") at the same dates. The reduction in the number of years on May 1 for each future scenario can be compared to the historical simulation at a later calendar date, showing little shift for the Warm/Wet scenario and a > 2 week shift for the Hot/Dry scenario. Scenarios are listed in Table 5-3.

**ADDENDUM: Elevations of known wolverine dens in Glacier area have been added as triangle symbols.**

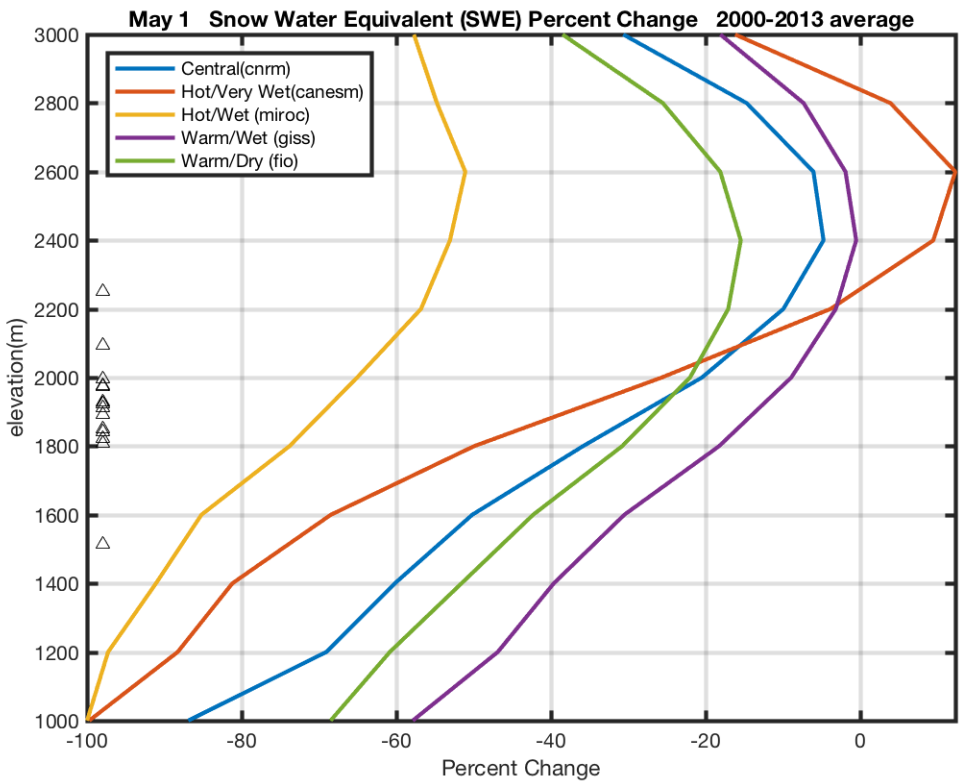


**Figure 5-22: Snow Water Equivalent (SWE, mm) at elevation bands for GLAC for five future scenarios on May 1.** Central (cnrm, red), Hot/Very Wet (canesm, green), Hot/Wet (miroc, purple), Warm/Wet (giss, aqua), Warm/Dry (fio, orange). Known wolverine den site elevations are shown by black triangles. Note that the highest elevation at GLAC tops out at 3000m, whereas the highest elevation band at ROMO tops out at 4000m.

DRAFT

ADDENDUM: This figure was missing from the 14 APRIL2017 draft

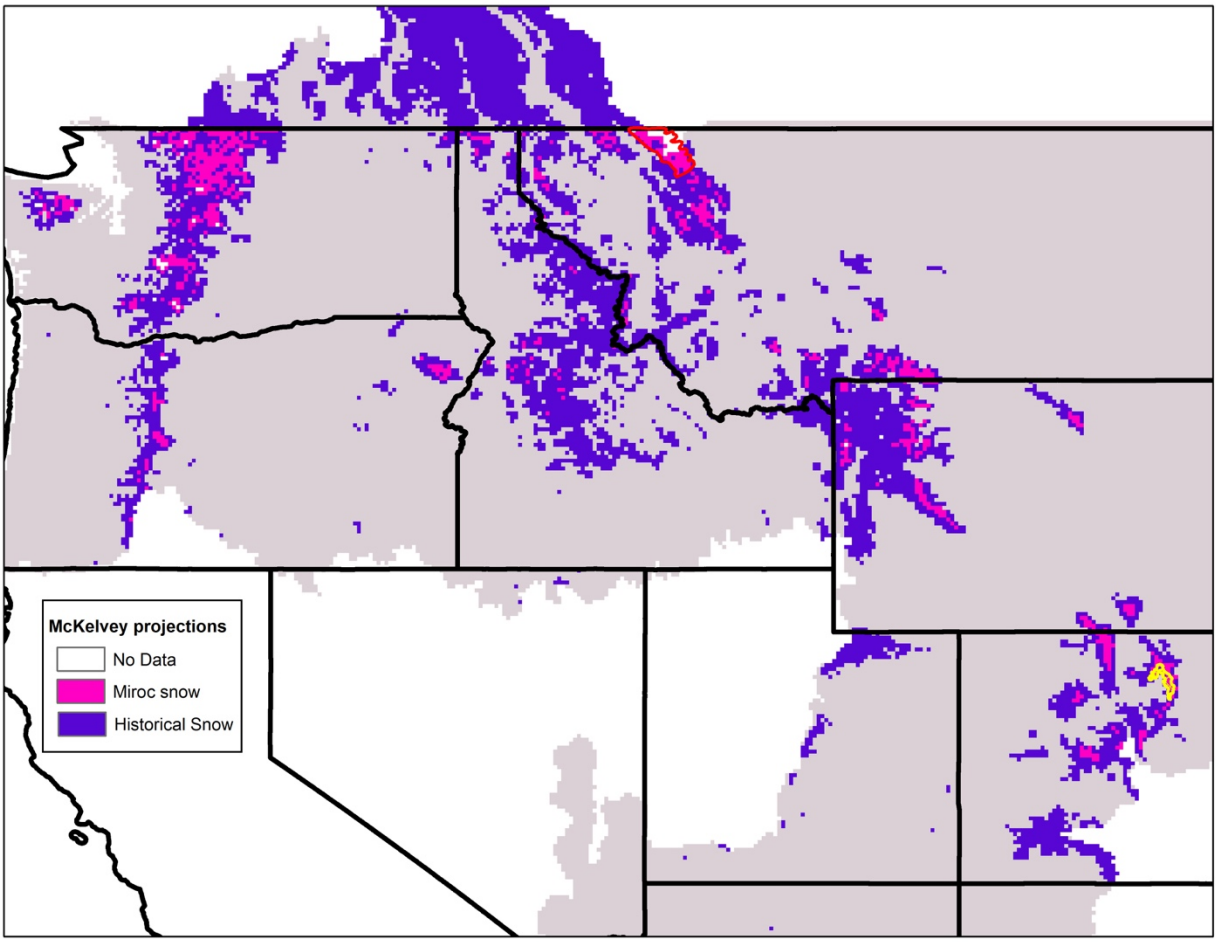


**Figure 5-24: Simulated May 15 average snow cover inferred from 13cm snow depth on May 1 from McKelvey et al. (2011). Historical simulation and "MIROC 2080s" projection are shown. No projection data were included for Canada. Outlined areas are shown from the present study: GLAC (red), ROMO (yellow). Note that the domain simulated in McKelvey et al. (2011) did not include all of the GLAC study area. (Data were generously provided by Jeff Copeland. Graphic prepared by John Guinotte).**

DRAFT

**From:** Grizzle, Betty
**To:** A J
**Subject:** Re: niches and bioclimatic envelopes
**Date:** Thursday, April 20, 2017 8:43:03 AM
**Attachments:** Elith and Graham_2009.pdf
Pearson 2007_SDM for practioners.pdf

---

FYI - Here are two references that explain species distribution modeling (SDM) concepts and model differences. I have many more on the use of Maxent, which can work well for some applications.

On Wed, Apr 19, 2017 at 5:07 PM, A J <222wsheridan@gmail.com> wrote:

> **It seems the Copeland et al. 2010 paper could have benefited from taking bias into consideration. Way more weight given to a handful of mountain study areas and dismissing lowland forest habitats. Mapping locations of female wolverines, whether denning or not, would have given a much more accurate picture of where wolverines reproduce, since so few females disperse very far from their natal areas. Many of the biases highlighted in the article below were true of the Copeland et al. paper.**
>
> Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias
>
> Yoan Fourcade , Jan O. Engler, Dennis Rödder, Jean Secondi
>
> Published: May 12, 2014https://doi.org/10.1371/journal.pone.0097122

--

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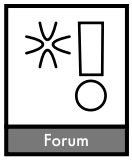


**Ecography 32: 66–77, 2009**
doi: 10.1111/j.1600-0587.2008.05505.x
© 2009 The Authors. Journal compilation © 2009 Ecography
Subject Editor: Miguel Araújo. Accepted 9 December 2008

# Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models

**Jane Elith and Catherine H. Graham**

*J. Elith (j.elith@unimelb.edu.au), School of Botany, The Univ. of Melbourne, Parkville, Victoria 3010, Australia. – C. H. Graham, Dept of Ecology and Evolution, 650 Life Sciences Building, Stony Brook Univ., Stony Brook, NY 11794, USA.*

Species distribution models (SDMs) are increasingly being used to address a diverse range of applied and theoretical questions (Guisan and Thuiller 2005, Jeschke and Strayer 2008). Also known as ecological niche models, bioclimatic envelopes, habitat models and resource selection functions, SDMs are correlative models that use environmental and/or geographic information to explain observed patterns of species occurrences. Their expanding use means that models are now being fitted to new forms of data, including a recent focus on modelling occurrence records from museums or herbaria (Graham et al. 2004). For some applications, such as climate change or invasive species research, model predictions are extended beyond the geographic or environmental region from which training samples were drawn (Araújo et al. 2005). SDMs are also being used in a variety of fields including evolutionary biology, where they are used to study topics such as speciation or hybrid zones (Kozak et al. 2008) and epidemiology, where they are used to predict the spread of disease (Peterson et al. 2002). As a result of these diverse uses of SDMs that have been spurred on by advances in geographic information systems (GTS, Foody 2008) and data analysis (Breiman 2001a), new modelling methods continue to be implemented. Model complexity has generally increased over time from simple environmental matching (e.g. BIOCLIM, Busby 1991; DOMAIN, Carpenter et al. 1993) to fitting more complex non-linear relationships between species presence and the environment (e.g. generalised additive models, GAM, Hastie and Tibshirani 1990, Yee and Mitchell 1991; and maximum entropy modelling, MaxEnt, Phillips et al. 2006). Recent emphases on machine-learning and Bayesian methods indicate that new methods will continue to be developed (Latimer et al. 2006).

This wide array of methods, data types and diverse research questions imply firstly, that there are many different requirements of modelling methods, and secondly, that when choosing a method, knowledge is required about which method is best suited to the available data and the intended application. However, the criteria and advice that would enable informed choice of method are currently scattered throughout the literature, and are incomplete. This makes it hard for most users to know whether it is worth adopting newer methods and for newcomers to know where to start.

How could species distribution modelling as a research field provide clearer advice as to what methods are best for a given application? To date research has focused on studies that compare model performance across multiple methods, address specific solutions to a given statistical or sampling issue, or provide detailed treatments of particular models. Some attempts have also been made to link ecological theory to choice of method (Table 1). While this research has provided information and guidance necessary for selecting relevant methods, it is our opinion that we need more syntheses of existing knowledge, more advice from statisticians and computer scientists expert in the algorithms, and a broader suite of evaluation methods that target not just whether there are differences in predictive performance, but why these differences occur. This forum piece focuses on the third of these, and aims to demonstrate the effectiveness of asking why.

There are various approaches for assessing why models differ in predictive performance, including developing strong theoretical knowledge of how a method works, testing multiple parameter settings for the method and observing effects on outputs, and using data with known characteristics to test model fit and prediction. The latter can be sets of data with known properties e.g. drawn from a known distribution, created from a known equation (Bio 2000, Moisen and Frescino 2002) or simulated (artificial) species (Austin et al. 2006). Simulated species are particularly useful if relevant features such as population processes, competition, or typical landscape properties can be included (Tyre et al. 2001, Reineking and Schröder 2006, Meynard and Quinn 2007, Kearney et al. 2008). While we encourage the use of any approach that gives insight into why methods differ, here we choose to use a simulated species within a real landscape.

We evaluate three applications of distribution modeling: 1) understand the relationships between the species and its environment; 2) predict which parts of the landscape are

Table 1. Examples of existing approaches addressing a variety of methodological, theoretical, statistical and applied questions.

| Category | Aim | Examples |
|---|---|---|
| Comparative studies | To quantify whether methods perform differently (in terms of model fit or prediction) and to search for any general patterns in the differences | Moisen and Frescino 2002, Seguardo and Araújo 2004, Reese et al. 2005, Elith et al. 2006, Hernandez et al. 2006, McPherson and Jetz 2007a, b, Graham et al. 2008, Loiselle et al. 2008 |
| Specific methods for treating specific problems | To use an appropriate method for data (or for a problem) that has characteristics violating assumptions of common models | Models for data with imperfect detection (MacKenzie et al. 2002); models for zero-inflated data (Martin et al. 2005); models that deal with spatial autocorrelation (Dormann et al. 2007); subsampling data or accounting for its bias |
| Detailed treatments of methods | To explain a method clearly and inform users of its characteristics, strengths and weaknesses for ecological analyses | Generalised additive models (Yee and Mitchell 1991), MaxEnt (Phillips and Dudik 2008), Resource Selection Functions (Manly et al. 2002) |
| Linking ecological theory to choice of method | To ensure the selected model is consistent with known ecological theory | Methods appropriate for modelling realistic species environment relationships (Austin 2002); quantile regression for modelling limiting factors (Huston 2002); multiplicative models for modelling interactions and overriding limitations (McCune 2006) |

more or less suitable for the species by creating a map of relative suitabilities; 3) extrapolate to environmental conditions outside those in the sample space. Because simulated species provide known species-environment relationships and spatial distribution we can evaluate differences among methods in relation to the truth and gain insight into why these differences exist.

## Simulating the species and sampling it

We created a simulated plant species and mapped it onto a landscape in southern Australia. The species responds to three variables: wetness, aspect (''southness'') and geology and prefers wet and south-facing (shaded) sites and fertile substrates. We created an interaction between the response to wetness and the summed responses to southness and geology, and weighted the terms so that wetness dominated the final distribution (eq. 1 and Fig. 1, top panel). Note from Fig. 1 that the responses to continuous variables are non-linear; details of how each component (SI.wetness etc.) was specified is presented in Supplementary material Appendix S1.

$$\text{Suitability of a cell} = \text{SI.wetness}*0.5*(\text{SI.southness} + \text{SI.geology}) \quad (1)$$

where SI = suitability index (Supplementary material)

The predictor variables (wetness, southness and geology) existed as real mapped data; the species' response to them was invented. The mapped distribution based on these relationships shows the suitability (scaled 0 to 1) of each grid cell for the plant (Fig. 2, top left). Whilst these data could be modelled as suitabilities, most species data exist as presence-only or presence-absence records, so we made a presence-absence realisation of the species. We used the suitability value in each grid cell of the map as the success rate for one sample of the binomial distribution, i.e. a cell with a suitability of 0.6 has a 60% chance of being occupied (rbinom function in R; R Development Core Team 2006). The binomial realisation is consistent with an interpretation of species relationships that says: ''if the environment is only partially suitable for the species, in some cases the species will occur there and in some it will not''. Our presence-absence realisation of the simulated species occupied 12% of the cells in the study region (Supplementary material Fig. S2a).

To provide the data set for modelling we sampled from the simulated presence-absence distribution by taking 1000 sites at random; these included 115 presences and 885 absences and together comprise what we will call the presence-absence (PA) sample. This number of sites is somewhat arbitrary, but is enough to fit models well, and is consistent with some real data sets used in modelling. Other protocols such as stratified sampling across environmental gradients could be used instead of random sampling. The PA sample is visualised in Fig. 3a. Note that, consistent with the full data set (Fig. 3b), samples at high wetness are relatively rare. For methods only requiring presence data, the presence records in the PA sample were used as presence-only (PO) data. In the online supplement (Supplementary material Appendix S5) we describe additional data samples, in which 1000 or 3000 pseudo-absences were selected and combined with the PO data, to test the effect of using presences with pseudo-absences instead of true absence data.

## Modelling and evaluation methods

We chose five algorithms to demonstrate what simulated data can show about differences between methods. For the PA data we selected a generalised linear model (GLM; McCullagh and Nelder 1989) as a standard regression model and two more recent methods, boosted regression trees (BRT; Friedman et al. 2000) and random forests (RF; Breiman 2001b). For the PO data, we used MaxEnt and GARP as featured in recent comparisons (Peterson et al. 2007, Phillips 2008). MaxEnt, GARP and RF are machine learning (ML) methods. The version of BRT used here is a ML method reinterpreted into a statistical paradigm. More details and references for all algorithms are given in the online supplement. These methods were selected because they allow a number of contrasts including comparison of

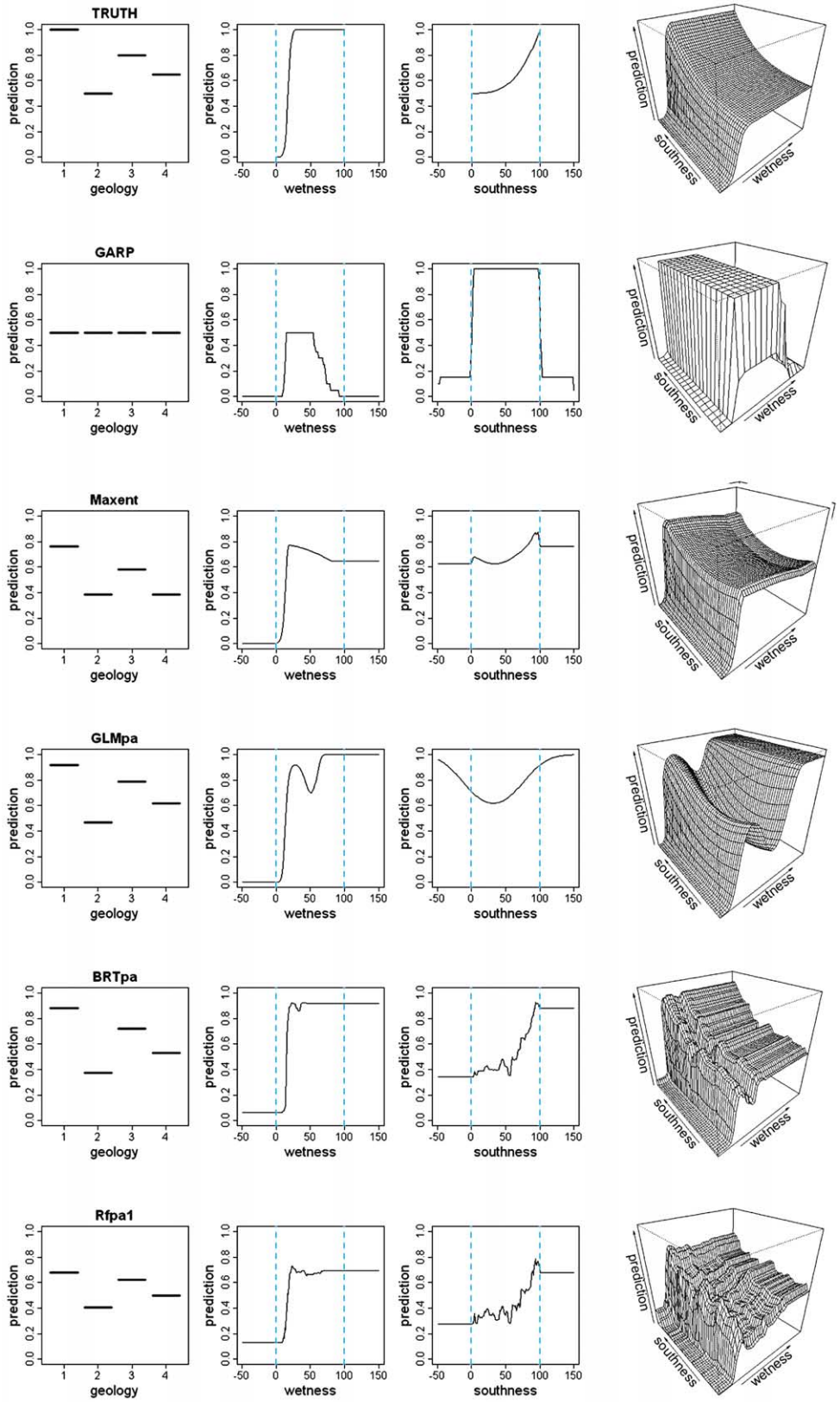


Figure 1. Partial responses to the 3 variables (left) and over co-varying wetness and southness (3D plots, right). The true responses (top panel) were generated by using the equations that define the simulated species to predict to the evaluation strip, then plotting the results (see Elith et al. 2005 for details). The blue vertical lines show the extent of the variable values in the mapped region; outside these the models are extrapolating. The range on the wetness and southness axes of the 3D plots is that within the blue lines of the 2D ones, and predictions range from 0 to 1.

