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Cc: [Betty Grizzle](#)
Subject: We request your review and comment on the Service's Wolverine Species Status Assessment
Date: Monday, October 30, 2017 2:03:10 PM
Attachments: [Draft Wolverine SSA Report_Oct 23 2017.pdf](#)

Dear Tribal Partners:

Attached please find the U.S. Fish and Wildlife Service's DRAFT Species Status Assessment (SSA) for the Wolverine - Contiguous United States Distinct Population Segment (DPS). The SSA is intended to provide the biological and scientific underpinnings for all decisions the Service must make in accordance with the Endangered Species Act (Act). The draft report will undergo concurrent peer review and review by State Fish and Wildlife Agencies and by Federal land management agencies (BLM, NPS, and USFS) within the DPS range.

The Service jointly respects and values the significant role of Indian Tribes in past and ongoing species conservation. We also respect the sovereignty of Tribal governments and our collective Trust responsibility to Tribes. Continuing this effective relationship with interested Tribes and others is essential to achieving conservation of species including wolverine. Therefore, we are providing this draft for review by members of your organization with expert knowledge of the species and its habitat. That review will help us ensure that we have appropriately considered the best scientific and commercial information when evaluating the current status and future viability of the wolverine DPS.

We request your organization's independent scientific perspectives on the comprehensiveness and logic of the document, as well as how well the technical conclusions are supported by the data and analyses. We ask that your comments on the draft SSA report focus specifically on whether the best available information was used, the quality of the scientific information, and our interpretation and analyses of the data with regard to the species' viability in the contiguous United States. We request that you direct your review to the scientific issues and assumptions related to your expertise.

We welcome consolidated comments from your tribe on the Draft SSA by November 30, 2017. Please send comments by that date to betty_grizzle@fws.gov. Thank you for your interest and assistance.

The Draft SSA is not intended to solicit public comment and will be revised after this scientific review. The Draft SSA does not predetermine any future agency decision under the Endangered Species Act.

General Information about SSAs:

The Species Status Assessment framework is a new tool the U.S. Fish and Wildlife Service is using to improve transparency while conducting listing determinations and other actions in accordance with the Act, and peer review of our analyses of the viability of species is part of that new process. The attached draft SSA report is a rough draft; we are seeking comments at this stage to ensure that we have time to incorporate any substantial comments as we finalize the report.

In reviewing the document, please note that this draft SSA report does not result in or predetermine a decision by the Service on whether the Canada lynx warrants protections of the Act. This document is strictly a characterization of the species' viability in the contiguous United States. As a reminder, all reviews and comments submitted to the Service will become public documents and part of our administrative record for this document.

If you have any questions regarding this SSA, please let me know.

Anna

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DRAFT
SPECIES STATUS ASSESSMENT
FOR THE
NORTH AMERICAN WOLVERINE
(Gulo gulo luscus)



Wolverines in southwestern Montana. *Photo credit: Mark Packila; used with permission.*

U.S. Fish and Wildlife Service

Version 1.0
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Executive Summary

The North American wolverine (*Gulo gulo luscus*; wolverine) is a medium-sized carnivore found across the west-northwestern contiguous United States, Alaska, and Canada. The most recent estimate of wolverine populations in the contiguous United States based on resource function modeling is 318 individuals, with a range from 249 to 949; however, systematic monitoring across the wolverine's North American range has not been conducted given the difficulty in surveying this highly mobile species, and its occupation across large and remote areas. A multi-state effort to determine wolverine occupancy in Montana, Idaho, and Washington was conducted in winter of 2016–2017 and in Wyoming for the winters of 2015 and 2016–2017. Results from this study are still being analyzed, but photographic detections of wolverines were found across all States, including areas where wolverines have not recently been observed. In Canada, the population is estimated to exceed 10,000 mature individuals and has been stable over the last two decades. Recent density estimates indicate no declining trend for wolverines in Alaska. Wolverine populations in Alaska are considered to be continuous with populations in the Yukon and British Columbia provinces of Canada. Wolverines that occupy the North Cascades region are known to move from Washington into British Columbia.

Wolverines are highly mobile, capable of moving and dispersing over great distances over short periods of time. Wolverine populations are also characterized by naturally low densities in North America. The species is highly territorial, with very little overlap between same-sex adults. Wolverines occupy a variety of habitats, but are generally found in remote locations, away from human settlements. Wolverines consume a variety of food resources and seasonal switching of prey likely allows for adjustment for nutritional needs throughout their life history. As observed in other arctic mammals, wolverines have the ability to dissipate body heat to balance the heat loss from 30°C to –40°C (86°F to –40°F), due in large part to vasodilatation and rise of skin temperature, and rapid and seasonal adjustments in fur insulation. Wolverines can also adapt to both cold and warm temperatures by movement and, relatedly, micro- and macro-habitat selection. Further, wolverines have been observed near and in lakes and other water bodies.

Wolverine reproduction includes the following characteristics: polygamous behavior (i.e., male mates with more than one female each year), delayed implantation (up to 6 months), a short gestation period (30–40 days), denning behavior, and an extended period of maternal care (3.5 months). The reproductive behavior in wolverines is temporally adapted to take advantage of the availability of food resources, limited interspecific competition, and snow cover in the winter.

Since the publication of the Service's 2013 proposed rule to list the distinct population segment of the North American wolverine in the contiguous United States (78 FR 7864; February 4, 2013), several new wolverine studies have been published, which has added to our understanding of wolverine biology while also highlighting new insights into identifying key species' needs and their interactions with both abiotic and biotic factors. In particular, wolverine populations and wolverine dens have been observed outside previously modeled projections of spring snow cover. Our evaluation of snow cover at previously recorded natal den site locations in the western United States indicated that 'melt-out' dates at these locations extend well past the May 15 date used in persistent spring snow cover models.

Overall, the best available information indicates that within the contiguous United States the wolverine's physical and ecological needs include:

- (1) large territories in remote landscapes; at high elevation (1,800 to 3,500 meters (5,906 to 11,483 feet));
- (2) access to a variety of food resources, that varies with seasons; and
- (3) physical/structural features (e.g., talus slopes, rugged terrain) linked to reproductive behavioral patterns.

In this Species Status Assessment (SSA) Report, we provide a discussion of the ecological needs of the wolverine, its current conditions, and projected future conditions. We evaluate potential stressors to the species, with a particular focus on the impacts associated with projected effects of climate change.

In our analysis, we applied the conservation biology principles of redundancy, resiliency, and representation (collectively known as the “3Rs”) to evaluate the current and projected future condition of the wolverine and its ability to sustain itself (as one or more populations) in the wild over time (Carroll *et al.* 1996, entire; Wolf *et al.* 2015, entire). This evaluation considers the unique demographic, distribution, and diversity characteristics unique to the species. After applying the framework of the 3Rs, we determined the following:

- (1) Redundancy: The wolverine occurs across the contiguous United States within a metapopulation structure. The best available information indicates that the species continues to expand into historical, previously occupied areas in the contiguous United States following decades of hunting and trapping.
- (2) Representation: The wolverine is currently found across the west-northwestern United States, as well as much of Canada, and Alaska. The best available information indicates that the species is found across a wide range of habitats. Modeled primary habitat for the wolverine in the contiguous United States has been estimated at 164,125 square kilometers (km²) (63,369 square miles (mi²)).
- (3) Resiliency: The wolverine appears resilient within its contiguous United States range. The species exhibits physiological (e.g., seasonal changes in fur) and behavioral plasticity in its life history (e.g., reproduction, feeding, movement and use of habitat). Estimated population size and growth rates across its North American range are uncertain, but the best available information does not suggest that abundance is declining in the contiguous United States, or in North America. The most significant stressor currently and in the future appears to be the effects of climate change, such as warming temperatures and loss of snowpack. However, based on the best available information, we have no indication that this species is unable to adapt or adjust to changing conditions.

Demographic risks to the species from either known or most likely potential stressors (i.e., effects from roads, disturbance due to winter recreational activities, effects of wildland fire, and overutilization) are low based on our evaluation of the best available information as it applies to current and potential future conditions for the wolverine and in the context of the attributes that affect its viability. We analyzed the potential effects of climate change to wolverine habitat, including snow persistence in the Northern and Southern Rocky Mountains. The future

timeframe evaluated in this analysis is approximately 40 to 50 years, which captures the range of time periods for proposed projects within the species range, as well as our best professional judgment of the projected future conditions related to climate change, wildland fire conditions, or other potential cumulative impacts. While population information is lacking for this subspecies in some parts of its range, the best available information does not indicate that, winter recreational activities, infrastructure features, mortality from road crossings or trapping (authorized and incidental), currently or in the future will result in a decline in the subspecies across its range. Our evaluation of climate change indicates that snow cover is projected to decline in response to warming temperatures and changing precipitation patterns, but this varies by elevation, topography, and by geographic region. In general, models indicate higher elevations will retain more snow cover than lower elevations, particularly in early spring (April 30/May1). Further, significant snow persistence (greater than 0.5 meters (20 inches)) is projected at high elevations.

Legal protections include State listing in California and Oregon (as threatened), as endangered in Colorado, as a candidate species in Washington, and protection as a non-game species in Idaho and Wyoming. In Canada, provincial designations range from endangered to threatened in eastern provinces, and sensitive/special concern to no ranking in other provinces. Legal trapping or hunting of wolverines is currently prohibited in the contiguous United States. Trapping effort along the U.S.–Canada border does not represent a significant barrier to wolverine movement and dispersal along the international border.

Within the contiguous United States, approximately 96 percent of modeled wolverine primary habitat is located on Federal lands, with 41 percent located in designated wilderness areas. Management actions, including State Wildlife Action Plans, the Idaho Wolverine Conservation Plan, and USDA Forest Service Land and Resource Management Plans, and other Federal and Tribal partners, include winter road closures, fire management, land acquisition or conservation easements.

Abbreviations and Acronyms Used

ADF&G = Alaska Department of Fish and Game
BLM = Bureau of Land Management
°C = degrees Celsius
CDFW = California Department of Fish and Wildlife
CNDDDB = California Natural Diversity Database
COSEWIC = Committee on the Status of Endangered Wildlife in Canada
cm = centimeter
DNA = deoxyribonucleic acid
EIS = Environmental Impact Statement
EPA = U.S. Environmental Protection Agency
°F = degrees Fahrenheit
ft = feet
GCMs = Global Climate Models
GHG = Greenhouse gas
GPS = Global Positioning System
IDFG = Idaho Department of Fish and Game
in = inch
IPCC = Intergovernmental Panel on Climate Change
IUCN = International Union for Conservation of Nature and Natural Resources
kg = kilogram
km = kilometer
lb = pound
m = meter
mi = mile
MODIS = Moderate-Resolution Imaging Spectroradiometer
Montana FWP = Montana Fish, Wildlife, & Parks
NRC = National Research Council
NRIS = Natural Resource Information System
ODFW = Oregon Department of Fish and Wildlife
RCPs = Representative Concentration Pathways
Service = U.S. Fish and Wildlife Service
SSA = Species Status Assessment
SCA = Snow Covered Area
SGCN = Species of Greatest Conservation Need
SWCC = Southwestern Crown of the Continent
SWE = Snow Water Equivalent
WAFWA = Western Association of Fish and Wildlife Agencies
WDFW = Washington Department of Fish and Wildlife
WGFD = Wyoming Game and Fish Department
WRCC = Western Regional Climate Center
WSWCP = Western States Wolverine Conservation Project
YBP = Years Before Present

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Introduction

The wolverine (*Gulo gulo*) is the largest member of the Mustelidae family (weasels, mink, marten, and others) and resembles a small bear with a bushy tail (Hash 1987, p. 575). Wolverines have a Holarctic distribution that includes the northern portions of Europe, Asia, and North America. In North America, they are found in Alaska, much of Canada, and the western-northwestern United States. The wolverine is important to the culture of Native Americans and Aboriginal Peoples in North America, as is its conservation status in aboriginal territory (Cardinal 2004, p. iv; Edmo 2016; pers. comm.; Miles 2017, pers. comm.).

Wolverines possess a number of morphological and physiological adaptations that allow them to travel long distances and they maintain large territories in remote areas (Pasitschniak-Arts and Larivière 1995, p. 6). They have been described as curious, intelligent, and playful, but cautious animals (e.g., Krott 1958, p. 241; Krott 1960, pp. 25–26; Magoun 1985, p. 94; Cardinal 2004, p. 7–8; Woodford 2014; entire), though their social behavior and social organization has not been well-studied.

During the late 1800s and early 1900s, the wolverine population declined or was extirpated in much of the conterminous United States (lower 48 States), which has been attributed to over-trapping and habitat degradation (Hash 1987, p. 583). Similar range reductions and extirpations of some wolverine populations were observed in parts of Canada during this time period (van Zyll de Jong 1975, entire; Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2014, p. iv), attributed largely to human exploitation and availability of food (e.g., decline in caribou (*Rangifer tarandus*)), not climate or habitat changes (van Zyll de Jong 1975, pp. 434, 436). Habitat loss (historic vs. current range) for the North American wolverine (i.e., Canada and United States) has been estimated at 37 percent (Laliberte and Ripple 2004, p. 126). Wolverine numbers have recovered to some extent from this decline; in the United States, wolverines are currently found in parts of Washington, Oregon, Idaho, Montana, Wyoming, and California, and, as recently as 2012 in Colorado and 2016 in Utah, though not all of these areas contain resident, reproductive populations.

Species Status Assessment Methodology

In preparing the Species Status Assessment (SSA) Report for the wolverine, we reviewed available reports and peer-reviewed literature, incorporated survey information, and contacted species experts to collect additional unpublished information for the North American subspecies (*Gulo gulo luscus*), including Canada and Alaska. We identified uncertainties and data gaps in our assessment of the current and future status of the species. We also evaluated the appropriate analytical tools to address these gaps and conducted discussions with species experts and prepared updated maps of the known species' range and denning areas across North America. In some instances, we used publications and other reports (primarily from Fenno-Scandinavia) of the Eurasian subspecies (*Gulo gulo gulo*) in completing this assessment.

Importantly, we note here that, since the publication of the 2013 proposed listing rule (78 FR 7864; February 4, 2013), many new wolverine studies have been published, which has added to our understanding of wolverine biology while also highlighting new insights into identifying key

species' needs and their interactions with both abiotic and biotic factors. This is particularly relevant for a difficult to study animal like the wolverine.

Using the species, individual, and population needs identified for the wolverine and location results from surveys and studies, we conducted a geospatial analysis to estimate the North American wolverine's current range. We then evaluated this range and previous estimates of potentially suitable habitat in the west-northwestern United States to assess the species' current conditions within that region. Our future condition analysis includes the potential conditions that the species or its habitat may face, that is, the most probable scenario if those conditions are realized in the future. This most probable scenario includes consideration of the sources that have the potential to most likely impact the species at the population or rangewide scales in the future, including potential cumulative impacts. Potential future impacts associated with climate change (probabilistic estimates for temperature and precipitation) were based on downscaled climate model projections, including a detailed study of two regions in the western United States (Glacier National Park and Rocky Mountain National Park).

For the purpose of this assessment, we generally define viability as “consisting of self-sustaining populations that are well distributed throughout the species' range,” and where “[s]elf-sustaining populations are those that are sufficiently abundant and have sufficient genetic diversity to display the array of life history strategies and forms that will provide for their persistence and adaptability in the planning area over time” (Committee of Scientists 1999, p. 38). We use a timeframe of approximately 40 to 50 years because it is within the range of the available modeling efforts related to climate change. We believe this is a reasonable timeframe to consider as it includes the potential for observing these effects over several generations of the wolverine.

Using the SSA framework (Figure 1), we consider what the species needs to maintain viability by characterizing the status of the species in terms of resiliency, redundancy, and representation (Wolf *et al.* 2015, entire).

- **Resiliency** is having sufficiently large populations for the species to withstand stochastic events (arising from random factors). We can measure resiliency based on metrics of population health; for example, birth versus death rates and population size. Resilient populations are better able to withstand disturbances such as random fluctuations in birth rates (demographic stochasticity), variations in rainfall (environmental stochasticity), or the effects of anthropogenic activities.
- **Redundancy** is having a sufficient number of populations for the species to withstand catastrophic events (such as a rare destructive natural event or episode involving many populations). Redundancy is about spreading the risk and can be measured through the

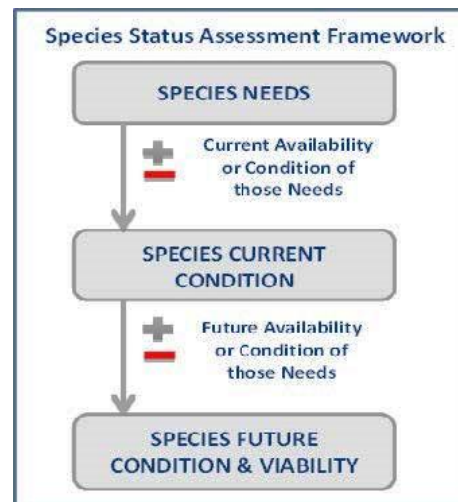


Figure 1. Species Status Assessment Framework.

duplication and distribution of populations across the range of the species. The greater the number of populations a species has distributed over a larger landscape, the better it can withstand catastrophic events.

- **Representation** is having the breadth of genetic makeup of the species to adapt to changing environmental conditions. Representation can be measured through the genetic diversity within and among populations and the ecological diversity (also called environmental variation or diversity) of populations across the species' range. The more representation, or diversity, a species has, the more it is capable of adapting to changes (natural or human caused) in its environment. In the absence of species-specific genetic and ecological diversity information, we evaluate representation based on the extent and variability of habitat characteristics within the geographical range.

Species Description

Taxonomy

The taxonomic relationship between North American and Eurasian wolverines has been a debated topic (Pasitschniak-Arts and Larivière 1995, p. 1). Most authorities consider all wolverines to belong to a single species, *Gulo gulo* (Rausch 1953, p. 114; Kurten and Rausch 1959, p. 19; Wozencraft 2008 [in *Wilson and Reeder's Mammal Species of the World*, online publication]). Some also further consider the New World and Old World wolverines to be two subspecies, *Gulo gulo luscus* and *G. g. gulo*, respectively, based on morphological measurements. Degerbøl (1935, pp. 35–43) noted slight color differences and very slight, if any, cranium differences, based on 10 North American (Hudson Bay) specimens examined, and regarded the North American and Old World wolverines as conspecific, but identified two subspecies. This reference also cites Coues (1877, p. 43), who, based on observations of a slight similar cranium difference, had posited that the wolverines of the Old World and New World were the same species (Degerbøl 1935, p. 35).

In their *Checklist of Palearctic and Indian Mammals* (1st and 2nd editions) Ellerman and Morrison-Scott (1951, p. 251; 1966, p. 251) identified one species of wolverine, but listed several subspecies. A comparative analysis of various measurements from 1 wolverine skull collected from the northern Ural Mountains to 41 Alaskan skulls by Rausch (1953, entire) reported “no appreciable differences,” noting the highly variable skull characteristics for the Alaskan specimens. Additionally, Krott (1960, p. 20) found no distinct differences between Old World and New World wolverines, and that pelt size and quality were not distinguishable. However, using biometric measurements of both newly collected and previously published cranial measurements (e.g., Degerbøl 1935; Rausch 1953), Kurtén and Rausch (1959, p. 19) reported that the North American and European wolverine were significantly different in several quantitative characters related to the size and shape of the skull size and teeth size. They concluded that the two wolverine populations represented two distinct subspecies, but were the same species, *Gulo gulo*.

The International Union for Conservation of Nature and Natural Resources (IUCN) states that “Most recent accounts [citing Jones *et al.* 1992, Pasitschniak-Arts and Larivière 1995, Wozencraft 2005] treat *luscus* as a subspecies of *Gulo gulo*, following Degerbøl (1935) and

Kurtén and Rausch (1959)” (Abramov 2016, p. 1). We reviewed the references cited by IUCN. Jones *et al.* (1992, p. 17) only considers *Gulo gulo*. Pasitschniak-Arts and Larivière (1995, p. 1) state there are differences in the taxonomic treatment, and that, while *Gulo gulo* is now considered by most to be the extant *species*, others (including the above-cited Kurtén and Rausch (1959) and Rausch (1953)) have considered two *subspecies*. The Wozencraft (2005) citation is from Wilson and Reeder’s previous 2005 publication, which was updated as of 2008. That account lists several “offspring” of *Gulo gulo*, but does not provide citations for the subspecies identified there, and at least two of those listed are not considered to be subspecific entities (e.g., *G. g. vancouverensis* and *G. g. luteus* (see Banci 1982, p. ii; Banci 1994, p. 104)). Finally, the COSEWIC Assessment and Status Report on the Wolverine (*Gulo gulo*) in Canada indicated that taxonomists recognize only a single subspecies (*Gulo gulo luscus*) in North America or consider *G. gulo* as single Holarctic taxon (COSEWIC 2014, p. 4).

Genetic analyses for the North American wolverine populations have primarily focused on genetic structure and variation of wolverine populations or subpopulations (see Kyle and Strobeck 2001; Kyle and Strobeck 2002; Zigouris *et al.* 2012, Zigouris *et al.* 2013). However, Frances’ (2008, pp. 20–21) assessment of wolverine spatial genetic structure and demographic history (using mitochondrial DNA) indicated incomplete lineage sorting between North American and Eurasian populations, though comprehensive sampling has not been conducted for some areas (e.g., eastern Asia). A study by Tomasik and Cook (2005, entire) also concluded that reciprocal monophyly (i.e., distinct *species*) had not been attained between Eurasian and North American wolverine populations. Until additional studies are published, including robust genetic analyses in conjunction with additional sampling, the Service recognizes the North American wolverine as *G. g. luscus*.

Physical Appearance

Detailed descriptions of the wolverine are described in Novikov (1962, pp. 196–202), Hash (1987, p. 575), Pasitschniak-Arts and Larivière (1995, pp. 1–2), and Wilson (1982, pp. 644–646), among others. Key distinguishing features are summarized here.

Wolverines are a medium-sized (about 1 meter (m) (3.3 feet (ft)) in length) carnivore, with a large head, broad forehead, and short neck (Pasitschniak-Arts and Larivière 1995, p. 1). Males are larger than females (Hall 1981, p. 1,007; Banci 1987, p. 35). Wolverines have heavy musculature and relatively short legs, and large feet with strong, curved claws for digging and climbing (Hash 1987, p. 575). Their feet are well-adapted for travel through deep snow and, during the winter, dense, stiff, bristle-type hairs are found between the toes and around the foot pad (Grinnell *et al.* 1937, pp. 265–266; Hash 1987, p. 575); this characteristic becomes diminished in the summer (Hash 1987, p. 575).

Adult wolverines are sexually dimorphic, with females weighing from 7 to 13 kilogram (kg) (15.4 to 29 pounds (lbs)) and males weighing between 10 to 18 kg (22 to 40 lbs) (North America) (Rausch and Pearson 1972, p. 264; Magoun 1985, pp. 19–21; Banci 1994, p. 99; Copeland 1996, p. 20; Cardinal 2004, p. 8; Lofroth 2001, p. 11; Inman 2013, pers. comm.; Magoun 2013, pers. comm.; Aubry *et al.* 2016, pp. 17–18). The skulls of wolverine are large and heavy, and the strong jaw structure allows animals to feed on frozen flesh and crush bone

(Haglund 1966, p. 269; Hash 1987, p. 575). Some geographic variation and sexual differences in skull morphology have been reported (Pasitschniak-Arts and Larivière 1995, p. 2). Wolverines have small, wide-set eyes, and are reported to have excellent hearing (Grinnell *et al.* 1937, p. 265; Krott 1960, p. 25; Bevanger 1992, p. 8).

Wolverine fur is short, thick, and uniform in thickness on the head and becomes longer towards the rear of the body (Hash 1987, p. 1). The coat consists of dense, woolly underfur (2-3 centimeters (cm) (0.8-1.2 inches (in) long) and coarse, stiff guard hairs, 6-10 cm (2.4-4 in) in length (Hash 1987, p. 1). The rich glossy coat can vary from medium brown to black (Banci 1994, p. 99; Pasitschniak-Arts and Larivière 1995, p. 1). Seasonal and individual variation in pelt color has been described (Degerbøl 1935, pp. 38–42; Grinnell *et al.* 1937, p. 252). In general, the head, tail and legs are darker than the face (Pasitschniak-Arts and Larivière 1995, p. 1). An upper body stripe, which varies from creamy, pale buff to light brown or reddish in color (Pasitschniak-Arts and Larivière 1995, p. 1), extends from the nape of the neck, along the sides of the body, to the base of the bushy tail (Banci 1994, p. 99). White or orange patches are commonly found on the throat or chest (Pasitschniak-Arts and Larivière 1995, p. 1; Magoun *et al.* 2008, p. 24; Figure 14). The unique property of wolverine fur to shed frost (Hardy 1948, p. 330; Quick 1952, pp. 492–493), along with its rarity, has made wolverine pelts valuable for trade (Hash 1987, p. 575).

Various accounts state that wolverines have a strong sense of smell (Grinnell *et al.* 1937, p. 265; Bevanger 1992, p. 8) that allows them to locate carrion from great distances (Hornocker and Hash 1981, p. 1,297; *in litt.* Bevanger 1992, p. 8, citing Røskaft 1990; Copeland 1996, p. 100; Cardinal 2004, p. 8); however, experiments with young wolverines indicated a poor sense of smell, and that wolverines may locate food (areas where previously located or cached) based on their memory skills (Magoun 2013, pers. comm.) or learning abilities (e.g., Krott 1958, p. 241).

Scent-marking is used by mammalian carnivores for chemical communication (Hutchings and White 2000, p. 160). For wolverines, this behavior commonly includes urination (e.g., trees, stumps, snow) (Copeland 1996, p. 115; Magoun 1985, p. 105), but also includes scat, and scratches and bites on trees (Haglund 1966, pp. 225, 277; Copeland 1996, p. 115). Scent rubbing (see review by Rieger 1979) of the ventral (abdomen/stomach) area and anal rubbing have also been observed in wolverines (Pulliainen and Oyaskainen 1975, pp. 268–269; Rieger 1979, p. 22, *in litt.* Goethe 1964; Magoun 1985, p. 105). Scent marking by wolverines may also be an important chemical communication signal for potential wolverine prey. Field experiments conducted by Sullivan *et al.* (1985, pp. 928, 930) and Sullivan (1986, p. 388) found that black-tailed deer (*Odocoileus hemionus columbianus*) and snowshoe hares (*Lepus americanus*) avoided feeding on seedlings that were marked with wolverine urine.

Life History and Ecology

In this section we provide a summary of the individual and population needs (collective, species needs), including its life history, physiology and behavior, resource functions necessary for each life stage (i.e., breeding, feeding, sheltering, dispersal), demographic information (abundance and distribution) and ecological setting.

Overview

Wolverines are active year-round and have been considered as primarily nocturnal (Iversen 1972b, p. 319; Pasitschniak-Arts and Larivière 1995, p. 7, and references cited therein). In his observational studies, Krott (1958, p. 168; 1960, p. 25) described periods of 3-4 hours of activity followed by 3-4 hours of sleep for wolverines in Scandinavia, a pattern also observed in Idaho (Copeland 1996, p. 77).

A study of body temperatures of caged wolverines, along with direct observations of animals obtained from Alaska and Sweden and previous studied animals (Alaska), suggested that wolverines were a day-active species, being very active in the morning, with periods of sleep during the night, a pattern that persisted in both winter and summer (Folk *et al.* 1977, p. 233). However, crepuscular activity (period just after dawn and just before sunset) may be a more accurate description for wolverine behavior (McCue *et al.* 2007, pp. 98–99). Others have remarked that wolverines exhibit a plasticity in their behavior (i.e., different behavior under different conditions) (Krott 1960, p. 26), a result attributed, in part, to their being a scavenging carnivore covering large areas (Stewart *et al.* 2016, pp. 1,495, 1,497). Several aspects of this plasticity are described below.

Wolverines are wide-ranging animals and known for traveling great distances in a short period of time (Krott 1960, p. 21; Gardner *et al.* 1986, p. 603; Woodford 2014, entire) (see Movement section below). This is due, in part, to their unique body structure. As described by Krott (1960, p. 20), they are “lumbrosacrally overbuilt” with heavy musculature and legs that are acutely angled when walking. Wolverine gait is characterized as either a 2X pattern (when patterns of two footprints repeat), used primarily in deep snow, and the more common 3X lopes (patterns of three footprints), for covering long distances over more compacted snow (Halfpenny *et al.* 1995, p. 104). The latter is described as a bouncing gait where all four feet may leave the ground at the same time (Halfpenny *et al.* 1995, p. 104).

As noted in our Species Description section above, in winter, the dense hairs on the foot pad and its body structure supports a low foot load, which has been estimated at 22 gram/cm² (Knorre 1959, p. 26) and 27–35 gram/cm² (Novikov 1962, pp. 22–23 (citing Dulkeit 1953)). This foot loading is believed to provide an advantage for wolverines preying on ungulates and other large mammals whose movements become restricted in deep snow (Knorre 1959, p. 26; Formozov 1963, pp. 40–41; van Zyll de Jong 1975, p. 435; Banci 1994, p. 113). However, a study of wolverines in boreal forest habitat in Canada present a differing interpretation of the wolverine foot adaptation based on tracking wolverines in snow over three winters (Wright and Ernst 2004a, pp. 58–59), in which they observed wolverines in their study area continuously selected for a path of least snow cover, where practicable, and only traveled in upland areas (Wright and Ernst 2004a, p. 59). They concluded that the low foot load is advantageous when snow crusts form, but, in deep snow, wolverines shift to an inefficient walking gait, which increases energy demand (Wright and Ernst 2004a, p. 59). They hypothesized that traveling in deep snow during winter in search of food may increase the risk of starvation due to the greater energy expenditure (Wright and Ernst 2004a, p. 59).

Physiology

The wolverine is a snow-adapted, cold climate animal in its physiology, morphology (Telfer and Kelsall 1984, p. 1,830), behavior, and habits. The wolverine was considered by Formozov (1963, p. 65) as one of several “chioneuphores,” or those vertebrates who tolerate snow but have no special adaptations; however, wolverines could also be considered as a “chionophile” or those animals with adaptations for snow (e.g., increased surface area on feet, pelt characteristics) (see definitions in Pruitt 1959, p. 172; Cathcart 2014, p. 22).

In general, mustelids weighing more than 1 kilogram (kg) (2.2 pounds (lbs)) have a basal metabolism (defined as the minimum metabolic rate for maintaining a comfortable warm temperature; Irving 1972, p. 121) that is about 20 percent higher than other mammals (Iversen 1972a, p. 343). For the wolverine, Young *et al.* (2012, p. 222) estimated a basal metabolic rate for a 15 kg (33 lbs) adult at 669.4 kcal/day, using Iversen’s derived equation [Metabolic rate (M)=84.6*Weight (W, in kg)^(0.78) ± 0.15] (Iversen 1972a, p. 343). By comparison, the estimated basal metabolic rate for a 53 g (1.9 ounce (oz)) least weasel (*Mustela nivalis*) is about 40 kcal/day, and approximately 250 kcal/day for a 3.8–5.5 kg (8.4–12 lbs) Arctic fox (*Vulpes lagopus*) (both sampled from Barrow, Alaska) (Irving 1972, p. 115; Figure 9.1).

Experimental studies by Iversen (1972, pp. 320–321; Figure 4) found that during their first 2½ months, the basal metabolic rate for young wolverines was substantially higher than rates reported for other mammals ($W^{1.41}$ vs. $W^{1.0}$), then declined after 3 months, and declined again after 8 months. Because the early period coincides with weaning, Wilson (1982, p. 646) suggested that the observed peak may be related to changes in food consumed as well as improved thermoregulation since the mother is leaving the young for longer periods of time.

Energy expenditure during pregnancy is relatively low for mustelids (Oftedal and Gittleman 1989, p. 374); however, energy requirements for lactation in mammals can be over 4 to 7 times basal metabolic rates (Allen and Ullrey 2004, p. 478). Thus, estimates of energetic requirements (e.g., less than 1 kg prey/day annually) may be too low to support reproductive activity (Young *et al.* 2012, p. 226). Wolverines are known to consume a variety of food resources and seasonal switching of prey likely allows for adjustment for nutritional needs throughout their life history (Krebs *et al.* 2007, p. 2,187 (Canada); Koskela *et al.* 2013a, pp. 103–104 (Finland); Yates and Copeland *in prep* (Montana)). Additional details on diet and feeding behavior for wolverines are provided below.

Relatedly, Casey *et al.* (1979, p. 335) evaluated metabolic and respiratory responses of eight terrestrial Arctic mammals to ambient temperature during summer months. For wolverines, they found that the frequency of respiration was generally constant (15–20 per minute), but their tidal volume (air moved per breath) increased nearly constantly with *decreasing* ambient temperature, unlike Canada lynx (*Lynx canadensis*), which is similar in body mass (Casey *et al.* 1979, p. 335). The researchers inferred that the increased ventilation of wolverines at low ambient temperatures was the result of an increased energy metabolism (Casey *et al.* 1979, p. 336).

Thermal neutrality (or **thermoneutrality**) is the temperature range at which resting metabolism is at minimum (Barnett and Mount 1967, p. 468) and animals produce heat at a minimum rate in

a thermal neutral environment (Barnett and Mount 1967, p. 413). For a resting mammal at thermal neutrality, body temperature is primarily maintained by “physical thermoregulation,” that is, control of circulation in the skin and by sweating (Barnett and Mount 1967, p. 413). The body temperature of wolverine (measured by an implanted temperature transducer) at thermoneutrality has been reported at 38°C (100.4°F) (Folk *et al.* 1977, p. 231; Casey *et al.* 1979, pp. 332–333). The **critical temperature** is the point at which the metabolic rate starts to rise; thus, animals with lower critical temperatures are able to better conserve their energy expenditure (Barnett and Mount 1967, p. 413). Studies of arctic mammals defined a zone of thermoneutrality in Eskimo dogs (*Canis lupus familiaris*) and Arctic foxes that extended to at least –40°C (–40°F), with an estimated critical temperature between –45°C (–49°F) and –50°C (–58°F) (Scholander *et al.* 1950a, p. 254).

Arctic mammals, including wolverine, Arctic fox, and wolf (*Canis lupus*), have a threshold of thermoneutrality of between –30°C to –40°C (–22°F to –40°F) (Iversen 1972b, p. 322; citing studies by Scholander *et al.* (1950b) and Hart (1956)). Relatedly, Casey *et al.* (1979, p. 340) estimated a critical temperature for wolverine (14 kg (31 lb)) in *summer* pelage of 5°C (41°F) based on an observed increase in oxygen uptake at air temperatures below this temperature. For comparison, measurements of metabolic rates for the red fox (*Vulpes vulpes alascensis*) (Alaska) observed critical temperatures of 8°C (46°F) in summer (Irving *et al.* 1955, p. 184). These Arctic mammals therefore have the ability to dissipate heat to balance the heat loss from 30°C to –40°C (86°F to –40°F), due in large part to vasodilatation and rise of skin temperature (Scholander *et al.* 1950a, p. 251).

Arctic mammals, particularly small mammals, also adapt behaviorally to cold temperatures by creating burrows and building nest sites under the snow. Wolverines are known to dig holes in snow for shelter (Pruitt 2005, p. 120), and wolverine reproductive den sites located under deep snow may provide a thermoneutrality advantage for newborn cubs (Magoun and Copeland 1998, p. 1,313). This topic is discussed in more detail below under Use of Dens and Denning Behavior.

Wolverines can also adapt to both cold and warm temperatures by movement and, relatedly, micro- and macro-habitat selection. Wolverines have been observed near and in lakes and other water bodies and are good swimmers, easily crossing lakes and rivers (Seton 1909, p. 950; Krott 1960, p. 23; Magoun 2017, pers. comm.). They likely use these areas more frequently during warmer months both for cooling and hydration, or possibly for hygienic reasons (Krott 1960, p. 23).

Changes in endocrine (hormone) function can also represent a physiological adaptation to cold by acting on organs to generate energy (Barnett and Mount 1967, p. 428). The best available information does not indicate that these functions have been evaluated in wolverines. However, one veterinarian reported an enlarged thyroid in a wolverine during a necropsy procedure (Copeland 2017, pers. comm.), which is suggestive of a high metabolism.

In addition to these physiological processes, rapid and seasonal adjustments of fur insulation provide an additional mechanism for mammals to overcome large seasonal changes in temperature (Casey *et al.* 1979, p. 340) and have been described for wolverine and other mammals in Alaska (Henshaw 1970, p. 522). The seasonal increase in fur depth for captive

wolverines was reported to be 65 percent (Henshaw 1970, p. 522). That study identified a metric termed seasonal insulative advantage (or SIA) as a measure of the degree to which insulative compensation changes seasonally in response to ambient temperature (Henshaw 1970, p. 522). For wolverines, this advantage was found to be less than unity; that is, the increase in fur did not fully compensate for average winter cold, and therefore other compensating mechanisms were needed (Henshaw 1970, p. 522).

Similarly, an evaluation of the seasonal change in the insulation of fur of wolverine (pelts from Canada) found a 41.2 percent change in mean insulation values (measured as °C/cal/m²/hr) from winter to summer (Hart 1956, p. 56). A single annual molting (between August and December) was noted in Grinnell *et al.* (1937, p. 251) (California), but twice yearly was described by Novikov (1962, p. 201) (Russia). The large seasonal change in insulation observed for wolverine and other larger mammals is, in large part, due to changes in fur depth, and can be interpreted as an adaptation to both high summer temperatures and low winter temperatures (Hart 1956, p. 57). The reported seasonal decrease in wolverine fur thickness also correlates with experimental results of Casey *et al.* (1979, p. 337) who indicated that a seasonal shift in oxygen consumption below critical temperature was likely due to an increased rate of heat loss in summer.

Range and Habitat Use

Historical Range and Distribution

Phylogeography/Phylogenetics

Results from a molecular study of phylogenetic relationships of the Mustelidae family suggest at least six radiation episodes within this family since the Early Eocene Epoch (approximately 50 million years before present (YBP)) (Marmi *et al.* 2004, pp. 488, 492). The split of the marten (*Martes*, *Gulo*) and weasel (*Mustela*) lineages occurred in the Early Middle Miocene Epoch (14 to 11 million YBP), with the separation of Old World and New World lineages (*Martes*, *Gulo*) occurring in the Late Miocene Epoch (8.6 to 5.8 million YBP) (Marmi *et al.* 2004, p. 488). The *Gulo* genus appears in the fossil record in the mid-Pleistocene in both Europe and North America (Bryant 1987, p. 659).

The dispersal of *Gulo* across Beringia (land mass that extended from Siberia into interior Alaska during the Pleistocene) is believed to have produced contemporaneous records for the species in Europe and North America (Bryant 1987, p. 659). Genomic data was examined using a molecular dating technique to estimate an approximate age of the *G. gulo* ancestor (Malyarchuk *et al.* 2015, entire). The researchers estimated a relatively recent origin of the species *Gulo gulo* at about 181,000 to 234,000 YBP (Malyarchuk *et al.* 2015, pp. 1,115–1,116). They note that this latter time period corresponds to the Riss glaciation period (187,000 to 230,000 YBP), a time of genetic divergence of amphi-Beringian (both sides of Beringia) species and speciation events (Hope *et al.* 2013, p. 426). Their results, along with fossil information, also indicate the divergence of the *Gulo* branch and the other *Martes* taxa occurred during the Late Miocene-Early Pliocene (5.6 million YBP), and lends support for strong evolutionary processes in the northern Siberian ecosystems in the Pliocene and Pleistocene Epochs (Malyarchuk *et al.* 2015, pp. 1,116–1,117).

An evolutionary trend was described in which *Gulo* increased in size from the mid- to late-Pleistocene, with a subsequent reduction in size post glaciation, as well as small changes in selected teeth, and a possible shift to colder habitats (Bryant 1987, p. 660). The Late Pleistocene and the Pleistocene-Holocene transition represent the end of prolonged period that was characterized by climate fluctuations followed by rapid warming (Post 2013, p. 28). This analysis also indicated that both the mid-Pleistocene European *Gulo schlosseri* and the early North American *Gulo* appear to be adapted to a warmer climatic environment, but are likely to have also occupied colder climates (Bryant 1987, p. 660). Other factors such as competition (Guilday 1971, p. 237), predator avoidance, and prey abundance may also have been important in creating significant shifts in geographic ranges for certain species during glacial cycles.

Wolverines are believed to have migrated to North America during the late Pleistocene, although fossil evidence from the Pleistocene Epoch for wolverine is limited (Anderson 1977, p. 15; Bryant 1987, p. 660), and most fossil material is either cranial or dental fragments (Bryant 1987, p. 660). A summary of records for both Pleistocene and extant *Gulo* (Bryant 1987, p. 659; Table 3) includes findings in the United States from Colorado, Idaho (e.g., White *et al.* 1984, p. 248 (lava tubes)), Alaska, Maryland, and Pennsylvania, and Canada (primarily the Yukon region) ranging from the Irvingtonian Age (1.8–2.4 million YBP) to Late Wisconsinan-Holocene (15,000 YBP to present day).

Genetic studies can provide an understanding of the postglacial recolonization of wolverines following the Last Glacial Maximum, a period of rapid cooling, and movement patterns due to changed climatic conditions (Frances 2008; Zigouris *et al.* 2013; McKelvey *et al.* 2014). Following the Last Glacial Maximum, beginning about 21,000 YBP, was a period of rapid warming, resulting in a second wave of extinction events, particularly of large mammalian megafauna that were cold-adapted (Post 2013, pp. 29, 31).

During the late Wisconsin period (10,000 to 25,000 YBP), approximately 60 percent of North America was covered by glacial ice (Rogers *et al.* 1991, p. 624). However, several ice-free refugia existed at that time including the Beringian refugium, which included eastern Siberia, most of Alaska, areas of northwestern Canada, and areas of the Bering Sea shelf that were exposed by lower sea levels, and this refugium harbored a number of mammalian species including wolverine (Rogers *et al.* 1991, pp. 624, 626). Analyses by Frances (2008, entire) and Zigouris *et al.* (2013, entire) supported a wolverine colonization of North America in which individuals “followed retreating glaciers” (Zigouris *et al.* 2013, pp. 10–11), beginning about 21,000 YBP, following the Last Glacial Maximum, when a period of rapid warming occurred that resulted in additional extinction events, particularly large mammalian megafauna (Post 2013, p. 29)

A phylogeographic analysis presented by McKelvey *et al.* (2014, p. 331) proposed that a unique haplotype (Cali 1) observed in historical wolverine samples from California was reflective of an independent evolutionary history resulting from isolation (i.e., southern ice-free refugium) of wolverines during glacial retreat. However, Zigouris *et al.* (2013, p. 10, Supplemental Table S5) found the Cali 1 haplotype described by Schwartz *et al.* (2007, p. 2,173; Tables 2 and 4) (relabeled as Haplotype 21) also occurred in historical wolverine samples from the eastern region

of Canada (Quebec-Labrador). In addition, as noted by Zigouris (2014, pp. 232–233) the historical samples analyzed by McKelvey *et al.* (2014, p. 327; Table 1) were primarily those from locations at the southwestern edge of the wolverine's North American range (e.g., California, Colorado, Idaho, Montana, Wyoming, Utah, Washington). Without additional sampling, it is unclear if this particular haplotype distribution from two of the most peripheral North American wolverine populations is a reflection of a skewed dispersal after post-glacial colonization, or was a more widely distributed haplotype that declined or was lost due to hunting and trapping pressures (beginning in 18th century) or fragmentation (late-20th century) (Zigouris *et al.* 2013, p. 10).

Additional discussion of our current understanding of wolverine genetic structure and diversity is provided in the *Population Structure* section below.

Historical Range

In North America, wolverines were historically distributed in much of the northern portion of the continent, extending southward to the northernmost region of the United States (Maine to Washington) or approximately north of the 38th parallel (Hash 1987, p. 576; Banci 1994, p. 102).

An estimate of wolverine observations and distribution in the contiguous United States was prepared by compiling 901 verifiable or documented records of wolverine occurrence dating from 1801 to 2005 from 24 states in the contiguous United States (Aubry *et al.* 2007, entire). This included a total of 809 verifiable or documented records for the Rocky Mountain and Pacific Coast mountains (west-northwestern United States) for this time period (Aubry *et al.* 2007, p. 2,151).

The historical population size of wolverines in Canada is not known (Fortin 2005, p. 4). Its historical distribution, as depicted by Seton (1909, p. 947; Map 51) and also later by van Zyll de Jong (1975, p. 435; Figure 9) shows a broad range across much of Canada. Examples of early descriptive accounts include de Puyjalon (1900, pp. 126–144), who described wolverines as inhabiting Labrador, Canada (de Puyjalon, p. 101), and extending in range to the 66th parallel and perhaps further (de Puyjalon 1900, p. 144); reports of both trapped and live wolverines in Labrador in the late 1700s (Townsend (ed.), 1911, pp. 73, 93, 228, 255); and reports of wolverines as “common” in Canada's Nunavut Territory (Hudson Bay region) during a 1920s Danish excursion (the Fifth Thule Expedition) to Arctic North America (Freuchen 1935, p. 101). The 2014 COSEWIC report presents a historical range distribution for Canada based on personal accounts and interpretation of the fur trade (COSEWIC 2014, pp. 12–13; Figure 3).

Current Range

We created a map depicting wolverine observations for the west-northwestern United States by requesting all available wolverine records from State agencies (e.g., wildlife agencies, natural heritage programs) and the Forest Service Natural Resource Information System (NRIS) Wildlife Database. We found a total of 4,215 records (1800s to 2017) for this portion of the United States (*cf.* 809 records from Aubrey *et al.* 2007; Table 1). Figure 2 presents a map of these compiled

observations, overlaid with the habitat suitability model results presented by Inman *et al.* (2013, p. 281). We acknowledge that some of these records may be in error or inaccurately located, and although wolverines have been reported from the Central Great Plains, Great Lakes region, Upper Midwest, or Northeast (Wilson 1982, p. 650), we did not create a historical range for these regions given the very low number (92) reported by Aubry *et al.* (2007, p. 2,151) from the 1880s to 2005, and to present day, and an incomplete historical record of trapping. We also found a few additional historical records that do not appear in Aubry *et al.* (2007, p. 2,151). For example, Nead *et al.* (1985, entire) identified several positive and probable reports of wolverines in Colorado in the late 1970s. A wolverine was reported from the Squaw Valley region of California in the summer of 1953 (Ruth 1954, pp. 594–595). Our intent in creating this map was to present an overall geographical depiction of the wolverine's estimated range only for the west-northwestern United States, and is not intended to represent an estimate of population numbers.

Using the best available information, we also created a current North American range based on results presented by COSEWIC (2014, p. 12) for Canada and Alaska, Forest Service NRIS data, and more recent observations (e.g., telemetry, camera traps, mortality reports) reported from California, Washington, Colorado, Wyoming, Utah, and North Dakota (e.g., California Natural Diversity Database (CNDDB); Forest Service NRIS; Idaho Department of Fish and Game; Utah Division of Wildlife; Wyoming Game and Fish Department). This range is illustrated in Figure 3.

We recognize that this depiction does not necessarily represent current areas where reproducing populations of wolverines are found, nor does it capture unverified accounts from New Mexico, described in Frey (2006, pp. 20–21) for the Sangre de Cristo Range, and visual observations reported by two individuals (2005 and 2016) in response to our *Federal Register* notice (81 FR71670; October 18, 2016) requesting information for our status review. In addition, we did not incorporate the Central Great Plains, Great Lakes region, Upper Midwest, or Northeast. However, we note here that a female wolverine was observed over several years (2004–2010) in the lower peninsula of Michigan, and genetic testing after her death in 2010 suggested she was more closely associated with eastern Canada wolverine populations (i.e., Manitoba and Ontario) (*in litt* Zigouris 2013, pers. comm.). It's unclear how this individual came to occupy this region, but given the long distant movements reported for this species (e.g., male wolverine that traveled from Wyoming into Colorado and then back to North Dakota), dispersal from Canada is plausible. Wilson (1982, p. 650) reported that wolverines on occasion may enter Minnesota from Canada. Jackson (1961, pp. 359–360) also reported several authentic records of wolverine in Wisconsin and in areas in Minnesota, along the Wisconsin-Minnesota border. However, the wolverine was likely never abundant in Wisconsin, even before trapping and hunting in the late 19th and early 20th centuries (Jackson 1961, p. 359).

We provide a discussion of wolverine population abundance and distribution in more detail in the *Biological Status–Current Condition* section below.

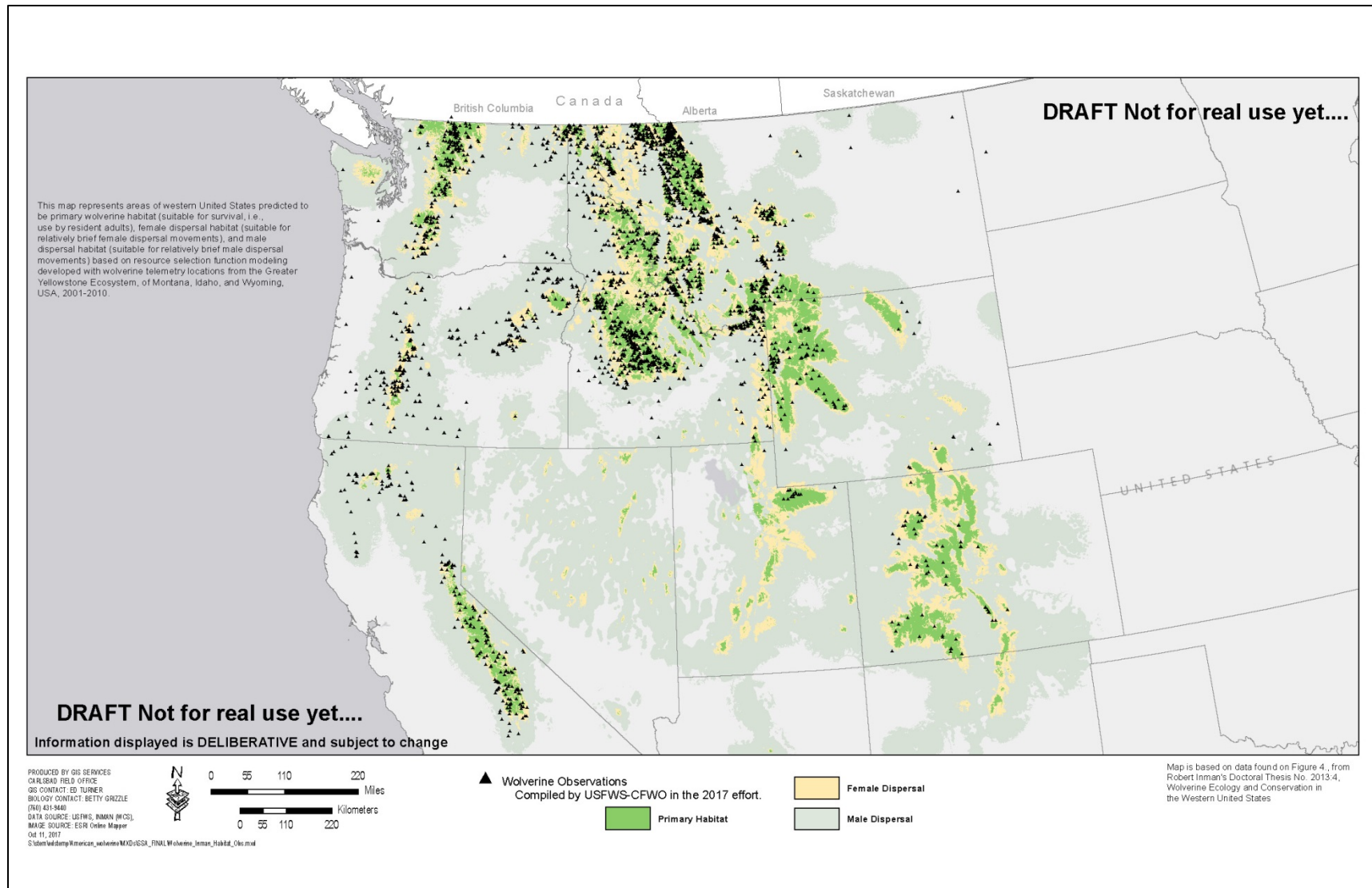


Figure 2. North America wolverine observations within the west-northwestern United States (1800s to 2017); shown with Inman *et al.* (2013) modeled habitat.