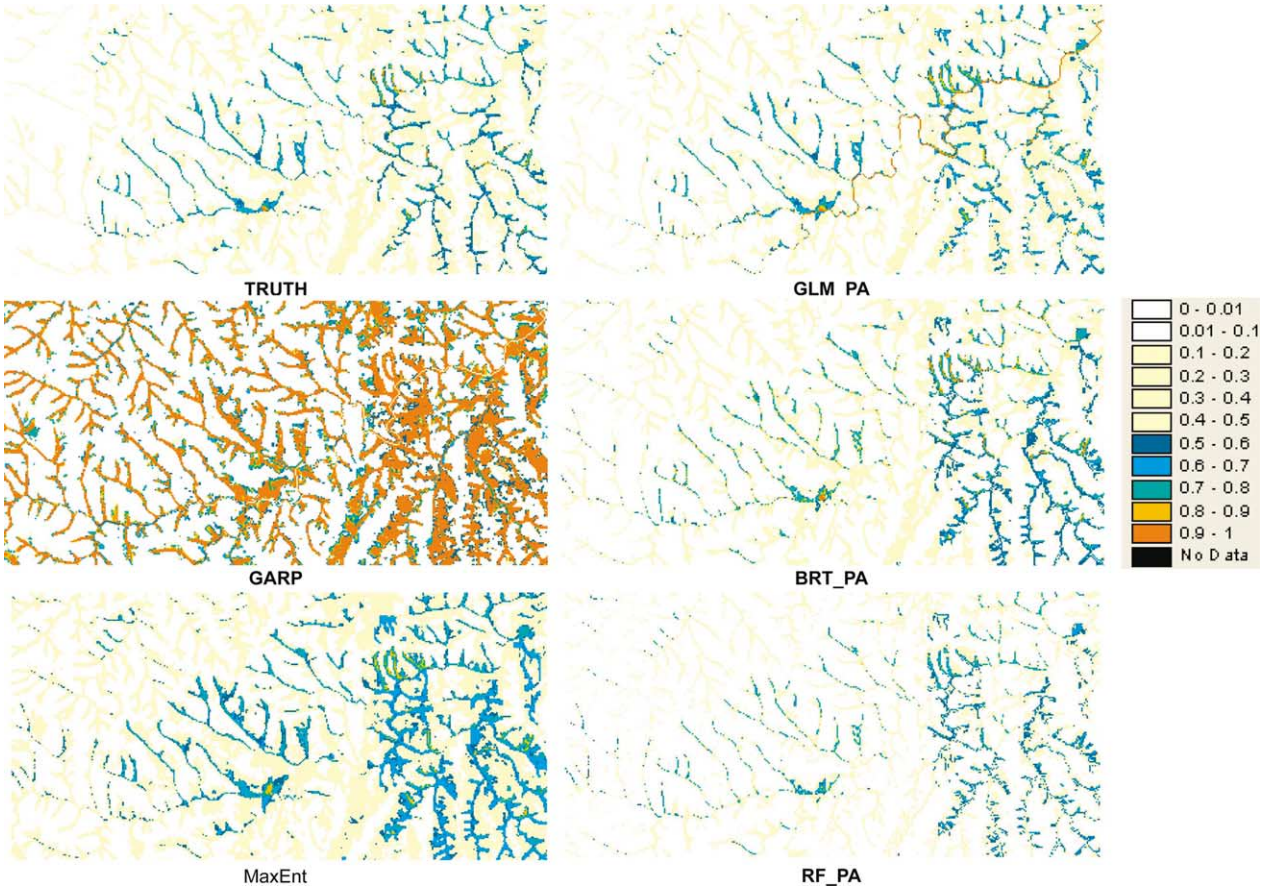


Figure 2. Mapped distributions of the virtual species (top left) and predictions of relative suitabilities from the methods detailed in the text, legend: white $<0.1$, cream 0.1–0.5, blue-light, blue-green-orange-vermillon at steps of 0.1 from blue (0.5–0.6) to vermillon (0.9–1).

models developed on PA compared with PO data, comparison of MaxEnt and GARP, and comparison of two methods using ensembles of trees, BRT and RF. Each of the methods is assumed capable for at least some of our three posed applications, and they have all been used for related tasks.

For details of model building methods see Table 2 and Supplementary material Appendix S2, S3 and S4. In those appendices the settings for some methods are tested in detail; this reflects our need to explore the effect of a range of settings for some methods, either because we were relatively inexperienced with that method or because the recommended settings did not produce good results.

The first of our applications was to understand the relationships between the species and its environment. The second – mapped predictions – would also benefit from knowledge of the modelled relationships, for understanding differences between the maps. However, not all methods provide visualization of fitted functions, so we created a second set of environmental grids with an evaluation strip inserted, following Elith et al. (2005). The strip is a simple data arrangement that holds two of the three environmental variables at a constant value (here, a value achieving maximum suitability for the species) whilst varying the value of the third environmental variable across its numerical range. To visualise interactions (and to check that results do not depend on the value at which variables are held constant), pairs of variables can be covaried. For this, we included a comprehensive set of combinations of wetness and southness for each of the four classes of geology. Predictions were made to the evaluation strip and then plotted, to illustrate the partial response to one or two variables while holding other variables constant. This method is analogous to the partial plots from standard regression methods (see Elith et al. 2005 for details). To determine how the models extrapolate we included values for variables in the evaluation strip that were outside the variable range in the study area for both wetness and southness. We acknowledge that this approach only measures one aspect of extrapolation, and that other possibilities exist including creating landscapes or evaluation data with new combinations of variables. The simple test of extrapolation outside limits will suffice here, as a first exploration of extrapolation behaviour.

Finally, to evaluate a method's ability to predict habitat, mapped predictions were visually and quantitatively assessed. Summary statistics were calculated across predictions in all 80 000 cells, and then used to compare the presence-absence realisation and the true suitabilities. Analyses using presence-absence data as truth focussed on: 1) the area under the receiver operating characteristic curve (AUC; Hanley and McNeil 1982); 2) the remaining per-observation deviance (i.e. the variation left unexplained, as measured by the mean binomial deviance across sites; Elith and Leathwick 2007); 3) the point biserial correlation coefficient (a Pearson correlation, Elith

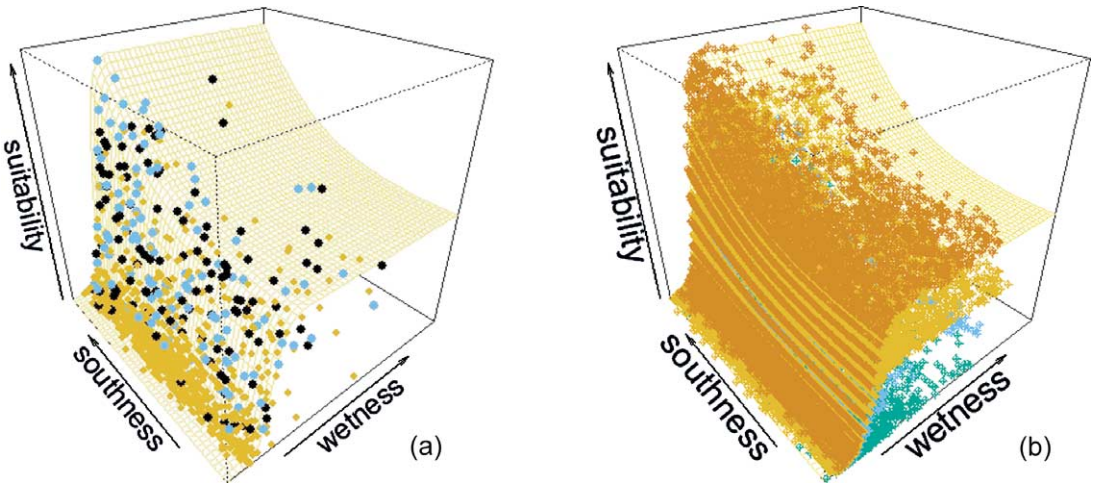


Figure 3. (a) The data samples for presence-absence models. Samples are shown at their original true suitability value (vertical axis), but were converted to presence (blue) or absence (orange) as described in the text. (b) The location of all 80 000 grid cells in environmental space. The pale yellow mesh shows the full suitability surface from the simulated species, for geology class 1. The points of varying colours show sites in the four geology classes. Note the few sites with high wetness values.

et al. 2006, COR.pa); and 4) elements of the confusion matrix for predictions converted to binary values, using a threshold described later. Predictions were compared with true suitabilities with a Pearson correlation coefficient (COR.si).

It is important to use more than one metric to assess model performance because each quantifies a different aspect of predictive performance (see Murphy and Winkler 1987 and Pearce and Ferrier 2000 for interesting discussions of this topic). Amongst the measures tested against PA observations, AUC measures the ability of predictions to discriminate between observed presence and absence, regardless of the absolute value of the predictions. COR.pa also measures discrimination, but includes consideration of the actual value of the prediction, and how it compares to the observation. Deviance puts more emphasis on the

Table 2. Details of model fitting procedures and settings.

| Method | Name for model | Data | Settings and notes on further tests |
|---|---|---|---|
| Genetic algorithm for ruleset prediction | GARP | PO | Used v 1.1.6. Details in Supplementary material Appendix S2 on tests to compare effects of different settings. Results presented here from: species data = 115 PO samples plus pseudo-absences selected by GARP. 50% data used for training, 50% for extrinsic evaluation. Created 500 models each with a convergence limit of 0.01 and 1000 maximum iterations. Allowed all rule types. From the 500 models chose 20% with mid extrinsic omission error and from those 20 with mid commission error. Final prediction is mean of these. For predicting to evaluation strip projected to grids with strip inserted. |
| Maximum entropy | MaxEnt | PO | Used ver. 3.2.1 from the command line. Modelled the 115 PO samples and allowed MaxEnt to select a random 10000 background samples (the default). All other settings were the defaults except: flagging geology as a categorical variable, providing a separate set of grids to project to that contained the evaluation strip, and using the ''-d'' flag (see help file for MaxEnt). The -d flag forces MaxEnt to calculate the probability distribution over the background samples alone (rather than the default, which calculates it over the joint background and presence data), and providing it with the best chance to be well calibrated. For predicting to evaluation strip projected to grids with strip inserted. |
| Generalised linear models | GLM.pa | PA | Used R[1] and function GLM. Created all possible subsets of models with the options for each variable being: exclude, or (if continuous): linear, quadratic or cubic fits. Used AIC to select the best model. |
| Boosted regression trees | BRT.pa | PA | Used R[1] and function GBM with custom scripts of Elith et al. 2008 to build an ensemble of regression trees. Selected tree complexity of 3, learning rate of 0.001, using prevalence-stratified cross-validation to determine optimal number of trees (4250). See Supplementary material Appendix S4 for details. |
| Random forests | RF.pa | PA | Used R[1] and function random forest to build an ensemble of classification trees. Tests of a range of settings are presented in Supplementary material Appendix S3. Model presented here had 500 trees with one variable randomly selected from the 3 candidates at each split. No class weights. |

[1]R Development Core Team 2006.

model calibration i.e. on whether predictions reliably predict frequencies of occurrence.

## Results

### Relationship of species to environment

Figure 1 shows the modelled responses to the 3 variables when others are held at their optima, and in the right column, the response to co-varying wetness and southness for geology class one. Here we analyse the results for the ranges of the variables in the data – i.e. within the blue vertical lines of Fig. 1. In the later section "Extrapolation" we deal with predictions outside the range of the data.

We would not expect any of the methods to fully retrieve the species environment relationship of the simulated species because a relatively small sample of a binary realisation of the data was used to build the models (Fig. 3a). Nonetheless, several of the methods were able to fit reasonably accurate functions. This was an easier task for the methods using smoothed functions (GLM and MaxEnt), given that the true relationships were smooth.

All methods except GARP modelled geology correctly (Fig. 1, left column). GARP's modelled response to geology varied across different data samples, runs, and summaries of the data (Supplementary material Appendix S2). GARP might be expected to model categorical data properly because it uses logistic rules, but the implementation is a genetic algorithm version of logistic regression and has not been coded to properly deal with unordered categorical variables (Elith unpubl. and Peterson pers. comm.). However, the atomic rules provide some opportunity to model geology correctly, and in some cases (Supplementary material Fig. S3 and S6) the result was better than the one presented.

The low suitability of dry areas (wetness $< 15$) was correctly captured by all methods (Fig. 1, second and fourth columns). At higher levels of wetness, where the data are more sparse, BRT modelled the overall shape of the response most accurately, followed by MaxEnt (slightly reduced amplitude), RF (smaller amplitude) and GLM (unnecessary complexity around wetness of 50) and last, GARP (small amplitude and wrongly predicted that high wetness was unsuitable). Whilst the general form of the fitted function was correct for BRT, it was overfitted to the sample, producing a dip in the response at wetness $\sim 30$. At this level of wetness the sample was sparse and happened to contain more zeros than would be expected for the suitabilities. RF showed even more overfitting (note the more uneven surface, Fig. 1, right column), which was only fractionally reduced by using more trees in the ensemble (Supplementary material Appendix S3).

Southness (Fig. 1, third and fourth columns) was difficult to model well, probably partly because the response included an interaction between southness and wetness, and also because it was less dominant than wetness in the suitability equation. RF, BRT and MaxEnt did best, GLM was reasonable but gave an increasing response at low values of southness and, without an interaction, could not capture the response to southness at high wetness (see right side of 3D plot). GARP did not manage to model the true response or anything close to it, and this result was consistent across all tests (Supplementary material Appendix S2).

### Mapped predictions; visual assessments

Differences between the methods were also evident based on the mapped predictions. We present the results as maps and plotted data so that any arbitrary impressions introduced by choice of legend in the map (Fig. 2, 4) can be checked against the plotted results (Fig. 5). Note that the COR.si in Table 3 acts as a summary measure of the plotted data in Fig. 5.

Because all methods predicted the response to low wetness correctly, they all correctly predicted absence at dry sites (the white areas on the maps, Fig. 2). Modelling this part of the response accurately meant that all methods produced a broadly correct mapped pattern. GARP tended to predict high values across any areas that had at least some suitability for the species, whereas the other methods predicted gradations in suitability more accurately (Fig. 2 and related close-up, Fig. 4). The overprediction can be traced to the errors in retrieving the true underlying species-environment relationships, and particularly the dominance given to the incorrectly modelled response to southness. In other words, why GARP overpredicts is partially answered; GARP could not retrieve the true relationships in the data. This is only a partial answer because we do not know what features of the algorithm cause this overprediction. Simulated data like these could be used to explore whether another simulated species or different settings for GARP improve model performance. We were unable to improve GARP model performance substantially when we used different settings or methods to combine individual GARP runs (Supplementary material Appendix S2). Nonetheless, the results of the different trials shown in the Supplementary material, are interesting in that they suggest that means of all runs of GARP are slightly better for these data than the subsets that are generally advised. They also demonstrate considerable run-to-run variation (where one run is 500 models and summaries thereof).

As expected, none of the methods perfectly retrieved the true mapped suitabilities; sample size, characterising the response with binary data rather than suitabilities, and algorithmic limitations all contribute to this result. MaxEnt recreated the general mapped pattern of the simulated species well and was only worse than the best method, BRT, with respect to calibration (Fig. 2, 4). Perfect calibration would have resulted in all records in Fig. 5 sitting on the diagonal, but a presence-only method cannot be perfectly calibrated unless information on the species prevalence in the region is available (but note that proportional calibration is possible for a PO method – records would follow a straight line, but the gradient and intercept would not be 1 and 0 respectively). In contrast, the three methods trained on the PA data should be properly calibrated. The results for these methods are all reasonable, with BRT predictions slightly less dispersed than RF and GLM (Fig. 2, 4, 5). We tested various settings for RF (seven combinations are presented in Appendix S4); the ones we present here are those that would have been selected from the out-of-bag

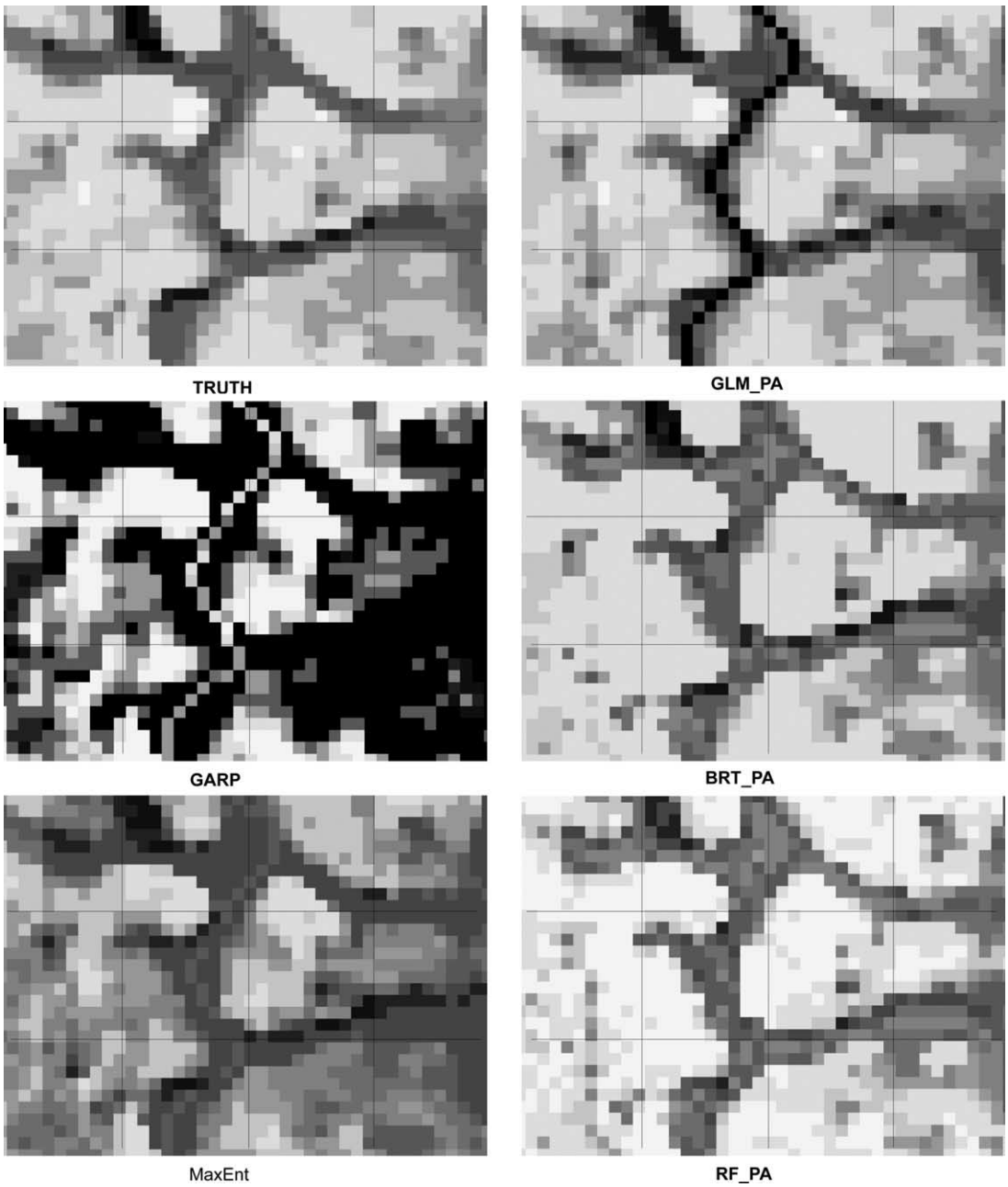


Figure 4. Close-up of predictions from Fig. 2. Choice of location was via random number selection for centre grid position. Predictions in greyscale, from white (zero) to black (one); fine grid lines are in the same position on each map.

error estimates, are consistent with those used in other published studies, and appear close to optimal (Supplementary material Appendix S4).

Before leaving the topic of calibration we note that, with PO data, MaxEnt calibration results may not always be as good as those presented here. Our simulated species was created to vary in suitability from 0 to 1. This range corresponds to that used in the MaxEnt logistic output (Phillips and Dudik 2008), so the MaxEnt predictions for this simulated species were reasonably well calibrated. However, if our truth was rescaled (say, by multiplying all suitabilities by 0.5), MaxEnt predictions would be more poorly calibrated (S. Phillips pers. comm.). This problem is not restricted to MaxEnt, as shown in Supplementary material, Appendix S5, where BRT and GLMs are fitted with PO data. There the choice of the number of pseudo-absences, and the optional weighting of them, affected calibration. Together, these issues demonstrate an inherent problem for models using PO data; they cannot be well calibrated without information on species prevalence (Ward et al. in press).

## Mapped predictions; quantitative analyses

The summary statistics presented in Table 3 focus on predictions as continuous values (i.e. in their default format, such as probabilities). These demonstrate some differences

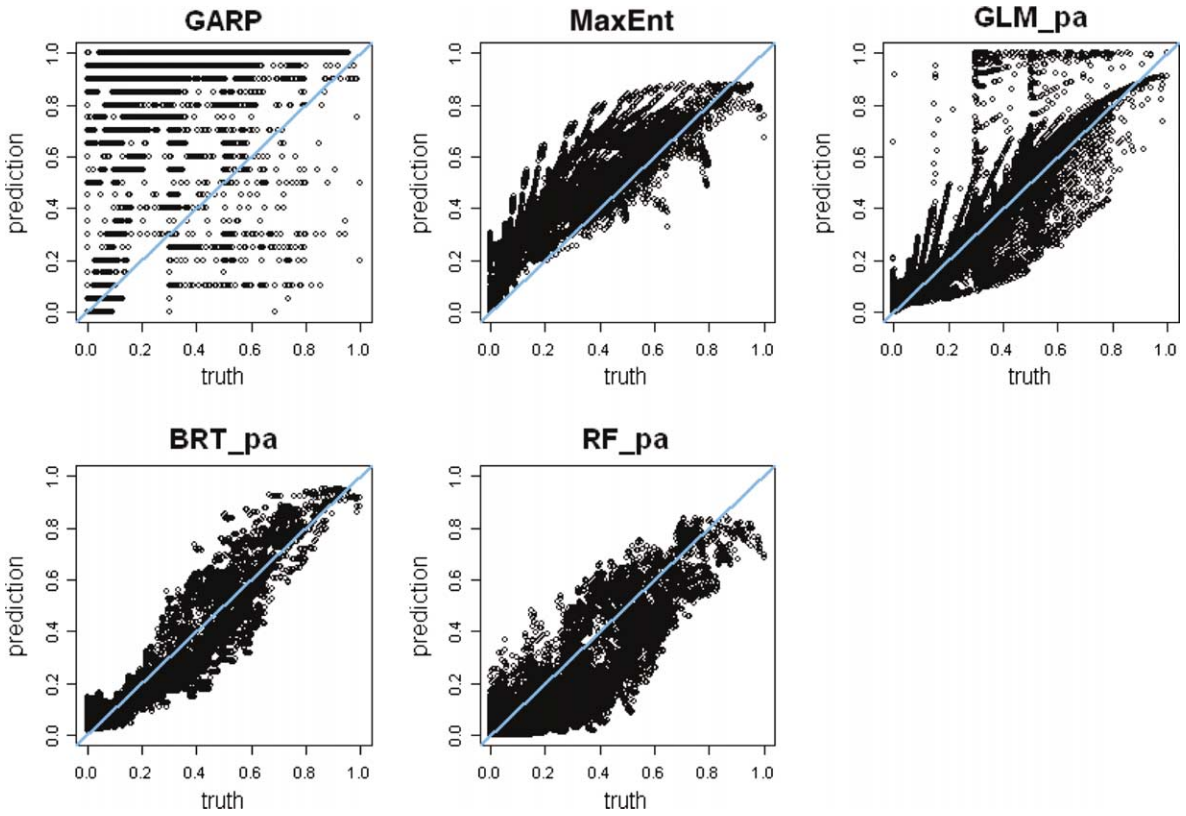


Figure 5. Predictions (*y* axis) versus the true suitability for all 80 000 grid cells in the maps in Fig. 2, covering five modelling methods described in Table 1. The blue diagonal line shows the 1:1 relationship.

between the methods, with the extent of the difference varying with the statistic. Note that the first row in Table 3 (''Truth'') indicates the best possible performance for AUC, Deviance and COR.pa, because it measures the relationship between the true presence-absence realisation (sampled for modelling) and the true suitability. The AUC indicated that all models discriminated the broad patterns of presence and absence reasonably well, but there was some variation between methods. The broad success in discriminating between presence and absence locations probably results from the correct modelling of dry conditions, because all the pair-wise comparisons between predictions in these areas and ones in the wetter areas would have been correctly ranked. Measures that include consideration of the actual value of the predictions (all others) emphasise more clearly that MaxEnt, BRT and GLM all do well, followed by RF then GARP (Table 3). Note that it is difficult to make a fair comparison across all methods, because the 3 models fitted to the PA data had more information than the PO methods, and this information allows the models to estimate probabilities and hence to be better calibrated. This particularly affects remaining deviance (Table 3). Nevertheless, for this exercise MaxEnt does well without this information (but see the earlier discussion about the scaling of suitabilities and its effects on calibration in MaxEnt). The fact that, for PA methods, the order of model performance is consistent across metrics shows that errors in prediction are related to both discrimination and calibration. Given that the general shapes of the fitted functions for RF are reasonable, it is likely that its reduced performance in these summary metrics results from the noisier fit compared with BRT (Fig. 1, right column) and the slightly poorer calibration.

Table 3. Comparison of model results with truth, as realised by the presence-absence map (columns 2, 3 and 4) and the suitability values (column 5). For all statistics except deviance, higher is better.

| Model | AUC | Remaining deviance | COR.pa | COR.si |
|---|---|---|---|---|
| Truth (suitabilities) | 0.872 | 0.514 | 0.508 | 1.000 |
| GARP | 0.822 | 3.391 | 0.401 | 0.793 |
| MaxEnt | 0.861 | 0.612 | 0.467 | 0.922 |
| GLM.pa | 0.863 | 0.546 | 0.480 | 0.941 |
| BRT.pa | 0.862 | 0.537 | 0.485 | 0.954 |
| RF.pa | 0.834 | 0.736 | 0.448 | 0.875 |

It is possible that using predictions as continuous values unfairly discriminates against GARP, because GARP works by producing a presence-absence prediction, and non-binary predictions are achieved from summaries across multiple runs. Because of this, the predictions for all methods were thresholded and a test of binary predictions applied. We did this without biasing the results towards methods with good calibration, by using thresholds that gave the same prevalence across the landscape for all methods (following Phillips et al. 2006). This meant that we used a threshold of 1 for GARP (to get prevalence as close to truth as possible and to restrict the overprediction of GARP), then set others in relation to that. The results (Table 4) are consistent with other results, though the differences are less extreme. Note that this thresholding method likely disadvantages methods other than GARP

Table 4. Comparisons among methods when predictions are reduced to binary results. Because GARP overpredicted, the highest possible GARP threshold (1) was used to convert GARP predictions to binary form, then thresholds were selected for all other methods that gave identical prevalence in the landscape (17.3%, compared with truth 11.9%). The values in the tables are the proportions of predictions that fell into each category (true negative etc.) when cross-tabulated with truth.

| Prediction: | true negative | true positive | false negative | false positive |
|---|---|---|---|---|
| GARP | 0.771 | 0.064 | 0.056 | 0.109 |
| MaxEnt | 0.778 | 0.071 | 0.049 | 0.102 |
| GLM | 0.780 | 0.073 | 0.047 | 0.100 |
| BRT | 0.780 | 0.073 | 0.047 | 0.100 |
| RF | 0.777 | 0.070 | 0.050 | 0.103 |

because others are likely to have lower optimal thresholds when set independently.

Information on BRT and GLM models fitted to the presence – pseudo-absence data are presented in Supplementary material Appendix S5. These show that in some (but not all) cases the fitted functions are reasonably accurate, and that across methods different ways of sampling and weighting the pseudo-absences have different effects on the discrimination and calibration of the models. We note that alternative implementations of BRT that are better suited to the presence/pseudo-absence data structure will be available soon (Ward et al. in press).

### Extrapolation

The extrapolation behaviours of the models are presented in Fig. 1, in which the responses to the highest and lowest values for the wetness and southness, outside the blue dashed lines, are where the models are extrapolating to unsampled conditions outside the range of these variables in the mapped region. The nonsensical negative values of wetness and southness don't matter here – the important question is how the models would extrapolate beyond the sampled values of data. We had no prior knowledge of GARP behaviour, and in this example extrapolation was either a stepped decline (at extremes of southness) or a constant value. The selected rules in the best-subsets models would explain this behaviour, but they are not accessible in the desktop program so could not be analysed. Extrapolation patterns varied in GARP according to the dataset, the particular run, and the selected subsets (Supplementary material Fig. S3). By contrast, MaxEnt acts consistently and by default is ''clamped'' so it extrapolates in a horizontal line from the fit at the most extreme environmental value in the training data, both presence and background. As expected from the way polynomials behave, a GLM fitted with cubic and quadratic functions extrapolates by continuing the fitted trend beyond the last observation, sometimes with unwanted results. For example, here the projected increase in suitability at the lower values of southness is not sensible; north-facing (low southness) sites should be least suitable for the species. Classification and regression trees always extrapolate at a constant value from the last ''known'' site, as seen for BRT and RF.

## Reflections on the simulation

Before considering the wider implications of this simulation, we want to first emphasise what it does not do. Whilst we built our simulated species to be somewhat ecologically realistic (the species is affected by more than one variable, and reacts to predictors in non-linear and non-additive ways), it is more simple than reality. We do not see that as a problem, though, if we appropriately restrict our conclusions to ones about the link between the algorithm, data and fitted functions. Other types of simulations could be used to test modelling abilities for other aspects of what influences species distributions in natural populations (e.g. interactions between species, sink and source habitats). We also only tested some of the many ways of fitting these methods – for example, a GLM can include interactions and use natural splines instead of polynomials to control behaviours at the extremes of the sample ranges. Finally, we did not attempt a comprehensive study, though we hope that our simulation inspires other explorations.

What then does this simulation demonstrate? First, knowing what an algorithm is doing can give insights into various features that are apparent in its predictions; it helps to answer why particular patterns are observed. We summarise in Table 5 some insights from this study, and some of the remaining open questions. Testing an algorithm's performance using a simulated species approach and multiple evaluation criteria reveals unique behaviours of the modelling methods we explored and therefore should help developers and modellers to understand and improve model performance. The systematic studies in Supplementary material Appendix S2, S3 and S5 demonstrate that carefully evaluating model performance across parameter settings reveals the effect of those parameters.

Second, our example clearly illustrates the value of evaluating models from several viewpoints. The summary statistics indicated which algorithm gave the best mapped predictions and, when taken together, the metrics gave some hints about why performance varied. AUC only measures rank so did not reveal the more extreme differences between methods that were more related to model calibration. We do not believe that this means that any of these statistics are misleading (Lobo et al. 2008), but simply that different statistics measure different aspects of performance, and that appropriate statistics relevant to the application of the model need to be selected. Being able to visualise fitted functions not only satisfied our application of exploring modelled relationships, but also allowed us to understand what caused differences among the methods and how different fitted functions influenced mapped predictions.

Third, comparing the results for the partial responses with the quantitative assessments gives some useful insights. For example, even though the GLM modelled unnecessary complexity in the wetness response (giving the wave-like forms in the 3D plots), the evaluation statistics implied it did nearly as well as BRT. This is in spite of the fact that BRT had a better controlled fit overall. The distribution of environments (Fig. 3b) gives the key; there are relatively few sites in the places where the GLM failed to model the true response. Similarly, the environmental distribution of the training data (Fig. 3a) explains why several methods (GLM, BRT and RF) tended to model a declining response (even if

Table 5. Information learnt from the case study, including explanations relating to ''why''.

| What | Why (demonstrated, postulated, or inferred) | What can be learnt? |
|---|---|---|
| Categories were modelled well with most methods | All algorithms, with the exception of GARP could identify the pattern correctly. GARP's logistic regression rules treat categories as ordered data. Atomic rules should be able to model categorical values but must not have done so in our example, or might have been overwhelmed by logistic rules. | Categorical data such as soil type or land-use can be used in most methods. Don't use categorical data with GARP, or present it as ordered categories or in binary format. |
| Wetness modelled reasonably but there was some variation across methods | Wetness was the dominant driver for the distribution so was probably the easiest to model correctly. All methods were capable of modelling non-linear trends but MaxEnt modelled amplitude imperfectly (i.e. it was not well calibrated) because it had no information on prevalence. When sampling was sparse (wetness $\sim$30) GLM responds with a strong incorrect "trough" in predictions, a consequence of the complexity of fit allowed, and BRT and RF both overfit the response. MaxEnt did not model the detail in the sparse area, probably because the regularization was strong enough to model a smoother trend. | Presence-absence data gives more information for calibration than presence-only. Strong environmental trends are easiest to model.<br>If there are "troughs" in fitted functions think about whether they make sense ecologically and look at data sparsity. Ignore small fluctuations in fitted functions for ensemble methods because they likely represent peculiarities of the sample, and watch for their effect on predictions. Produce error estimates to see where data sparsity creates uncertainty. |
| Southness harder to model | Southness was less dominant in the model, and interactions complicate the response. GLM is likely to have done better if we modelled the interactions. | It is possible to model weaker trends, but this varies more across methods. Need to test if GARP's tendency to overpredict stems from an inability to capture all but the strongest trends.<br>Failing to allow interactions will compromise models. |
| Mapped predictions differ | Mapped predictions differ because the underlying fitted functions differ.<br>Also some clues about why they differ can be gleaned from the various evaluation stats – e.g. models with higher unexplained deviance should produce maps less consistent with the true pattern. | Differences in maps can be understood by looking at underlying models. It would be useful to develop tools to link the map to the functions to show, for any grid cell, what part of the function is relevant. This would be part of the more comprehensive evaluation toolbox that is needed. |
| Extrapolations differ | Extrapolations differ because of how the functions are or are not constrained at the edges of the environmental response variables. | Knowledge is required about 1) what a method is doing when extrapolating into novel environments, and 2) what is sensible. Again, it would be useful to have tools to link maps to fitted functions for exploring what is behind the predictions. |

only a small trough) to wetness at values early on the plateau of the true response – the samples are sparse in some parts of this environment, and several have been realised as ''absence'' in this particular sample. These results demonstrate that understanding the environmental distribution of the data in the region of interest, in the sample, and in regions that might be used for projection, is a critical part of understanding the implications for modelling and prediction.

Finally, the demonstration prompts a range of questions about what characteristics we want from models in certain situations. For example, when using species distribution models to predict how species ranges will shift with climate change or how they will extrapolate to new regions it is critical that we understand how the algorithm performs when projected into new environmental combinations not sampled by the training data. In other words, is the way that the algorithm extrapolates appropriate from an ecological perspective? Different behaviours are apparent in the implementations of the methods that we tested, but the choice as to which (if any) is correct is as much an ecological and/or a physiological question, as a statistical one. In fact, operationally there are more choices than we demonstrated – for example, GLMs can include natural splines in which knots can be specified and extrapolation controlled; MaxEnt has options to predict zero outside the range of the data. For a full investigation of extrapolation or forecasting behaviour a much larger range of tests is required including prediction to new combinations of environments. The important point is that we need to first recognise what different modelling applications require of SDMs and then research the best means for achieving what they require. Understanding how the models work and devising evaluation criteria that are closely matched to the questions being asked can inform decisions about the best modelling approach.

## Conclusion

We suggest that the SDM literature has not yet matured to the point that it provides clear guidance for selecting relevant methods. Additional model comparison studies may not be fruitful unless they start to ask why certain methods perform better than others. Deeper insights into the causes of varying model performance require an expansion of model evaluation approaches (Araújo and Guisan 2006), syntheses of existing knowledge, and contributions from experts. Given that applications of SDM have grown and are likely to continue to proliferate, insight into the characteristics of models that influence model performance is essential. For instance, there are applications

that do not satisfy the underlying assumptions of species equilibrium with environment (Dormann 2007) such as range shifts with climate, or species invasions into a new area. Likewise, there is an increased demand for models that capture realistic species-environment relationships for theoretical studies in both ecology (i.e. niche differentiation among related species) and evolution (i.e. trait conservatism and its influence on species distributions). For each case, what methods are particularly suitable for the intended use? By providing an example that we believe gives useful insight into model performance, we hope that both developers and users will increasingly question what their models are doing and whether that is most appropriate for the intended applications and outcomes.

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# Species' Distribution Modeling for Conservation Educators and Practitioners

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# Species' Distribution Modeling for Conservation Educators and Practitioners

Richard G. Pearson

## Abstract

Models that predict distributions of species by combining known occurrence records with digital layers of environmental variables have much potential for application in conservation. Through using this module, teachers will enable students: to develop species' distribution models; to apply the models across a series of analyses; and to interpret predictions accurately. Part A of the synthesis introduces the modeling approach, outlines key concepts and terminology, and describes questions that may be addressed using the approach. A theoretical framework that is fundamental to ensuring that students understand the uses and limitations of the models is then described. Part B of the synthesis details the main steps in building and testing a distribution model. Types of data that can be used are described and some potential sources of species' occurrence records and environmental layers are listed. The variety of alternative algorithms for developing distribution models is discussed, and software programs available to implement the models are listed. Techniques for assessing the predictive ability of a distribution model are then discussed, and commonly used statistical tests are described. Part C of the synthesis describes three case studies that illustrate applications of the models: 1) Predicting distributions of known and unknown species in Madagascar; 2) Predicting global invasions by plants of South African origin; and 3) Modeling the potential impacts of climate change on species' distributions in Britain and Ireland.