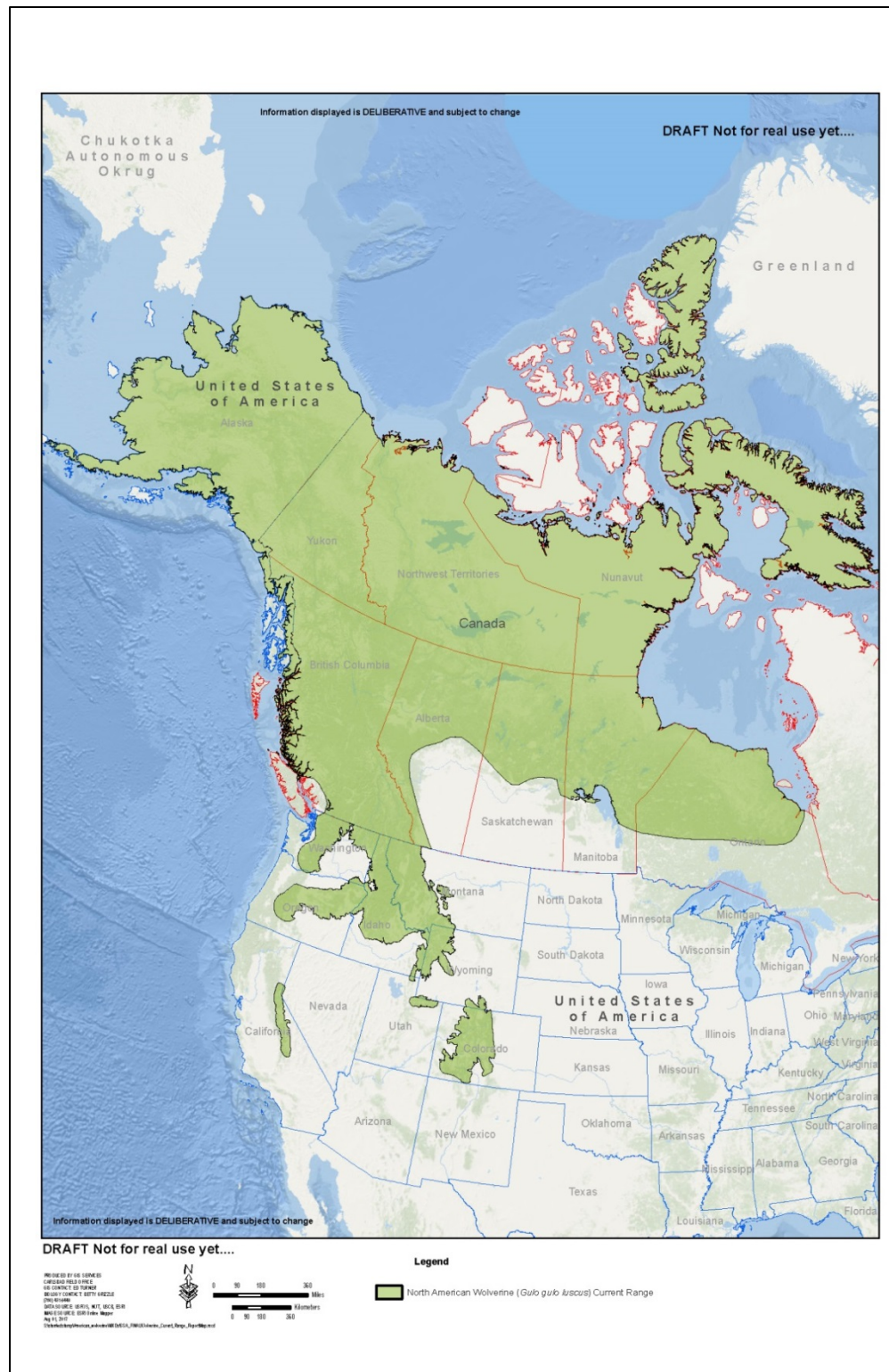


Figure 3. Current range of North American wolverine. Adapted from COSEWIC (2014), EPA (2010), Inman *et al.* (2013), records from CNDDDB; Forest Service NRIS; Idaho Department of Fish and Game; Utah Division of Wildlife; Wyoming Game and Fish Department, and den records from CNDDDB, Inman, and Copeland.

Habitat Use

Wolverines occupy a variety of habitats within their current range, including Arctic tundra, subarctic-alpine tundra, boreal forest, mixed forest, redwood forest, and coniferous forest (Banci 1994, p. 114). However, these broad, landscape-scale vegetation associations can obscure other habitat variables important for wolverines, including features found within peripherally occupied areas or areas of high elevation (Banci 1994, p. 114). In Canada, wolverines use a wide variety of forested and tundra vegetation, at all elevations (COSEWIC 2014, p. 18).

When viewed by ecoregion (U.S. Environmental Protection Agency (EPA) 2010), in general, wolverine observations in the contiguous United States are most commonly found in the Northwestern Forested Mountains ecoregion. In Canada, our estimate of current range includes Northwestern Forested Mountains, Northern Forests, Marine West Coast Forest, Hudson Plain, Taiga (Boreal Forest), Tundra, and parts of the Arctic Cordillera (northeastern fringe of Nunavut and northern Labrador); in Alaska, Marine West Coast Forest, Northwestern Forested Mountains, Taiga, and Tundra are represented. **Appendix A** provides an illustration of these ecoregions of North America in relationship to our Current Range map presented in Figure 3.

Studies of wolverines in central Idaho found that montane coniferous forests comprised two-thirds of available habitat (Copeland 1996, p. 120). Wolverine in this region also exhibited a seasonal preference, with subalpine rock habitats used in summer and montane coniferous forests used most often in winter (Copeland 1996, p. 120). In addition, individuals within this study population commonly crossed natural openings and those areas with little cover, including burn areas, meadows, or open mountain-top areas (Copeland 1996, p. 124).

Observations of summer movements of wolverines in northwestern Montana indicated that both males and females moved to higher, cooler elevations and remained there throughout the summer (Hornocker and Hash 1981, p. 1,299). In the Greater Yellowstone Ecosystem, wolverines selected areas that contained steep terrain with tree cover, high elevation meadows, boulder or talus fields, and avalanche chutes (Inman *et al.* 2012a, p. 785). In this region, wolverines selected elevations at and above the treeline during summer, moved slightly lower during winter, but avoided low-elevation winter ranges occupied by potential prey (e.g., elk) or areas with little human activity (Inman *et al.* 2012a, p. 785). The avoidance of these areas may be the result of lack of tree or talus field cover at these low elevations, in combination with presence of potential predators (e.g., wolf, mountain lion (*Puma concolor*) or competitors (e.g., coyote (*Canis latrans*), bobcat (*Lynx rufus*) (Inman *et al.* 2012a, p. 785).

Several habitat association-type models have been developed for both North American and European wolverines. In the northern Rockies (including Canada and the United States), Carroll *et al.* (2001, p. 975) found that elevation and north-facing cirque habitat variables (i.e., alpine areas), when incorporated into empirical habitat models, were significantly correlated with wolverine occurrence; however, results from multiple regression analyses of these and other habitat variables indicated a high degree of unexplained variance for predicting wolverine habitat relationships, and underscores the inherent difficulty in identifying appropriate metrics to represent difficult to measure underlying factors, or other unrecognized limiting variables (Carroll *et al.* 2001, pp. 971, 973–974). Copeland *et al.* (2007, entire) also evaluated habitat

associations for wolverines in central Idaho. Wolverines were found to be associated with high elevations (2,200 to 2,600 m (7,218 to 8,530 ft)) with a slight downward shift in summer (Copeland *et al.* 2007, p. 2,207). These movements correspond with a shift in cover types, from high-elevation whitebark pine (*Pinus albicaulis*) communities in summer to mid-elevation Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) in winter (Copeland *et al.* 2007, pp. 2,207–2,208). Results from a study of wolverines in Scandinavia suggested that topography may be important in providing refugia from predators and may therefore facilitate the co-existence of wolverines with larger carnivores such as wolves (Khalil *et al.* 2014, p. 636).

In interior Alaska, wolverines were also found to be positively associated with high elevations (Gardner *et al.* 2010, p. 1,901). The authors concluded that wolverines avoided human influences based on observations that both elevation and human influence were found to have significant effects on wolverine occurrence probabilities, but were not correlated (Gardner *et al.* 2010, p. 1,901). However, they indicate that their sampling design was not able to determine which human activities influenced wolverine behaviors; a combination of intensity of development and harvest activities was suggested (Gardner *et al.* 2010, p. 1,901). Current studies are underway in the North Slope region of Alaska to evaluate fine-scale habitat selection of wolverines related to denning, caching, day bed use, and snow holes (Dorendorf 2016, p. 6). Day beds were also described by Haglund (1966, p. 268) for wolverines studied in Sweden.

A study also found that habitat associations, at least for females, are more complex, and include combinations of several modeled variables that supported hypotheses related to food (prey distribution), predation risk (based on a ruggedness index), or human disturbance (winter recreation activity, roads, and forest harvesting) for both summer and winter in two study areas located in northcentral and southeast British Columbia (Krebs *et al.* 2007, pp. 2,186–2,187). Wolverines in the Rocky Mountains of Alberta, Canada, were found to more likely occupy areas with increasingly rugged terrain (Fisher *et al.* (2013, pp. 710–712).

Camera trapping was used to study wolverine behavior in varying habitat in the Rocky Mountains of Alberta, Canada (Stewart *et al.* 2016, entire). That study found that wolverine behavior differed in landscapes that had been significantly modified by human activities as compared to those with light modifications or in protected areas (Stewart *et al.* 2016, p. 1,499). They concluded that wolverine occurrence in their study areas varied more strongly with linear features (seismic lines created from oil and gas exploration, pipelines, transmission lines, roads, and rail lines) than with the degree of snowpack, and supports the idea that human “footprint” as a driver of habitat suitability for wolverines; that is, if snowpack conditions was the only driver for suitable habitat, then a behavioral signal would not be expected (Stewart *et al.* 2016, p. 1,501).

Aboriginal knowledge holders (the knowledge Aboriginal Peoples have accumulated about wildlife species and their environment) in Canada have reported that while wolverines appear to avoid human habitation and developed areas, some wolverine will visit these areas if they do not appear to be threatened or if development activities cease (Cardinal 2004, p. 22). Wolverines have also been described as occupying deserted snow huts (Nunavut Territory, Canada) during winter months (Freuchen 1935, p. 98).

A negative association with roads and wolverine (and caribou) occurrence in boreal forest habitat was reported in northwestern Ontario, Canada, and wolverines in that study area avoided deciduous forests (Bowman *et al.* 2010, p. 464). However, a study of wolverines in upland boreal forests of Canada found that wolverines followed open linear corridors that offered compact snow conditions, including winter roads, recent seismic lines, snowmobile trails, and all-terrain vehicle tire tracks for travel of distances up to 3 kilometers (km) (1.86 miles (mi)) (Wright and Ernst 2004b, p. 59). In central Idaho, wolverines were reported using snowmobile winter access (unmaintained) roads for travel (Copeland *et al.* 2007, p. 2,210).

A study of wolverine selection patterns in boreal forests in northwestern Alberta using resource selection function (RSF) modeling techniques¹ and data from telemetered wolverines found that, for the winter season, both male and female wolverines selected for streams, forested areas (broadleaf, coniferous, and mixed) and bogs or fens, while avoiding active oil and gas well sites and low-traffic winter roads (Scrafford *et al.* 2017, pp. 31, 32). That study also found that wolverines did not avoid older seismic lines, likely due to the intermediate stage of regeneration found in their study area as well as availability of small prey in conjunction with minimal risk of human or wolf presence (Scrafford *et al.* 2017, p. 34).

RSF-based modeling was used to quantify the relationship between the observed distribution of the wolverine and variables representative of habitats and human disturbance in the taiga and tundra ecoregions (shown in Appendix A) of the Canadian central Arctic (Nunavut and Northwest Territories) (Johnson *et al.* 2005, p. 10). Using a range defined by previous studies of collared wolverines, researchers identified two seasons for wolverines, based on presence or absence of barren-ground caribou (*Rangifer tarandus groenlandicus*) (Johnson *et al.* 2005, p. 8). They found that, in winter, the occurrence of wolverines was correlated with patches of heath rock and rock association, and areas dominated by sedge (Johnson *et al.* 2005, pp. 23–25). Results for models for summer season were less clear, but models that included grizzly bear (*Ursus arctos*), caribou, and wolf were found to be positively associated with wolverine, likely due to the scavenging opportunities and hunting of caribou provided by these other carnivores (Johnson *et al.* 2005, p. 24). In Finland, the presence of wolves was found to be one of the most important variables influencing habitat selection of wolverines (Koskela 2013, p. 35) likely due to the increased scavenging opportunities provide by wolf kills (Koskela 2013, p. 36).

A RSF model was also used to develop a predictive map of wolverine habitat for the western United States (Inman *et al.* (2013, p. 281), as shown in the background of our Figure 3. Their best fit model found that, in general, wolverine were most likely to be distributed at high elevations, with steeper terrain, more snow, fewer roads, and reduced human activity, but also in proximity to high elevation talus, tree cover, and areas that had snow cover on April 1 (Inman *et al.* 2013, pp. 280–281). Primary habitat for the wolverine in the western United States was estimated at 164,125 km² (63,369 mi²) (Inman *et al.* 2013, p. 281). Additional information

¹ RSF is any mathematical function that is proportional to the probability of use of a resource unit (Manly *et al.* 2002, p. 15). A RSF contains several coefficients that quantify the selection for or avoidance of an environmental feature, and the sign/strength of those coefficients represents a differential variation in the distribution of each environmental feature measured at a sample of locations to a comparable set of random sites. Thus, when an animal's observed use of a resource is greater than those random sites, selection of that feature is inferred (Johnson *et al.* 2005, p. 10).

related to the results of this modeling effort is discussed in the *Population Distribution and Abundance* section below.

Movement

Wolverine movements are related to both territoriality (within home ranges) and dispersal (adults and young). Movement within home ranges by adult male and female wolverines is extensive. For example, wolverines monitored in the Greater Yellowstone Ecosystem traveled a distance that was equivalent to their average home range diameter in less than 2 days, which is also about the size of their home range circumference in less than 1 week (Inman *et al.* 2012a, pp. 782–783). This study also found that, for a 24-hour period, the average minimum distance traveled was 15.5 (km) (9.63 (mi) for males and 7.5 km (4.66 mi) for females (Inman *et al.* 2012a, p. 783). Telemetry studies of wolverines in south-central Alaska indicate an average distance traveled per day of approximately 12 km (7.46 mi) for females and 8–21 km (4.97–13 mi) for males (Woodford 2014, no page number). Observations from snow tracking studies have found instances where two individual wolverines traveled together (Wright and Ernst 2004b, p. 63).

A study of female Fennoscandinavian wolverines found that most (86 percent) females remained stationary in their established territories, with 8 percent vacating and 6 percent expanding their territory (Aronsson 2017, p. 40). In addition, this study of 42 female wolverines in 122 territories reported that females with established territories only moved to available territories that were higher than average in quality (Aronsson 2017, p. 41). In central Norway, a study of spatial and temporal patterns in wolverines using noninvasive genetic sampling methods also found that individuals tended to stay in the same general area from one year to the next (Bischof *et al.*'s 2016, p. 1,533).

A number of factors can affect wolverine movements within territories, such as availability of food, temperature, and breeding activity. Seasonal shifts in elevation have also been observed for wolverines in the contiguous United States. An ecological study of wolverines in southcentral Alaska found significant movement up in elevation during late winter and early spring as well as significant movement down in elevation during the late fall and winter (Gardner 1985, p. 21). Wolverines were also observed moving to and occupying higher and presumably cooler elevations in summer months in northwestern Montana (Hornocker and Hash 1981, p. 1,299). In Central Idaho, wolverines exhibited a preference for higher elevation areas containing rock and talus cover in summer months, but moved to lower elevations in winter; this was likely the result of an increase in availability of carrion related to the fall hunting season (Copeland 1996, p. iv). Two aboriginal knowledge holders in the Kivalliq region (Nunavut, Canada) reported that wolverines will move closer to communities during caribou migration in the fall, likely attracted by the large number of caribou carcasses left by hunters (Cardinal 2004, p. 22).

A study of wolverine movement in boreal forest habitat in Canada (northwestern Alberta and northeastern British Columbia) during winter months found that wolverines chose the most direct travel route with the least snow cover (Wright and Ernst 2004a, pp. 58–59). Woodford's (2014, no page number) account of wolverine observations from studies in Alaska indicated that, when pursued, wolverines will run uphill, which may represent a predator-avoidance adaptive behavior.

As discussed in more detail below (*Diet and Feeding*), several studies have shown that wolverines exhibit a seasonal shift in diet, and Hornocker and Hash (1981, p. 1298) concluded that food availability was the primary factor determining both movements and home ranges for wolverines studied in northwestern Montana. Movement patterns of adult males during the summer months are also likely influenced by breeding activity (Magoun 1985, p. 66).

Males and females maintain large territories with very little overlap between same-sex adults (Magoun 1985, p. 38; Banci 1994, p. 118; Inman *et al.* 2012a, p. 783; Bischof *et al.* 2016, pp. 1,532–1,533; Regehr and Lacroix 2016, p. 249), but breeding pairs have overlapping territories (Copeland 1996, pp. 55–61; Hedmark *et al.* 2007, p. 19; Dawson *et al.* 2010, p. 413; Persson 2010, p. 52; Inman *et al.* 2012a, p. 787). However, ranges of young males, who have not yet dispersed, can overlap with resident adult male home ranges (Alaska) (Magoun 1985, p. 64). Studies of wolverines in the Greater Yellowstone Ecosystem found a mean percent overlap of 12.7 percent for same sex, adult–sub-adult pairs and about 24 percent for opposite sex, adult–sub-adult pairs (Inman *et al.* 2012a, p. 787). In addition, Inman *et al.* (2012a, p. 783) found that when a resident adult wolverine died, same-sex adults (not known to be located within the dead wolverine’s home range) would begin using (within 3–7 weeks) areas of the unoccupied home range, or same-sex subadults would expand into and then occupy most or all of the dead wolverine’s former home range. A study of territoriality of wolverines in central Norway (using scat analysis) indicated that within their study population, wolverines were also more likely to choose a home range area that was previously used by a neighboring same sex individual after that individual’s death (Bischof *et al.* 2016, p. 1,533).

Table 1 below presents a summary of annual home ranges of resident wolverines.

Table 1. Home Range Size for Adult, Resident Wolverines.

Region	Female, km ² (mi ²)	Male, km ² (mi ²)	Reference
Central Idaho	384 (148)	1,582 (610)	Copeland 1996
Central Idaho / Yellowstone Region	357 (138)	1,138 (439)	Heinemeyer and Squires 2015
Greater Yellowstone Ecosystem	303 (117)	797 (308)	Inman <i>et al.</i> 2012a
Glacier National Park (MT)	139 (54)	521 (201)	Copeland and Yates 2008
Alaska (Northwestern)	53-232 (20-89.6)	488-917 (188-354)	Magoun 1985
Canada Northwest Ontario	50-400 (19-154) 423 (163)	230-1,580 (89-610) 2,563 (990)	COSEWIC 2014 Dawson <i>et al.</i> 2010
Central Norway	331 (128)	757 (292)	Bischof <i>et al.</i> 2016
Southern Norway	274 (106)	663 (256)	Landa <i>et al.</i> 1998
Northern Sweden	170 (66)	669 (258)	Persson <i>et al.</i> 2010

Home range use is smaller for female wolverines during the reproductive period. For a parturient (about to bear young) female, estimates of home range size in the Greater Yellowstone region were significantly smaller, with a minimum of 100–150 km² (39–58 mi²) (i.e., during year raising young) (Inman *et al.* 2012a, p. 782). The average home range size for lactating females rearing young was estimated at 70 km² (27 mi²) from March through August (Alaska) (Magoun 1985, p. 36). In northwestern Ontario, researchers reported a home range of 262 km² (101 mi²) for a lactating female (Dawson *et al.* 2010, pp. 141–142). In general, the distance traveled by female wolverines depends on the location of the reproductive den site within the home range, the areas used for locating food/prey, and the territory border (Myhr 2017, no page number).

In summary, habitat diversity, food availability, and competition for resources can collectively or individually influence home range sizes of wolverines (Magoun 1985, p. 63; Inman *et al.* 2012a, p. 785), which affects wolverine densities and population structure. Home range sizes of male wolverines are likely influenced by the density and reproductive condition of female wolverines (Magoun 1985, p. 63).

Dispersal relates to the successful establishment of a breeding territory, generally by juveniles, at a location removed from the natal denning area, and can be confused with long-range movements of wolverines and other carnivores (Ruggiero *et al.* 1994, pp. 4–5).

Based on telemetry studies, wolverines have been observed to disperse over very long distances. Both male and females can move long distances (Flagstad *et al.* 2004, pp. 684–686), but young (yearling) females tend to establish home ranges closer to their natal ranges than do young males (COSEWIC 2014, p. 24), which supports a male-biased dispersal pattern (from natal range) for wolverine populations. Vangen *et al.* (2001, p. 1,647) indicated that dispersal patterns of females were likely determined by competition for resources (that is, high quality territories) while male dispersal patterns were likely determined by competition for mates.

As noted above, wolverines readily cross water bodies such as rivers, and can cross rugged terrain (COSEWIC 2014, p. 24; Woodford 2014, entire). Dispersing wolverines in Idaho traveled over 200 km (124 mi) following routes across isolated subalpine habitat (Copeland 1996, p. 130). Inman *et al.* (2012a, p. 784) recorded dispersal-related movements of wolverines in the Greater Yellowstone Ecosystem and found that the maximum dispersal distance of subadults from the home range of their mothers was 170 km (106 mi) for males and 173 km (108 mi) for females, with an average maximum distance per dispersal movement of 102 km (63 mi) for males and 57 km (35 mi) for females (Inman *et al.* 2012a, p. 784). In the Ontario, Canada, region a juvenile male reportedly dispersed 100 km (62 mi) (COSEWIC 2014, p. 24, citing unpublished data from Dawson *et al.* 2013).

Two recent examples illustrate the extensive dispersal capability of wolverines. A male wolverine apparently dispersed (2008 or earlier) from the western edge of the Rocky Mountain region to the Sierra Nevada region of California (Moriarty *et al.* 2009, p. 160). Another male wolverine (designated as M56), whose natal area was the Greater Yellowstone Ecosystem (northwest Wyoming), moved south to Colorado (about 500 miles), where it remained for about 3 years (2009–2012), when its tracking signal was lost. In April 2016, M56 was legally shot and

killed by a rancher in western North Dakota, about 1126.5 km (700 mi) from where it was last seen (Wyoming Game and Fish Department (WGFD) 2016, pers. comm).

Additional discussion of population distribution and density estimates is provided below (see Biological Status–Current Conditions).

Reproduction and Growth

Wolverine reproduction includes the following characteristics: polygamous behavior (i.e., a male mates with more than one female each year), delayed implantation (up to 6 months), short gestation period (30–40 days), denning behavior, and an extended period of maternal care (Rausch and Pearson 1972, pp. 255–256; Pasitschniak-Arts and Larivière 1995, p. 5; Magoun and Copeland 1998, pp. 1,315–1,316; Hedmark *et al.* 2007, p. 19; Persson *et al.* 2017 *in prep*).

Table 2 below presents a summary of wolverine reproductive chronology (extent and peak of reproductive events) based on a review of the literature and personal knowledge from field studies (Inman *et al.* 2012b, entire), and studies from Scandinavia (Aronsson 2017; Persson *et al.* 2017 *in prep*).

Table 2. Chronology of wolverine reproductive events (adapted from Inman *et al.* 2012b).

Reproductive Biology Event	Time Interval
Mating Season	May – August; <i>peak in June</i>
Nidation (implantation of embryo)	November – March; <i>peak in late December–early February</i>
Gestation (45 days)	November – April; <i>peak in January–mid-March</i>
Parturition (birth of young)	late January – mid-April; <i>peak in February–mid-March</i> (Sweden: <i>peak in mid-February</i> , range from end of January to early March) ^a
Reproductive Den Use	late January – end of June; most commonly, <i>early February–mid-May</i>
Lactation	About 10 weeks; generally February–June
Weaning	April – June; most commonly, <i>late April–May</i>
Rendezvous Sites	April – June; <i>peak in early May</i>
Independence	August – January; <i>peak in September–December</i>
Dispersal	Peak period at <i>10–15 months of age</i> ; February–mid-April

^a Persson *et al.* (2017, *in prep*).

Wolverine mating is generally assumed to occur in May, June, and July (Pulliainen 1968, p. 341; Rausch and Pearson 1972, p. 249). A review of both the literature and personal observations by Inman *et al.* (2012, p. 636) indicated that June represented the peak in a wolverine mating season, but began in at least May and extended into early August. Female wolverines have been reported as not breeding in their first summer (under 1 year of age) based on examination of reproductive tracts from wolverine carcasses obtained from trappers (Yukon) (Banci and Harestad 1988, p. 268) and ages of pregnant female wolverines were estimated at 1 to 11-plus years of age (Banci and Harestad 1988, p. 266). In another study of wolverine carcasses (also in Yukon), some female wolverines were said to be mature at about 1 year (about 15 months), but first litters were not produced until 2 years of age (Rausch and Pearson 1972, p. 253). In Scandinavia, the mean age of first reproduction for female wolverines was 3.4 years, based on

monitoring of telemetered animals (Persson *et al.* 2006, p. 76). Breeding ages were reported at 2 to 13 years of age for wolverines in Sweden (mean age of first birth was 3.4, range of 2 to 5 years), based on monitoring/observations of female wolverines (Rauset *et al.* 2015, p. 3,157).

A genetic-based wolverine study in Scandinavia found that “females often reproduced with the same male in subsequent breeding years” (Hedmark *et al.* 2007, p. 18). However, this study also found (with some assumptions regarding sampling and paternity) that 8 of 13 female wolverines bred with different males, and, based on telemetry results, 2 females bred with a new male even though their previous breeding partner was still alive (Hedmark *et al.* 2007, p. 18). This shift in partners may have resulted from a change in the resident male wolverine in the area (Hedmark *et al.* 2007, p. 19).

The reproductive rate of wolverines is relatively low. An early study of 31 wolverine dens in Finland, as reported by hunters, found an average of 2 young per den (range 1–4) (Pulliainen 1968, pp. 338–341). Average litter size for northern Europe (161 litters) was 2.5 (range 1–4) (Pulliainen 1968, p. 343). In Alaska, average litter size was reported as 1.75 young, with a reproductive rate of 0.69 young per adult female per year (Magoun 1985, p. 28). A summary of average litter size for earlier studies of New World and Old World wolverines, based on method of determination, was presented in Magoun (1985, p. 29), indicating a range of 2.2 to 3.5. Anderson and Aune (2008, entire) evaluated pregnancy rates based on presence of corpora lutea (CL) and fetuses in trapper-harvested wolverines from western Montana. That study found median CL counts for pregnant adults ranging from 1.6 to 3.0, depending on the subpopulation (Anderson and Aune 2008, p. 22), with a mean litter size based on number of fetuses for pregnant adult females of 2.6 (Anderson and Aune 2008, p. 23). Studies of telemetered female wolverine in Scandinavia, from 1993 to 2002, reported a mean litter size of 1.88, with a range of 1 to 4 young, with a mean annual birth rate of 0.74 young per female (Persson *et al.* 2006, pp. 76–77). More recently, the average number of young per female per year reported for wolverines in Sweden was 0.84 (range 0–3); however, for those animals with recorded denning behavior, this value increased to 1.38 (range 0–3) (Rauset *et al.* 2015, p. 3,157).

Results from studies of telemetered female wolverines indicate that studies of wolverine reproductive tracts are likely to overestimate wolverine productivity (Persson *et al.* 2006, p. 77). Their findings suggest that young are either lost during pregnancy and/or shortly after birth, and are not likely to occur before implantation due, in part, to presumed delayed implantation (Persson 2006, p. 77). Delayed implantation (or reabsorption) of fetuses has been observed in other mustelids, including mink (Hansson 1947, p. 62; and references cited therein, pp. 65–66). However, the factors that contribute to the observations that female wolverines do not give birth during some years are not well understood, and could be due to failure to breed, pseudo-pregnancy (as demonstrated by Mead *et al.* 1993, entire), failure of a fetus to implant, absorption of implanted fetus, stillbirth, or mortality before emerging from den (e.g. infanticide, etc.) (Magoun 2013, pers. comm.).