This synthesis document is part of an NCEP (Network of Conservation Educators and Practitioners; http://ncep.amnh.org/) module that also includes a presentation and a practical exercise:

- An introduction to species' distribution modeling: theory and practice (presentation by Richard Pearson)
- Species' distribution modeling using Maxent (practical by Steven Phillips)

This module is targeted at a level suitable for teaching graduate students and conservation professionals.

### Learning objectives

Through use of this synthesis, teachers will enable students to:

1. Understand the theoretical underpinnings of species' distribution models
2. Run a distribution model using appropriate data and methods
3. Test the predictive performance of a distribution model
4. Apply distribution models to address a range of conservation questions

## Introduction and Theory

### Introduction

Predicting species' distributions has become an important component of conservation planning in recent years, and a wide variety of modeling techniques have been developed for this purpose (Guisan and Thuiller, 2005). These models commonly utilize associations between environmental variables and known species' occurrence records to identify environmental conditions within which populations can be maintained. The spatial distribution of environments that are suitable for the species can then be estimated across a study region. This approach has proven valuable for generating biogeographical information that can be applied across a broad range of fields, including conservation biology, ecology, and

evolutionary biology. The focus of this synthesis is on conservation-oriented applications, but the methods and theory discussed are also applicable in other fields (see Table 1 for a list of some uses of species' distribution models in conservation biology and other disciplines).

This synthesis aims to provide an overview of the theory and practice of species' distribution modeling. Through use of the synthesis, teachers will enable students to understand the theoretical basis of distribution models, to run models using a variety of approaches, to test the predictive ability of models, and to apply the models to address a range of questions. Part A of the synthesis introduces the modeling approach and describes the usefulness of the models in addressing conservation questions. Part B details the main steps in building a distribution model, including selecting and obtaining suitable data, choosing a modeling algorithm, and statistically assessing predictive performance. Part C of the synthesis provides three case studies that demonstrate uses of species' distribution models.

*What is a species' distribution model?*

The most common strategy for estimating the actual or potential geographic distribution of a species is to characterize the environmental conditions that are suitable for the species, and to then identify where suitable environments are distributed in space. For example, if we are interested in modeling the distribution of a plant that is known to thrive in wet clay soils, then simply identifying locations with clay soils and high precipitation can generate an estimate of the species' distribution. There are a number of reasons why the species may not actually occupy all suitable sites (e.g. geographic barriers that limit dispersal, competition from other species), which we will discuss later in this synthesis. However, this is the fundamental strategy common to most distribution models.

The environmental conditions that are suitable for a species may be characterized using either a *mechanistic* or a *correlative* approach. Mechanistic models aim to incorporate physiologically limiting mechanisms in a species' tolerance to environmental conditions. For example, Chuine and Beaubien (2001) modeled distributions of North American tree species by estimating responses to environmental variables (including mean daily temperature, daily precipitation, and night length) using mechanistic models of factors including frost injury, phenology, and reproductive success. Such mechanistic models require detailed understanding of the physiological response of species to environmental factors and are therefore difficult to develop for all but the most well understood species.

Correlative models aim to estimate the environmental conditions that are suitable for a species by associating known species' occurrence records with suites of environmental variables that can reasonably be expected to affect the species' physiology and probability of persistence. The central premise of this approach is that the observed distribution of a species provides useful information as to the environmental requirements of that species. For example, we may assume that our plant species of interest favors wet clay soils because it has been observed growing in these soils. The limitations of this approach are discussed later in the synthesis, but it has been demonstrated that this method can yield valuable biogeographical information (e.g., Raxworthy et al., 2003; Bourg et al., 2005). Since spatially explicit occurrence records are available for a large number of species, the vast majority of species' distribution models are correlative. The correlative approach to distribution modeling is the focus of this synthesis.

The principal steps required to build and validate a correlative species' distribution model are outlined in Figure 1. Two types of model input data are needed: 1) known species' occurrence records; and 2) a suite of environmental variables. 'Raw' environmental variables, such as daily precipitation records collected from weather stations, are often processed to generate model inputs that are thought to have a direct physiological role in limiting the ability of the species to survive. For example, Pearson et al. (2002) used a suite of seven climate variables and five soil variables to generate five model input variables, including maximum annual temperature, minimum temperature over a 20-year period, and soil moisture availability. At this stage, care should be taken to ensure that data are checked for errors. For example, simply plotting the spe-

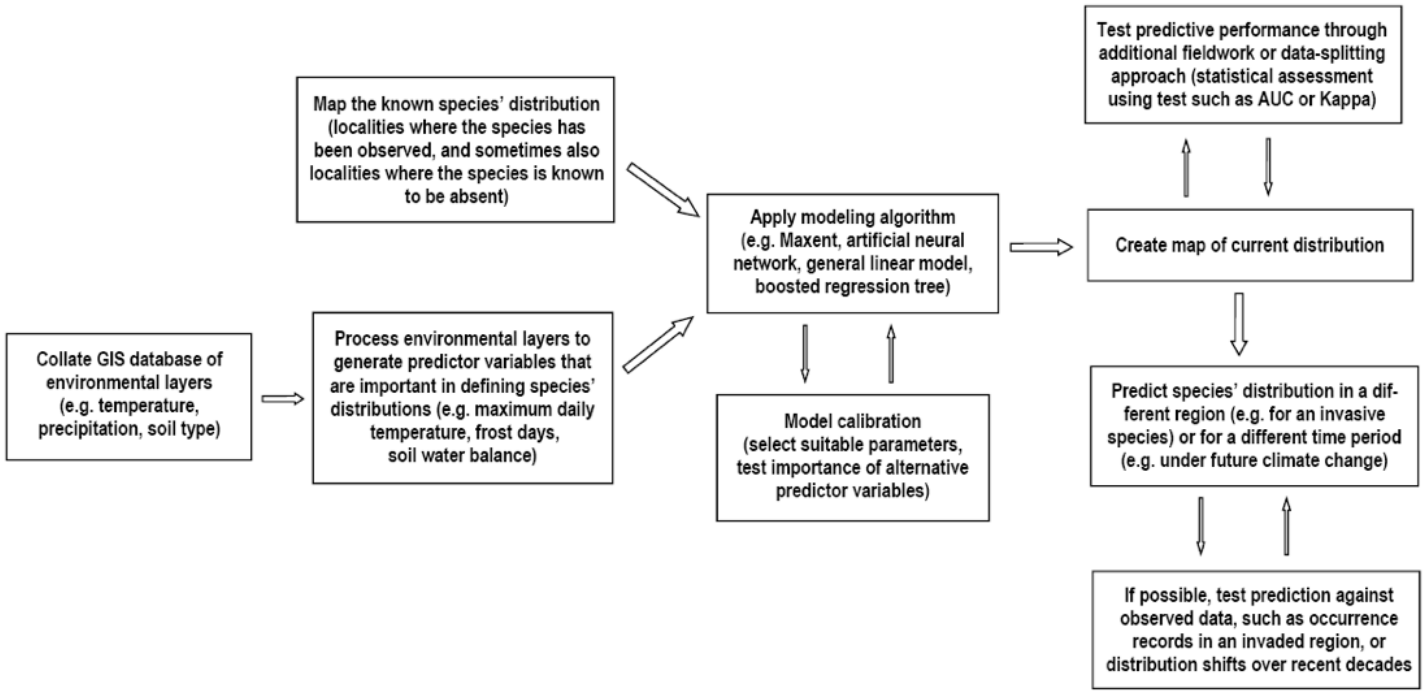


Figure 1. Flow diagram detailing the main steps required for building and validating a correlative species distribution model.

cies' occurrence records in a GIS can help identify records that are distant from other occupied sites and should therefore be checked for accuracy. Data types and sources are discussed in detail in the Section 3: 'Data types and sources'.

The species occurrence records and environmental variables are entered into an algorithm that aims to identify environmental conditions that are associated with species occurrence. If just one or two environmental variables were used, then this task would be relatively straightforward. For example, we may readily discover that our plant species has only been recorded at localities where mean monthly precipitation is above 60mm and soil clay content is above 40%. In practice, we usually seek algorithms that are able to integrate more than two environmental variables, since species are in reality likely to respond to multiple factors. Algorithms that can incorporate interactions among variables are also preferable (Elith et al., 2006). For example, a more accurate description of our plant's requirements may be that it can occur at localities with mean monthly precipitation between 60mm and 70mm if soil clay content is above 60%, and in wetter areas (>70mm) if clay content is as low as 40%.

A number of modeling algorithms that have been applied to this task are reviewed in Section 4. Depending on the method used, various decisions and tests will need to be made at this stage to ensure the algorithm gives optimal results. For example, a suitable 'regularization' parameter will need to be selected if applying the Maxent method (see Phillips et al., 2006 and Box 3), or the degrees of freedom must be selected if running a generalized additive model (see Guisan et al., 2002). The relative importance of alternative environmental predictor variables may also be assessed at this stage so as to select which variables are used in the final model.

Having run the modeling algorithm, a map can be drawn showing the predicted species' distribution. The ability of the model to predict the known species' distribution should be tested at this stage. A set of species occurrence records that have not previously been used in the modeling should be used as independent test data. The ability of the model to predict the independent data is assessed using a suitable test

statistic. Different approaches to generating test datasets and alternative statistical tests are discussed in the section: 'Assessing predictive performance'. Since a number of modeling algorithms predict a continuous distribution of environmental suitability (i.e. a prediction between 0 and 1, as opposed to a binary prediction of 'suitable' or 'unsuitable'), it is sometimes useful to convert model output into a prediction of suitable (1) or unsuitable (0). This is a necessary step before applying many test statistics; thus, methods for setting a threshold probability, above which the species is predicted as present, are also outlined in the section: 'Assessing predictive performance'.

Once these steps have been completed, and if model validation is successful, the model can be used to predict species' occurrence in areas where the distribution is unknown. Thus, a set of environmental variables for the area of interest is input into the model and the suitability of conditions at a given locality is predicted. In many cases the model is used to 'fill the gaps' around known occurrences (e.g., Anderson et al., 2002a; Ferrier et al., 2002). In other cases, the model may be used to predict species' distributions in new regions (e.g. to study invasion potential, for review see Peterson, 2003) or for a different time period (e.g. to estimate the potential impacts of future climate change, for review see Pearson and Dawson, 2003). Three examples of the use of predictions from species distribution models are presented in Part C. Ideally, model predictions in different regions or for different time periods should be tested against observed data; for example, Thuiller et al. (2005; see Case Study 2) tested predictions of invasion potential using occurrence records from the invaded distribution, while Araújo et al. (2005a) tested predictions of distribution shifts under climate change using observed records from different decades.

This modeling approach has been variously termed 'species distribution', 'ecological niche', 'environmental niche', 'habitat suitability' and 'bioclimate envelope' modeling. Use of the term 'species distribution modeling' is widespread but it should be noted that the term is somewhat misleading since it is actually the distribution of suitable environments that is being modeled, rather than the species' distribution *per se*. Regardless of the name used, the basic modeling process is essentially the same (see Part B) and the theoretical underpinnings of the models are similar. It is essential that these theoretical underpinnings are properly understood in order to interpret model outputs accurately. The following section describes this theoretical framework.

**Section 2. Theoretical Framework**

This section outlines some of the fundamental concepts that are crucial for understanding how species' distribution models work, what types of questions they are suitable for addressing, and how model output should be interpreted.

*Geographical versus environmental space*

We are used to thinking about the occurrence of species in geographical space; that is, the species' distribution as plotted on a map. To understand species' distribution models it is important to also think about species occurring in *environmental space*, which is a conceptual space defined by the environmental variables to which the species responds. The concept of environmental space has its foundations in ecological niche theory. The term 'niche' has a long and varied history of use in ecology (Chase and Leibold, 2003), but the definition proposed by Hutchinson (1957) is most useful in the current context. Hutchinson defined the *fundamental niche* of a species as the set of environmental conditions within which a species can survive and persist. The fundamental niche may be thought of as an '*n*-dimensional hypervolume', every point in which corresponds to a state of the environment that would permit the species to exist indefinitely (Hutchinson, 1957). It is the axes of this n-dimensional hypervolume that define environmental space.

Visualizing a species' distribution in both geographical and environmental space helps us to define some basic concepts that are crucial for species' distribution modeling (Fig. 2). Notice that the observed localities constitute all that is known about the species' *actual distribution*; the species is likely to occur in other areas in which it has not yet been detected (e.g., Fig. 2, area *A*). If the actual distribution is plotted in envi-

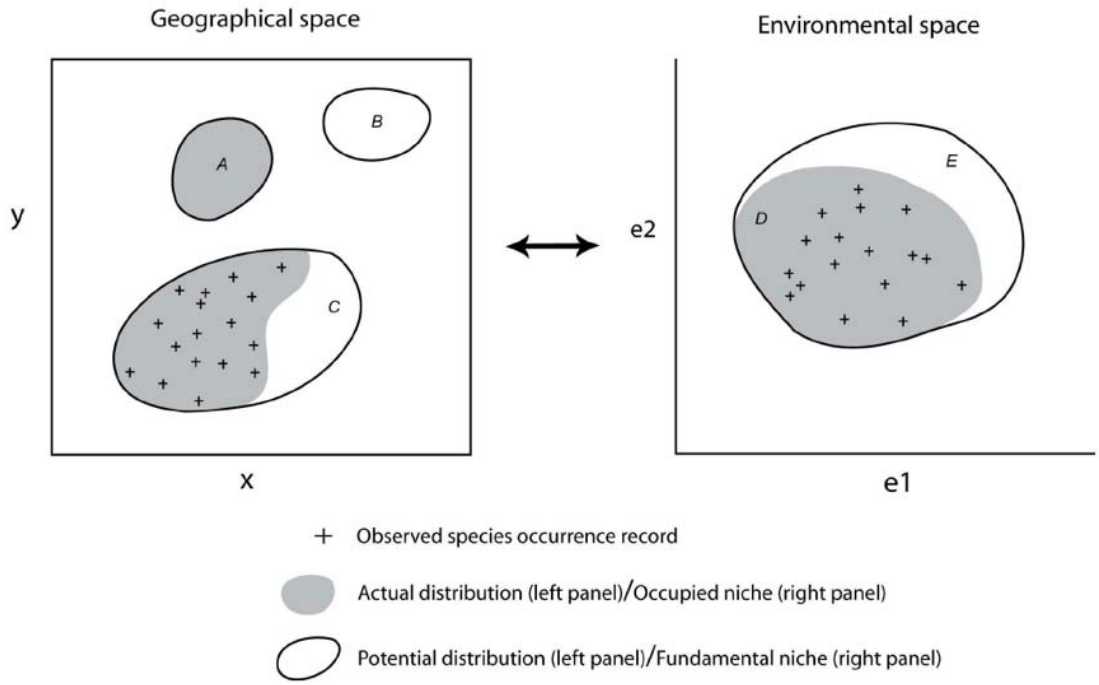


Figure 2. Illustration of the relationship between a hypothetical species' distribution in geographical space and environmental space. Geographical space refers to spatial location as commonly referenced using *x* and *y* coordinates. Environmental space refers to Hutchinson's *n*-dimensional niche, illustrated here for simplicity in only two dimensions (defined by two environmental factors, $e_1$ and $e_2$). Crosses represent observed species occurrence records. Grey shading in geographical space represents the species' actual distribution (i.e. those areas that are truly occupied by the species). Notice that some areas of actual distribution may be unknown (e.g. area A is occupied but the species has not been detected there). The grey area in environmental space represents that part of the niche that is occupied by the species: the occupied niche. Again, notice that the observed occurrence records may not identify the full extent of the occupied niche (e.g. the shaded area immediately around label D does not include any known localities). The solid line in environmental space depicts the species' fundamental niche, which represents the full range of abiotic conditions within which the species is viable. In geographical space, the solid lines depict areas with abiotic conditions that fall within the fundamental niche; this is the species' potential distribution. Some regions of the potential distribution may not be inhabited by the species due to biotic interactions or dispersal limitations. For example, area B is environmentally suitable for the species, but is not part of the actual distribution, perhaps because the species has been unable to disperse across unsuitable environments to reach this area. Similarly, the non-shaded area around label C is within the species' potential distribution, but is not inhabited, perhaps due to competition from another species. Thus, the non-shaded area around label *E* identifies those parts of the fundamental niche that are unoccupied, for example due to biotic interactions or geographical constraints on species dispersal.

ronmental space then we identify that part of environmental space that is occupied by the species, which we can define as the *occupied niche*.

The distinction between the occupied niche and the fundamental niche is similar, but not identical, to Hutchinson's (1957) distinction between the realized niche and the fundamental niche. With reference to the case of two species utilizing a common resource, Hutchinson described the realized niche as comprising that portion of the fundamental niche from which a species is not excluded due to biotic competition. The definition of the occupied niche used in this synthesis broadens this concept to include geographical and historical constraints resulting from a species' limited ability to reach or re-occupy all suitable areas, along with biotic interactions of all forms (competition, predation, symbiosis, and parasitism). Thus, the occupied niche reflects all constraints imposed on the actual distribution, including spatial constraints due to

limited dispersal ability, and multiple interactions with other organisms.

If the environmental conditions encapsulated within the fundamental niche are plotted in geographical space then we have the *potential distribution*. Notice that some regions of the potential distribution may not be inhabited by the species (Fig. 2, areas B and C), either because the species is: excluded from the area by biotic interactions (e.g., presence of a competitor or absence of a food source); the species has not dispersed into the area (e.g., there is a geographic barrier to dispersal, such as a mountain range, or there has been insufficient time for dispersal); or the species has been extirpated from the area (e.g. due to human modification of the landscape).

Before we go on to discuss how these concepts are used in distribution modeling, it is important to appreciate that the environmental variables used in a distribution model are unlikely to define all possible dimensions of environmental space. Hutchinson (1957) originally proposed that all variables, "both physical and biological" are required to define the fundamental niche. However, the variables available for modeling are likely to represent only a subset of possible environmental factors that influence the distribution of the species. Variables used in modeling most commonly describe the physical environment (e.g. temperature, precipitation, soil type), though aspects of the biological environment are sometimes incorporated (e.g. Araújo and Luoto 2007, Heikkinen et al. 2007). However, the distinction between biotic and abiotic variables is often problematic; for example, land cover type is likely to incorporate both abiotic (e.g. urban) and biotic (e.g. deciduous forest) classes.

Another important factor that we must be aware of is source-sink dynamics, which may cause a species to be observed in unsuitable environments. 'Source-sink' refers to the situation whereby an area (the 'sink') may not provide the necessary environmental conditions to support a viable population, yet may be frequently visited by individuals that have dispersed from a nearby area that does support a viable population (the 'source'). In this situation, species occurrence may be recorded in sink areas that do not represent suitable habitat, meaning that the species is present outside its fundamental niche (Pulliam, 2000). We can logically expect this situation to occur most frequently in species with high dispersal ability, such as birds. In such cases, it is useful to only utilize records for modeling that are known to be from breeding distributions, rather than migrating individuals. Because correlative species distribution models utilize observed species occurrence records to identify suitable habitat, inclusion of occurrence localities from sink populations is problematic. However, it is often assumed that observations from source areas will be much more frequent than observations from sink areas, so this source of potential error is commonly overlooked.

One more thing to be aware of before we move on is that some studies explicitly aim to only investigate one part of the fundamental niche, by using a limited set of predictor variables. For example, it is common when investigating the potential impacts of future climate change to focus only on how climate variables impact species' distributions. A species' niche

Bog rosemary (*Andromeda polifolia*), which was modeled by Berry et al. (2002). See Case Study 3. Source: Mako, from Kangasala, Suomi.

defined only in terms of climate variables may be termed the *climatic niche* (Pearson and Dawson, 2003), which represents the climatic conditions that are suitable for species existence. An approximation of the climatic niche may then be mapped in geographical space, giving what is commonly termed the *bioclimate envelope* (Huntley et al., 1995; Pearson and Dawson, 2003).

*Estimating niches and distributions*

Let us now consider the extent to which species' distribution models can be used to estimate the niche and distribution of a species. We will assume in this section that the model algorithm is excellent at defining the relationship between observed occurrence localities and environmental variables; this will enable us to focus on understanding the ecological assumptions underlying distribution models. The ability of different modeling algorithms to identify the relationship between occurrence localities and environmental variables is discussed in the section: 'Modeling Algorithms'.

Let us first ask what the aim of the modeling is: what element of a species' distribution are we trying to estimate? There are many potential uses of the approach (Table 1) and these require modeling either the actual distribution or the potential distribution. For example, if a model is being used with the purpose of selecting sites that should be given high conservation priority, then modeling the actual distribution will be the aim (since there would be less priority given to conserving sites where the environment is suitable for the species, but the species is not present). In contrast, if the purpose is to identify sites that may be suitable for the reintroduction of an endangered species, then modeling the potential distribution is an appropriate aim. We will now consider the degree to which alternative aims are achievable using the species' distribution modeling approach.

Correlative species' distribution models rely on observed occurrence records for providing information on the niche and distribution of a species. Two key factors are important when considering the degree to which observed species occurrence records can be used to estimate the niche and distribution of a species:

**Table 1. Some published uses of species' distribution models in conservation biology (based in part on Guisan and Thuiller, 2005).**

| Type of use | Example reference(s) |
|---|---|
| Guiding field surveys to find populations of known species | Bourg et al., 2005; Guisan et al., 2006 |
| Guiding field surveys to accelerate the discovery of unknown species | Raxworthy et al., 2003 |
| Projecting potential impacts of climate change | Iverson and Prasad, 1998; Berry et al., 2002; Hannah et al., 2005; for review see Pearson and Dawson, 2003 |
| Predicting species' invasion | Higgins et al., 1999; Thuiller et al., 2005; for review see Peterson, 2003 |
| Exploring speciation mechanisms | Kozak and Wiens, 2006; Graham et al., 2004b |
| Supporting conservation prioritization and reserve selection | Araújo and Williams, 2000; Ferrier et al., 2002; Leathwick et al., 2005 |
| Species delimitation | Raxworthy et al., 2007 |
| Assessing the impacts of land cover change on species' distributions | Pearson et al., 2004 |
| Testing ecological theory | Graham et al., 2006; Anderson et al., 2002b |
| Comparing paleodistributions and phylogeography | Hugall et al., 2002 |
| Guiding reintroduction of endangered species | Pearce and Lindenmayer, 1998 |
| Assessing disease risk | Peterson et al., 2006, 2007 |

1) *The degree to which the species is at 'equilibrium' with current environmental conditions.*

   A species is said to be at equilibrium with the physical environment if it occurs in all suitable areas, while being absent from all unsuitable areas. The degree of equilibrium depends both on biotic interactions (for example, competitive exclusion from an area) and dispersal ability (organisms with higher dispersal ability are expected to be closer to equilibrium than organisms with lower dispersal ability) (Araújo and Pearson, 2005). When using

the concept of 'equilibrium,' we should remember that species distributions change over time, so the term should not be used to imply stasis. However, the concept is useful for us here to help understand that some species are more likely than others to occupy areas that are abiotically suitable.

2) *The extent to which observed occurrence records provide a sample of the environmental space occupied by the species.*
In cases where very few occurrence records are available, perhaps due to limited survey effort (Anderson and Martinez-Meyer, 2004) or low probability of detection (Pearson et al., 2007), the available records are unlikely to provide a sufficient sample to enable the full range of environmental conditions occupied by the species to be identified. In other cases, surveys may provide extensive occurrence records that provide an accurate picture as to the environments inhabited by a species in a particular region (for example, breeding bird distributions in the United Kingdom and Ireland are well known) (Gibbons et al., 1993). It should be noted that there is not necessarily a direct relationship between sampling in geographical space and in environmental space. It is quite possible that poor sampling in geographical space could still result in good sampling in environmental space.

Each of these factors should be carefully considered to ensure appropriate use of a species' distribution model (see Box 1). In reality, species are unlikely to be at equilibrium (as illustrated by area B in Fig. 2, which is environmentally suitable but is not part of the actual distribution) and occurrence records will not completely reflect the range of environments occupied by the species (illustrated by that part of the occupied niche that has not been sampled around label D in Fig. 2). Fig. 3 illustrates how a species' distribution model may be fit under these circumstances. Notice that the model is calibrated (i.e. built) in environmental space and then projected into geographical space. In environmental space, the model identifies neither the occupied niche nor the fundamental niche; instead, the model fits only to that portion of the niche that is represented by the observed records. Similarly, the model identifies only some parts of the actual and potential distributions when projected back into geographical space. Therefore, it should not be expected that species' distribution models are able to predict the full extent of either the actual distribution or the potential distribution.

This observation may be regarded as a failure of the modeling approach (Woodward and Beerling, 1997; Lawton, 2000; Hampe, 2004). However, we can identify three types of model predictions that yield important biogeographical information: species' distribution models may identify 1) the area around the observed occurrence records that is expected to be occupied (Fig. 3, area 1); 2) a part of the actual distribution that is currently unknown (Fig. 3, area 2); and/or 3) part of the potential distribution that is not occupied (Fig. 3, area 3). Prediction types 2 and 3 can prove very useful in a range of applications, as we will see in the following section.

*Uses of species' distribution models*

Consider modeled area 2 in Fig. 3, which identifies part of the actual distribution for which no occurrence records have been collected. Although the model does not predict the full extent of the actual distribution, additional sampling in the area identified may yield new occurrence records. A number of studies have demonstrated the utility of species' distribution modeling for guiding field surveys toward regions where there is an increased probability of finding new populations of a known species (Fleishman et al., 2002; Bourg et al., 2005; Guisan et al., 2006; also see Case Study 1). Accelerating the discovery of new populations in this way may prove extremely useful for conservation planning, especially in poorly known and highly threatened landscapes.

Consider now predicted area 3 in Fig. 3. Here, the model identifies an area of potential distribution that is environmentally similar to where the species is known to occur, but which is not inhabited. The full extent of the potential distribution is not predicted, but the model can be useful for identifying sites that may be suitable for reintroduction of a species (Pearce and Lindenmayer, 1998) or sites where a species is most likely to become invasive (if it overcomes dispersal barriers and if

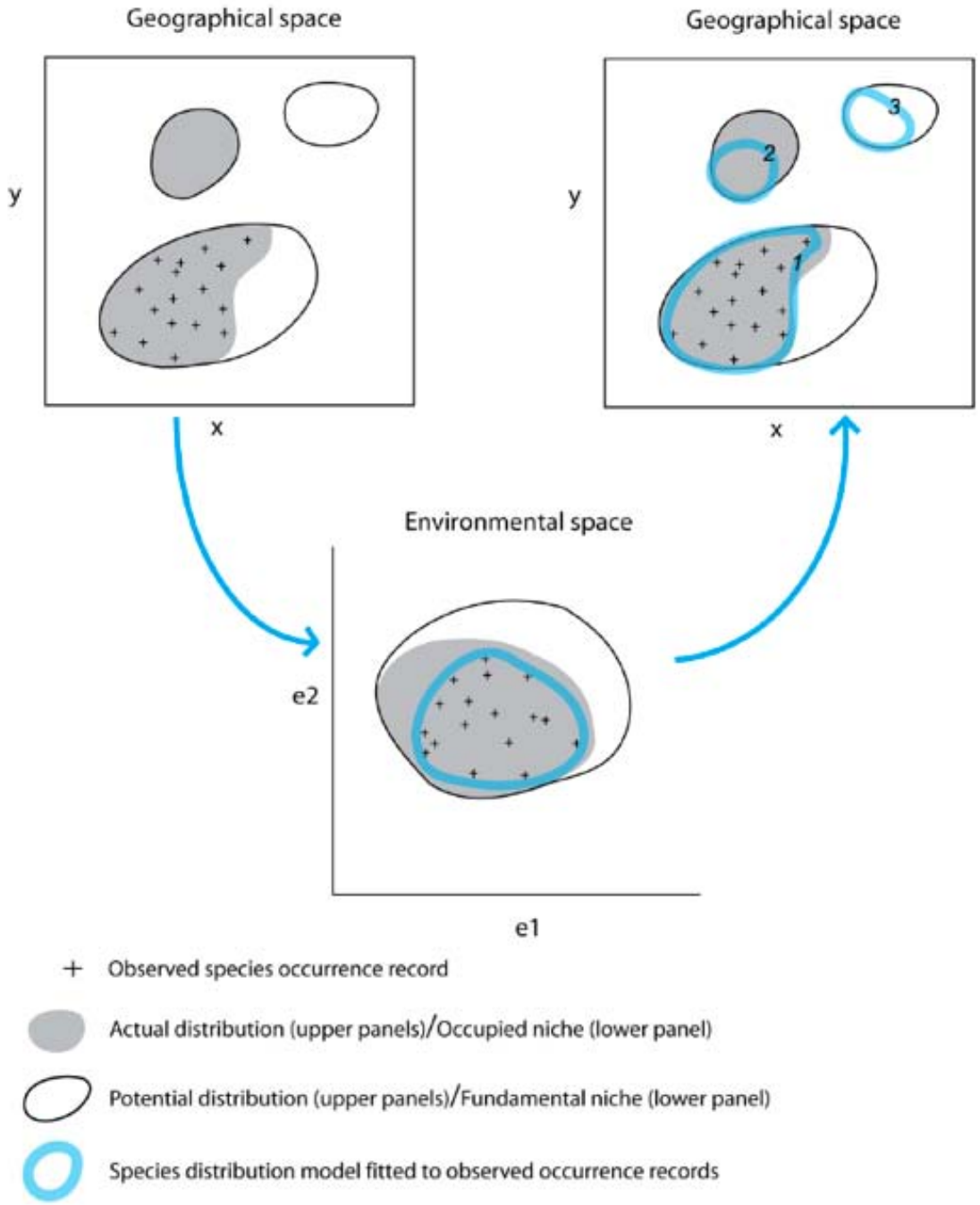


Figure 3. Diagram illustrating how a hypothetical species' distribution model may be fitted to observed species occurrence records (using the same hypothetical case as in Fig. 2). A modelling technique (e.g. GARP, Maxent) is used to characterize the species' niche in environmental space by relating observed occurrence localities to a suite of environmental variables. Notice that, in environmental space, the model may not identify either the species' occupied niche or fundamental niche; rather, the model identifies only that part of the niche defined by the observed records. When projected back into geographical space, the model will identify parts of the actual distribution and potential distribution. For example, the model projection labeled *1* identifies the known distributional area. Projected area *2* identifies part of the actual distribution that is currently unknown; however, a portion of the actual distribution is not predicted because the observed occurrence records do not identify the full extent of the occupied niche (i.e. there is incomplete sampling; see area *D* in Fig. *2*). Similarly, modeled area *3* identifies an area of potential distribution that is not inhabited (the full extent of the potential distribution is not identified because the observed occurrence records do not identify the full extent of the fundamental niche due to, for example, incomplete sampling, biotic interactions, or constraints on species dispersal; see areas *D* and *E* in Fig. 2).

biotic competition does not prevent establishment) (Peterson, 2003). Model predictions of this type also have the potential to accelerate the discovery of previously unknown species that are closely related to the modeled species and that occupy similar environmental space but different geographical space (Raxworthy et al., 2003; see Case Study 1).

Model predictions as illustrated in Fig. 3 therefore have the potential to yield useful information, even though species are not expected to inhabit all suitable locations and sampling may be poor. Additional uses of species' distribution modeling include identifying potential areas for disease outbreaks (Peterson et al., 2006), examining niche evolution (Peterson et al., 1999; Kozak and Wiens, 2006) and informing taxonomy (Raxworthy et al., 2007). However, some potential applications require an estimation of the actual distribution of a species. For example, if a model is being used with the purpose of selecting priority sites for conservation, then an estimate of the actual species' distribution is desired since it would be inefficient to conserve sites where the species is not present (Loiselle et al., 2003). In such cases, it should be remembered that modeled distributions represent environmentally suitable regions but do not necessarily correspond closely with the actual distribution. Additional processing of model output may be required to improve predictions of the actual distribution. For example, predicted areas that are isolated from observed occurrence records by a dispersal barrier may be removed (Peterson et al., 2002) and the influence of competing species may be incorporated (Anderson et al., 2002b).

It is useful to note that mechanistic distribution models (e.g., Chuine and Beaubien, 2001) are subject to the same basic caveat as correlative approaches: the models aim to identify areas with suitable environmental conditions, but do not inform us which areas are actually occupied. Mechanistic models are ideally suited to identifying a species' fundamental niche, and hence its potential distribution. This is because mechanistic approaches model physiological limitations in a species' environmental tolerance, without relying on known occurrence records to define suitable environments. However, the detailed understanding of species' physiology that is required to build mechanistic models prohibits their use in many instances.

The discussion in this section should help clarify the theoretical basis of the species' distribution modeling approach. It is crucial that any application of these models has a sound theoretical basis and that model outputs are interpreted in the context of this framework (see Box 1). It should now be apparent why the terminology used to describe these models is so varied throughout the literature. The terms 'ecological niche model', 'environmental niche model', 'bioclimate envelope model' and 'environmental suitability model' usually refer to attempts to estimate the potential distribution of a species. Use of the term 'species distribution model' implies that the aim is to simulate the actual distribution of the species. Nevertheless, each of these terms refers to the same basic approach, which can be summarized as follows: 1) the study area is modeled as a raster map composed of grid cells at a specified resolution; 2) the dependent variable is the known species' distribution; 3) a suite of environmental variables are collated to characterize each cell; and 4) a function of the environmental variables is generated so as to classify the degree to which each cell is suitable for the species (Hirzel et al., 2002). Part B of this synthesis details the principal steps required to build a distribution model, including selecting and obtaining suitable data, choosing a modeling algorithm, and statistically assessing predictive performance.

## Developing a Species' Distribution Model

### Data Types and Sources

Correlative species' distribution models require two types of data input: *biological data*, describing the known species' distribution, and *environmental data*, describing the landscape in which the species is found. This section discusses the types of data that are suitable for distribution modeling, and reviews some possible sources of data (see Table 2).

Data used for distribution modeling are usually stored in a Geographical Information System (GIS; see Box 2). The data may be stored either as point localities (termed 'point vector' data; e.g. sites where a species has been observed, or locations

**Box 1. Caution! On the use and misuse of models**

*Garbage in, garbage out:* This old adage is as relevant to distribution modeling as it is to other fields. Put simply, a model is only as good as the data it contains. Thus, if the occurrence records used to build a correlative species' distribution model do not provide useful information as to the environmental requirements of the species, then the model cannot provide useful output. If you put garbage into the model, you will get garbage out.

*Model extrapolation:* 'Extrapolation' refers to the use of a model to make predictions for areas with environmental values that are beyond the range of the data used to calibrate (i.e. develop) the model. For example, suppose a distribution model was calibrated using occurrence records that spanned a temperature range of 10–20°C. If the model is used to predict the species' distribution in a different region (or perhaps under a future climate scenario) where the temperature reaches 25°C, then the model is extrapolating. In this case, because the model has no prior information regarding the probability of the species' occurrence at 25°C, the prediction may be extremely uncertain (see Pearson et al., 2006). Model extrapolation should be treated with a great deal of caution.

*The lure of complicated technology:* Many approaches to modeling species' distributions utilize complex computational technology (e.g. machine learning tools such as artificial neural networks and genetic algorithms) along with huge GIS databases of digital environmental layers. In some cases, these approaches can yield highly successful predictions. However, there is a risk that model users will be swayed by the apparent complexity of the technology: "it is so complicated, it must be correct!" Always remember that a model can only be useful if the theoretical underpinnings on which it is based are sound.

For additional discussion of the limitations of ecological models, see the NCEP module: *Applications of Remote Sensing to Ecological Modeling.*

of weather stations), as polygons defining an area (termed 'polygon vector' data; e.g. areas with different soil types) or as a grid of cells (termed 'raster' data; e.g. land cover types derived from remote sensing [see NCEP module: *Remote Sensing for Conservation Biology*]). For use in a distribution model, it is usual to reformat all environmental data to a raster grid. For example, temperature records from weather stations may be interpolated to give continuous data over a grid (Hijmans et al., 2005). Formatting all data to the same raster grid ensures that environmental data are available for every cell in which biological data have been recorded. These cells, containing both biological data and environmental data, are used to build the species' distribution model. After the model is constructed, its fit to test occurrence records is evaluated (see section: 'Assessing Predictive Performance') and, if the fit is judged to be acceptable, the occurrence of species in cells for which only environmental data are available can be predicted. Note that in some applications the model may be used to predict the species' distribution in a region from which data were not used to build the model (e.g. to predict the spread of an invasive species) or under a future climate scenario. In these cases, environmental data for the new region or climate scenario must also be collated.

A consideration when collating data is the spatial scale at which the model will operate. Spatial scale has two components: *extent* and *resolution* (see NCEP module *Applications of remote sensing to ecological modeling*). Extent refers to the size of the region over which the model is run (e.g. New York state or the whole of North America) whilst resolution refers to the size of grid cells (e.g. 1 $km^2$ or 10 $km^2$). Note that it is common for datasets with large extent to have coarse resolution (e.g. data for North America at 10 $km^2$) and datasets with small extent to have fine resolution (e.g. New York state at 1 $km^2$). Spatial scale can play an important role in the application of a species' distribution model. In particular, ideally the data resolution should be relevant to the species under consideration: the appropriate data resolution for studying ants is

likely to be very different from that for studying elephants.

*Biological data*

Data describing the known distribution of a species may be obtained in a variety of ways:

1) *Personal collection*: occurrence localities can be obtained during field surveys by an individual or small group of researchers. For example, Fleishman et al. (2001) built models using butterfly occurrence records collected by the researchers during surveys in Nevada, USA.
2) *Large surveys*: distribution information may be available from surveys undertaken by a large number of people. For example, Araújo et al. (2005a) built distribution models using data from *The New Atlas of Breeding Birds in Britain and Ireland*: *1988-1991* (Gibbons et al., 1993), which represents the sampling effort of hundreds of volunteers.
3) *Museum collections:* occurrence localities can be obtained from collections in natural history museums. For example, Raxworthy et al. (2003) utilized occurrence records of chameleons in Madagascar that are held in museum collections.
4) *Online resources:* distributional data from a variety of sources are increasing being made available over the internet (see Table 2). For example, the Global Biodiversity Information Facility (www.gbif.org) is collating available datasets from a diversity of sources and making the information available online via a searchable web portal.