Carnivorous mammals generally have altricial young (poorly developed and dependent young (Derrickson 1992, p. 58)), and prepare shelter in dens where the mother can feed their young and keep them warm (Irving 1972, p. 174). Young wolverines (kits or cubs) weigh about 0.1 kg (3.5 oz) at birth and are blind until about 4 weeks of age (Krott 1960, p. 23). Newborns are covered

with whitish to yellow hair (Krott 1958, p. 87; Mehrer 1976, p. 570), 4.5 millimeters (mm) (0.18 in) in length (Shilo and Tamarovskaya 1981, p. 147), with unerupted teeth (Mehrer 1976, p. 570; Pasitschniak-Arts and Larivière 1995, p. 5) and closed ear canals (Shilo and Tamarovskaya 1981, p. 147). They are generally not left alone at the den during the first 3-4 weeks (Krott 1958, pp. 88, 108). A study of telemetered wolverines in Scandinavia found that, on average, a female wolverine spends most of her time within 1,000 m (3,281 ft) of the reproductive den during the denning period (Myhr 2017, no page number).

Mustelids, in general, have a short period of growth (Iversen 1972b, p. 317). As noted above, the metabolism of young wolverines is highest during the first 2.5 months, and individuals are almost two-thirds grown by the fall (at about 6 months) (Krott 1960, p. 25). As described by Shilo and Tamarovskaya (1981, p. 146), 45-50 day old cubs (Norway) have woolly coats, are muddy grey in color, with teeth beginning to erupt at this age. At about 150 days, all permanent teeth have been established (Shilo and Tamarovskaya 1981, p. 147). After 2.5 months, young wolverines replace their juvenile coat with the adult summer coat (Shilo and Tamarovskaya 1981, p. 147). With growth ending at about 8 months (Iversen 1972b, p. 320; Magoun 1985, p. 23), cubs are generally full grown by October or November.

Use of Dens and Denning Behavior

Dens and breeding burrows of animals are, in general, carefully constructed, well-camouflaged, and located in areas not easily accessible (Novikov 1962, p. 25). Wolverines use both natal dens (used for birthing) and maternal dens (used subsequent to natal den and before weaning) for rearing young (Magoun and Copeland 1998, p. 1,314). The average relocation distance to maternal den sites for active wolverine den sites studied in Norway was 268 m (879 ft) (95% confidence interval: 40–497 m (131–1,631 ft)) (May *et al.* 2012, p. 199). The young remain at the natal den site for 6 to 8 weeks (Krott 1960, p. 24), and are weaned at 9 to 10 weeks (Copeland 1996, p. iv (Central Idaho); Koskela *et al.* 2013a, p. 101 (Finland)) (*cf.* 7 to 8 weeks reported by Myhre and Myrberget, 1975, p. 754 (Norway)). After weaning, the young are dependent on the mother and begin to travel with her by late April (Koskela *et al.* 2013a, p. 101 (Finland)). Observations of wolverines in central Idaho reported that females traveled up to 17.9 km (11 mi) from maternal dens to forage (Copeland 1996, p. 97).

The exact timing of when females abandon natal dens and begin using maternal dens is difficult to establish (Inman *et al.* 2012b, p. 638). In general, studies have found that den abandonment (natal) occurs before May (Magoun and Copeland 1998, p. 1,315; Table 1; Inman *et al.* 2012b, p. 637; Figure 2). A study by Aubry *et al.* (2016, p. 24) reported that a female wolverine moved her single young (estimated to be at least 9 weeks old) from a natal den in *late April* in the North Cascades region of Washington. More recently, a comprehensive study of wolverines in Scandinavia found that females begin to shift den locations more frequently beginning in *late April* as young are more mobile and are more reliant on solid food brought to them by the mother (Aronsson 2017, p. 46). Natal den abandonment in Alaska and Idaho reportedly “coincided with a period when maximum daily temperatures rose above freezing for a number of days for the first time since denning commenced” (Magoun and Copeland 1998, p. 1,316). Factors other than temperature can influence shifts in the locations of these den, including intraspecific predation, parasites, or other disturbances (Inman *et al.* 2012b, p. 638). In central Idaho, Copeland (1996, p.

iv) concluded that human disturbance at maternal den sites resulted in den abandonment, but not *abandonment of young*.

Rendezvous sites are locations in which the female leaves young while she hunts for food, and from which they will not leave without her (Magoun 1985, pp. 16, 77). These areas provide security to young (Copeland 1996, p. 94) and serve as locations at which females bring food to the young, or from which she will guide them to a food source (Inman *et al.* 2012b, p. 638). Rendezvous sites of wolverines studied in central Idaho consisted of large boulder talus or riparian areas associated with mature overstory and dense timber deadfall (Copeland 1996, p. iv). Magoun (1985, p. 76) reported that rock caves and hilltops containing boulders without large snowdrifts were used as rendezvous sites in Alaska. Females may move their young to new rendezvous sites several times over a two month period (Magoun 1985, p. 73), and distances between consecutive sites have been reported as far away as 8.5 km (5.3 mi) (Magoun 1985, p. 76).

Studies of adult female wolverines in Scandinavia (northern Sweden) have provided additional details regarding the temporal patterns of reproductive behavior and den site use. Aronsson (2017, p. 45) (see also Persson *et al.* 2017, in prep) found that, in general, most births occurred in mid-February. Females spend very little time outside the natal den for the first 2 weeks (Aronsson 2017, p. 45). During the first period of den site use, or approximately 2 to 2.5 months from mid-February (when females generally give birth and are lactating), females will move short distances and do not need to bring food to young (Aronsson 2017, p. 46). This time period generally coincides with snow cover and favorable conditions for food caching, and dens offer protection from predators and the environment (Aronsson 2017, p. 46). In addition, during the first 1.5 months of the denning period, females rarely changed den sites, but begin to move outside the den in early March (Aronsson 2017, p. 45). In the later denning period (after April 15), females begin to move more frequently and at greater distances between den sites (Aronsson 2017, p. 45). By late April, the young are more active and also begin to rely more on solid food that is brought back to them by their mother (Aronsson 2017, p. 46). This also corresponds to a time period when prey are more available (reindeer migration and calving period in Sweden) and expected shorter distance movements by the mother back to denning or rendezvous sites (Aronsson 2017, p. 46). These observations are consistent with Inman *et al.*'s (2012b, entire) proposed cold, low productivity niche for wolverines based on studies of wolverines in the Greater Yellowstone Ecosystem. That is, reproductive chronology in wolverines is considered to be adapted to take advantage of the availability of food resources, limited interspecific competition, and snow cover in the winter (Inman *et al.* 2012b, p. 635).

In summary, as described by Inman *et al.* (2012b, entire) and Persson *et al.* (2017, in prep), reproductive behavior of wolverines reflect seasonal shifts in resource abundance within the wolverine's range; that is, adaptation that matches the time of birth and development of young to changes in the availability of resources and foraging strategies (Persson *et al.* 2017, in prep). We present in Figure 4 a visual summary of wolverine feeding strategies relative to resource availability from time of birth to post-weaning.

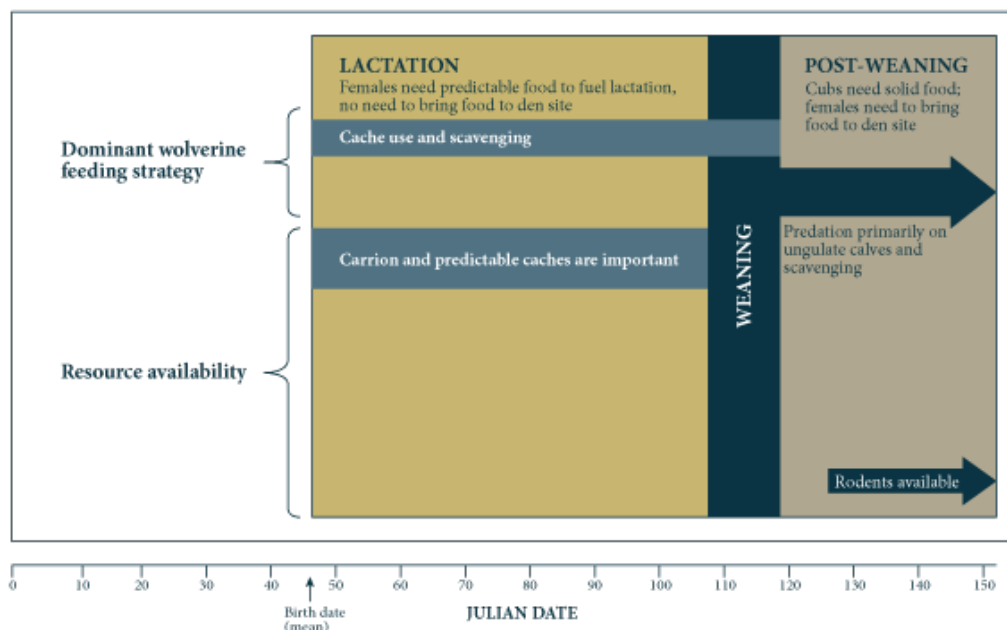


Figure 4. Wolverine feeding strategies relative to resource availability. Adapted from Persson *et al.* 2017, in prep.

Denning Habitat

Given the wolverine's observed association with snow, we provide in **Box 1** a summary of the importance of snow, in general, for ecological systems. This summary provides a detailed perspective of how various physical properties of snow can influence ecological systems occupied by snow-adapted wildlife, including insulating properties, differences in snow cover in mountainous vs. forested habitat, and changes in snow cover due to wind and slope/aspect. However, we also emphasize here that there have been limited comprehensive studies of wolverine behavior, or its physical and ecological requirements outside of the winter months in North America (*cf.* Banci 1987 (Yukon); Hornocker and Hash 1981 (Montana); Gardner 1985 (Alaska); Magoun 1985 (Alaska); Copeland 1996 (Idaho); Krebs *et al.* 2007 (Canada); Inman *et al.* 2013 (Greater Yellowstone Ecosystem)) due, in part, to the difficulty in tracking animals when snow cover is absent and their ability to move great distances across rugged terrain. In addition, den site locations for North America reported in the past have been biased to tundra regions where dens are more readily observed and located (Banci 1994, p. 110). In Scandinavia, snow cover has also been found to be a poor technique for tracking female wolverines during the time when they give birth and initiate denning (Aronsson and Persson 2016, p. 266).

Box 1. Snow Cover in an Ecological Context

Formozov (1961; 1963) prepared comprehensive reviews of the unique properties of snow in the context of its role in the ecology of animals and plants in Russia. In his 1963 review (translated from the 1946 original), he identified two important factors attributed to snow cover — *nastization* (the thickness of the crust on the surface of mature snow cover) and *firnization* (process of snow compaction) — relative to its ecological influence (Formozov 1963, p. 8). Snow cover provides not only a substrate that allows some animals to move across the landscape, it also provides a matrix within which other animals can create tunnels and build nests (Formozov 1963, p. 8). Additional fundamental concepts described in this study are provided below:

- Snow has very low thermal conductivity which promotes cooling at the surface while at the same time protects the deeper layers from chilling; but this property varies by region, by depth, by season, and by year (e.g., the more continuous the snow cover during winter, the greater the warming effect); as snow changes to ice (through compaction and melting), the thermal conductivity decreases (Formozov 1963, pp. 7, 8, 108)
- Snow therefore creates a thermo-insulating layer, which allows for a unique temperature regime on the surface and underneath; as an example, soil temperatures measured in January (near Saint Petersburg, Russia) averaged 15°C higher with snow cover than without snow cover, with up to a 32°C difference, depending on the day and depth measured (Formozov 1963, p. 109)
- Snow cover in mountains:
 - Depth of snow cover and its duration increases with elevation; even minor elevation differences are noticeable (Formozov 1963, p. 123)
 - This spotty distribution is also affected by unequal distribution of snow precipitation on slopes with different exposures, transport of snow by wind, melting of snow on sun-exposed slopes, avalanche or rolling down of snow from steeper areas, and vegetation (Formozov 1963, p. 123)
 - Snow cover areas near Arctic limits and at treeline in mountain regions is more strongly influenced by wind (which compacts and re-works snow cover) (Formozov 1963, p. 29)
- Snow cover in forests:
 - The maximum depth, density, duration and date of melting, thickness of snow surface crust are all much different in forested areas as compared to open treeless areas (Formozov 1963, p. 19)
 - Snow accumulates slowly under trees and is generally thicker the further away from the forest than within the forest; thus, the compaction and settling of snow under a forest canopy is less than tundra or open fields (with a less icy crust), so for some vertebrates, forested areas can provide a more preferable place to winter or migrate (Formozov 1963, pp. 24, 26)
 - Snow cover in forested areas also melts slower than open fields and clearings (Formozov 1963, p. 28)
- Snow cover also plays an important role in the overwintering conditions for insect eggs, caterpillars, pupae, and adult insects in litter and soil, and some plants (Formozov 1963, p. 121)

Although it has been assumed that wolverines have an obligate relationship with snow for natal denning, including persistent spring snow cover, the key elements or combination of elements that define this relationship have not been empirically analyzed. As noted above, adult wolverines have a wide range of thermoneutrality. However, newborns, who are born with lighter, less dense fur are likely to have a more limited ability to control their internal temperature, though huddling (a thermotactic behavior) of small mammals in dens can conserve heat (Barnett and Mount 1967, p. 439). Relatedly, basal metabolic production of heat is the source of heat that maintains bodily warmth, and is not easily modifiable unlike the flexibility of insulation (Irving 1972, p. 121). However, metabolic heat above an animal's basal rate for preservation of warmth is restricted by its limited capacity for metabolic production of heat, but also by food availability and the time and opportunity for nourishment (Irving 1972, p. 121). In general, metabolic production of heat is costly to animals, but variable insulation represents a conservative strategy (Irving 1972, p. 121).

Another key element related to den location is the protection that dens provide to a nursing female and her young. Because wolverines are known to den in a variety of structures, it is unclear if the apparent relationship to snow cover is based on selecting den locations in remote, high elevation areas to avoid predators. Bare rock and boulders at den sites can offer dry and secure cavities and enhance the ruggedness of the landscape (May *et al.* 2012, p. 198). "Ruggedness," a measure derived from elevational changes and irregularity of land surface (density of contour lines) traversing a given area (Beasom *et al.* 1983, p. 1,163) has been found to be an important variable (i.e., secure habitat from predation risk) for female wolverines in winter (British Columbia, Canada) (Krebs *et al.* 2007, p. 2,188) and for den site selection at site-specific, home range, and landscape scales (southcentral Norway) (May *et al.* 2012, pp. 200–201).

Wolverine denning habitat varies across its Holarctic range. For example, in southcentral Norway, wolverine dens were snow tunnels dug into deep snow at the tree line (elevation 1,100 m (3,609 ft)), but most of the tunnel systems extended down to boulder fields, talus slopes, or rock crevices such that young could crawl around within these structures (May *et al.* 2012, p. 201). Snow tunnels are also reported for wolverine natal dens in Alaska (Magoun 1985, pp. 84, 185, 190). However, reproductive dens are not always excavated in deep snow. In Canada, female wolverines are said to give birth in dens where snow cover persists at least until April, and can den under snow-covered rocks, logs, or within snow tunnels (COSEWIC 2014, p. v). As an example, in northwestern Ontario, den site habitat for a female in lower Boreal Forest habitat (elevation 250 to 500 m (820 to 1,640 ft), 51°N) included large boulders and downed trees, similar to dens described for wolverines in montane ecosystems (Dawson *et al.* 2010, p. 139). In Finland, Pulliainen (1968, p. 340) reported a den site (January) at the base of a tree and not covered in snow, and also described other structural features such as rocks, fallen trees, and deep ravines as denning habitat (likely both natal and maternal dens) (Pulliainen 1968, pp. 338–341). In Russia, where wolverine habitat has been described as located far from human-inhabited areas within boreal forests and, to some extent, tundra, and taiga (Novikov 1962, pp. 199, 200), den locations were described as "clefts in rocks, among stones, and under roots of upturned trees" (Novikov 1962, p. 200). A study from northwestern Ontario noted that, because lowland boreal forest habitat in this region does not support deep, wind-hardened snowdrifts, other structural

elements within snow layers such as trees and boulders can be important components of wolverine denning habitat (Dawson *et al.* 2010, p. 142).

Limited studies to date have evaluated the importance of denning habitat to reproductive success, or the key physiological and ecological characteristics, including avoidance and/or protection from predators, prey availability, availability of caching habitat, that define denning behavior and den site selection. Population density, trapping pressure, population genetics, and other measures of habitat quality may also influence wolverine fecundity (Anderson and Aune 2008, p. 28). In addition, studies of wolverine denning activity have not reported the condition of the natal or maternal den location following abandonment; that is, what is the persistence and/or depth of snow at the natal den at the end of the denning season and how does this affect survival of young?

A bioclimatic model was used by Copeland *et al.* (2010, p. 234) to test the following hypothesis: "...wolverine distribution **at the broadest spatial scale** is constrained within a climatic envelope defined by an obligate association with persistent spring snow cover and by an upper limit of thermoneutrality." However, this hypothesis was based on the premise "**If persistence of wolverine populations is linked to** the availability of suitable reproductive den sites ([citing] Banci 1994), snow cover that persists throughout the denning period **may be** a critical habitat component **that limits the wolverine's geographic distribution**" (Copeland *et al.* 2010, p. 234). The authors tested this hypothesis by "comparing and **correlating** the locations of wolverine reproductive dens from throughout their circumboreal range, and telemetry locations from 10 recent wolverine studies in western North America and Scandinavia, with spatial models representing the distribution of spring snow cover and average maximum August temperatures" (Copeland *et al.* 2010, p. 234) (emphasis added).

Bioclimatic models "use associations between aspects of climate and known occurrences of species across landscapes of interest to define sets of conditions under which species are likely to maintain viable populations" (Araújo and Peterson 2012, p. 1,527). They are correlational by nature and are often applied to study a variety of conservation issues, including forecasting potential climate change effects on species' distributions (Araújo and Peterson 2012, p. 1,527). However, these types of correlational models have received some criticisms and require careful framing to avoid misapplication (Sieck *et al.* 2011, p. 6; review by Araújo and Peterson 2012, entire). They generally represent a first step for evaluating current and future species distributions, and, when coupled with climate change scenarios, results are presented at a coarse scale that may not accurately project shifts in species distribution at a smaller scale (Sieck *et al.* 2011, p. 6). In particular, when used to estimate extinction risk, these types of models provide only an estimate of the empirical relationships between a species' current distribution and climate variables and then use inferred relationships to identify potential areas where the species is distributed under future climate scenarios (Araújo and Peterson 2012, p. 1,553). Extinction risk is not represented in the model's input data and therefore is not the targeted parameter of the model; thus, a bioclimatic model's usefulness may be limited in these types of applications given that it only offers partial explanatory evidence for reasons for potential extinction related to the shifts in climate suitability within the time frame being modeled (Araújo and Peterson 2012, p. 1,533 and citations therein). In addition, climate niche projections generally do not incorporate factors such as competition, dispersal, and evolutionary capacity, which also influence range

boundaries (Michalak *et al.* 2017, p. 370). Thus, these types of models are more applicable at broad scales in which the effects of fine-scaled topography and biological interactions play a more limited role (Michalak *et al.* 2017, p. 370); however, both of those factors are important for wolverine, particularly at the den-site scale.

Finally, Post (2013, p. 50) suggested that the niche conservatism approach may not be appropriate in predicting changes to species' distributions under future climate change scenarios. He concluded that, based on redistribution patterns of flora and fauna throughout the Pleistocene epoch, but particularly the Late Pleistocene period of rapid warming, species movement is not always predictable in directions or rates based simply on their association with the more predictably changing environmental/abiotic measures.

As noted above, Copeland *et al.* (2010, entire), used a bioclimatic model to evaluate an assumed association not at the den site scale, but at a broad scale. The results presented in Copeland *et al.* (2010, entire) were based not on the condition of snow cover at a particular den site at the time of denning, but rather their evaluation of snow persistence (April 24 to May 15) was based on satellite images summed over a 7-year period (2000 to 2006) for the den locations. The spatial resolution of the snow measurement used to detect daily snow cover was 500 m (1,640 ft), using Moderate-Resolution Imaging Spectroradiometer (MODIS). If persistent snow cover was observed in any one year, it was included in the bioclimatic model regardless of whether denning occurred during that particular year.

In addition, although the study found that 69 percent of dens for North American wolverines were located within satellite images (pixels) in areas that had snow cover for 6–7 years, just over one-third (31 percent) of the identified den locations were located in areas that were identified as having spring snow cover 5 years or less out of 7 years. Also, the den location attributes (e.g., den structure, how long it was used) were not recorded relative to the observed persistent snow cover and some of the 560 dens (e.g., Norway) were identified by snow tracking rather than direct observation. In essence, the results presented by Copeland *et al.* (2010, entire) provided a fairly accurate, though preliminary, assessment of where **wolverine populations** are expected to be observed, but did not evaluate (model) snow persistence at the den site scale based on location and denning period (emphasis added).

We also note here that results from group scoring exercises using modified (no consensus) Delphi techniques (i.e., group discussions followed by group scoring exercises with points allocated for beliefs on wolverine habitat needs and behavior, as well as uncertainty in allocation of points) of a panel of scientists convened by the Service in April 2014 (Wolverine Science Panel Workshop), indicated that most panelists allocated points to an obligate relationship of wolverines with deep snow at the den-site scale, but there was a wide range of scores from the panel as to whether contiguous snow was limiting at the home-range or species-range scales (Wolverine Science Panel Workshop Report 2014, pp. 9–11).

Since the 2013 (78 FR 7864; February 4, 2013) and 2014 (79 FR 47522; August 13, 2014) proposed rules for the wolverine, several publications have presented additional study results related to wolverine distribution and snow cover. In Alberta, Canada, Webb *et al.* (2016, entire) found that, based on wolverine harvest data, wolverine occurrence relative to spring snow cover (percent of area covered, with greater than 75 percent snow coverage, on April 1 and 15) varied

based on the different regions of Alberta. This study used meteorological data from 2009 to 2015, in northern Alberta (north of 54°N) and differentiated between spring snow cover that persisted in ≥ 1 of 7 years and more frequently (≥ 4 of 7 yr) (Webb *et al.* 2016, pp. 1462–1464). Although the study found an overall positive trend of more frequent wolverine harvests in those areas expected to have spring snow cover, the study did not find consistent large differences between these areas, and did not typically detect significant relationships with frequent spring snow cover (4–7 years) in all regions (Webb *et al.* 2016, p. 6). The Rocky Mountains region was the only region in which wolverines were reported in areas with more frequent spring snow cover (4–7 years) (Webb *et al.* 2016, p. 5). This region, which is located along the western border of Alberta, contains montane, subalpine and alpine habitat, with elevations from 1,000 m (3,281 ft) to 3,700 m (12,139 ft) (Webb *et al.* 2016, p. 9). Conversely, the study found that in the Boreal Forest region of Alberta (i.e., wetland habitat interspersed with coniferous, mixed wood, and deciduous forests, with elevations between 1,500 m (4,921 ft) to 1,100 m (3,609 ft)), a female wolverine denned under large boulders and downed trees (Webb *et al.* 2016, p. 8). The authors noted that wolverine den locations within low elevation, forest habitats have not been well-described (Webb *et al.* 2016, p. 8). As noted above (Novikov 1962, p. 200), in boreal forested habitat, wolverines den in rock areas and in tree root structures. A similar finding was reported in Sweden, where a majority of dens ($n=49$) were in boulder areas located within mature, mixed coniferous forests (i.e., not alpine or tundra habitat) (Makkonen 2015, p. 14); all den sites provided cover for young *without snow* (Makkonen 2015, p. 17). A recently published study reported two wolverine natal dens in logged areas (cutblocks) in northern Alberta, Canada; specifically, within a slash pile and log deck (Scrafford *et al.* 2017, p. 35).

A study of wolverine populations and distribution in Sweden observed that wolverine populations were found outside areas with persistent spring snow cover (mean snow depth and proportion of years with snow cover on March 15; 1961–1990) and expanding into boreal forest habitat located to the east and south of alpine areas (Aronsson and Persson 2016, p. 266). This southern and eastern expansion (from 1996 to 2014) indicates recolonization of their historical distribution in Sweden, and is thought to be the result of an increase in population, with more dispersers colonizing forest habitat, and an increase in year-round scavenging opportunities due to an increase in Scandinavian wolf packs (Aronsson and Persson 2016, p. 266; Aronsson 2017, pp. 43–44). As of the spring of 2017, over 80 reproductive dens have been observed outside the boundary of the snow model presented in Copeland *et al.* (2010) (Persson 2017, pers. comm.). Similarly, in Finland, Koskela (2013, p. 38) found that 10 observed wolverine dens observed were determined to be “snow dens,” but 8 of the 10 dens were located in areas outside the Copeland *et al.* (2010) modeled, satellite-based spring snow cover area.

Snow depth can be affected at a local level by terrain, ruggedness, slope and aspect; slope and aspect together will affect the exposure to snow accumulation (May *et al.* 2012, p. 198). In an effort to document and compare snow persistence at the wolverine den-site scale, Magoun *et al.* (2017, entire) evaluated the use of low-altitude aerial photography during late May 2016 in areas within the Rocky Mountains (Idaho and Montana) and northwestern Alaska. In Idaho and Montana, flight lines were established along transects through the long axis of previously documented home ranges of denning female wolverines and, in Alaska, known den sites (from 2016) were visited by helicopter and remaining snow was photographed (Magoun *et al.* 2017, p. 383). Transect segments in the Rocky Mountain study areas documented snow on May 31 in all but one segment, with 82 percent classified in low to heavy snow retention categories, and 58 percent considered as moderate to heavy (Magoun *et al.* 2017, p. 383). In the Alaska study area,

photographs documented widely scattered patches of snow on May 29, with remnant snowdrifts observed at all four wolverine den sites (Magoun *et al.* 2017, p. 383). The documentation of the existence of scattered patches of snow in the Rocky Mountains persisting into late May in areas previously detected to be bare of snow on May 29 (MODIS persistent spring snow cover, McKelvey *et al.* 2011, p. 2,889, Figure 4D; Magoun *et al.* 2017, p. 384, Figures 2b and 2d) suggests that persistent spring cover may not always be detectable at the den-site scale using remote sensing methods (Magoun *et al.* 2017, p. 384), and is affected by terrain, ruggedness, slope, and aspect.

To evaluate snow cover at previously recorded den site locations in the western United States, we reviewed natal, maternal, and known den sites relative to derived ‘melt-out’ dates using MODIS/Terra Snow Cover, 8-day series (Hall and Riggs 2016). Melt-out dates represent the first day of the 8-day composite series when the cell in which the den was located switches from “snow” to “no snow.” The spatial resolution for these data is 500 m by 500 m (1,640 ft by 1,640 ft). Because MODIS data was only available from the years 2000 to present, we were only able to evaluate 21 of the 34 den sites documented in our records. As shown in Table 3, the earliest melt-out date was May 14 (2006) and the latest was July 12 (2002).