Species distribution data may be either *presence-only* (i.e. records of localities where the species has been observed) or *presence/absence* (i.e. records of presence and absence of the species at sampled localities). Different modeling approaches have been developed to deal with each of these cases (see section on: 'Modeling Algorithms'). In some instances, the inclusion of absence records has been shown to improve model performance (Brotons et al., 2004). However, absence records are often not available and may be unreliable in some cases. In particular, absences may be recorded when the species was not detected even though the environment was suitable. These cases are often referred to as 'false absences' because the model will interpret the record as denoting unsuitable environmental conditions, even though this is not the case. False absences can occur when a species could not be detected although it was present, or when the species was absent but the environment was in fact suitable (e.g. due to dispersal limitation or metapopulation dynamics). Inclusion of false absence records may seriously bias analyses, so absence data should be used with care (Hirzel et al., 2002).

There are a number of additional potential sources of bias and

**Box 2. The Role of Geographic Information Systems (GIS)**

GIS is a vital tool in species' distribution modeling. The large datasets of biological and environmental data that are used in distribution modeling are ideally suited to being stored, viewed, and formatted in a GIS. For example, useful GIS operations include changing geographic reference systems (it is essential that all data are referenced to a common coordinate system, so occurrence records can be matched with the environmental conditions at the site), reformatting spatial resolution, and interpolating point locality data to a grid. GIS is also crucial for visualizing model results and carrying out additional processing of model output, such as removing predicted areas that are isolated from observed species records by a dispersal barrier (Peterson et al., 2002). However, the distribution modeling itself is usually undertaken outside the GIS framework. With few exceptions (e.g. Ferrier et al., 2002), the distribution model does not 'see' geographical coordinates; instead, the model operates in environmental space (see section: 'Theoretical Framework'). Some GIS platforms now incorporate distribution modeling tools (e.g. DIVA GIS: www.diva-gis.org/, IDRISI: http://www.clarklabs.org/), or have add-in scripts that enable distribution models to be run (e.g. BIOCLIM script for ArcView: http://arcscripts.esri.com/details.asp?dbid=13745), but running the model within a GIS is not necessary.

**Table 2. Some example sources of biological and environmental data for use in species' distribution modeling**

| Type of data | Source |
|---|---|
| *Species' distributions* | |
| - Data for a wide range of organisms in many regions of the world | Global Biodiversity Information Facility (GBIF): www.gbif.org |
| - Data for a range of organisms, mostly rare or endangered, and primarily in North America | NatureServe: www.NatureServe.org |
| *Climate* | |
| - Interpolated climate surfaces for the globe at 1km resolution | WorldClim:http://www.worldclim.org/ |
| - Scenarios of future climate change for the globe | Intergovernmental Panel on Climate Change (IPCC): http://www.ipcc-data.org/ |
| - Reconstructed palaeoclimates | NOAA: http://www.ncdc.noaa.gov/paleo/paleo.html |
| *Topography* | |
| - Elevation and related variables for the globe at 1km resolution | USGS: http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html |
| *Remote sensing (satellite)* | |
| - Various land cover datasets | Global Landcover Facility: http://glcf.umiacs.umd.edu/data/ |
| - Various atmospheric and land products from the MODIS instrument | NASA:http://modis.gsfc.nasa.gov/data/ |
| *Soils* | |
| - Global soil types | UNEP: http://www.grid.unep.ch/data/data.php?category=lithosphere |
| *Marine* | |
| - Various datasets describing the world's oceans | NOAA: www.nodc.noaa.gov |

error that should be carefully considered when collating species' distribution data. Errors may arise through the incorrect identification of species, or inaccurate spatial referencing of samples. Biases can also be introduced because collectors tend to sample in easily accessible locations, such as along roads and rivers and near towns or biological stations (Graham et al., 2004a). In some cases, biased sampling in geographical space may lead to non-representative sampling of the available environmental conditions, although this is not necessarily the case. When utilizing records from museum collections, it should be remembered that these data were not generally collected with the purpose of determining the distributional limits of a species; rather, sampling for museum collections tends to be biased toward rare and previously unknown species.

*Environmental data*

A wide range of environmental input variables have been employed in species' distribution modeling. Most common are variables relating to climate (e.g. temperature, precipitation), topography (e.g., elevation, aspect), soil type and land cover type (see Table 2). Variables tend to describe primarily the abiotic environment, although there is potential to include biotic interactions within the modeling. For example, Heikkinen et al. (2007) used the distribution of woodpecker species to predict owl distributions in Finland since woodpeckers excavate cavities in trees that provide nesting sites for owls.

As noted in the previous section: 'Introduction' variables are

often processed to generate new variables that are thought to have a direct physiological or behavioral role in determining species' distributions. In general, it is advisable to avoid predictor variables that have an indirect influence on species' distributions, since indirect associations may cause erroneous predictions when models are used to predict the species' distribution in new regions or under alternative climate scenarios (Guisan and Thuiller, 2005). For example, species do not respond directly to elevation, but rather to changes in temperature and air pressure that are affected by elevation. Thus, a species characterized as living at high elevation in a low latitude region may, in fact, be associated with lower elevations in areas with higher latitude, since the regional climate is cooler.

Environmental variables may comprise either *continuous data* (data that can take any value within a certain range, such as temperature or precipitation) or *categorical data* (data that are split into discrete categories, such as land cover type or soil type). Categorical data cannot be used with a number of common modeling algorithms (see section: 'Modeling Algorithms'). In these cases, it may be possible to generate a continuous variable from the categorical data. For example, Pearson et al. (2002) estimated soil water holding capacity from categorical soil data, and used these values within a water balance model to generate continuous predictions of soil moisture surplus and deficit.

Modern technologies, including remote sensing (see NCEP module *Applications of remote sensing to ecological modeling*), the internet, and GIS have greatly facilitated the collection and dissemination of environmental datasets (see Table 2). In addition, global climate models have been used to generate scenarios of future climates and to simulate climatic conditions since the end of the last glacial period (see Table 2). Predicted future climate scenarios can be used to estimate the potential impacts of climate change on biodiversity (e.g. Thomas et al. 2004; see case study 3), whilst simulations of past climates can be used to test the predictive ability of models (e.g. Martinez-Meyer et al., 2004). Given the vast amounts of data that are available, it is especially important to remain critical as to which variables are suitable for inclusion in the model. Some studies have demonstrated good predictive ability using only three variables (e.g., Huntley et al., 1995), whilst other studies have applied methodologies that can incorporate many more variables (e.g., Phillips et al., [2006] utilized 14 environmental variables, although some of these variables are likely to have been rejected by the algorithm applied because they did not provide useful information beyond that which was included in other variables).

**Modeling Algorithms**

A number of alternative modeling algorithms have been applied to classify the probability of species' presence (and absence) as a function of a set of environmental variables. The task is to identify potentially complex non-linear relationships in multi-dimensional environmental space. In the section: 'Theoretical Frameworks', we assumed that the modeling algorithm is excellent, enabling us to identify three expected types of model prediction, illustrated by modeled areas *1, 2* and *3* in Fig. 3. If we now admit some degree of error in the algorithm's ability to fit the observed records, then a fourth type of prediction will occur: the model will predict as suitable areas that are part of neither the actual nor the potential distribution. The most useful algorithms will limit these erroneous 'type 4' predictions.

Table 3 lists some commonly used approaches for species' distribution modeling. Some methods that have been applied are statistical (e.g. generalized linear models [GLMs] and generalized additive models [GAMs]), whilst other approaches are based on machine-learning techniques (e.g., maximum entropy [Maxent] and artificial neural networks [ANNs]). Published studies have often applied one or more of these algorithms and have given the resulting model a name or acronym (e.g., 'Maxent' refers to an implementation of the maximum entropy method, while 'BIOMOD' is the acronym given to a model that implements a number of methods, including GLMs and GAMs). Often these models have been implemented in user-friendly software that is free and easy to obtain (Table 3).

There are some important differences between among model algorithms that should be carefully considered when selecting which method(s) to apply. One key factor is whether the algorithm requires data on observed species absence (see 'Data Types and Sources'). Some algorithms operate by contrasting sites where the species has been detected with sites where the species has been recorded as absent (e.g., GLMs, GAMs, ANNs). However, reliable absence data often are not available (see: 'Data Types and Sources'), so other methods have been applied that do not require absence data. We can distinguish three types of presence-only methods:

1) Methods that rely solely on presence records (e.g. BIOCLIM, DOMAIN). These methods are truly 'presence-

**Table 3. Some published methods for species' distribution modeling**

| Method(s)[1] | Model/software name[2] | Species data type | Key reference/URL |
|---|---|---|---|
| Gower Metric | DOMAIN★ | presence-only | Carpenter et al., 1993<br>http://www.cifor.cgiar.org/docs/_ref/research_tools/domain/<br>http://diva-gis.org |
| Ecological Niche Factor Analysis (ENFA) | BIOMAPPER★ | presence and background | Hirzel et al., 2002<br>http://www2.unil.ch/biomapper/ |
| Maximum Entropy | MAXENT★ | presence and background | Phillips et al., 2006<br>http://www.cs.princeton.edu/~schapire/maxent/ |
| Genetic algorithm (GA) | GARP[3]★ | pseudo-absence[4] | Stockwell and Peters, 1999<br>http://www.lifemapper.org/desktopgarp/ |
| Artificial Neural Network (ANN) | SPECIES | presence and absence (or pseudo-absence) | Pearson et al., 2002 |
| Regression:<br>generalized linear model (GLM), generalized additive model (GAM), boosted regression trees (BRT), multivariate adaptive regression splines (MARS) | Implemented in R[5] | presence and absence (or pseudo-absence) | Lehman et al., 2002<br>Elith et al., 2006<br>Leathwick et al., 2006<br>Elith et al., 2007 |
| Multiple methods | BIOMOD | presence and absence (or pseudo-absence) | Thuiller, 2003 |
| Multiple methods | OpenModeller | depends on method implemented | http://openmodeller.sourceforge.net/ |

[1] 'Method' refers to a statistical or machine-learning technique. [2]'Model/software name' refers to a name (or acronym) given to a published model that implements the method(s) stated. Software to implement the method for species' distribution modeling is readily available at no cost for those models marked with an asterisk (★); other models are available at the discretion of the author(s). [3]The genetic algorithm for rule-set prediction (GARP) includes within its processing multiple methods, including GLM. [4]Note that Pseudo-absence here refers to the sampling approach implemented in the GARP software; in principle, any presence-absence method can be implemented using pseudo absences. [5]R is a freely available (at no cost) software environment for statistical computing and graphics (http://www.r-project.org/). Based in part on Elith et al. (2006) and Guisan and Thuiller (2005).

only' since the prediction is made without any reference to other samples from the study area.

2) Methods that use 'background' environmental data for the entire study area (e.g. Maxent, ENFA). These methods focus on how the environment where the species is known to occur relates to the environment across the rest of the study area (the 'background'). An important point is that the occurrence localities are also included as part of the background.
3) Methods that sample 'pseudo-absences' from the study area. In principle, any presence/absence algorithm can be implemented using pseudo-absences. The aim here is to assess differences between the occurrence localities and a set of localities chosen from the study area that are used in place of real absence data. The set of 'pseudo-absences' may be selected randomly (e.g., Stockwell and Peters, 1999) or according to a set of weighting criteria (e.g., Engler et al., 2004; Zaniewski et al., 2002). An important difference between the pseudo-absence approach and the background approach is that pseudo-absence models do not include occurrence localities within the set of pseudo-absences.

Another key difference among model algorithms is their ability to incorporate categorical environmental variables (see the section: Data Types and Sources'). Methods also differ in the form of their output, which is most commonly a continuous prediction (e.g. a probability value ranging from 0 to 1) but may be a binary prediction (with '0' as a prediction of unsuitable environmental conditions or species absence, and '1' a prediction of highly suitable environmental conditions or species presence). To generate a binary prediction from a model that gives continuous output, it is necessary to set a threshold value above which the prediction is classified as 'highly suitable' or 'present' (see the section: 'Assessing Predictive Performance').

A further consideration when selecting a modeling algorithm is whether it is important to determine the relative influence of different input variables on the model's fit or predictive capacity. Some models may have excellent predictive power but do not enable us to easily understand how the algorithm is operating; such models are often termed 'black box' since the model takes input and produces output but the internal workings are somewhat opaque. For example, artificial neural networks have shown good predictive ability (e.g., Pearson et al., 2002; Thuiller, 2003; Segurado and Araújo, 2004), but identifying the relative contribution of each input variable to the prediction is difficult (sensitivity analysis may be used, but this requires additional analyses). In contrast, a GLM builds a regression equation from which the relative contributions of different variables are immediately apparent (Guisan et al., 2002).

**Box 3. Maximum Entropy (Maxent) Modeling of Species Distributions (based on Phillips et al., 2006)**

Maxent is a general-purpose method for characterizing probability distributions from incomplete information. In estimating the probability distribution defining a species' distribution across a study area, Maxent formalizes the principle that the estimated distribution must agree with everything that is known (or inferred from the environmental conditions where the species has been observed) but should avoid making any assumptions that are not supported by the data. The approach is thus to find the probability distribution of maximum entropy (the distribution that is most spread-out, or closest to uniform) subject to constraints imposed by the information available regarding the observed distribution of the species and environmental conditions across the study area.

The Maxent method does not require absence data for the species being modeled; instead it uses background environmental data for the entire study area. The method can utilize both continuous and categorical variables

**Box 3. Maximum Entropy (Maxent) Modeling of Species Distributions (Continued)**

and the output is a continuous prediction (either a raw probability or, more commonly, a cumulative probability ranging from 0 to 100 that indicates relative suitability). Maxent has been shown to perform well in comparison with alternative methods (Elith et al., 2006; Phillips et al., 2006; Pearson et al., 2007). One drawback of the Maxent approach is that it uses an exponential model that can predict high suitability for environmental conditions that are outside the range present in the study area (i.e. extrapolation, see Box 1). To alleviate this problem, when predicting for variable values that are outside the range found in the study area, these values are reset (or 'clamped') to match the upper or lower values found in the study area.

For a concise mathematic definition of Maxent and for more detailed discussion of its application to species distribution modeling see Phillips et al. (2004, 2006). These authors have developed software with a user-friendly interface to implement the Maxent method for modeling species distributions (for free download see web link in Table 3). The software also calculates a number of alternative thresholds (see Section 5), computes model validation statistics (see section: 'Assessing Predictive Performance'), and enables the user to run a jackknife procedure to determine which environmental variables contribute most to the model prediction (see the practical exercise by Steven Phillips that accompanies this synthesis).

It is not possible within the scope of this synthesis to describe the theory, advantages and disadvantages of a large number of modeling algorithms; the reader is referred to the literature cited in Table 3. However, see Box 3 and the practical exercise by Steven Phillips that accompanies this Synthesis for a more detailed description of one method, Maxent.

The model algorithm is in some ways the 'core' of the distribution model, but it should be remembered that the algorithm is just one part of the broader modeling process; other factors, including selection of environmental variables (see section: 'Data Types and Sources') and application of a decision threshold (see section: 'Assessing Predictive Performance'), are key elements of the modeling process that affect model results and may be varied regardless of the model algorithm being used. Nevertheless, studies comparing different modeling algorithms have demonstrated substantial differences between predictions from alternative methods. The importance of selecting an appropriate algorithm is discussed below.

*Differences between methods and selection of 'best' models*

Given the variety of possible modeling methods (Table 3), it is important to consider the degree to which different methods yield different results. Furthermore, if model predictions differ substantially, how should we choose which method to apply? This is an active area of research, and unfortunately there are no simple answers.

A number of studies have demonstrated that different modeling approaches have the potential to yield substantially different predictions (e.g., Loiselle et al., 2003; Thuiller, 2003; Brotons et al., 2004; Segurado and Araújo, 2004; Thuiller et al., 2004; Elith et al., 2006; Pearson et al., 2006). Pearson et al. (2006) found especially large differences among predictions of changes in range size under future climate change scenarios based on nine alternative modeling methods. Predicted changes in range size differed in both magnitude and direction (e.g. from 92% range reduction to 322% range increase for a single species). In another study, Loiselle et al. (2003) demonstrated markedly different results when alternative distribution models were used alongside a reserve selection algorithm for identifying priority sites for conservation.

The most comprehensive model comparison to date was provided by Elith et al. (2006). The authors compared sixteen modeling methods using 226 species across six regions of the world. All of the models included in the study were implemented using presence-only data for calibration (some methods required the use of pseudo-absence data), but model performance was assessed using data on both presence and

absence. These analyses found differences between predictions from alternative methods, but also found that some methods consistently outperformed others. In general, models classified as 'best' were those that were able to identify complex relationships that existed in the data, including interactions among environmental variables.

Several additional factors that lead to differences among predictions from alternative algorithms have been identified. These include (1) whether the model uses presence-absence or presence-only data (Brotons et al., 2004; Pearson et al., 2006), (2) if the model does not use absence data, whether the model uses solely presence records, 'background' data, or 'pseudo-absences' (Elith et al., 2006), (3) whether the algorithm is parametric or non-parametric (Segurado and Araújo, 2004), and (4) how the model 'extrapolates' beyond the range of data used for its calibration (Pearson et al., 2006; and see Box 1).

In view of these differences among models, selection of an appropriate algorithm is both difficult and crucial. Identifying models that are generically 'best' is problematic since the approach used to assess predictive performance depends on the aim of the modeling. For example, Elith et al. (2006) assessed the ability of models to simulate *actual* distributions by using statistical tests that reward models for correctly classifying both presences and absences (see Section 5). In contrast, Pearson et al. (2007) assessed predictive performance based only on the model's ability to predict observed presences, arguing that the purpose of the modeling was to identify *potential* distributions (in which case use of absence data in assessing performance is invalid since a site classified as absent still may be environmentally suitable). The relative merits of aiming to predict actual versus potential distributions were discussed in Section 2. We will also return to the question of how to identify 'best' models when describing various statistical approaches for assessing predictive performance in Section 5. However, the important point is that it is not straightforward to identify which methods are best, and it is therefore not possible to recommend use of one method over another.

In practice, model selection will be influenced by factors including whether observed absence data are available, whether data on some of the environmental variables are categorical, and whether it is important to evaluate the influence of different variables on the model prediction. We recommend that modeling efforts apply and examine predictions from a range of methods in order to quantify uncertainty arising from the choice of method and to identify when different models are in agreement. Perhaps most importantly, it is vital that the assumptions and behavior of any model are properly understood (e.g. how does the model deal with environmental conditions that are beyond the range of the data used to calibrate the model?) so that model output can be accurately interpreted.

**Assessing Predictive Performance**

Assessing the accuracy of a model's predictions is commonly termed 'validation' or 'evaluation', and is a vital step in model development. Application of the model will have little merit if we have not assessed the accuracy of its predictions. Validation thus enables us to determine the suitability of a model for a specific application and to compare different modeling methods (Pearce and Ferrier, 2000). This section discusses different approaches for assessing predictive performance, including strategies for obtaining data against which the predictions can be compared, methods for selecting thresholds of occurrence, and various test statistics. As in previous sections, there is no single approach that can be recommended for use in all modeling exercises; rather, the choice of validation strategy will be influenced by the aim of the modeling effort, the types of data available, and the modeling method used.

*Strategies for obtaining test data*

In order to test predictive performance it is necessary to have data against which the model predictions can be compared. We can refer to these as *test data* (sometimes called *evaluation data*) to distinguish them from the *calibration data* (sometimes called *training data*) that are used to build the model. It is fairly common for studies to assess predictive performance by simply testing the ability of the model to predict the calibration

data (i.e. calibration and test datasets are identical). However, this approach makes it difficult to identify models that have over-fit the calibration data (meaning the model is able to accurately classify the calibration data, but the model performs poorly when predicting test data), making it impossible for users to judge how well the model may perform when making predictions (Araújo et al., 2005a). It is therefore preferable to use test data that are different from the calibration data.