Table 3. Wolverine Den Site Melt-Out Dates, 2002–2008.

Den #	Den Type	Melt-out Date	Elevation, meters (feet)	Structure	State
1	Unknown	7/12/2002	1,814 m (5,951 ft)	None Listed	WA
2	Natal	5/25/2003	1,928 m (6,326 ft)	Log Complex	MT
3	Maternal	5/25/2003	1,995 m (6,545 ft)	Log Complex	MT
4	Natal	6/4/2004	1,807 m (5,923 ft)	Log Complex	MT
5	Natal	6/9/2004	2,399 m (7,871 ft)	None Listed	WY
6	Natal	6/17/2004	2,487 m (8,160 ft)	None Listed	MT
7	Maternal	6/29/2004	1,823 m (5,981 ft)	Downed Log	MT
8	Maternal	6/29/2004	1,893 m (6,211 ft)	Log/Boulder	MT
9	Maternal	6/11/2005	1,912 m (6,273 ft)	Spider Tree	MT
10	Maternal	6/11/2005	1,973 m (6,473 ft)	Spider Tree	MT
11	Natal	6/11/2005	1,977 m (6,486 ft)	Spider Tree	MT
12	Natal	7/12/2005	2,693 m (8,835 ft)	None Listed	MT
13	Unknown	5/14/2006	1,514 m (4,967 ft)	Log Complex	MT
14	Unknown	5/25/2006	2,093 m (6,867 ft)	None Listed	MT
15	Maternal	5/31/2006	1,851 m (6,073 ft)	Log Complex	MT
16	Natal	5/31/2006	1,843 m (6,047 ft)	Log Complex	MT
17	Unknown	6/7/2006	2,252 m (7,389 ft)	None Listed	MT
18	Natal	6/18/2006	2,695 m (8,842 ft)	None Listed	MT
19	Natal	5/25/2007	2,820 m (9,252 ft)	None Listed	MT
20	Natal	6/4/2007	1,922 m (6,306 ft)	Log/Boulder	MT
21	Unknown	7/3/2008	2,505 m (8,219 ft)	None Listed	ID

For natal den sites only, the range for melt-out dates was May 25 to July 12. All of these sites indicate a melt-out date that is past the May 15 date used for the persistent spring snow cover model presented in Copeland *et al.* (2010), which suggests that snow is persistent at these locations past the time when young begin moving out of natal dens (i.e., late April; see Use of Dens and Denning Behavior section). Additional studies are needed to further document wolverine den structure, snow conditions at dens, and how long dens are used, particularly for those locations outside of areas expected to have spring snow cover, to better understand the relationship of wolverines and snow cover (Webb *et al.* 2016, p. 8; Magoun *et al.* 2017, pp. 6–7).

Other physical or biotic variables are also likely to be important for wolverine den site locations. Elevation affects snow depth and persistence at the landscape scale (May *et al.* 2012, p. 198). Inman *et al.* (2012a, p. 782) found that wolverines (12 females and 6 males) monitored in the Greater Yellowstone Ecosystem selected, on an annual basis, areas above 2,600 m (8,530 ft) latitude-adjusted elevation. In central Idaho, natal dens were also found in secluded, high elevation (above 2,500 m (8,202 ft)) cirque basins (Copeland 1996, p. 94).

We evaluated 34 den sites in the lower United States using a linear regression model to evaluate whether the elevation of wolverine den sites is related to latitude. We note here that not all of these dens were characterized as to whether they were natal or maternal dens and a few records were not verified through tracking of females or direct observations. Given these caveats, our examination of these records indicated that, in general, wolverine dens at lower latitudes (36 to 38°N) occur at higher elevations (range: 2,688 to 3,562 m) (8,819 to 11,686 ft) while the converse is seen for those dens at higher latitudes, or approximately 44 to 49°N (range: 1,514 to 2,820 m) (4,967 to 9,252 ft). Given our assumptions (small sample size, test of normality (i.e., Shapiro test for elevation is just met)) we used linear regression (R Software; R Development Core Team, 2014) to test this association. We found a significant association with elevation and latitude [adjusted $R^2 = 0.76$, $F = 108.1$, $df=32$; $p\text{-value} = 8.24 \times 10^{-12}$], such that dens found at lower elevation were associated with higher latitudes. However, the results of this simple model indicate that 76 percent of the elevation for this sample is explained by latitude; thus, other potential explanatory variables or interactions between variables should be considered using multiple regression techniques.

The steep slopes found at higher elevations also provide conditions conducive to avalanches, which result in debris and talus/boulder piles that provide structure for dens (Inman 2013, pers. comm.). Steep slopes and the availability of rocks were found to be important to wolverine den site selection for wolverines studied in Norway (May *et al.* 2012, p. 200). These areas also offer either exclusive or higher frequencies of maternal food sources during the high energy demands for reproducing females, such as marmot emerging from hibernation and neonatal ungulates (Inman 2013, pers. comm.) (see *Diet and Feeding* discussion below).

In summary, wolverines select den sites for different characteristics depending on location. Dens located under snow cover may be related to wolverine distribution based on other life history traits, including morphological, demographic, and behavioral adaptations that allow them to successfully compete for food resources (Inman 2013, pers. comm.). Structure (e.g., uprooted trees, boulders and talus fields) appears to be essential for natal den sites with or without snow cover. Sensitivity to human disturbance and predator avoidance are also likely important factors

in selecting both natal and maternal den sites. However, reproductive success of wolverines has not been evaluated relative to the depth and persistence of snow cover, or in combination with these or other important characteristics, including prey availability and predator avoidance.

Demography

The lifespan of the wolverine is variable. Jackson (1961, p. 361) reported an upper range of 8–10 years in the wild and potentially up to 18 years in captivity. Based on trapper-submitted carcasses from the Yukon, an upper age of 11.9 years for a male wolverine and 12.9 years for (pregnant) female was reported (Jung and Kukka 2013, pp. 8, 12). Inman *et al.* (2012a, p. 781) classified wolverines less than 1 year old as juveniles (or cub), those 1 to 2 years old as subadults, and those at least 3 years old as adults. Generation time for wolverines has been estimated at 7.5 years (COSEWIC 2014, p. 23).

Survival of adult female wolverines is considered to be an important demographic parameter in the wolverine's life history (Sæther *et al.* 2005, entire). As noted by Aronsson (2017, p. 13), because most polygamous species display a dispersal pattern that is sex-based, their population distribution is generally limited by the dispersal behavior of the sex that is more philopatric (the tendency of a species to remain within or return to its birth area). Thus, the distribution of wolverine populations and colonization is generally limited by dispersal of female wolverines (Aronsson *et al.* 2017, p. 2).

Stochastic factors (both demographic and environmental) also strongly influence the population dynamics of the wolverine (Sæther *et al.* 2005, p. 1,011–1,012). Given the rapid maturity of young wolverines, survival of female wolverines with young is likely dependent on the availability and distribution of food sources during the “snow-free season” (late spring and summer) (Banci 1994, p. 114). For example, a study of wolverines in Norway found that survival of young was primarily influenced by the abundance of small rodents (Landa *et al.* 1997, p. 1,293).

Evaluating how variations in demographic rates are influenced by the interactions between costs of reproduction, individual quality (e.g., breeding status), and environmental factors can provide a better understanding of the dynamics and viability of animal populations (Robert *et al.* 2012; p. entire; Rauset *et al.* 2015, entire). The interactions between individual age, environmental resources, and reproductive costs of wolverines in Sweden were recently examined (Rauset *et al.* 2015, entire). The results of this study provide important details regarding the influences on wolverine reproduction productivity. The study found that age-related variation in reproductive output for female wolverines is driven by the interactions between age, reproductive costs, and availability of resources (Rauset *et al.* 2015, p. 3,160). As an example, female wolverines were found to be more likely to give birth and nurse young in home ranges with greater food resource abundance at the time of fetal development (Rauset *et al.* 2015, p. 3,158). The study also concluded that a favorable reproductive strategy for female wolverines is a conservative one, wherein older female wolverines do not “trade” current reproduction against their own survival (Rauset *et al.* 2015, p. 3,161).

Intraspecific predation of wolverines is another important influence on wolverine population dynamics (Persson *et al.* 2003, p. 26). The altricial life history stage (early May to end of July) is likely a period of high juvenile mortality in solitary carnivores, such as the wolverine, since females are balancing the energetic demands of lactation (Sadleir 1984, pp. 179–180) and providing protection to young (Persson *et al.* 2003, p. 22). Young (juveniles) wolverines are vulnerable to predation during the time period when left unattended in the natal den (generally March–April) and when they first exit the natal den and are left at rendezvous sites, or around May–June (Magoun 1985, pp. 49, 73, 77). An additional vulnerability occurs when juvenile wolverines are required to become nutritionally independent and begin exploratory movements away from their mother’s protection, generally August–September (Vangen *et al.* 2001, p. 1,644).

Mortality

There are a few natural predators of wolverines, but interactions with wolves can lead to severe injury and death (Burkholder 1962, p. 264; Banci 1987, pp. 81, 91; White *et al.* 2002, p. 132). Mountain lions are suspected of killing wolverines (Copeland 1996, p. 46; Krebs *et al.* 2004, p. 497; Aubry *et al.* 2016, pp. 27, 32). Starvation has also been identified as a cause of mortality in wolverines (Hornocker and Hash 1981, p. 1,296; Banci 1987, pp. 91, 110; Krebs *et al.* 2004, p. 497). Intraspecific predation also contributes to wolverine deaths. Persson *et al.* (2003, p. 25) found that juvenile survival rate tended to be lower during the altricial period (May–July), and intraspecific predation was the most common cause of mortality, occurring either as infanticide or after independence. Avalanches have also been documented as a cause of wolverine deaths (Inman *et al.* 2007, p. 89).

In North America, anthropogenic causes of mortality for wolverine populations include hunting, trapping, and road kill. Discussion of the effects of hunting, trapping, and human development is provided below (see Biological Status–Current Condition section).

Diet and Feeding

Wolverines have been described as opportunistic foragers (Inman *et al.* 2012b, p. 639) and as a “seasonal scavenger on the fringe of the food web” (Larsen 1980, p. 399). They are both scavengers and predators, with a diet that varies between seasons and years, and switching between food sources depending on availability (Magoun 1987, p. 396; Cardinal 2004, pp. 19–22; Mattisson *et al.* 2016, p. 9). The term “polyphagous” was used by Landa *et al.* (1997, p. 1,292) to describe the switching of food sources depending on prey availability by wolverines. Regional variations in diet have also been observed for wolverine populations (Nunavut, Canada) (Awan and Szor 2012, p. 9). The availability of ungulate carrion is believed to be more important than a particular habitat type for wolverines (Cardinal 2004, p. 20).

Early studies from northwestern Montana using scat analysis found that carrion (deer or elk) was an important component of wolverine diet (Hornocker and Hash 1981, p. 1,297). However, during winter, hoary marmots (*Marmota caligata*) were also important food items consumed and, in the spring, Columbian ground squirrels (*Urocitellus columbianus*) were heavily preyed upon (Hornocker and Hash 1981, p. 1,298). As reported by Cardinal (2004, pp. 20–21), wolverines in Canada have a large and varying diet based on reports from aboriginal traditional

knowledge holders; in addition to large animals as prey or carrion, wolverine diet includes rabbits and ptarmigans (*Lagopus* sp.), porcupine (*Erethizon dorsatum*), mice, beaver (*Castor canadensis*), fish, ducks, seals, gulls and gull eggs, and lemmings, as well as antlers, bones, and skulls. Native mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*), that occupy high elevation winter ranges in portions of North America, have also been suggested as important components of wolverine winter diet, particularly during the reproductive denning period (Buell Environmental 2016, pers. comm.). Snowshoe hares may also be an important food item for wolverines in parts of Canada (Jung and Kukka 2013, p. 20).

In northwestern Alaska, analyses of wolverine winter diet using carcasses collected from hunters (1996–2002) within the migratory range of the Western Arctic Caribou Herd found that caribou represented the most common food item, likely through scavenging behavior, followed by moose (*Alces alces*), and to a lesser degree, microtine rodents, Arctic ground squirrels (*Spermophilus parryii*), porcupines, wolverines, red fox (*Vulpes vulpes*), sheep and ptarmigan (Dalerum *et al.* 2009, p. 249). One study year found stomach contents contained a large portion of muskoxen (*Ovibos moschatus*) and Dall's sheep (*Ovis dalli*) (Dalerum *et al.* 2009, p. 249). Wolverines were found to be the main predator of caribou calves (less than 14 days of age) in northern British Columbia, Canada (Gustine *et al.* (2006, pp. 13–14). Wolverine diets in winter (scat analysis) and summer (primarily direct observation) were evaluated by Magoun (1987, entire) in northwestern Alaska. Results from that study indicate a large number of Arctic ground squirrels were eaten in summer, while the winter diet consisted primarily of caribou and Arctic ground squirrels (Magoun 1987, p. 393). Scavenging was found to be an important feeding strategy in winter, including remnants of buried caribou carcasses or bone/hide in the tundra (Magoun 1987, p. 396).

Food habits of wolverines from 2002 to 2007 in Glacier National Park were evaluated by Yates and Copeland (*in prep*) by reviewing prey remains and scat samples, or direct observations of feeding behavior. Their scat analysis found that 72 percent of samples contained more than one prey species, and 89 percent contained plant material, primarily conifer needles (Yates and Copeland, *in prep*). The latter may be related to scent-marking behavior of territories, either by defecation after chewing on twigs/shrubs or terpenes released during urination, or the result of stomach contents found within their consumed herbivorous prey (Yates and Copeland, *in prep*). Overall, deer and elk represented the most frequent prey item (37 percent), but hibernating rodents were also common in scats (36 percent). Other prey items included mice, voles, lemmings, bovids (e.g., bighorn sheep, mountain goat), birds, and hares (Yates and Copeland, *in prep*). Temporal differences in the occurrence of prey were also observed.

Snow tracking in Montana found that wolverines hunted in brush piles, log jams, and heavy cover, and routinely entered "tree wells," areas immediately under dense, low growing conifers where snow does not accumulate, that provide easy access to small, ground-dwelling mammals (Hornocker and Hash 1981, p. 1298). Wolverines have been described as moving and lifting large stones in order to access human-cached meat (Freuchen 1935, p. 98).

Several foraging strategies have been described for wolverines. Predation behavior on reindeer (Sweden) was detailed by Haglund (1966, p. 275). A study of elk in Siberia, Russia, noted that, in most instances, wolverines will attack young, pregnant females, young of the year, and

wounded or sick animals (Knorre 1959, p. 27). Elk were chased, sometimes by two wolverines during periods of heavy snow (Knorre 1959, pp. 10, 27) and wolverines have been observed feeding in groups on large animal carcasses (Cardinal 2004, p.21). However, wolverines have been described as neither an effective predator of large game animals, nor a serious competitor with other predators (Cardinal 2004, p. 21).

Based on studies in Alaska, Dalerum *et al.* (2009, p. 251) suggested that wolverines occupying this region are large ungulate specialists, but use a generalist feeding strategy by switching between ungulate food sources (e.g., caribou and moose) depending on their availability. Thus, during periods of low caribou abundance, wolverines can switch from caribou (migratory) to moose (non-migratory) while still maintaining their ecological role as a scavenger on ungulate carcasses (Dalerum *et al.* 2009, p. 251).

A study of wolverine diet using scat samples in Finland found that breeding female wolverines opportunistically used carrion and hunted less on small prey as compared to males and non-breeding females (Koskela 2013, p. 35). In addition, in areas with low densities of mid-size ungulates, smaller prey and carcasses may be important in the wolverine diet (Koskela 2013, p. 35). These results supported an optimal foraging theory; that is, wolverines will opportunistically use foods that are the most energy-efficiently available (Koskela 2013, p. 41). In other words, hunting ungulates or smaller prey (rabbits, birds) may incur greater energetic costs than scavenging for food, but searching for wolf- or human-killed carcasses will take more time (Koskela 2013, p. 41).

Finally, diet and feeding strategies of wolverines were evaluated in Scandinavia (Mattisson *et al.* 2016, entire). Wolverine feeding strategies were found to be flexible and temporarily shifted from scavenging to predation and heavily influenced by seasonal dependent responses to availability of prey and the supply of carrion (Mattisson *et al.* 2016, p. 9). Predictable anthropogenic food sources (i.e., remains from hunted ungulates) also influenced wolverine feeding strategies in their study area by increasing scavenging behavior relative to predation (Mattisson *et al.* 2016, p. 10).

Aboriginal traditional knowledge holders in Canada have reported wolverines as being largely dependent on wolves or another large predator to obtain large mammal carrion such as caribou, but also scavenge off polar bear (*Ursus maritimus*) and grizzly bear (summer) kills (Cardinal 2004, p. 20). Wolverine were observed following the tracks of Eurasian lynx (*Lynx lynx*) and then scavenging on prey left behind from lynx kills (Haglund 1966, pp. 272–273). Myhre and Myrberget (1975, p. 756) noted that the hunting abilities of wolverine and Eurasian lynx are not the same and that the two animals use the meat of their prey differently, which, together, may allow the two carnivores to coexist in the same environment.

In Sweden, Mattisson *et al.*'s (2011b, p. 1,326) study of Global Positioning System (GPS)-collared wolverines found that they spent three times longer scavenging ungulate carrion as compared to feeding on wolverine-killed prey, and more than half of the reindeer carcasses scavenged by wolverines were killed by Eurasian lynx. That study concluded that lynx can increase the availability of food for wolverines and other scavengers and that lynx behavior around kill sites minimizes potential encounter conflicts (Mattisson *et al.* 2011b, p. 1,328). In

their study area, Eurasian lynx do not appear to pose a significant threat to wolverines, neither by exclusion in space or time (Mattisson *et al.* 2011a, p. 79) nor from mortality (Persson *et al.* 2009, p. 327). We are not aware of similar evaluations for North American populations of wolverines and Canada lynx. This lack of study on interspecific processes in the more predator-diverse North American landscape is an important gap in our understanding of wolverine distribution (Fisher *et al.* 2013, p. 712).

Large carnivores can act as “sympatric ungulate predators” (Dalerum *et al.* 2009, p. 251), generating carrion at kill sites, particularly during winter months, but also as competitors and potential sources of mortality (White *et al.* 2002, p. 132; Krebs *et al.* 2004, p. 497; Koskela *et al.* 2013b, p. 221). Wolverines apparently balance their exposure to the risk of predation with foraging opportunities (Scrafford *et al.* (2017, p. 32). Thus, even though wolverines may not be dependent on lynx or other sympatric predators for their survival or reproduction, an increase in the availability of carrion likely has a positive influence on the reproductive rate (e.g., number of offspring) in wolverine populations (Mattisson *et al.* 2011b, p. 1,328).

Caching of food is an important behavior of wolverines and is a key component of wolverine population dynamics (Hornocker and Hash 1981, p. 1,297; Inman *et al.* 2012b, p. 640). Food is cached in both summer and winter, by both sexes, and allows for food to be available past the peak periods of mortality and predation (Inman *et al.* 2012b, p. 639). Wolverines will typically move between carcasses and cache sites and are able to remove large parts of a carcass in a short time (Mattisson *et al.* 2011b, p. 1,327). Caching behavior in Sweden was reported most commonly in snow, as well as crevices in rock piles, and found that wolverines carried food to cache sites over long distances (8 and 10 km (5 and 6 mi)) (Haglund 1966, p. 274). As an example, Bjärvall (1982, p. 319) reported a female wolverine carried a reindeer head (with antlers) about 22 km (13.67 mi) back to a den site in Sweden. In northwestern Alaska, wolverines fed on cached ground squirrels during winter (Magoun 1987, p. 395).

A study of wolverine caching behavior in boreal forest habitat in Canada reported that cache sites varied from simple caches, a single feeding site or excavation, to cache complexes, which included feeding stations, latrines, resting sites, and climbing trees dispersed over varying spatial landscapes (Wright and Ernst 2004b, pp. 61–62). All cache sites included bones and hides of moose, which were likely scavenged from wolf kills (Wright and Ernst 2004b, p. 62). Cache sites were often excavated in snow, but also in the ground under boughs of large spruce (*Picea* spp.) trees (Wright and Ernst, 2004b, p. 62). Wolverines also appeared to select cache sites and resting areas that offered good visibility of approaching competitors or predators (Wright and Ernst 2004b, pp. 63–64).

Wolverine energetic demands and food requirements are related to their foraging strategies. Caching provides important energy for female wolverines during the lactation period and helps ensure survival of newborns (Inman *et al.* 2012b, p. 640). Wolverines were found to have high energetic needs compared to other mammalian carnivores (Young *et al.* (2012, p. 2,252), similar to results previously presented by Iversen (1972a, p. 343), who concluded the basal metabolism of mustelids weighing over 1 kg (2.2 lbs) is approximately 20 percent higher than for other mammals. A study by Andrén *et al.* (2011, p. 36) estimated a 1.2 kg/day (2.65 lbs/day) (range: 1.0–1.4 kg/day (2.2–3 lbs/day)) food requirement for wolverines, while Young *et al.* (2012, p.

223) estimated a male wolverine would require an average of 0.85 kg (1.87 lb) of prey/day in winter and 0.95 kg/day (2.1 lbs/day) in “snow-free” periods.” Based on energy equivalent value of various prey sources, Young *et al.* (2012, pp. 223, 225) estimated that a winter diet for a male wolverine would include the equivalent of 1.8 ungulates, 70.7 sciurids (squirrels), 20.6 lagomorphs (rabbits), and 832.7 small mammals, while in snow free season this would include the equivalent of 0.9 ungulates, 122.9 sciurids, and 3362.1 small mammals.

The study by Young *et al.* (2012, p. 225) concluded that wolverines consume 0.1 kg (0.22 lb) of prey per day more outside winter season, but that prey expected to be consumed in winter had a higher caloric content than other seasons; thus, the mass requirement is lower. As an example, they cite the higher proportion of ungulates consumed in winter, which provide about 1.3 times more energy (kilojoules per kilogram) than squirrels (Young *et al.* 2012, p. 225). Other researchers have also noted that food during the summer is just as important as the availability of cached ungulate food in the winter (e.g., during the energy demanding lactation period) (Inman *et al.* 2012b, pp. 640–642). The post-weaning growth period (May–August) was identified as a high energetic demand for food by a wolverine family group (Inman *et al.* 2012b, p. 640). Taken together with the lactation period, the calories available to wolverines therefore likely reaches a maximum from March to April (Inman *et al.* 2012b, p. 640).

Population Structure

As discussed above, wolverines recolonized much of North America after periods of glaciation and then experienced heavy human persecution in much of their range. As shown in our current range map (Figure 3) and described below in our *Population Abundance and Distribution* section, wolverines occur across a broad expanse of North America, where the contiguous United States represents the southern extent of the species’ range. A number of biological factors can affect wolverine populations, including the species’ low intrinsic rate of population increase, naturally low densities, and need for large, intra-sexual home ranges (Banci and Proulx 1999, p. 180). Their extensive dispersal abilities make possible the recolonization of individuals into vacant habitats (Vangen *et al.* 2001, p. 1,647; Aronsson 2017, p. 43). As noted above (*Diet and Feeding*), interactions with sympatric predators and the availability of prey and carrion can also directly and indirectly affect wolverine populations.

Wolverines in the contiguous United States are considered to represent a metapopulation (set of local or subpopulations within a larger area and where migration is possible between patches (Hanski and Simberloff 1997, p. 11)) (Inman *et al.* 2013, p. 277) and occupy habitat in high alpine patches at low densities, dispersing into suitable areas (Inman *et al.* 2012a, pp. 782–784). Wolverine populations in Canada are considered to occur as a single large group as they are easily able to move between areas of good habitat and because wolverine habitat is relatively contiguous (Harrower 2017, pers. comm.). Wolverine populations in Alaska are considered to be continuous with populations in the Yukon and British Columbia provinces of Canada based on genetic studies (COSEWIC 2014, p. 37).

Studies of wolverines in the North Cascades region have documented movement of wolverines from Washington into British Columbia (Aubry *et al.* 2016, pp. 16, 20). The 2014 COSEWIC Report indicated that rescue (immigration from another population) of Canadian wolverine

populations along the Canada-Alaska international boundary was likely (based on nuclear DNA evidence), but was negligible *from* the contiguous United States (COSEWIC 2014, p. 37). Based on mitochondrial DNA studies, Tomasik and Cook (2005, p. 390) concluded the gene flow in wolverines in northwestern North America is likely male-mediated, and is primarily due to long distance dispersal between low-density populations. Genetic studies of North American wolverines conducted by Kyle and Strobeck (2002, entire) found high levels of gene flow across northern populations (Canada and Alaska).

Genetics

Evaluation of genetic material can provide an understanding of population dynamics (Cegelski *et al.* 2006, p. 209). The geographical genetic structure of wolverines is believed to be largely structured around the strong female philopatry characteristic of this species (Rico *et al.* 2015, p. 2), and, given the species polygamous behavior, wolverine population distributions (at least in Scandinavia) are considered to be primarily limited by dispersal of the more philopatric sex (females) (Aronsson 2017, p. 13). However, the extensive and often asymmetrical movement of male wolverines from core populations to the periphery of their range can result in the addition of nuclear genetic material to these edges (Zigouris *et al.* 2012, p. 1,553). Thus, the dispersal pattern for male wolverines may help explain why allelic richness (i.e., nuclear DNA) can be similar across regions, but haplotype richness (mitochondria DNA) is lower at the periphery of the species' range (Zigouris *et al.* 2012, p. 1,553). Additionally, the extensive dispersal movements of both male and female wolverines can produce gene flow among diverged populations, making it difficult to distinguish, without additional sampling and analysis, between long-distance dispersal and fragmentation based on the patchy distribution of some haplotypes (Zigouris *et al.* 2013, p.10).

Studies evaluating the genetic structure of wolverines, primarily within its core range in North America, were presented in Chappell *et al.* (2004) and Kyle and Strobeck (2001, 2002). Using microsatellite markers, Kyle and Strobeck (2002) and Zigouris *et al.* (2012) found a greater genetic structure of wolverines toward their eastern and southern peripheries of their North American distribution, likely due to a west-to-east recolonization during the Holocene (Zigouris *et al.* 2013, p. 9). Similarly, based on mitochondria DNA, McKelvey *et al.* (2014, p. 330) concluded that modern wolverine populations in the contiguous United States are the result of recolonization (following persecution from hunting and trapping) from the north.

Genetic diversity and population genetic structure of a larger sample size of wolverines were examined by Cegelski *et al.* (2006, entire) for the southern extent of their North American range using both microsatellite markers and mitochondrial DNA. They concluded that the wolverine populations in the contiguous United States were not sources for dispersing individuals into Canada (Cegelski *et al.* 2006, p. 208). They found that there was significant differentiation between most of the populations in Canada and the United States (Cegelski *et al.* 2006, p. 208). However, they cautioned that their statistical analysis may not have been able to detect "effective migrants" and that sample size can affect the detection of dispersers (Cegelski *et al.* 2006, p. 208). They concluded that some migration of wolverines was occurring between the Rocky Mountain Front region (northwestern Montana) and Canada as well as among wolverine populations in the United States, with the exception of Idaho (Cegelski *et al.* 2006, p. 208). In

addition, results from testing of allelic differences among the populations were interpreted by the authors as likely inadequate to counter the effects of genetic drift due to low numbers of migrants (Cegelski *et al.* 2006, p. 208). They estimated that, based on genetic diversity observed at that time, two effective migrants from either Canada or Wyoming into the Rocky Mountain Front population would be needed to maintain the levels of genetic diversity in that population, and one effective migrant was needed to maintain levels of diversity in the Gallatin, Crazybelt, or Idaho populations (Cegelski *et al.* 2006, p. 209). The authors concluded that migration is essential for maintaining diversity in wolverine populations in the contiguous United States since effective population size may never be reached due to the naturally low population densities of wolverines (Cegelski *et al.* 2006, p. 209).

Effective population size (N_e) (see **Box 2**) is defined as “the size of an idealized population that would experience the same amount of genetic drift and inbreeding as the population of interest. In popular terms, N_e is the number of individuals in a population that contribute offspring to the next generation” (Hoffman *et al.* 2017, p. 507). It represents a metric for quantifying rates of inbreeding and genetic drift and is often used in conservation management to set genetic viability targets (Olsson *et al.* 2017, p. 1). It is not the same as the more commonly used metric, census population size (N), but is often assumed to represent the *genetically* effective population size.

An effective population size analysis for wolverines in the contiguous United States was presented in Schwartz *et al.* (2009, p. 3,225) using wolverine samples from the main part of the Rocky Mountains populations (e.g., central and eastern Idaho, Montana, northwestern Wyoming). Excluded in this analysis, were subpopulations from Crazy and Belt Mountains in Montana (based on suggestion by Cegelski *et al.* (2003) that they represented separate groups) (Schwartz *et al.* 2009, p. 3,225). Samples were divided into three time frames and the computer program ONEsAMP was used to estimate effective population size in each time frame [sample size appears to be between 142 and 210]. The summed effective population size was estimated at 35, with credible limits from 28–52, and the summed values for the three time frames was reported as follows: $N_{e\ 1989-1994} = 33$, credible limits 27–43; $N_{e\ 1995-2000} = 35$, credible limits 28–57; $N_{e\ 2001-2006} = 38$, credible limits 33–59 (Schwartz *et al.* 2009, p. 3,226).

However, Cegelski *et al.*’s (2006, p. 203) evaluation of nuclear DNA population structure in wolverines in Canada (sample size of 101) and the contiguous United States (sample size of 116), as depicted by a principle component analysis plot and dendrogram, found that all of the Canadian wolverine populations clustered together. In the contiguous United States, the Rocky Mountain Front subpopulation clustered with the Wyoming subpopulation, the Crazybelt Mountains' area subpopulation clustered with the Gallatin (Montana) population, and the Idaho population was highly differentiated (Cegelski *et al.* 2006, p. 203). That study concluded that some exchange of migrants is occurring between the Gallatin and Crazybelt wolverine populations (Cegelski *et al.* 2006, p. 207), but noted that this grouping is more genetically differentiated and isolated from the other populations they sampled *when compared to* the Rocky Mountain Front population (Cegelski *et al.* 2003).

In addition, the map presented in Schwartz *et al.* (2009, p. 3,223) depicting the locations of the wolverine samples used in preparing their effective population size estimate shows significant gaps within the wolverine’s range in Idaho and parts of Montana (e.g., interior of the Bob

Marshall Wilderness area). Thus, other wolverine subpopulations and/or individuals were likely missed for this analysis. Studies within the Southwestern Crown of the Continent (SWCC) in northwestern Montana have detected cross-valley movements of wolverines, which researchers believe is an indication of good connectivity in this region (SWCC Wildlife Working Group 2016, pers. comm.). Current efforts to collect additional wolverine hair samples for genetic analyses are underway through a multi-state occupancy survey project (see *Population Abundance and Distribution* section below).

Another evaluation of mitochondria DNA was conducted by Francis (2008), who found an overall lack of regional (geographic) genetic structure for North American wolverines, but noted that a few populations (Crazybelts (Montana), Southeast Alaska, Nunavut (Canada), and Kenai Peninsula) appeared to be isolated from the others (Francis 2008, p. 12). However, statistical testing did not identify any genetically defined sampling localities (Francis 2008, p. 13). Minimal differences were found between core and peripheral wolverine populations, as grouped in that analysis (Francis 2008, p. 21; Table 4). Conversely, the study by Zigouris *et al.* (2012, p. 1,554; Table 5) did find support for genetic clusters for wolverine populations in Canada, and Zigouris *et al.* (2013, p. 5; Table 3) identified several worldwide regional genetic groups. In addition, an analysis of estimated population growth found signals of population expansion in several wolverine populations (Francis 2008, p. 13; Table 5) including Rocky Mountain Front, Wyoming, Central, South, and Northwestern Alaska, British Columbia, Northwest Territories, and Nunavut.

Box 2. Effective Population Size and Genetic Variation

The concept of effective population size (N_e) (see review by Wang *et al.* 2016) and, relatedly, minimum viable population, has been a topic of debate, particularly the 50/500 rule, which was developed over 30 years ago. As noted by Laikre *et al.* (2016, p. 280), the concept and guidelines for *genetically* effective population size were developed for single, isolated populations, but it's unclear which of the various N_e metrics was referenced in the original concept proposed by Franklin (1980) (i.e., inbreeding effective size, realized effective size, total inbreeding effective size of a metapopulation, or eigenvalue effective size (Laikre *et al.* 2016, p. 288)).

There are differing interpretations of the values proposed for effective population size. For example, should the minimum viable effective population size be derived genetically to set a threshold for a minimum viable population? Here, the rule is interpreted as 50 being the short-term number (for inbreeding depression) and 500 as the long-term number (for retention of genetic variation). Or should the N_e value of 500 be interpreted as a long-term goal for maintaining a healthy, genetically robust population, and not a threshold trigger that predicts extinction risk? In addition, some view the 500 value to be a global reference value rather than a local value, and that it may not be necessary to maintain a local N_e of 500 as long as there is some gene flow into a population (Jamieson and Allendorf 2012, p. 580).

Finally, others have recommended changes to the 50/500 rule. Laikre *et al.* (2016, entire) presented an analysis of the metapopulation effective size for the Fennoscandian wolf population and recommended that long-term conservation genetic target for metapopulations ($N_{eMeta} \geq 500$), but also a realized effective size of *each subpopulation* ($N_{eRx} \geq 500$). Frankham *et al.* (2014, p. 59) have recommended modifying the 50/500 rule to 100/1000.

It can be difficult to make inferences about the relationship between population size and point estimates of genetic diversity without continued genetic monitoring and an understanding of the demographic history of a species' population (Hoffman *et al.* 2017, p. 507), including factors that have influenced movement patterns and connectivity. It's also important to note that genetic diversity can be a reflection of favorable adaptations (natural selection) and is necessary for species to locally adapt to environmental stressors or to facilitate range shifts (Zigouris *et al.* 2012, p. 1,544). Genetic distinctiveness in peripheral populations may play a role in both maintaining and generating biological diversity for a species (Zigouris *et al.* 2012, p. 1,544; citing results presented in Channell and Lomolino 2000, p. 84). Genetic variation that is adaptive is a better predictor of the long-term success of populations as compared to overall genetic variation (Hoffman *et al.* 2017, p. 510). The challenge is to be able to determine whether genetic variation is adaptive and is a reflection of remnants of high genetic diversity from ancestral populations, or whether that variation is a reflection of accumulated deleterious, nonadaptive genes due to genetic drift in small populations (Hoffman *et al.* 2017, p. 509).

In summary, the currently known spatial distribution of genetic variability in wolverines in North America appears to be a reflection of a complex history where population abundance has fluctuated since the time of the last glaciation, and insufficient time has passed since human persecution for a full recovery of wolverine densities (Cardinal 2004, pp. 23–24; Zigouris *et al.* 2012, p. 1,554). Zigouris *et al.* (2012, p.1,545) noted that the genetic diversity reported in Cegelski *et al.* (2006) and Kyle and Strobeck (2001, 2002) for the southwestern edge of the North American range represented only part of the diversity in the northern populations of wolverines. Zigouris *et al.* (2012, p. 1,545) posit that the irregular distribution of wolverines in the southwestern periphery and the genetic diversity observed in those analyses is a result of population bottlenecks that were caused by range contractions from a panmictic (random mating) northern core population approximately 150 years ago coinciding with human persecution. Demographic studies as well as additional genetic analyses from contemporaneous wolverines currently occupying the contiguous United States are needed to evaluate the current status of wolverine populations in North America. In addition, ecological, phenotypical, and environmental information should be used to complement genomic data when interpreting the strength of conclusions or inferences of spatial patterns of adaptation or for adaptively divergent populations (Jamieson and Allendorf 2012, p. 492).

Summary

In this SSA report, we have incorporated information from several new studies related to the wolverine published since our 2013 proposed rule and previous studies that were not considered (e.g., Magoun *et al.* 2017). We have also reviewed new publications and publications in preparation from wolverine researchers in Scandinavia (e.g., Aronsson 2017; Bischof *et al.* 2016; Makkonen 2015; Mattisson *et al.* 2016; Myhr 2015; Persson *et al.* 2017, *in prep*). This information informs our assessment of the most current information regarding the description of the wolverine and its life history and ecology across its North American range. We have included in this SSA Report detailed discussions of wolverine physiology, and spatial and temporal patterns and trends related to reproduction and diet/feeding. We also prepared a revised current range map (see Figure 3) based on information we received from Federal, State, and others, including Canada.

A species' current and future conditions and overall viability (in terms of resiliency, redundancy, and representation), are largely impacted by the availability of what the species needs at the individual, population, and species level. The needs described below are necessary for wolverines to have resources for the basic requirements of life (breeding, feeding, and sheltering) at all levels. Overall, the best available information indicates that within the contiguous United States the wolverine's physical and ecological needs include:

- (1) large territories in remote landscapes; at high elevation (1,800 to 3,500 meters (5,906 to 11,483 feet))
- (2) access to a variety of food resources, that varies with seasons; and
- (3) physical/structural features (e.g., talus slopes, rugged terrain) linked to reproductive behavioral patterns.

Biological Status – Current Condition

This section provides an overview of the wolverine's current condition, including those stressors that may be impacting the species or its habitat. In this SSA Report, we have identified stressors based on impacts that may negatively affect the physical and ecological needs of the species, including temporary or permanent impacts to habitat features that the species relies on for survival and reproduction.

Population Abundance and Distribution

Since our 2013 proposed rule, we have received additional reports of wolverine observations including Utah, Colorado, and Oregon, and an updated Canadian status review for the wolverine has been prepared (COSEWIC 2014, entire). Additional studies have also been published related to wolverine populations in British Columbia and Alberta (e.g., Regehr and Lacroix 2016; Stewart *et al.* 2016; Webb *et al.* 2016). As noted above, we developed a Current Range map for the North American wolverine (see Figure 3). For the conterminous United States, this map was based on several resources, including the primary habitat model developed by Inman *et al.* (2013), EPA Ecoregion mapping (2010), Forest Service NRIS data, and information received from State agencies. We used the 2014 COSEWIC Assessment and Status Report's current range map for Canada and Alaska. For Canada, the range of occurrence includes the Yukon, Northwest Territories, Nunavut, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Québec, Newfoundland, and Labrador (COSEWIC 2014, p. vii).

Contiguous United States

Areas in the western contiguous United States were identified by Inman *et al.* (2013, entire) as suitable for wolverine survival (long-term survival; used by resident adults), or **primary habitat** (Inman *et al.* 2013, p. 279), reproduction (used by reproductive females), and dispersal (female and male) of wolverines (see methodology in Inman *et al.* 2013, pp. 279–280; Figure 2). From these results, the researchers estimated potential and current distribution and abundance of wolverines in the western contiguous United States (Inman *et al.* 2013, p. 282). They estimated current population size of wolverines to be 318 (range 249–626) located within the Northern Continental Divide (Montana) and areas within the following ecoregions: Salmon-Selway

(Idaho, portion of eastern Oregon), Central Linkage (primarily Idaho, Montana), Greater Yellowstone (Montana, Idaho, Wyoming), and Northern Cascades (Washington) (Inman *et al.* 2013, p. 282). Potential wolverine population capacity based on their RSF habitat modeling was estimated to be 644 (range: 506–1881) (Inman *et al.* 2013, p. 282). However, these estimates did not consider spatial characteristics related to behavior, such as territoriality, of wolverine populations. The discussion below provides a summary of recent studies of wolverine detections and observations in the western United States; however, no comprehensive surveys have been conducted across the species' entire range.

In the northern Cascades region of Washington and Canada, researchers tracked activity areas for 14 wolverines via satellite telemetry from 2007 through 2015 (Aubry *et al.* 2016, entire). This study demonstrated that the region supports a resident population, with 9 of 11 study animals documented primarily within Washington (Aubry *et al.* 2016, p. 40).

The Oregon Department of Fish and Wildlife (ODFW) reports that wolverines have been found in the Oregon Cascades on Three-fingered Jack (glaciated volcano) in Linn County, on the Steens Mountain in Harney County, and Broken Top Mountain in Deschutes County, in the Eagle Cap Wilderness Area in the Wallowa Mountains of northeastern Oregon, and, more recently (2012), in Wallowa County, northeast Oregon (ODFW 2017, no page number).

In California, camera trap data indicate the continued presence of a single male wolverine in the Truckee area, as of March 2017 (Shufelberger 2017, pers. comm.). The California Department of Fish and Wildlife (CDFW) has received reports of wolverine detections from the public over past several years, particularly the region near Carson Pass, as well as near Meeks Bay, Lake Tahoe (Stermer 2017, pers. comm.). CDFW researchers are conducting multi-species predator surveys, targeting the potential occurrence of Sierra Nevada red fox and wolverine using camera trapping with hair snares in an effort to determine occupancy, detection probability, distribution, and habitat associations (Stermer 2017, pers. comm.).

A pilot study to evaluate wolverine occupancy was conducted in Wyoming from February through June in 2015 (Inman *et al.* 2015, entire). Results from that survey (hair snares and camera traps in 18 stations across 5 mountain ranges) indicated at least three individual wolverines (at five stations) with at least one individual in the Gros Ventre and Wind River mountain ranges, and at least two individuals in the Southern Absaroka mountain range (Inman *et al.* 2015, p. 9). Occupancy modeling estimated a probability of occupancy for sampled sites of 62.9 percent (Inman *et al.* 2015, p. 8).

In an effort to assess wolverine occupancy in the western United States, the Western Association of Fish and Wildlife Agencies (WAFWA), in coordination with Tribal partners, have formed a multi-state, multi-agency working group (Western States Wolverine Working Group) to design and implement the Western States Wolverine Conservation Project (WSWCP)—Coordinated Occupancy Survey (see Bjornlie *et al.* 2017 for details of protocol). The primary objectives of the WSWCP include: 1) implement a monitoring program to define a baseline wolverine distribution and genetic characteristics of the metapopulation across Montana, Idaho, Wyoming, and Washington, 2) model and maintain the connectivity of the wolverine metapopulation in western United States, and 3) develop policies to address socio-political needs to assist wolverine

population expansion as a conservation tool, including translocation of wolverines (IDFG 2016, pers. comm.; Montana Fish, Wildlife, & Parks (FWP) 2016, pers. comm.; WGFD 2016, pers. comm.).

The WGFD began implementation of the survey in Wyoming in the Greater Yellowstone Ecosystem region and the Bighorn Mountains (25 grid cells) in the winter of 2015–2016 (WGFD 2016, pers. comm.). That initial survey detected, based on unique fur markings, at least two unique wolverines in the Wind River and southern Absaroka Mountain Ranges (WGFD 2016, pers. comm.). The WGFD reported 26 independent wolverine visits, and detections at least once within their study area during each of the four sampling periods (December 2015 through March 2016) (Bjornlie *et al.* 2017, pp. 4–5). Genetic analyses of collected hair samples, including sex and individual identification, are underway.

The monitoring effort was expanded in the winter of 2016–2017 to 187 cells (cell area of 225 km² (87 mi²)) across four states (Washington, Idaho, Montana, and Wyoming). Preliminary results for the 2016–2017 winter detected wolverines in 85 survey cells (WAFWA 2017).

Photographic detections of wolverine include 18 from Idaho, 48 in Montana (including detection of wolverines in all 10 cells surveyed in the SWCC region (Davis 2017, pers. comm.)), 10 in Washington, including detections south of Interstate 90 (Davis 2017, pers. comm.), and 9 in Wyoming; genetic analyses, to date, have reported a total of 157 wolverine samples (WAFWA 2017). It has not yet been determined from the camera-trap images and hair samples how many of these detections are the same individual. **Appendix B** contains a map illustrating these preliminary detections (as of July 2017).

Based on a 6-year study of monitoring resident wolverines (live trapping and camera stations) in central Idaho (Centennial, Smoky, and Salmon Mountains) and the western Yellowstone region (Teton Mountains), Heinemeyer (2016, pers. comm.) suggested that subpopulations of the species at this southern periphery of their North American range are still unstable with low rates of recruitment. We therefore requested additional information from State and Federal agencies regarding the most recent wolverine detections in the Winter Recreation Project study areas of Idaho and Wyoming. In the Teton Mountains region, two wolverines were detected in March 2017, in two different areas (Dewey 2017, pers. comm.). In addition, at least one wolverine was detected on the east side of the Teton Mountains during the winter of 2016–2017, as part of the Western States Wolverine Conservation Project–Coordinated Occupancy Survey monitoring and occupancy study, and a member of the public reported wolverine tracks within Grand Teton National Park in March 2017, while skiing (Walker 2017, pers. comm.). In Idaho, IDFG reported 5 wolverine detections in the Salmon Mountains in Central Idaho in the winter of 2016 (Mack 2017a and 2017b, pers. comm.). These recent detections are displayed in **Appendix C** relative to the study areas of the Winter Recreation Project study areas for the McCall, Idaho, and Teton Mountains. A wolverine was also detected in the winter of 2016–2017 in the Gravelly Range in southwestern Montana about 25 km (15.5 mi) north of the Centennial Mountains area surveyed during the winter recreation project (Inman 2017b, pers. comm.).

Alaska

The ADF&G Trapper Questionnaire Annual Reports include estimates of relative abundance and trends of wolverines and other furbearers as reported by trappers (Parr 2016, p. 38). Table 4 below provides a summary of abundance and trends from 2010–2016 of those reports by region.

Table 4. Relative Abundance and Trend of Wolverine Populations, Alaska (as reported by trappers), 2010-2016.* For Trend, + indicates increase, – indicates declining/decrease, and n/c indicates no change. Sources: ADF&G 2012, 2013a, 2013b; Parr 2016.

Region	Relative Abundance				Trend			
	2010-2011	2011-2012	2012-2013	2015-2016	2010-2011	2011-2012	2012-2013	2015-2016
Region I – Southeast Alaska	scarce	scarce	scarce	scarce	n/c	n/c	n/c	–
Region II – Southcentral Alaska	scarce	scarce	scarce	scarce	n/c	n/c	n/c	–
Region III – Interior Alaska	scarce	scarce	scarce	scarce	n/c	n/c	n/c	–
Region IV – Central and Southwest Alaska	N/A	N/A	N/A	scarce	N/A	N/A	N/A	–
Region V - Northwest	N/A	N/A	N/A	scarce	N/A	N/A	N/A	–
Southwest	common	scarce	scarce	N/A	n/c	–	n/c	N/A
Arctic and Western	common	common	scarce	N/A	n/c	n/c	n/c	N/A

*No reports written for years 2009-2010, 2013-2015.

However, relying exclusively on trapping reports is likely to present an incomplete assessment of wolverine populations. The accuracy of information provided in the most recent report is dependent on how many trappers reply to the annual survey; for 2016 the response rate was only 11.7 percent (Parr 2016, p. 3). Trapping effort was reported to have increased by some trappers (45 percent of those reporting) during the 2015–2016 season, and 80 percent of those who increased their efforts reported an increase in their overall catch (Parr 2016, p. 15). However, this assessment does not consider how this increased trapper effort relates to harvest levels for wolverine, nor does it account for an unknown and unreported number of wolverines taken for subsistence purposes (Gardner *et al.* 2010, p. 1,894). Estimates of density, described below, provide a better depiction of wolverine population status in Alaska.

Canada

Similar to Alaska, determining wolverine population abundance and trends in Canada is difficult as numbers are developed from harvest activity (COSEWIC 2014, p. 25). Wolverine harvest trends are also difficult to estimate given the temporal and spatial variability in trapping effort and reporting of harvest, and not all regions use mandatory pelt sealing, compulsory reporting, or fur export permits/fur dealer records (COSEWIC 2014, p. 26).

According to the most recent COSEWIC Assessment and Status Report on the Wolverine, *Gulo gulo* in Canada (COSEWIC 2014, entire), Canada’s western subpopulation has been estimated at 15,688 to 23,830 adults, though this value is based on several assumptions (consistent trapping effort and uniform densities across the species’ range); the eastern population is estimated at less than 100 individuals or may be extirpated (COSEWIC 2014, p. 36). Population trends across all

of Canada are not known, but wolverine populations have been stable over areas within the country's northern range for the last three generations (22.5 years) (COSEWIC 2014, p. v).

In northern Manitoba and Ontario, wolverines may be increasing in number as aerial surveys in northern Ontario have indicated an eastward reoccupation of its former range (towards James Bay and Québec) (COSEWIC 2014, p. v). However, although observations of wolverines continue to be reported within Québec and Labrador (the eastern sub-population), there have been no verifiable observations since 1978, and wolverines are likely extirpated from much of southeastern Canada (COSEWIC 2014, p. v). In addition, declines in the southern regions (within parts of British Columbia and Alberta) may be occurring (COSEWIC 2014, p. 36). Table 5 presents a more detailed summary of wolverine populations in Canada.

Table 5. Wolverine Population Estimates for Canadian Territories. Source: COSEWIC, 2014.

Territory	Number of wolverines
Yukon Territory	3,500–4,500
Northwest Territories	3,430–7,325 (with an additional 220–470 juveniles)
Nunavut	Estimated at 2,000–2,500
British Columbia	2,700–4,760
Alberta	Estimated at 1,500–2,000
Saskatchewan	Less than 1,000
Manitoba	1,100–1,600
Ontario	458–645
Québec	Very rare, at non-detectable level, or extirpated
Labrador (including mainland Newfoundland)	Very rare or extirpated

In addition to the 2014 COSEWIC summary, Cardinal 2004 (entire) prepared a complimentary summary report of wolverine trends in Canada based on Aboriginal traditional knowledge. Trends reported indicate: (1) high, relatively stable levels of wolverines in the Yukon; (2) high levels of wolverines in the North Slave region of the Northwest Territories, though population levels are estimated to be stable to decreasing; (3) high levels of wolverine along forested areas in the northern portions of the mainland within the Inuvialuit Settlement Region (ISR) (located in the northwest corner of the Northwest Territories) and Kitikmeot region of Nunavut; (4) an increase in wolverines in the Kivalliq region of Nunavut, but at lower levels than populations in the Boreal and North Mountain ecological areas; and (5) least abundant in the northeastern corner of Nunavut and the Arctic Islands (Cardinal 2004, pp. 22–29). In sum, the majority of traditional knowledge holders in Nunavut, Northwest Territory, and Yukon Territory describe wolverine populations as either stable or increasing in northern Canada and is now found in areas where they occurred in the past; however, they are still considered naturally uncommon; only in Yellowknife did people report that wolverines might be decreasing (Cardinal 2004, pp. iii– iv, 10, 23).

Other inventory and occupancy studies include an inventory of wolverines conducted by Regehr and Lacroix (2016, entire) in the winter of 2012 on the east side of the Coast Mountains in British Columbia using a multi-method approach. They identified six individuals using genetic analysis, and one additional individual by photography, which was higher than expected as compared to model predictions of density and habitat quality (Regehr and Lacroix 2016, pp.

248–249). Estimates of wolverine occupancy were also evaluated for the Canadian Crown of the Continent ecosystem (central and southern Canadian Rockies) (Clevenger *et al.* 2016, entire). Occupancy estimates were found to vary from year-to-year and exhibited a north-south gradient, likely due to the differences in habitat quality among areas that were sampled by year (Clevenger *et al.* 2016, p. 4). For 2016, estimated wolverine occupancy probability was 0.40 for their British Columbia Rockies study area, with a declining pattern from north to south (Clevenger *et al.* 2016, p. 4). In general, their research has found that wolverines are more abundant in rugged, remote areas that have minimal human activity and landscape disturbance (Clevenger *et al.* 2016, p. 5). This study projected an expected number of wolverines in their study area of about 28 (Clevenger *et al.* (2017, p. 6). To the south, in the Southwestern Crown of the Continent (SWCC) region (northwestern Montana, approximately 1.5 million acres), wolverine surveys (snow tracking, bait stations/hair snares) have been conducted since 2012 (SWCC Wildlife Working Group 2016, pers. comm.). These survey efforts have detected 22 unique wolverines (11 males, 11 females) across three U.S. Forest Service districts, and they reported an increase in the frequency of detections from 2012 to 2015 (SWCC Wildlife Working Group 2016, pers. comm.).

The 2014 COSEWIC report indicates that trends in wolverine populations in the northern range, while uncertain, appear to be stable or increasing, but also notes that there is some concern for populations in the southern areas of British Columbia and parts of the northern United States (COSEWIC 2014, p. 22, and references cited therein). In British Columbia, researchers are currently conducting a multi-phase project using landscape genetic analyses to identify and delineate functional populations of wolverines and provide an estimate of size and sustainable harvest within each functional population (Weir 2017, pers. comm.).

Estimates of Density

Wolverine densities vary across North America, and have been described as “naturally low” (van Zyll de Jong 1975, p. 434) and “naturally uncommon” (Cardinal 2004, p. iii) given the species’ large home range, wide-ranging movements, and solitary characteristics. The most recent estimates (at that time) of density (number of wolverines per 1,000 km² (386 mi²)) for North America were prepared by Inman *et al.* (2012a, p. 789; Table 5). In the contiguous United States, density estimates ranged from 3.5 for the Greater Yellowstone region (2001–2008) (areas above 2,150 m (7,054 ft) (latitude-adjusted elevation), 4.5 for central Idaho (1992–1995), to 15.4 for northwestern Montana (1972–1977).