Ideally, test data would be collected independently from the data used to calibrate the model. For example, Fleishman et al. (2002) modeled the occurrence of butterfly species in Nevada, USA, using species inventory data collected during the period 1996-1999, and then tested the models using data collected from new sites during 2000-2001 (see Case Study 1 for a comparable study). Other researchers have undertaken validation using independent data from different regions (e.g. Beerling et al., 1995; Peterson, 2003), data at different spatial resolution (e.g., Pearson et al., 2004; Araújo et al., 2005b), data from different time periods (e.g., Araújo et al., 2005a), and data from surveys conducted by other researchers (Elith et al., 2006).

However, in practice it may not be possible to obtain independent test data and it is, therefore, common to partition the available data into calibration and test datasets. Several strategies are available for partitioning data, the simplest being a one-time split in which the available data are assigned to calibration and test datasets either randomly (e.g., Pearson et al., 2002) or by dividing the data spatially (e.g., Peterson and Shaw, 2003). The relative proportions of data included in each data set are somewhat arbitrary, and dependent on the total number of locality points available (though using 70% for calibration and 30% for testing is common, following guidelines provided by Huberty (1994)). An alternative to a one-time split is 'bootstrapping', whereby the data are split multiple times. Bootstrapping methods sample the original set of data randomly with replacement (i.e. the same occurrence record could be included in the test data more than once). Multiple models are thus built, and in each case predictive performance is assessed against the corresponding test data. Validation statistics can then be reported as the mean and range from the set of bootstrap samples (e.g., Verbyla and Litaitis, 1989; Buckland and Elston, 1993). An approach similar to bootstrapping, but sampling without replacement (i.e. the same occurrence record cannot be included in the test data more than once), can also be applied and may be termed 'randomization' (Fielding and Bell, 1997).

Another useful data partitioning method is *k*-fold partitioning. Here, data are split into *k* parts of roughly equal size ($k > 2$) and each part is used as a test set with the other *k*-1 sets used for model calibration. Thus, if we select $k = 5$ then five models will be calibrated and each model tested against the excluded test data. Validation statistics are then reported as the mean and range from the set of *k* tests (Fielding and Bell, 1997). An extreme form of *k*-fold partitioning, with *k* equal to the number of occurrence localities, is recommended for use with very low sample sizes (e.g., $< 20$; Pearson et al., 2007). This method is termed 'jackknifing' or 'leave-one-out' since each occurrence locality is excluded from model calibration during one partition.

The following sub-sections describe validation statistics that can be calculated after test data have been obtained using one of the above approaches.

*The presence/absence confusion matrix*

If a model is used to predict a set of test data, predictive performance can be summarized in a *confusion matrix*. Note that binary model predictions (i.e. predictions of suitable and unsuitable, rather than probabilities; see section 4) are required in order to complete the confusion matrix. Later subsections describe methods for converting continuous model outputs into binary predictions (see *Selecting thresholds of occurrence*) and for assessing predictive performance using continuous predictions (see *Threshold-independent assessment*). However, in order to understand these later sections it is important to first look at the confusion matrix.

The confusion matrix is rather more straightforward than its name suggests, and is alternatively termed an 'error matrix' or

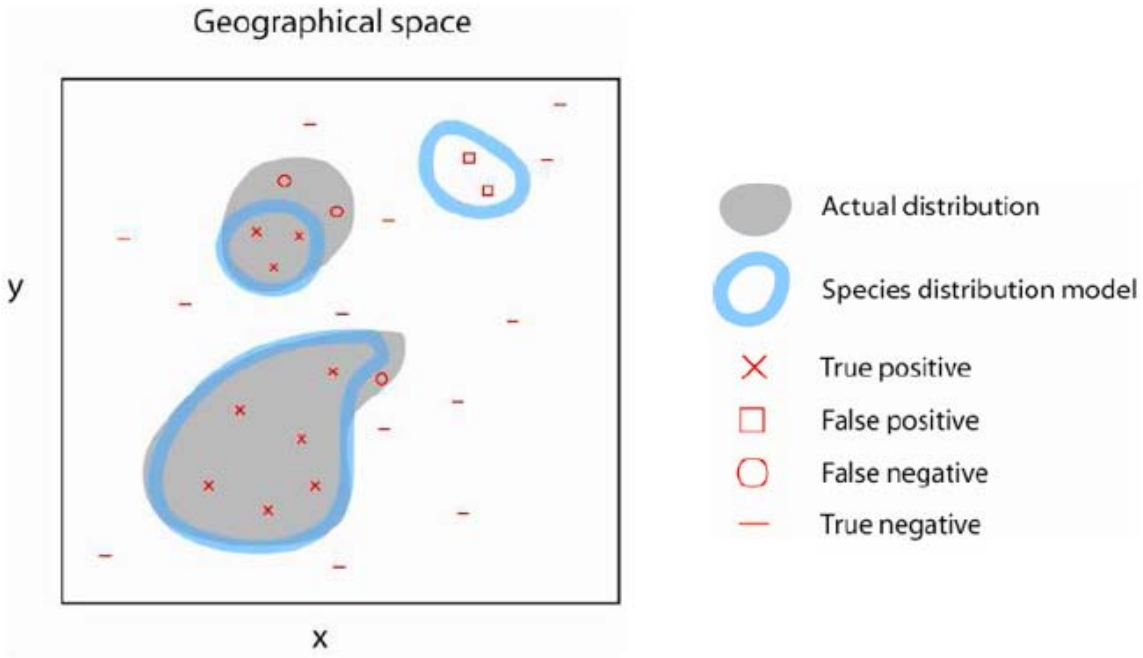


Figure 4. Diagram illustrating the four types of outcomes that are possible when assessing the predictive performance of a species distribution model: true positive, false positive, false negative and true negative. The diagram uses the same hypothetical actual and modeled distributions as in Figure 3. Each instance of a symbol (x, □, o, -) on the map depicts a site that has been surveyed and presence or absence of the species recorded (it is assumed here that if a site falls within the actual distribution then the species will be detected). These survey records constitute the test data. Frequencies of each type of outcome are commonly entered into a confusion matrix (see main text).

a 'contingency table'. The confusion matrix records the frequencies of each of the four possible types of prediction from analysis of test data: (a) true positive (the model predicts that the species is present and test data confirms this to be true), (b) false positive (the model predicts presence but test data show absence), (c) false negative (the model predicts absence but test data show presence), (d) true negative (the model predicts and the test data show absence). Frequencies are commonly recorded in a confusion matrix with the following form:

| | recorded present | recorded absent |
|---|---|---|
| predicted present | *a (true positive)* | *b (false positive)* |
| predicted absent | *c (false negative)* | *d (true negative)* |

Each element of the confusion matrix can be visualized in geographical space as illustrated in Figure 4. In the example depicted, 27 test localities have been sampled and presence or absence of the species recorded at each site. The use of test data comprising only presence localities (i.e. species occurrence records) is discussed below, but for completion of the confusion matrix we require both presence and absence records. Thus, the hypothetical case shown in Figure 4 would yield the following confusion matrix:

| | recorded present | recorded absent |
|---|---|---|
| predicted present | *9* | *2* |
| predicted absent | *3* | *13* |

The frequencies in the confusion matrix form the basis for a variety of different statistical tests that can be used to assess model performance. Most of the commonly used tests are described below. Terminology related to model performance often varies from study to study and is sometimes not intuitive. In particular, false negative predictions are commonly

termed errors of 'omission', whilst false positive predictions are termed errors of 'commission'.

*Test statistics derived from the confusion matrix*

A simple measure of predictive performance that can be derived from the confusion matrix is the proportion (or percentage) of test localities that are correctly predicted, calculated as

$$(a+d)/(a+b+c+d)$$

This measure may be termed 'accuracy' or 'correct classification rate'. The concept of accuracy is simple and logical, but it is possible to obtain high accuracy using a poor model when a species' prevalence (the proportion of sampled sites in which the species is recorded present) is relatively high or low. For example, if prevalence is 5% then 95% of test localities can be correctly classified simply by predicting all sites as 'absent'. To circumvent this problem, Cohen (1960) introduced a measure of accuracy that is adjusted to account for chance agreement between predicted and observed values. The statistic, Kappa (k), is similar to accuracy but the proportion of correct predictions expected by chance is taken into account (for full derivation see Monserud and Leemans, 1992). Kappa is calculated as:

$$\frac{[(a+d)-(((a+c)(a+b)+(b+d)(c+d))/n)]}{[n-(((a+c)(a+b)+(b+d)(c+d)/n]}$$

Accuracy and Kappa statistics use all values in the confusion matrix and therefore require both presence and absence data. However, absence data are often unavailable (e.g. when using specimens from museum collections) and are inappropriate for use when the aim is to estimate the *potential distribution* (since the environment may be suitable even though the species is absent).

When only presence records are used, the proportion of observed occurrences correctly predicted can be calculated as:

$$a/(a+c)$$

This measure is sometimes termed 'sensitivity' or 'true positive fraction'. Alternatively, we may calculate:

$$c/(a+c)$$

which is often termed 'omission rate' or 'false positive fraction'. Note that these two measures – sensitivity and omission rate – sum to 1. Thus, high sensitivity means low omission, and low sensitivity means high omission. Although sensitivity and omission rate avoid the use of absence records, a serious disadvantage of these tests is that it is possible to achieve very high sensitivity (and low omission) simply by predicting that the species is present at an excessively large proportion of the study area. In short, it is possible to cheat: if the model predicts the entire study area to be suitable, then sensitivity will equal 1, and omission rate will be zero. To avoid this problem, it is necessary to test the statistical significance of a sensitivity or omission rate score.

To test for statistical significance, we ask whether the accuracy of our predictions is greater than would be expected by chance. Imagine, for example, that we are blindfolded and asked to throw darts at a map of our study area. The sites identified by our random throws are then used as species' occurrence localities for model testing. The probability of landing darts in the area predicted by the model to be suitable for the species is equal to the proportion of the study area that is predicted as suitable. Thus, if the model predicts that the species will be present in 40% of the study area, then our probability of successfully landing a dart in the area predicted as suitable is 0.4.

We can apply the same logic to assess the statistical significance of a sensitivity (or omission rate) score. In this case, we use an exact one-tailed binomial test (or for larger sample sizes a chi-square test; for description of binomial and chi-square tests see Zar, 1996) to calculate the probability of obtaining a sensitivity result by chance alone (Anderson et al., 2002a). For example, suppose that the model in Figure 4 predicts that 30% of the study area is suitable for the species. The probabil-

ity of success by chance alone for each test locality is therefore 0.3. We can calculate from the confusion matrix that the sensitivity = 9/(9+3) = 0.75, and we can use an exact one-tailed binomial test to calculate that the probability of making nine or more successful predictions of presence by chance alone is 0.0017. We may therefore conclude that our result is statistically significant ($p < 0.01$).

A similar assessment of predictive performance can be conducted when only very few occurrence localities are available and test data have been generated using a jackknifing approach (see subsection *Strategies for obtaining test data*). In this case the number of successful predictions from a set of jackknife trials can be calculated (e.g., 9 successes in 12 jackknife trials) and a *p*-value can be calculated using the method presented in Pearson et al. (2007).

In practice, binomial and chi-square tests can be performed in most standard statistical packages, whilst the jackknife *p*-value can be calculated using software provided as Supplementary Material to the Pearson et al. (2007) paper. Various test statistics and thresholds (including those discussed in the remainder of this section) are sometimes calculated automatically by software designed for species distribution modeling (see Table 3), and test statistics may also be calculated using more general applications such as DIVA-GIS (for free download see http://www.diva-gis.org/).

Another statistic that can be derived from the confusion matrix is the proportion of observed absences that are correctly predicted, calculated as:

$$d/(b+d)$$

This statistic is commonly termed 'specificity' or 'true negative fraction'. Specificity is rarely used as a test statistic on its own, since specificity focuses solely on observed absence records. However, specificity is an important measure used in setting decision thresholds and in ROC analysis, which are described in the following two subsections.

*Selecting thresholds of occurrence*

Binary predictions of 'present' or 'absent' are necessary to test model performance using statistics derived from the confusion matrix. It is therefore often useful to convert continuous model output into binary predictions by setting a threshold probability value above which the species is predicted to be present. Although an alternative test statistic that does not require a threshold is available (Area Under the ROC curve; see the following subsection), this approach is not suitable in many circumstances (notably when absence records are not available, Boyce et al., 2002, but see Phillips et al., 2006). Furthermore, it is essential to learn the techniques described in this subsection to understand how the AUC test operates.

A number of different methods have been employed for selecting thresholds of occurrence (Table 4). Perhaps the simplest approach is to use an arbitrary value, but this method is subjective and lacks ecological reasoning (Liu et al., 2005). Other methods use criteria that are based on the data used to calibrate the model. One approach is to use the lowest predicted value of environmental suitability, or probability of presence, across the set of sites at which a species has been detected. This method assumes that species presence is restricted to locations equally or more suitable than those at which the species has been observed. The approach therefore identifies the minimum area in which the species occurs whilst ensuring that no localities at which the species has been observed are omitted (i.e. omission rate = 0, and sensitivity = 1). An alternative approach is to set the threshold to allow a certain amount of omission (e.g. 5%), which is analogous to setting a fixed sensitivity (e.g. 0.95). This method is less sensitive than the lowest predicted value method to 'outliers' (i.e. locations in which the species is detected despite a low predicted probability of occurrence or suitability), but errors of omission are imposed (i.e. some observed localities will be omitted from the prediction).

Many methods for setting thresholds can be implemented by calculating statistics derived from the confusion matrix across the range of possible thresholds. For example, sensitivity and

**Table 4. Some published methods for setting thresholds of occurrence**

| Method | Definition | Species data type[1] | Reference(s) |
|---|---|---|---|
| Fixed value | An arbitrary fixed value (e.g. probability = 0.5) | presence-only | Manel et al., 1999<br>Robertson et al., 2001 |
| Lowest predicted value | The lowest predicted value corresponding with an observed occurrence record | presence-only | Pearson et al., 2006<br>Phillips et al., 2006 |
| Fixed sensitivity | The threshold at which an arbitrary fixed sensitivity is reached (e.g. 0.95, meaning that 95% of observed localities will be included in the prediction) | presence-only | Pearson et al., 2004 |
| Sensitivity-specificity equality | The threshold at which sensitivity and specificity are equal | presence and absence | Pearson et al., 2004 |
| Sensitivity-specificity sum maximization | The sum of sensitivity and specificity is maximized | presence and absence | Manel et al., 2001 |
| Maximize Kappa | The threshold at which Cohen's Kappa statistic is maximized | presence and absence | Huntley et al., 1995<br>Elith et al., 2006 |
| Average probability/suitability | The mean value across model output | presence-only | Cramer, 2003 |
| Equal prevalence | Species' prevalence (the proportion of presences relative to the number of sites) is maintained the same in the prediction as in the calibration data. | presence and absence | Cramer, 2003 |

[1] Species occurrence records required to set the threshold. Based in part on Liu et al. (2005).

specificity may be calculated at thresholds increasing in increments of 0.01 from 0 to 1 (i.e. 0, 0.01, 0.02, 0.03…0.99, 1). As the threshold increases, the proportion of the study area predicted to be suitable for the species, or in which the species is predicted to be 'present,' will decrease. Consequently, the proportion of observed presences that are correctly predicted decreases (i.e. decreasing sensitivity) and the proportion of observed absences that are correctly predicted increases (i.e. increasing specificity) (Figure 5A). From these data we can select the threshold at which sensitivity and specificity are equal (labeled *a* in Figure 5A) or at which their sum is maximized. Similarly, it is common to calculate Kappa across the range of possible thresholds and to select the threshold at which the statistic is maximized (Figure 5B).

Choice of an appropriate decision threshold is dependent on the type of data that are available and the question that is being addressed. Some methods require presence and absence records, while others require presence-only records (Table 4). When using both presence and absence records, the general approach is to balance the number of observed presences and absences that are correctly predicted; in effect, to maximize agreement between observed and predicted distributions. Thus, we must be willing to increase the omission rate (i.e. decrease sensitivity) in order to increase the proportion of observed absences that are correctly predicted (i.e. increase specificity). Liu et al. (2005) tested twelve methods for setting thresholds using presence and absence data for two European

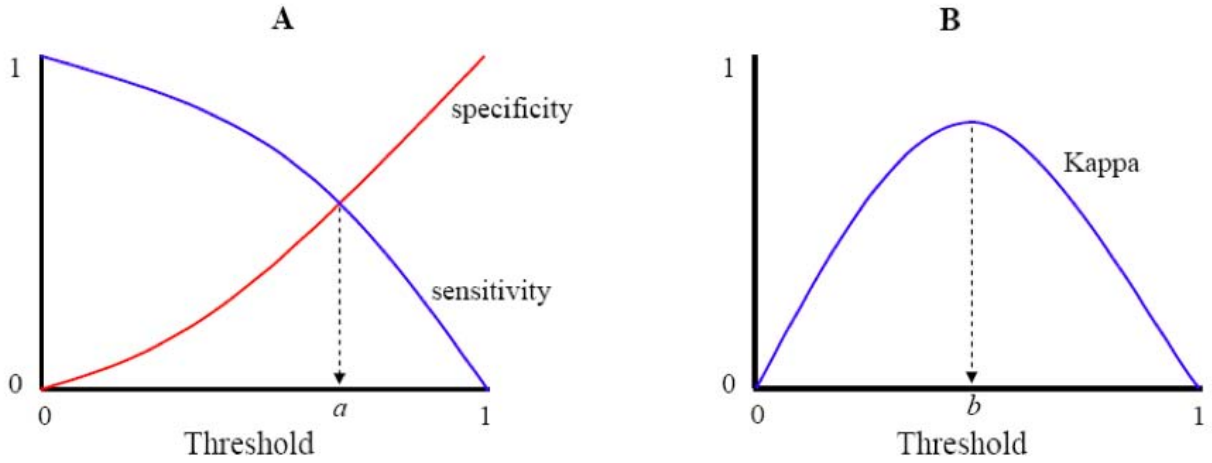


Figure 5. Plots showing changes in test statistics as the threshold of occurrence is adjusted. **A** Decrease in sensitivity and increase in specificity as the threshold is increased. The threshold labeled *a* corresponds to the specificity-sensitivity equality threshold. **B** Changes in the Kappa statistic as the threshold is adjusted. The threshold labeled *b* corresponds to that threshold at which Kappa is maximized.

plant species. Based on four assessments of predictive performance (sensitivity, specificity, accuracy and Kappa), they concluded that the best methods for setting thresholds included maximizing the sum of sensitivity and specificity, using the average probability/suitability score, and setting equal prevalence between the calibration data and the prediction (Table 4). Maximizing Kappa did not perform well, and use of an arbitrary fixed value performed worst.

Methods that use only presence records for setting a threshold are required for cases in which absence data are unavailable. Presence-only methods can also be justified on the grounds that they avoid false absences (Section 3): it may be argued that we should be primarily concerned with maximizing the number of observed presences that are correctly predicted, rather than minimizing the number of absences that are incorrectly predicted as presences (since some absences may be recorded in apparently suitable environments; Pearson et al., 2006). For example, Pearson et al. (2007) used a dataset comprising very few presence-only records for geckos in Madagascar. Because confidence was high that the localities and species identification were correct, and because these species are not highly mobile and are therefore unlikely to be found in unsuitable habitat (i.e. sink habitat; see Section 2), omission of any occurrence record was considered a clear model error. Therefore, the minimum predicted value corresponding to an observed presence was selected as a threshold to ensure zero omission. Distribution models thus predicted that many regions of the study area were suitable although no presences had been detected there. This approach suited the aim of the study, which was to prioritize regions for future surveys by estimating the potential distribution (see Case Study 1).