In Alaska and Yukon, density estimates presented by Inman *et al.* (2012a, p. 789) range from 3 to about 14 wolverines per 1000 km² (386 mi²), using a number of methods. For example, Royle *et al.* (2011, p. 609) estimated wolverine densities for southeastern Alaska (Tongass National Forest; 2008) from 8.2 to 9.7 per 1000 km² (386 mi²) (using mark-recapture), where the higher estimate incorporates a positive, trap-specific behavioral response. Density of wolverines were recently reported as an estimated 5–10 wolverines per 1000 km² (386 mi²) (based on snow tracking) for southcentral Alaska, and approximately 10 per 1000 km² (386 mi²) (based on DNA mark-recapture methods) for southeast Alaska (Golden 2017, pers. comm.). A wolverine occupancy study in 2015 within an area of central Alaska reported a density estimate of 9.48 wolverines per 1,000 km² (386 mi²) (ADF&G 2015a, p. 7).

Wolverine density estimates for Canada varies across regions, from 5 to 10 per 1000 km² (386 mi²) in northern mountain and boreal regions to 1 to 4 per 1000 km² (386 mi²) in southern boreal areas (COSEWIC 2014, p. 27). More recently, Clevenger *et al.* (2017, entire) presented a density estimate (using spatial capture/recapture models) for the Kootenay region of British Columbia of 0.78 wolverines per 1000 km² (386 mi²), for 3 study years (2014–2016), which they reported as lower than expected (Clevenger *et al.* 2017, p. 6).

Stressors – Causes and Effects

We reviewed the best available information to identify current conditions and potential stressors that may be affecting wolverine populations or its habitat. These include roads and other infrastructure, recreational activity and other human disturbances, wildland fire, disease or predation, and overutilization for commercial, recreational, scientific, or educational purposes. Because wolverines in North America move between both borders of Canada (i.e., contiguous United States, Alaska), we included in our evaluation stressors identified for wolverines in Canada and Alaska that are also relevant for wolverine populations in the contiguous United States.

As an initial step, we reviewed the land ownership of the area defined as primary habitat by Inman *et al.* (2013, entire) in the contiguous United States, and determined that 96 percent of that modeled habitat is located on Federal land (see **Appendix D**). Lands managed by the Forest Service represent the largest portion of Federal lands (89 percent) within this modeled primary habitat.

Effects from Roads

Roads and rail lines can be a cause of mortality to wolverines and habitat models have identified road density as an important association (avoidance) for selection of habitat (e.g., Rowland *et al.* 2003; Bowman *et al.* 2010; Inman *et al.* 2013). Road density has been listed as a threat to wolverines occupying the boreal/western mountain regions of Canada (Canadian Boreal Forest Agreement 2014, p. 2). In the wolverine's southern Canadian range, roads may be facilitating direct mortality by improving motorized access of hunters, trappers, and recreational users into remote areas (COSEWIC 2014, p. 21).

In their review of 12 radio-telemetry studies (1972 to 2001) of wolverines in North America, Krebs *et al.* (2004, p. 497) reported 3 mortalities of wolverines from road-rail kills. More recently, road mortalities have been recorded in Idaho (1 confirmed in 2014) (IDFG 2017a) and 2 in Montana (2004) (Kociolek *et al.* 2016, p. 68); one in Utah (2016) (Hersey 2017, pers. comm.); and two other wolverine road-rail fatalities in Montana were reported in 2015 (Inman 2017a, pers. comm.). In Canada, anthropogenic causes of mortality for wolverine populations also include road kill (COSEWIC 2014, p. v). One road mortality of a male wolverine was reported in a lowland boreal forest region of Ontario, Canada (Dawson *et al.* (2010, p. 142). More recently, Scrafford *et al.* (2017, p. 34) described a report in which 9 wolverines were struck and killed by vehicles in the Hay-Zama region of northwestern Alberta, Canada (2013–2015), and 1 road mortality occurred within the town of Rainbow Lake in Alberta.

Roads may also affect den site selection (May *et al.* 2012, p. 202), particularly areas within their range where they cannot select for high elevation habitat (e.g., central lowland forests of Canada) (Dawson *et al.* 2010, p. 143). In Norway, May *et al.* (2012, p. 202) found that wolverine dens were generally located far from infrastructure (public roads and private roads and/or recreational cabins). The authors reported a minimum threshold in den site selection relative to infrastructure of 1.4 km (0.87 mi) from private roads and 7.5 km (4.7 mi) from public roads (May *et al.* 2012, p. 202). However, they found that wolverines in their study area had a wide tolerance range at the home-range scale (1.0–2.75 km (0.62–1.7 mi) for private roads and 6.0–11.0 (3.7–6.8 mi) for public roads) (May *et al.* 2012, p. 201; Figure 4), supporting conclusions from other studies that have found that, once a general area is used, it appears to be re-used in subsequent years including by successive individuals colonizing the sites (May *et al.* 2012, p. 202).

Wolverine road crossings were evaluated in the western Greater Yellowstone region through telemetered animals and visual observations of snow tracks, direct observations of crossings, and road-kill mortality (Packila *et al.* 2007, entire). That study documented 43 crossings of U.S. and State highways by 12 wolverines (Packila *et al.* 2007, p. 105). Within the Big Sky, Montana, area, they documented 67 crossings of MT64/Jack Creek Road by 4 wolverines (Packila *et al.* 2007, p. 105). Most (76%) road crossings were made by subadult wolverines, dispersing or otherwise exploring new areas (Packila *et al.* 2007, p. 105). One road-caused mortality was observed and the authors report two others from additional sources during their study period (Inman *et al.* 2007, p. 89). The study results indicate that roads do not act as absolute barriers to movement by wolverines, but they can directly affect individuals (road kill) and may have secondary effects at the population level (Packila *et al.* 2007, p. 105).

In an effort to evaluate the potential impact of major roads to wolverine (individuals and populations), we conducted a spatial analysis of roads² found within Inman *et al.*'s (2013, p. 281) primary wolverine habitat and female wolverine dispersal habitat in the western United States, as measured by number of kilometers (miles). In our analysis, we identified four road classes: Interstate Highway, U.S. Highway, State Highway, and secondary roads. Secondary roads encompassed all roads not included in any of the first three categories and include paved and unpaved roads, including Forest Service roads, and are generally likely to have less traffic volume than major highways in the regions evaluated. Our analysis found that secondary roads represented 97 percent (29,892 km (18,574 mi)) of all roads (30,805 km (19,141 mi)) within modeled primary habitat, and 97.5 percent (144,279 km (89,650 mi)) of all roads (148,029 km (91,980 mi)) within modeled female dispersal habitat.

We then evaluated the type of roads at high elevation within our estimated Current Range (shown in Figure 3). Using the 2,300 m (7,546 ft) elevation as a benchmark (based on its use as a predictor variable for wolverine occurrence in Inman *et al.* 2013, and results from predictive models presented in Copeland *et al.* 2007, p. 2,205), we evaluated the length of roads above and below this elevation, and also the type of roads at or above 2,300 m (7,546 ft). The results are illustrated in **Appendix E**. Overall, we found that approximately 85 percent of *all* roads were

² Using U.S. Geological Survey National Transportation Dataset Downloadable Data Collection based on TIGER/Line data provided through U.S. Census Bureau and supplemented with 'HERE' road data to create tile cache base maps.

below 2,300 m (7,546 ft). Of the roads located at or above 2,300 m (7,546 ft), 95 percent are *secondary* roads (see charts in **Appendix E**).

Using the same dataset, we evaluated road density (km/km²) based on regional blocks of primary wolverine habitat in the western United States delineated by Inman *et al.* (2013; Figure 3). Those results are shown in Table 6. With the exception of the Southern Rockies (at 0.47 km/km²), the mean road densities at elevations equal to or greater than 2,300 m (7,546 ft) are very low.

Table 6. Mean Road Density in Wolverine Primary Habitat.

Geographic Region [‡]	Mean density (km/km ²), all roads	Mean density (km/km ²), all roads $\geq$ 2,300 m (7,546 ft)
Northern Cascade	0.54	0.00
North Continental Divide	0.54	0.00
Salmon-Selway	0.70	0.03
Central Linkage	0.84	0.06
Greater Yellowstone	0.24	0.06
Southern Rockies	0.55	0.47
Sierra Nevada	0.09	0.03
Uinta	0.15	0.12
Bighorn	0.00	0.00
Great Basin	0.06	0.03
Oregon Cascade	0.72	0.00

[‡]Regions defined in Inman *et al.* (2013; Figure 3).

We also reviewed den site locations (natal, maternal, or unknown dens) within our database relative to roads (see map in **Appendix E**). Our results indicate that wolverine dens are located in areas with minimal roads, including secondary roads; however, we caution that this analysis is based on a limited den site dataset and should be viewed in the context of other abiotic and biotic variables including landscape features at the den site scale and availability of food. Additionally, most den locations in much of the wolverine's range in the contiguous United States are at high elevations and roads in these areas would likely be impassable or closed entirely to vehicles during the time of denning (January–March).

In summary, wolverines are associated with habitat found in high elevation areas, but are known to disperse across great distances. Major highways can present mortality risks to dispersing individuals and affect immigration to open territories, but roads do not represent absolute barriers to wolverine movements. Wolverines den during winter months in remote locations that are often inaccessible or restricted to motorized vehicles, though, secondary roads and trails are used for winter recreational activity. Although we recognize there are likely additional events that have not been reported, we estimated the total number of wolverine mortalities due to roads from 1972 to 2016 (44 years) in North America was 20, at least 11 of which are from Canada (see citations above). As discussed above, we calculated a low proportion of major highways in both modeled primary habitat and female dispersal habitat, and a low mean density of roads at high elevations where wolverines have been observed, with the exception of the southern Rocky Mountains. Roads present a low stressor to wolverines at the individual and population level in most of its current contiguous United States range.

Disturbance due to Winter Recreational Activity

Wolverine behavior patterns, such as denning, rearing of young, movement and dispersal, and foraging/scavenging, may be affected by recreational activities (COSEWIC 2014, p. 42). As noted above, in Norway, May *et al.* (2012, p. 201) found, at the home range scale, a minimal threshold distance of approximately 1.5 km (0.93 mi) for wolverine den sites from private roads and/or recreational cabins. Krebs *et al.* (2007, entire) evaluated habitat use associations for wolverines in two multiple use areas in British Columbia, Canada. Using logistic regression models, the authors found that in an area of active recreation (Columbia Mountains), female wolverines were negatively associated with helicopter and backcountry skiing in their winter models (Krebs *et al.* 2007, pp. 2,187–2,188). However, in summer months, Copeland *et al.* (2007, p. 2,210) reported that wolverines in their study area of central Idaho were not uncommonly found near maintained trails and active campgrounds.

The Wolverine–Winter Recreation Study represents an on-going project to evaluate the potential effects of backcountry winter recreation (e.g., backcountry skiers, heli-skiers, cat-skiers, snowmobilers) on wolverines (Heinemeyer 2016, pers. comm.). The multiyear study areas include central Idaho and areas in the western Yellowstone region ('Island Park' and Teton Mountains) (Heinemeyer and Squires 2015, p. 3). The study has been monitoring wolverines using GPS collars using movement rates and percent of time active (vs. resting) as indicators of potential responses of wolverines to winter recreation activities (Heinemeyer 2013, pers. comm.). Backcountry winter recreation activities are monitored through GPS units voluntarily carried by recreationists (Heinemeyer 2016, pers. comm.). Early analysis of the data suggest that wolverines demonstrate a behavioral response to recreation activities, such as increased movement rates and a reduction in resting periods in areas of high recreation activity, especially high recreation days (Saturday and Sunday) (Heinemeyer and Squires 2013, pp. 5, 7–8).

However, this research has also found that wolverines maintained their home ranges within areas with relatively high winter recreation activity over several years of monitoring, including some areas found to contain the highest recreational activities (Heinemeyer 2016, pers. comm.). The study has not been able to determine whether these resident wolverines are reproductively successful due to the limited monitoring information available for reproductive females (Heinemeyer 2016, pers. comm.).

Conservation measures currently being implemented that address the effects of roads in the Teton Mountains include winter closures in certain areas (generally from November 1 through May 1), including road closures in the Bridger-Teton and Caribou-Targhee National Forests and in Grand Teton National Park as shown in **Appendix F** (additional details for Grand Teton National Park are described in Superintendent's Compendium (National Park Service (NPS) 2017; pp. 8–9); see also maps at <https://jhalliance.org/campaigns/dont-poach-the-powder/> Jackson Hole Conservation Alliance 2017). These closures are being implemented to help minimize disturbance to wildlife (e.g., migration pathways).

State Wildlife Action Plans prepared for individual western States identify recreation management strategies within wolverine habitats. For example, in the State of Oregon, the

ODFW Conservation Strategy identifies management of winter recreation use in order to avoid impacts to wolverines (ODFW 2016). In Montana's State Wildlife Action Plan, conservation actions are identified for addressing potential impacts from recreation, such as consideration of seasonal closures during breeding season (Montana FWP 2015, p. 63). The IDFG *Management Plan for the Conservation of Wolverines in Idaho* also includes conservation strategies related to winter recreation (e.g., characterizing wolverine response to recreational activities (IDFG 2014, p. 35)), and the State continues to support the Wolverine-Winter Recreation Study. **Appendix F** provides additional details on individual State conservation strategies.

In summary, wolverine behavior (movement) can be affected by winter recreational activity. Results from one long-term study in parts of the wolverine's range in the contiguous United States have found that wolverines can maintain residency in high winter recreational use areas. Wolverines have recently been detected in areas that experience winter recreational activity. Conservation strategies and actions have been identified in several western States' Wildlife Action Plan to address potential impacts of this stressor to wolverines. Based on the best available scientific and commercial information, the effect of winter recreational activity represents a low stressor to wolverines in the contiguous United States at the individual and population level.

Other Human Disturbance

Infrastructure, such as pipelines, active logging or clearcuts, seismic lines, and activities associated with mining (e.g., producing mines, mines under development, mineral exploration areas), may also affect individual wolverine behavior (e.g., avoidance) or loss or modification of wolverine habitat. As discussed above (see Habitat Use section), Johnson *et al.* (2005, entire) evaluated habitat relationships for the wolverine and other arctic wildlife, including the cumulative effects of human activities and associated infrastructure on the distribution of wolverines in the Canadian central Arctic using RSF modeling. However, because human disturbance factors (i.e., major developments, mineral explorations, seasonal outfitter camps) were mostly absent from the range of monitored wolverines, the researchers were not able to reliably model their effects (Johnson *et al.* 2005, p. 23).

The 2014 COSEWIC status review identified several potential stressors to wolverines and their habitat in Canadian territories. They indicated potential permanent, temporary, and functional losses to wolverine habitat from forestry; oil, gas and mineral exploration and development; and large hydroelectric reservoirs (COSEWIC 2014, p. 21). As discussed above, Scrafford *et al.* (2017, entire) evaluated habitat selection of wolverines in response to human disturbance in the western Canadian boreal forest in both winter and summer months. Their analysis found that wolverines were attracted to some industrial infrastructure (older seismic lines exhibiting latter stages of regeneration) and disturbance (areas of active logging), likely related to foraging opportunities (e.g., small prey), but avoided interior areas of intermediate-aged cutblocks (areas authorized for logging) (Scrafford *et al.* 2017, pp. 32–34). Their results found evidence of road avoidance, but wolverines were attracted to all-season road sections with borrow pits, which they suggest was related to foraging opportunities at these pits (e.g., presence of beavers in water-filled pits) and less predation risk, since wolves avoid these roads (Scrafford *et al.* 2017, p. 34). In sum, these authors concluded that wolverine selection patterns relative to industrial activity

and infrastructure in their study area represent a balance between exposure to predators and foraging opportunities (Scrafford *et al.* 2017, p. 32).

Additional studies of wolverine behaviors related to the effects of disturbance due to infrastructure and other human activities are needed. Based on the best available scientific and commercial information, these effects are small or narrow in scope and scale and appear to represent a trade-off between foraging opportunities in areas that provide minimal risk of predation and avoidance of open areas and/or higher predation risk (Scrafford *et al.* 2017, pp. 33–34).

Effects from Wildland Fire

Wildland fire can produce both direct and indirect effects to wildlife. Direct effects include injury and mortality as well as escape or emigration movement away from fires (Lyon *et al.* 2000, pp. 17–21). Small mammals will generally find refuge underground or within sheltered places within the burning area, while larger mammals will move to safe areas in unburned patches or outside the burn (Lyon *et al.* 2000, p. 18). For animals that emigrate during fire events, the length of time before they return is dependent on the degree to which fire has altered habitat structure and food supply (Lyon *et al.* 2000, p. 20).

We are unaware of any studies evaluating direct effects of wildland fire to wolverines. Wildland fire is likely to temporarily displace wolverines, which could affect home range dynamics. Given that wolverines can travel long distances in a short period of time, individuals would be expected to move away from fire and smoke (Luensmann 2008, p. 14). In addition, because young are born during winter months, fire risk at that critical life stage is very low (Luensmann 2008, p. 14).

Indirect effects of wildland fire can include habitat-related effects or effects to prey and competitors/predators; however, we are unaware of empirical studies evaluating these potential effects as they relate to wolverines. In a study area within the Yukon (Canada), wolverines were reported occupying regenerating forested habitat that contained remnants of mature timber which had burned 30 years prior (Slough and Mowat 1996, p. 948). Additionally, fire suppression in conjunction with logging activities in boreal forests (northwestern Ontario) can increase the prevalence of deciduous tree habitats, at least at a regional level, which is negatively associated with wolverine occurrence (Bowman *et al.* 2010, p. 464).

A study in northern Idaho of the effects of multiple wildland fires over several years, including very large fires, to forest habitat occupied by another mustelid, the American marten (*Martes americana*) found that fire events had created a mosaic of vegetation that supported a diverse assemblage of cover and food resources that was favorable to this species (Koehler and Hornocker 1977, p. 503). Similar to wolverines, the summer and fall diet of the American marten is represented by diverse prey, and wildland fire events can create and maintain forest openings for ground squirrels and voles (Koehler and Hornocker 1977, p. 504). The development of these types of mosaic forest communities following certain wildland fire events also provides discontinuous fuel loads, which in turn should result in smaller and cooler wildland fires, with less replacement of marten habitat (Koehler and Hornocker 1977, p. 504). However, large,

uniform burns would be expected to result in more severe impacts to American marten habitat (Lyon *et al.* 2000, p. 21).

Studies of the effects of wildland fire to a key prey species for the wolverine in parts of its North American range, the caribou, was reviewed by Klein (1982, entire). This review highlighted the importance of separating short-term effects of wildland fire in boreal forests to caribou ecology from long-term effects (Klein 1982, p. 393). Given that long-term benefits to the species' ecology can be disproportionate to the short-term detrimental effects on populations and herds, (including the species' lack of reproductive plasticity), caribou may be more appropriately considered as fire-influenced, rather than fire-adapted (Klein 1982, p. 393). Other ungulate prey species respond more positively to fire. An increase in spring and summer grasses following fall burns can provide forage for elk and deer, and sprouting of deciduous trees, such as aspen, birch and willow, following burns provides forage for moose (Luensmann 2008, p. 18).

Management measures to address this potential stressor are identified in USDA Forest Service National Forest Land Management Plans. Examples of these goals and objectives are described in **Appendix G**. In addition, the Idaho State Wildlife Action Plan includes measures to address fire threats to the wolverine and its habitat, including removal of perceived barriers to allow more prescribed natural fire on State and private forest lands and promoting/facilitating the use of prescribed fire as a habitat restoration tool, on both public and private lands where appropriate, and leaving fire-killed trees standing as wildlife habitat if they pose no safety hazard, all in an effort to restore a more natural fire interval that allows for return to historical forest conditions (IDFG 2017b, pp. 91, 134, 180).

Given the diversity of habitats occupied by wolverines, their occupancy of high elevations, and extensive mobility, wildland fire represents a limited stressor, in scope and scale, to wolverine habitat and its prey in the contiguous United States range.

Disease or Predation

Disease

We are unaware of comprehensive surveys evaluating the prevalence of diseases in wolverines in the contiguous United States. Early accounts of endoparasites species and their prevalence in wolverines include a review by Erickson (1946, p. 503), and a report by Rausch (1959, entire), who documented 7 species of helminth parasites in 86 percent of wolverines examined from trapper-supplied carcasses in Alaska. In 1994, Copeland (1996, p. 26) collected a single specimen of the parasite *Toxascaris* sp. from wolverine scat in Idaho. In Alaska, carcasses sampled (during necropsy or predator control activities) in 2012–2014 to determine the prevalence of *Trichinella* and its genotypes reported one wolverine with *Trichinella* T6 genotype in that single sample (ADF&G 2015b, p. 8). Results from Alaska trapper questionnaires for the prevalence of ectoparasites on wolverines were either scarce or not present across all reporting regions in 2015–2016 (Parr 2016, p. 21).

Rabies is endemic to Alaska in Arctic and red fox along north and west coasts of Alaska (ADF&G 2013c). Under the ADF&G enhanced rabies surveillance program, the agency

confirmed rabies in one wolverine (out of 49 sampled) in 2012, a female found dead in the North Slope region (Woodford and Beckman 2012). This was the first confirmed case of rabies in wolverines in North America (Woodford and Beckham 2012).

The 2014 COSEWIC Assessment and Status Report for the wolverine presented a summary of reported parasitic species observed in wolverines in Canada (COSEWIC 2014, p. 25). These observations included: parasitic nematode roundworms (*Trichinella* spp.) in 88 percent of wolverine samples tested from Nunavut and 26 percent from the lower MacKenzie region; helminth parasites (trematodes, cestodes and nematodes) in wolverine digestive tracts from the lower Mackenzie River valley; and, from the Nunavut region, protozoan parasites infections including *Sarcosystis* spp. (80 percent) and *Toxoplasma gondii* (41 percent) (citations omitted). Banci (1987, pp. 81, 110) reported parasitic pneumonia as a cause of mortality in southwest Yukon Territory, a female thought be nutritionally-stressed following the raising of young.

An evaluation of trapper-submitted wolverine carcasses harvested was conducted for the Yukon Territory in the fur trapping seasons 2005–2006 through 2011–2012 (Jung and Kukka 2013, entire). No samples tested positive for rabies (Jung and Kukka 2013, p. 17). Another study of intestinal parasites of wolverine carcasses from both the Yukon and Northwest Territories reported *Trichinella* spp. in 74 percent of carcasses and several intestinal parasites, including cestodes (parasitic flatworms) such as *Taenia* spp. (Luck *et al.* 2016, no page number).

In summary, other than a parasitic pneumonia mortality event and the single rabies case, we are not aware of any other studies documenting impacts of disease to wolverines in North America. At this time, based on the best available scientific and commercial information, we do not find that disease is a population or species level stressor to the wolverine in the contiguous United States.

Predation

As discussed above (*Diet and Feeding* section), a number of potential natural predators have been identified for wolverines across its North American range, including intraspecific predation. However, we have no information that suggests this predation represents a significant stressor to the wolverine at either an individual or population level.

In summary, the best scientific and commercial information available indicates that disease or predation is not a stressor the wolverine. We are unaware of any management or conservation measures currently in place to reduce potential impacts associated with disease or predation.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

There is currently no allowable trapping or harvesting of wolverines in the contiguous United States, though incidental trapping mortalities have been documented as we reported in our proposed rule (78 FR 7881; February 4, 2013). Two mortality events from shootings of wolverines were documented in Idaho (2001, 2007) (Idaho Department of Fish and Game (IDFG) 2014, p. 26).

In Montana, wolverines were a legally harvested furbearer in Montana up until 2012; however, the trapping season is currently suspended with a zero statewide quota (Montana Natural Heritage Program and Montana FWP 2017). Unlike populations in Eurasia, wolverines rarely prey on livestock in North America (*cf.* domestic sheep predation in Wyoming reported (Mead 2013, pers. comm.)) and therefore they are not directly targeted for predator control (COSEWIC 2014, p. 41). However, incidental trapping can result in the capture of non-target species such as wolverine. In Idaho, the IDFG has a mandatory furtaker harvest report that requests all live incidental catches be reported by species and any wolverine catch that results in mortality is required to be reported (IDFG 2013, pers. comm.). Since 1965, over a period of just over 50 years, 16 incidentally-trapped wolverines were reported during the State's furbearing seasons, with 6 animals known to be released alive and 6 mortalities (IDFG 2013, pers. comm.; IDFG 2016, pers. comm.). This total includes four wolverines caught during the 2013-2014 furbearer season, with three released alive and one mortality (IDFG 2014, p. 26). Within the State of Wyoming, there are two confirmed reports of incidental take, one in 1996 (Mead 2013, pers. comm.) one in 2006. The 2006 animal was released unharmed (Inman 2012, pers. comm.). In Montana, since the closing of the trapping season for wolverine in 2013 (2013 through 2016), four wolverines have been incidentally trapped, one in 2013 and three in 2014 (Inman 2017c, pers. comm.). The 2013 capture was released unharmed and the three caught in 2014 were all mortalities (Inman 2017c, pers. comm.).

Predator control programs targeting wolves, including poison and incidental trapping, can result in incidental losses of wolverines (COSEWIC 2014, p. 41). Specific to wolf control for livestock protection in Idaho, three wolverines have been trapped incidental to authorized wolf control activities since 1995, with two released alive and one animal euthanized (IDFG 2014, p. 26). Preventive measures have been adopted to reduce these incidental captures, including implementation of educational programs to minimize incidental capture of wolverines during trapping seasons (IDFG 2014, p. 27). Licensed wolf trappers are required to complete a Wolf Trapper Education course with specific instruction for reducing incidental trapping of wolverine, Canada lynx, and other non-target species (IDFG 2014, p. 27). In addition, the U.S. Department of Agriculture Wildlife Services (Wildlife Services) agency has also temporarily stopped (as of April 2017) using cyanide predator control devices in the State of Idaho (Moeller 2017).

In Alaska, wolverine trapping and hunting is controlled by seasons and bag limits, with about 550 animals harvested each year (Alaska Department of Fish and Game (ADF&G) 2017a). For the 2015–2016 reporting period, wolverine harvest, based on furbearer sealing records,³ totaled 527 animals (Parr 2016, p. 42). This level of harvest has been fairly consistent since 2010, as shown in Table 7 below.

³ Wolverine taken in Alaska are required to be sealed by an authorized department representative before pelts are shipped to an out-of-state buyer or auction house (Parr 2016, p. 44). For those species that require sealing, the number of animals sealed represents the best information regarding the statewide harvest (Parr 2016, p. 41).

Table 7. Number of wolverines harvested in Alaska, as reported from regulatory year sealing records, 2010–2015. Adapted from Parr (2016, p. 42; Table 10).

Alaska Region	2010	2011	2012	2013	2014	2015
I	25	20	25	31	14	15
II	25	29	50	31	16	37
III	233	235	261	358	268	214
IV	180	160	170	158	99	150
V	140	110	135	133	109	111
Total	603	554	641	711	506	527

Trapping and harvesting of wolverines occurs over much of the range in Canada, as summarized in the 2014 COSEWIC wolverine status review (COSEWIC 2014, pp. 10, 29–35). Specifically, wolverines are harvested in the northern and western territories—Manitoba, Saskatchewan, Alberta, British Columbia, Yukon, Northwest Territories, and Nunavut (COSEWIC 2014, p. 43). Non-aboriginal harvest of wolverines has not been permitted since 2001–2002 in Québec and Labrador (COSEWIC 2014, p. 43). Trapping is closed in Ontario (except through treaty rights), though incidental trapping results in 1 to 4 mortalities per year (Bowman *et al.* 2010, p. 465). Harvest levels in western provinces have remained relatively stable since 1992 (COSEWIC 2014, p. 38; Table 1).