As a final illustration of the importance of selecting an appropriate decision threshold, we can return to an example raised in Section 2. If the purpose of modeling is to identify areas within which disturbance may impact a species negatively (e.g. as part of an environmental impact assessment), then the threshold may be set low to identify a larger area of potentially suitable habitat. In contrast, if the model was intended to identify potential introduction or reintroduction sites for an endangered species or species of recreational value, then it would be appropriate to choose a relatively high threshold. Choosing a high threshold reduces the risk of choosing unsuitable sites by identifying those areas with highest suitability (Pearce and Ferrier, 2000).

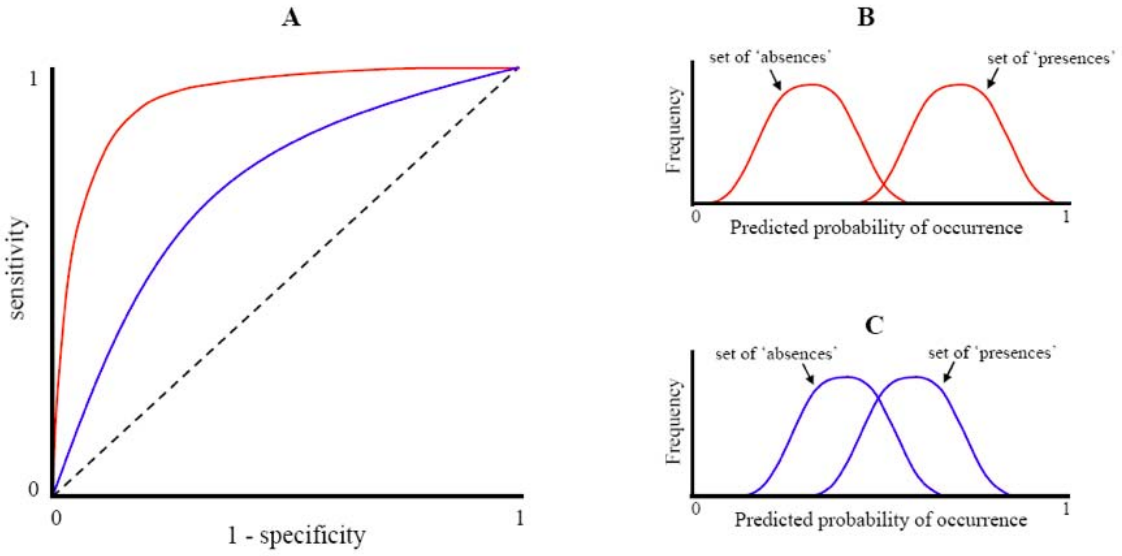


Figure 6. Example Receiver Operating Characteristic (ROC) Curves and illustrative frequency distributions. **A** ROC curves formed by plotting sensitivity against '1 – specificity'. Two ROC curves are shown, the upper curve (red) signifying superior predictive ability. The dashed 1:1 line signifies random predictive ability, whereby there is no ability to distinguish occupied and unoccupied sites. **B** and **C** show example frequency distributions of probabilities predicted by a model for observed 'presences' and 'absences'. The results shown in **B** reveal good ability to distinguish presence from absence, whilst results in **C** show more overlap between the frequency distributions thus revealing poorer classification ability. The case shown in **B** would produce an ROC curve similar to the upper (red) curve in **A**. The case shown in **C** would give an ROC curve more like the lower (blue) curve in **A**.

*Threshold-independent assessment*

When model output is continuous, assessment of predictive performance using statistics derived from the confusion matrix will be sensitive to the method used to select a threshold for creating a binary prediction. Furthermore, if predictions are binary, the assessment of performance does not take into account all of the information provided by the model (Fielding and Bell, 1997). Therefore, it is often useful to derive a test statistic that provides a single measure of predictive performance across the full range of possible thresholds. This can be achieved using a statistic known as AUC: the Area Under the Receiver Operating Characteristic Curve.

The AUC test is derived from the Receiver Operating Characteristic (ROC) Curve. The ROC curve is defined by plotting sensitivity against '1 – specificity' across the range of possible thresholds (Figure 6A). Sensitivity and specificity are used because these two measures take into account all four elements of the confusion matrix (true and false presences and absences). It is conventional to subtract specificity from 1 (i.e. 1 – specificity) so that both sensitivity and specificity vary in the same direction when the decision threshold is adjusted (Pearce and Ferrier, 2000). The ROC curve thus describes the relationship between the proportion of observed presences correctly predicted (sensitivity) and the proportion of observed absences incorrectly predicted (1 – specificity). Therefore, a model that predicts perfectly will generate an ROC curve that follows the left axis and top of the plot, whilst a model with predictions that are no better than random (i.e. is unable to classify accurately sites at which the species is present and absent) will generate a ROC curve that follows the 1:1 line (Figure 6A).

In order to summarize predictive performance across the full range of thresholds we can measure the area under the ROC curve (the AUC), expressed as a proportion of the total area of the square defined by the axes (Swets, 1988). The AUC thus ranges from 0.5 for models that are no better than random to

1.0 for models with perfect predictive ability. We can think of AUC in terms of the frequency distributions of probabilities predicted for locations at which we have empirical data on presence and absence (Figure 6, B and C). A high AUC score reflects that the model can discriminate accurately between locations at which the species is present or absent. In fact, AUC can be interpreted as the probability that a model will correctly distinguish between a presence record and an absence record if each record is selected randomly from the set of presences and absences. Thus, an AUC value of 0.8 means the probability is 0.8 that a record selected at random from the set of presences will have a predicted value greater than a record selected at random from the set of absences (Fielding and Bell, 1997; Pearce and Ferrier, 2000).

AUC is a test that uses both presence and absence records. However, Phillips et al. (2006) have demonstrated how the test can be applied using randomly selected 'pseudo-absence' records in lieu of observed absences. In this case, AUC tests whether the model classifies presence more accurately than a random prediction, rather than whether the model is able to accurately distinguish presence from absence.

A number of different methods can be used to compute the AUC (Pearce and Ferrier, 2000). Some distribution modeling programs automatically calculate the AUC (e.g. Maxent; Table 3). The statistic can also be calculated using numerous other free software packages (e.g. R, for free download see http://www.r-project.org/).

*Choosing a suitable test statistic*

The choice of test statistic depends largely on how the model will be applied. If the aim is to predict the actual distribution (Section 2) then use of a test that incorporates both presence and absence records may be preferable (e.g. accuracy or Kappa). A good model will successfully predict both presences and absences with equal frequency. However, when using this approach it is important to realize that predictions that an unoccupied area is environmentally suitable (type 3 predictions, Figure 3) are considered model errors. Because type 3 predictions are theoretically expected (Section 2), models may be judged poor although they make biologically sound predictions.

If the aim of the modeling is to estimate the potential distribution (Section 2) then presence-only assessment of model performance using sensitivity and statistical significance is likely to be preferable. In this case we cannot test if the model is *correct* (since we do not know the true potential distribution), but rather we test if the model is *useful*. Our criteria for usefulness are that the model successfully predicts presence in a high proportion of test localities (i.e., known occurrences) whilst not predicting that an excessively large proportion of the study area is suitable. Thus, a model that successfully predicts whether the species is present at all test localities whilst classifying most of the study area as suitable may be correct (the environment may truly be suitable throughout most of the study area); however, the model is not useful because it is not more informative than a random prediction.

Subjective guidelines can be used to decide what values of a test statistic correspond to 'good' model performance. For example, Landis and Koch (1977) suggested that Kappa scores >0.75 represent an 'excellent' model, whilst Swets (1988) classified any AUC score >0.9 as 'very good'. However, the only true test of the model is whether it is useful for a given application. There are numerous potential applications of these methods (Table 1) and the final part of this synthesis describes three representative case studies.

## Case Studies

### Case Study 1: Predicting Distributions of Known and Unknown Species in Madagascar (based on Raxworthy et al., 2003)

Our knowledge of the identity and distribution of species on Earth is remarkably poor, with many species yet to be described and catalogued. This problem has two key elements, which may be termed the 'Linnean' and 'Wallacean' shortfalls (Whittaker et al., 2005). The Linnean shortfall refers to our

lack of knowledge of how many, and what kind, of species exist. The term is a reference to Carl Linnaeus, who laid the foundations of modern taxonomy and the 18th century. The Linnean shortfall concerns our highly incomplete knowledge of the diversity of life that exists on Earth.

The Wallacean shortfall refers to our inadequate knowledge of the distributions of species. This term is a reference to Alfred Russel Wallace who, as well as contributing to the early development of evolutionary theory, was an expert on the geographical distribution of species (he is sometimes referred to as 'the father of biogeography'). The Wallacean shortfall thus refers to our poor knowledge of the biogeography of most species. Species distribution modeling offers a powerful tool to address both the Linnean and Wallacean shortfalls, as demonstrated in a study by Raxworthy et al. (2003).

Raxworthy et al. (2003) modeled the distributions of 11 species of chameleon that are endemic to the island of Madagascar. They used species occurrence records from recent surveys and from older specimens deposited in collections of natural history museums. No observed absence records were available for building the models. Environmental variables were derived from remote sensing data, from a digital elevation model, and from weather station data that had been interpolated to a grid (i.e. converted from point vector to raster data). In all, 25 GIS layers were used in the modeling, including environmental variables describing temperature, precipitation, land cover, and elevation. All analyses were undertaken at a resolution of 1 $km^2$. The modeling algorithm used was GARP (see Table 3), which generated an output ranging from 0 – 10 at increments of 1. Two alternative thresholds of occurrence were used: threshold = 1 (termed by the authors "any model predicts"), and threshold = 10 (termed "all models predict").

Predictive performance of the models was first evaluated by splitting the available data into two parts, 50% for calibrating the model and 50% for testing the model. The authors calculated the number of test localities at which the species was correctly predicted to be present and tested the statistical significance of the results using a chi-square test. Performance of the 11 models was generally good, with overall prediction success as high as 83%. Predictions usually were better than random. A second evaluation tested model performance using independent test data from herpetological surveys undertaken at 11 sites after the models had been built. In this case, model evaluation was based on both presence and absence records, since surveys were sufficiently thorough that detection probability was high. The success of these predictions was more than 70% and levels of statistical significance were uniformly high.

Raxworthy et al. (2003) thus demonstrated the potential for species' distribution models to be used to guide new field surveys toward areas in which the probability of species presence was high. This approach takes advantage of the type of model prediction illustrated by area *2* in Figure 3: the model identifies an area that is environmentally similar to where the species has already been found, but for which no occurrence data are available. The models can thus help to address the Wallacean shortfall, by improving our knowledge of the distributions of known species.

Raxworthy et al. (2003) also demonstrated that the models can help to address the Linnean shortfall by guiding field surveys toward areas where species new to science are most likely to be discovered. In this case, the approach makes use of the type of model prediction illustrated by area *3* in Figure 3: areas are identified that are unoccupied by the species being modeled, but where closely-related species that occupy similar environmental space are most likely to be found. By surveying sites identified by the distribution models for known species, Raxworthy et al. (2003) discovered seven new species, considerably greater than the number that would usually be expected on the basis of similar survey effort across a less-targeted area.

**Case Study 2: Species' Distribution Modeling as a Tool for Predicting Invasions of Non-Native Plants (based on Thuiller et al., 2005)**

Invasive species are increasingly a global concern, with inva-

sions altering ecosystem functioning, threatening native biodiversity, and negatively impacting agriculture, forestry, and human health. Species' distribution modeling can be used to identify areas that are most likely to be colonized by a known invader. The general approach is to model the distribution of a species using occurrence records from its native range, then project the model into new regions to assess susceptibility to invasion. The approach makes use of the type of model prediction illustrated by area *3* in Figure 3: areas are identified that are part of the potential, but not actual, distribution. Thuiller et al. (2005) used this method to identify parts of the world that are potentially susceptible to invasion by plant species native to South Africa.

Thuiller and colleagues developed distribution models for 96 South African plant taxa that are invasive in other regions of the globe. Species distribution data were extracted from large databases of occurrence records that have been collated for South Africa. Since the surveys incorporated within these databases were fairly comprehensive, the authors argued that absences within the databases are reliable and the modeling was thus undertaken using presence and absence data. Four climate-related variables that are known to affect plant physiology and growth were developed and used as input to the models. These included two measures of temperature (growing degree days and temperature of the coldest month) along with indexes of humidity and plant productivity. All the analyses were undertaken at a resolution of 25x25 km, which was considered sufficiently fine to identify environmental differences between regions at a global scale. Generalized Additive Models (implemented using the Splus-based BIOMOD application; Table 3) were used to build the distribution models.

The first step in the study was to model each species' distribution based on its native range in South Africa. Models were calibrated using 70% of the available records for each species, with the remaining 30% retained for model testing. The AUC validation test was applied using presence and absence test data. Because AUC assesses predictive performance based on continuous model output, it was not necessary to set a threshold of occurrence. Validation statistics for the test data were generally very good, with a median AUC score across all 96 species of 0.94 (minimum = 0.68, maximum = 1.0).

The second step in the study was to project the calibrated models worldwide. The accuracy of the global predictions was assessed for three example species using presence-only records from their non-native distributions (for example, in Europe, Australia, and New Zealand). Absence records were not available for these tests, so model performance was assessed using chi-square tests (see section 5). For each of the species, predictions of potentially suitable areas outside South Africa showed considerable agreement with observed records of invasions (chi-square test, $P<0.05$).

In a further step, Thuiller and colleagues summed the probability surfaces for all 96 taxa to produce a global map for risk of invasion by species of South African origin. Parts of the world most susceptible to invasion included six biodiversity 'hotspots', including the Mediterranean Basin, California Floristic Province, and southwest Australia. This study demonstrates that species distribution modeling can be a valuable tool for identifying sites prone to invasion. Such sites may be prioritized for monitoring and quarantine measures can be put in place to help avoid the establishment of invasive species.

**Case Study 3: Modeling the Potential Impacts of Climate Change on Species' Distributions in Britain and Ireland (based on Berry et al., 2002)**

Climate change has the potential to significantly impact the distribution of species. Species' distribution models have been used in a number of studies that aim to predict the likely redistribution of species under projected climate change over the coming century. The general approach is to calibrate the models based on current distributions of species and then predict future distributions of those species across landscapes for which the environmental input variables have been perturbed to reflect expected changes.

Berry et al. (2002) modeled 54 species that were chosen to

represent a range of habitats common in Britain and Ireland. Species distribution data were obtained for the whole of Europe (i.e. European extent) from range maps for European plants, amphibians, butterflies, and mammals. Since survey effort across Europe is generally very high, areas where a species had not been recorded were considered reliable measures of absence, and both presence and absence data were therefore used in the modeling. Five environmental variables describing temperature, precipitation, and soil type were used. These variables were generated using both current climate data and predictions of future climate from a General Circulation Model (GCM). GCMs are complex simulations that predict future climates using scenarios of greenhouse gas emissions. The environmental variables were calculated at a coarse resolution (~50x50 km) for Europe, and also at a finer resolution (10x10 km) for Britain and Ireland. The modeling algorithm was an Artificial Neural Network (Table 3), which gave predictions of relative suitability ranging from 0 to 1. These continuous predictions were converted into binary predictions of presence and absence by applying a threshold of occurrence that maximized the Kappa statistic.

An important part of Berry et al.'s (2002) method was that calibration of the distribution model was carried out at the European scale (large extent and coarse resolution) and then the model was used to predict distributions in Britain and Ireland (smaller extent and finer resolution). This approach ensured that when distributions were predicted under future climate scenarios in Britain and Ireland, the model was not required to extrapolate beyond the range of data for which it was calibrated (since future climates in Britain and Ireland are expected to be similar to conditions currently experienced elsewhere in Europe).

Evaluation of the models was undertaken at the European scale by comparing model predictions against a test dataset, which comprised one third of the available data that had been randomly selected and not used in model calibration. Since both presence and absence records were available, the Kappa statistic was applied. Results from these tests revealed generally good model performance, with 27 out of 54 species achieving Kappa scores >0.75, and only 7 of 54 species with Kappa scores <0.6.

The models calibrated for Europe were then used to predict distributions in Britain and Ireland under current and projected future climates. Berry et al. (2002) emphasized that they did not predict actual distributions, but rather 'bioclimate envelopes', or suitable climate space. It is important to remember that actual future distributions will be determined by many factors that are not taken into account in the modeling, including the ability of species to colonize areas that become suitable. Nevertheless, the distribution models enabled each species to be placed in one of three categories: those expected to lose suitable climate space, those expected to gain suitable climate space, and those showing little change. Species' distribution modeling thus enables preliminary assessments of the possible impacts of climate change to be made, providing information that may be valuable in developing conservation policies to address the threat.

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Changed: Confirmed: FWS Wolverine project meeting

Changed: Hold the time for now, but I don't think we'll need everyone at this meeting. We'll let you know Friday afternoon or monday morning when we see the comments from John and Kevin Doherty. Kevin was at our presentation in Lakewood, and is filling in for Steve on this while Steve is out on medical leave for a couple of weeks.

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No <https://www.google.com/calendar/event?action=RESPOND&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MjRUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&rst=2&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmYyOTllODg3OTgyZWMzY2FjMWVkMTdkMDZhZWNmYTMzMzU3YzdiMDE&ctz=America/Denver&hl=en>
more options » <https://www.google.com/calendar/event?action=VIEW&eid=MnE2M3R1NHFkcHBmOXRyM2w1Mmt1ZThhaG9fMjAxNzA0MjRUMjEwMDAwWiBqb2huX2d1aW5vdHRlQGZ3cy5nb3Y&tok=MTkjYW5kcmVhLnJheUBub2FhLmdvdmYyOTllODg3OTgyZWMzY2FjMWVkMTdkMDZhZWNmYTMzMzU3YzdiMDE&ctz=America/Denver&hl=en>

Invitation from Google Calendar <https://www.google.com/calendar/>

You are receiving this email at the account john_guinotte@fws.gov because you are subscribed for updated invitations on calendar john_guinotte@fws.gov.

To stop receiving these emails, please log in to https://www.google.com/calendar/ and change your notification settings for this calendar.

Forwarding this invitation could allow any recipient to modify your RSVP response. Learn More <https://support.google.com/calendar/answer/37135#forwarding> .

achment 20170420 151542_EM_Confirmed_ FWS Wolverine project meeting.ics (3851 Bytes) cannot be converted to PDF for

**From:** Grizzle, Betty
**To:** A J
**Subject:** Re: Looking for wolverine photo
**Date:** Wednesday, April 26, 2017 12:28:59 PM

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Not for at least another month. I just wanted to give you advance notice.

On Wed, Apr 26, 2017 at 11:26 AM, A J <222wsheridan@gmail.com> wrote:

> Betty
> By when would you need the photo?
>
> Sent from my iPhone
>
> > On Apr 26, 2017, at 10:14 AM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
> >
> > Hi Bob and Audrey - I am writing to ask if either of you has a nice adult wolverine photo that our agency can add to the cover of our Species Status Assessment Report. We will add a photo credit, but we need to have permission for its use in our administrative record.
> > No rush, however.
> >
> > Thank you,
> > Betty
> > --
> >
> > Betty J. Grizzle, D.Env.
> > Fish and Wildlife Biologist
> > U.S. Fish and Wildlife Service
> > Carlsbad Fish and Wildlife Office
> > 2177 Salk Ave, Suite 250
> > Carlsbad, CA 92008
> > 760-431-9440, ext. 215
> > 760-431-5901 fax

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