The management of wolverine harvest in Canada incorporates spatial and temporal elements such as season length, quotas, limited entry, and trapline management by trappers (reviewed by Slough *et al.* 1987). Wolverine harvest levels in Canada are monitored using mandatory pelt sealing, annual harvest reporting, or through monitoring of fur exports (COSEWIC 2014, p. 43). In some northern communities, wolverine pelts are used locally and harvests are monitored through carcass collection programs (COSEWIC 2014, p. 43).

The COSEWIC Assessment and Status Report for the wolverine also noted that range contraction and habitat trends of wolverines in Canada are not solely the result of habitat or trapping pressure (COSEWIC 2014, p. 20). Reductions in ungulate (e.g., caribou) populations, which provide an important winter food resource, were also likely an important factor in range contractions of wolverines in its northern range (COSEWIC 2014, p. 20), and likely continue to influence populations today. Snowmobiles have allowed for better access for hunters and trappers and may be increasing the number of wolverine harvested in its northern North America range; however, the areas of exploitation are still relatively small concentrated areas, and large areas of refugia continue to be found (Cardinal 2004, p. 31).

Population growth rate scenarios for North American wolverines were modeled by Krebs *et al.* (2004, p. 499), including trapped and untrapped populations. Of note, at the time of this study, wolverines were considered furbearer or game animals and trapped or hunted in 8 of their 12 study areas in North America, including Montana (Krebs *et al.* 2004, p. 495; Table 1). Estimated (logistic) rates of population growth (λ) were found to be lower for trapped populations ($\lambda = 0.878$) as compared to untrapped populations ($\lambda = 1.064$) (Krebs *et al.* 2004, p. 499). Based on their analysis, harvesting was considered to be an “additive mortality” in the populations studied and is likely sustained by dispersal from untrapped areas that provide refugia (Krebs *et al.* 2004,

pp. 499–500). However, as described in the 2014 COSEWIC report, trends in wolverine populations in the northern range, while uncertain, appear to be stable or increasing, with some concern for populations in the southern areas of British Columbia and parts of the northern United States (COSEWIC 2014, p. 22, and references cited therein). Similarly, in Alaska, over the past 6 years, on average, 590 wolverines are taken each year (see Table 7). The consistent harvest levels in these regions suggest relatively stable wolverine populations.

We evaluated trapping of wolverines in British Columbia and Alberta regions of Canada in an effort to document potential impacts to dispersing wolverines along the U.S.–Canada border. As described above (*Population Abundance and Distribution*), the population of wolverines in British Columbia is estimated to be 2,700–4,760 and 1,500–2,000 animals in Alberta (COSEWIC 2014, p. 36). We obtained 9 years (2007–2015) of harvest data for southern BC wildlife management units from the British Columbia Ministry of Environment, Ecosystems Branch for our analysis. Twenty seven years (1989–2015) of harvest data was obtained for Alberta in addition to locations of wolverines from a 2012–2015 study and other sources (Webb *et al.* 2016, p. 1,465; Webb 2017, pers. comm.).

Figure 5 presents the results from our spatial analysis and indicates a total of 77 wolverines were trapped in British Columbia wildlife management units within 110 km (68.35 mi) of the U.S.–Canada border from 2007–2015 (average of 8.5 animals per year). We used this distance since it's similar to both the average maximum distance per dispersal movement of 102 km (63 mi) for male wolverines reported by Inman *et al.* (2012a, p. 784) for the Greater Yellowstone region of Montana, and a reported 100 km (62 mi) dispersal distance for a juvenile male for Ontario, Canada (COSEWIC 2014, p. 24, citing unpublished data from Dawson *et al.* 2013). As shown below, one management area contains nearly one-third (23 individuals) of this total number. The other management units along the international border indicate very few animals harvested over this 8-year period (i.e., areas on map identified as zero). There is no open trapping season or hunting season on wolverines in the management units in the Okanagan (Region 8) (north of Washington State) or South Coast (Region 2) (southwest corner of British Columbia) with a trapping season for wolverines only in the Kootenay (Region 4, the eastern half of the southern part of the province) (Weir 2017b, pers. comm.). In addition, there has not been an open trapping season in Region 2 since at least 1985 and since 1993 in the Okanagan region (Weir 2017c, pers. comm.). For Alberta, we identified a total of 15 wolverines harvested by trappers and data presented in other studies within 110 km (68.35 mi) of the U.S.–Canada border from 1989–2014 (average of less than 1.0 animal per year). Researchers in Canada are currently conducting a landscape level analysis to estimate the size and sustainable harvest for wolverine populations within British Columbia (Weir 2017a, pers. comm.).



Legal Status/Protection

63

Administrative Code lists wolverines as a protected mammal (NAC 503.030), which provides full legal protection. There is no protected status for wolverines in the State of Alaska. The State of New Mexico Department of Game and Fish does not recognize the wolverine as a native mammal. Additional discussion regarding State regulatory mechanisms that provide protections for wolverines is provided in **Appendix G**.

The Idaho Department of Fish and Game issues permits allowing live capture, handling, and release of wolverines for scientific studies, which usually involved log box-traps that do not cause physical injury to the captured animals (IDFG 2014, p. 27). The agency also issues scientific collection permits to various agencies and organizations and to IDFG biologists that can include the capture, chemical immobilization, and placement of radio-collars/radio-markers on wolverines (IDFG 2014, p. 27). These permittees (and IDFG staff) are required to comply with animal trapping and handling protocols approved by IDFG's Wildlife Health/Forensic Laboratory and other animal welfare and research institutions. Over the past 20 years, there have been two documented wolverine deaths due to live capture activities in Idaho (IDFG 2014, p. 27).

In Wyoming, the Wyoming Game and Fish Commission (Commission) Regulation Chapter 52, Nongame Wildlife, authorizes take of wolverine only for scientific or educational purposes as regulated by Commission Regulation Chapter 33 (Regulation Governing Issuance of Scientific, Research, Educational, or Special Purpose Permits). We received information from the State of Wyoming indicating that a search of electronic records of Chapter 33 permits (issued since 1997) found (as of May 2013) three permits have been issued for scientific purposes to further understanding of wolverine ecology in Wyoming (Mead 2013, pers. comm.).

In California, research permits for State-listed, State-candidate, and fully protected species in California are issued as a Memorandum of Understanding (MOU). Currently, there are no active MOUs for research on wolverine in California (Burkett 2017, pers. comm.).

In Canada, provincial designations for the wolverine include Endangered in Labrador, and Threatened in Ontario and Québec ('Threatened' is equivalent to Endangered in Québec), with the remaining provincial designations ranging from no ranking to Sensitive or Special Concern and the Vancouver Island population designated as Imperilled (COSEWIC 2014, p. 44). Recovery planning for the wolverine is focused on the eastern population (Canadian Boreal Forest Agreement Secretariat 2015, p. 3).

In summary, overutilization does not represent a stressor to the wolverine the contiguous United States at the individual, population, or species level. Wolverine populations in the contiguous United States are currently protected under several State laws and regulations. Hunting and trapping activities for wolverines are currently suspended or closed entirely for animals within the contiguous United States, though occasional incidental trapping can occur. Trapping in Alaska and Canada has been and appears to be sustainable given large areas of available refugia in these regions. Trapping or harvesting of wolverines along the contiguous U.S.–Canada border does not represent a stressor to wolverines migrating into the contiguous United States at the individual or population level. In addition, wolverine populations along the Alaska–Canada

border are continuous with the Yukon region of Canada, which suggests a rescue effect for Canadian populations along this international boundary (COSEWIC 2014, p. 37).

Summary of Current Conditions

Wolverine populations in much of North America are still recovering from large losses of individuals from intensive hunting and persecution pressures in the late 1880s into the mid-20th century. Although there is limited rangewide survey information, based on the best available information, wolverines continue to be detected across suitable habitat within the contiguous United States. Studies are currently underway to estimate the species' current distribution and genetic characteristics of the metapopulation across Montana, Idaho, Wyoming, and Washington. In Canada, the total wolverine population is estimated at over 10,000 adults (COSEWIC 2014, p. 47). In Alaska, estimates of populations are not available and are best evaluated based on density (Parr 2017, pers.comm.), which are naturally low for this species. Recent density estimates range from 5 to 10 wolverines per 1000 km² (386 mi²) for Alaska (Parr 2017, pers. comm).

Based on our collection of observations and detections of wolverines in the contiguous United States and the 2014 status review for Canada, we prepared a Current Range map to illustrate the species' North American range (Figure 3). We estimated that the proportion of the current North American range of the wolverine encompassed within the contiguous United States is approximately 6 percent.

We determined that 96 percent of the previously modeled primary habitat (Inman *et al.* 2013) in the lower United States is considered to be lands owned or managed by the Federal government (see **Appendix D**). We also estimated that 41 percent of this modeled primary habitat is located in designated wilderness areas. **Appendix G, Regulatory Mechanisms and Conservation Measures**, provides a more detailed summary of management actions.

We evaluated several potential stressors that may be affecting wolverine populations or its habitat, including effects from roads, disturbance due to winter recreation and other activities, effects from wildland fire, disease and predation, and overutilization for (primarily) commercial purposes. We determined that the effects of roads (evaluated by number of miles, density, and location) and disturbance represent low level stressors to the wolverine in the contiguous United States. Wildland fire was determined to be a short-term stressor to wolverine habitat and its prey. Disease and predation are not considered stressors to the wolverine.

Legal trapping or hunting of wolverines is currently prohibited in the contiguous United States. Incidental trapping of wolverines is infrequent in the contiguous United States, and, in Idaho, education programs are being implemented to reduce this stressor. In Alaska, the level of harvest of wolverines has been fairly consistent since 2010, and, as noted above, density estimates indicate no declining trend in wolverine populations.

Wolverines are harvested in several Canadian provinces with management and monitoring oversight based on spatial and temporal elements. We reviewed trapping information from Canada (within 110 km (68.35 mi) of the contiguous U.S.–Canada border) to assess potential impacts to dispersing wolverines into the United States. We found that, in Alberta, 15 wolverines

were harvest over a 25 year period (average of less than 1.0 animal per year), and, for British Columbia, we found an average of 8.5 animals per year, though one management area contained nearly one-third (23 individuals) of this total. Researchers in Canada are currently conducting a landscape level analysis to estimate the size and sustainable harvest for wolverine populations within British Columbia (Weir 2017, pers. comm.). Based on the best available commercial and scientific information, overutilization does not represent a stressor to the wolverine in the contiguous United States.

Status – Future Conditions

The future timeframe evaluated in our analysis is approximately 40 to 50 years, which captures the range of time periods for proposed projects within the species' range, as well as our best professional judgment of the projected future conditions related to trapping/harvesting, climate change, or other potential cumulative impacts.

After considering the current conditions for the wolverine and its habitat, we describe here the most likely future scenario to potentially have an effect on wolverine at the population level in the contiguous United States:

- Climate change effects (i.e., significantly elevated temperatures resulting in decline in snowpack) may modify suitable habitat, which could also change the scope of the wildland fire stressor.

Based on our review of the best available information, we determined that there were no other plausible scenarios that were likely to have population level impacts to wolverine in the contiguous United States. We expect that the effects of trapping and roads, human disturbance, effects of wildland fire to continue to be at low levels in the future. We have no information that indicates that mortality from roads or disease would increase within the range of wolverine in the contiguous United States in the future.

Climate Change Effects

In this section, we consider climate changes that may affect environmental conditions that the wolverine relies on. As defined by the Intergovernmental Panel on Climate Change (IPCC), the term “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 2013a, p. 1450). The term “climate change” thus refers to a change in the mean or the variability of relevant properties, which persists for an extended period, typically decades or longer, due to natural conditions (e.g., solar cycles) or human-caused changes in the composition of atmosphere or in land use (IPCC 2013a, p. 1,450).

Scientific measurements spanning several decades demonstrate that changes in climate are occurring. In particular, warming of the climate system is unequivocal and many of the observed changes in the last 60 years are unprecedented over decades to millennia (IPCC 2013b, p. 4). The change in temperature reported in the Northern Hemisphere in recent history (past 150 years) at +0.6°C (1.08°F) is twice the change reported for the Southern Hemisphere (+0.3°C (0.54°F)) and there is much year-to-year variation (Post 2013, p. 4). With regard to precipitation over land,

there has been a decline in global total annual precipitation, but the variability between years in total precipitation has increased since about the 1970s (Post 2013, p. 9). The Palmer Drought Severity Index (PDSI) compares the actual amount of precipitation received in an area during a certain time period with the normal or average amount expected during that same period (National Weather Service (NWS) 2015) and is generally used as a measure of water stress. Time series analysis of the PDSI indicates worsening persistent drought-like or drought-potential conditions across the globe since 1980, a reflection of the influence of temperature on atmospheric dynamics (Post 2013, pp. 10–11).

Comprehensive assessments of other observed and projected changes in climate and associated effects and risks, and the basis for them, are provided for global and regional scales in recent reports issued by the IPCC (2013c, 2014), and similar types of information for the United States and regions within it can be found in the National Climate Assessment (Melillo *et al.* 2014, entire). Results of scientific analyses presented by the IPCC show that most of the observed increase in global average temperature since the mid-20th century cannot be explained by natural variability in climate and is “extremely likely” (defined by the IPCC as 95 to 100 percent likelihood) due to the observed increase in greenhouse gas (GHG) concentrations in the atmosphere as a result of human activities, particularly carbon dioxide emissions from fossil fuel use (IPCC 2013b, p. 17 and related citations).

Scientists use a variety of climate models, which include consideration of natural processes and variability, as well as various scenarios of potential levels and timing of GHG emissions, to evaluate the causes of changes already observed and to project future changes in temperature and other climate conditions. Model results yield very similar projections of average global warming until about 2030, and thereafter the magnitude and rate of warming vary through the end of the century depending on the assumptions about human population levels, emissions of GHGs, and other factors that influence climate change. Thus, absent extremely rapid stabilization of GHGs at a global level, there is strong scientific support for projections that warming will continue through the 21st century, and that the magnitude and rate of change will be influenced substantially by human actions regarding GHG emissions (IPCC 2013b, 2014; entire).

Global climate projections are informative, and, in some cases, the only or the best scientific information available. However, projected changes in climate and related impacts can vary substantially across and, as noted above, within different regions and hemispheres (e.g., IPCC 2013c, 2014; entire) and within the United States (Melillo *et al.* 2014, entire). Therefore, we use “downscaled” projections when they are available and have been developed through appropriate scientific procedures, because such projections provide higher resolution information that is more relevant to spatial scales used for analyses of a given species (see Glick *et al.* 2011, pp. 58–61, for a discussion of downscaling). We note here that multiple lines of evidence, not just projections derived from quantitative models, should be examined when conducting climate vulnerability assessments (Michalak *et al.* 2017, entire). Thus, we provide below projected effects from climate change in the western United States relative to both abiotic (e.g., temperature, precipitation, snow cover) and biotic (e.g., phenology, behavior) factors.

Abiotic Factors

California

Regional temperature and precipitation observations for assessing climate change are often used as an indicator of how climate is changing. For evaluating climate trends in California, the Western Regional Climate Center (WRCC) has defined 11 climate regions (Abatzoglou *et al.* 2009, p. 1,535). The relevant region for our assessment is the north/north-central Sierra Nevada region (Tahoe National Forest), currently occupied by a male wolverine, or the northeast region as defined in Abatzoglou *et al.* (2009, p. 1,535) .

Two indicators of temperature, the increase in mean temperature and the increase in maximum temperature, are important for evaluating trends in climate change in California. For the climate region that encompasses the Tahoe National Forest region, the 100-year linear trends provided by the WRCC indicate an increase in mean temperatures (Jan–Dec) of approximately 0.92°C/100 yr ($\pm 0.29^\circ\text{C}/100 \text{ yr}$) ($1.66^\circ\text{F} \pm 0.53^\circ\text{F}/100 \text{ yr}$) since 1895 from present day; 1.55°C/100 yr ($\pm 0.67^\circ\text{C}/100 \text{ yr}$) ($2.79^\circ\text{F} \pm 1.21^\circ\text{F}/100 \text{ yr}$) since 1949 to present day; and 2.41°C/100 yr ($\pm 1.54^\circ\text{C}/100 \text{ yr}$) ($4.33^\circ\text{F} \pm 2.78^\circ\text{F}/100 \text{ yr}$) since 1975 to present day (WRCC 2017). Thus, the increase in mean temperature has not been constant—the rate of increase over the past 42 years in this region has been 2.6 times higher than the past 122 years. We assume the rate of temperature increase for this region is higher for the second and third time periods (since 1949 and 1975, respectively) than for the first time period (since 1895) due to the increased use of fossil fuels in the later part of the 20th and early 21st century.

Although these observed trends provide information as to how climate has changed in the past, climate models can be used to simulate and develop future climate projections. Both state-wide and regional probabilistic estimates of temperature and precipitation changes for California (by the 2060s) using downscaled data from 16 global circulation models and 3 nested regional climate models were presented by Pierce *et al.* (2013, entire). The study looked at a historical (1985–1994) and a future (2060–2069) time period using the IPCC Special Report on Emission Scenarios A2 (Pierce *et al.* 2013, p. 841), which is an IPCC-defined scenario used for the IPCCs Third and Fourth Assessment reports, and is based on a global population growth scenario and economic conditions that result in a relatively high level of atmospheric GHGs by 2100 (IPCC 2000, pp. 4–5; see Stocker *et al.* 2013, pp. 60–68, and Walsh *et al.* 2014, pp. 25–28, for discussions and comparisons of the prior and current IPCC approaches and outcomes). Importantly, the projections by Pierce *et al.* (2013, pp. 852–853) include daily distributions and natural internal climate variability.

Simulations using these downscaling methods project an increase in *yearly* temperature for the area that encompasses the Tahoe National Forest (Sierra Nevada) ranging from 2.1°C (3.78°F) to 3.2°C (5.76°F) by the 2060s time period (Pierce *et al.* 2013, p. 844), compared to 1985–1994. The simulations indicated a yearly *upper* temperature increase of 2.5°C (4.5°F) from 1985–1994 to 2060–2069 (averaged across models) for this area, and an increase of 1.9°C (3.42°F) for the December–February period (Pierce *et al.* 2013, p. 842).

Beginning in 2012 and continuing into 2016, California experienced a severe drought throughout most of the state (Griffin and Anchukaitis 2014, p. 9,020). Although three-year droughts in California are not unusual when evaluated over the past 1000 years, the severity of these drought conditions during this period was demonstrated in the 2014 summer PDSI, which was estimated to be the lowest on record (1901–2014) (Williams *et al.* 2015, p. 6,823). An evaluation of how unusual this drought event was in the context of the last millennium using blue oak (*Quercus douglasii*) tree ring data from four sampling sites (with additional tree sampling following the 2014 growth season) was conducted by Griffin and Anchukaitis (2014, entire). Their paleoclimate drought and precipitation reconstructions for Central and Southern California show that, although the precipitation during this drought has not been anomalously low, it was not outside the range of variability (Griffin and Anchukaitis 2014, p. 9,017). However, the 2014 drought was the worst single drought year of at least the last 1,200 years in California and the 2012–2014 drought was the most severe of three consecutive drought years, based on three events found in the record for the last 1,200 years (Griffin and Anchukaitis 2014, pp. 9,020–9,021). The study concluded that low precipitation combined with high temperatures was responsible for creating this worst short-term drought episode (Griffin and Anchukaitis 2014, pp. 9,021–9,022).

A study by Williams *et al.* (2015, entire) estimated the anthropogenic contribution to California's drought during 2012–2014. They found that the intensifying effect of high potential evapotranspiration on this drought event (measured by summer PDSI) was almost entirely the result of high temperatures (18–27 percent in 2012–2014; 20–26 percent in 2014) (Williams *et al.* 2015, p. 6,825). Another study evaluating the influence of temperature on the drought in water year 2014 in California found that, although the low level of precipitation was the primary driver for the drought conditions, temperature was an important factor in exacerbating the drought, noting that the water year 2014 was the third year of the multiyear drought event and therefore conditions were drier than normal at the beginning of the water year (Shukla *et al.* 2015, p. 4,392).

In sum, these projections indicate that increased temperatures are likely to occur in the Tahoe National Forest region by the 2060s due to the effects of climate change.

Precipitation patterns can also be used as an indicator of potential climate change. We obtained yearly snowfall data for the Tahoe City station located in the northern Sierra Nevada region from the WRCC (<https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8758>) since that dataset was the most complete for the area. We then conducted a nonparametric correlation test, the Mann-Kendall statistical test (Hipel and McLeod 1994, pp. 63–64, 856–858), which is commonly used for analyzing climatic time series (e.g., Ahmad *et al.* 2015, entire), to evaluate trends in snowfall over time. This analysis was conducted using the R and R Studio software programs (Version 3.1.2; R Development Core Team, 2014) with the “Kendall” package (Version 2.2) (McLeod 2011). We found that annual snowfall amounts showed no statistically significant trend (increasing or decreasing) from 1909–2017 ($\tau = -0.0289$, two-sided p -value of 0.6705) for the Tahoe City station.

State-wide and regional probabilistic estimates of precipitation changes for California were also evaluated by Pierce *et al.* (2013, entire). When averaged across all models and downscaling

methods, small annual mean decreases in precipitation were found for the Sierra Nevada region of California, but that study also found an increase in precipitation for the December through February period (wetter winters) (Pierce *et al.* 2013, pp. 849, 855). There was significant disagreement across the models, with percent changes ranging from a 12 percent decrease to a 9 percent increase (Pierce *et al.* 2013, p. 851), and the projected changes in seasonal-mean precipitation were generally small when compared to natural internal climate variability (Pierce *et al.* 2013, p. 850; Figure 9).

Columbia River Basin Region

This region covers a large area within Washington, Oregon, and Idaho, and parts of British Columbia, Canada, and includes portions of the current range of the wolverine. Rupp *et al.* (2017, entire) used simulations from 35 Global Climate Models (GCMs) to provide projections of climate in the Columbia River Basin into the 2080s under two emissions scenarios, Representative Concentration Pathways (RCP) (RCP 4.5, which represents moderate reduction in GHG emissions (“intermediate emissions”), and RCP 8.5, which represents a continued increase in GHG emission “high emission”). The results of their multi-model ensemble for the RCP 4.5 scenario indicate mean annual temperature increases (above Bonneville Dam), above the 1970–1999 baseline average, of 1.3°C (2.34°F) for the 2010–2039 period, 2.3°C (4.14°F) for the 2040–2069 period, and 2.8°C (5.04°F), for the 2070–2099 future period (Rupp *et al.* 2017, p. 1,788). By season, the winter period (December–February) mean change result indicates an increase of 1.1°C (2.52°F) for 2010–2039, 2.2°C (3.96°F) for 2040–2069, and 2.7°C (4.86°F) for 2070–2099, as compared to the 1970–1999 baseline average (Rupp *et al.* 2017, p. 1,788).

For the RCP 8.5 scenario, the multi-model ensemble projections indicate mean annual temperature increases, above the 1970–1999 baseline average, of 1.4°C (2.34°F) for the 2010–2039 period, 3.1°C (5.58°F) for the 2040–2069 period, and 5.0°C (9.0°F), for the 2070–2099 period (Rupp *et al.* 2017, p. 1,788). For the winter season (December–February) mean change increase of 1.4°C (2.34 °F) for 2010–2039, 2.9°C (5.22°F) for 2040–2069, and 4.7°C (8.46°F) for 2070–2099, as compared to the 1970–1999 baseline average (Rupp *et al.* 2017, p. 1,788). The anthropogenic-forced (human caused or influenced) change for these projections is higher than the annual variability; thus, by the year 2050, it is very unlikely that the temperature for this year or any year following during this century would be as low as the historical average (Rupp *et al.* 2017, p. 1,788).

Precipitation projections were much less robust; the multi-model ensemble mean precipitation projections indicate an increase above baseline of up to 8 percent by 2099 for RCP 8.5 and slightly less for RCP 4.5 (Rupp *et al.* 2017, p. 1,788). When viewed seasonally, for the winter season, the ensemble projections indicate increases in precipitation for all three future time periods for both the RCP 4.5 and RCP 8.5 scenarios (ranging from 3 to 14 percent) as compared to the baseline period (1970–1999) (Rupp *et al.* 2017, p. 1,788). The projections of anthropogenic-forced increases in precipitation are lower than the interannual variability; however, despite these increases, the authors indicate that years of anomalously low precipitation relative to baseline would be expected with high frequency throughout the 21st century (Rupp *et al.* 2017, p. 1,788).

Within three subregions of the Pacific Northwest within the current range of the wolverine, Sheehan *et al.* (2015, p. 20; Table 4) also found that, when compared to a historical baseline (1971–2000), all future climate projections (RCP scenarios 4.5 and 8.5; 2036–2066, 2071–2100) indicate a rise in both minimum and maximum monthly temperatures, and a generally positive change in mean annual precipitation, though the latter results varied across projections.

Upper Snake River Basin

The Upper Snake River Tribe Foundation and its Tribal members prepared a climate change vulnerability assessment for the Upper Snake River Watershed (Petersen *et al.* 2017, entire). The assessment covers large areas of southern Idaho and eastern Oregon, and small areas of northern Nevada, northern Utah, and western Wyoming (Petersen *et al.* 2017, p. 15). Within three geographic/model domains of this larger region, downscaled climate projections were created from 20 GCMs run with two emissions scenarios (RCPs 4.5 and 8.5) and these outputs were then used to calculate potential future changes in temperature and precipitation (Petersen *et al.* 2017, pp. 15–16). The projections were analyzed in reference to a baseline period (1950–2005) for three future time periods—the 2030s (2020–2049), the 2050s (2040–2069), and the 2080s (2070–2099) (Petersen *et al.* 2017, p. 16).

For temperature, their projections indicated an increase in average annual temperatures in both future emission scenarios and across all time periods. Under RCP 8.5 (high emissions scenario), the ensemble mean temperature increase was about 6.11°C (11°F), and 2.78°C (5°F) under the RCP 4.5 intermediate emissions scenario across all three geographic/model domains (Petersen *et al.* 2017, Appendix A, p. 2). For the North and East domains (areas with greater topographical variability), there was some indication of a small increase in total annual precipitation by the end of the century, though there was less agreement among the models (Petersen *et al.* 2017, Appendix A, p. 2).

For all geographic/model domains, the average temperature is projected to increase under both emissions scenarios for all seasons (Petersen *et al.* 2017, Appendix A, p. 2). For the winter months (December, January, February), for RCP 4.5, the average seasonal temperature is projected to increase by 3.89 to 5°C (7 to 9°F) by the end of the century, and an increase of approximately 2.22 to 3.33°C (4 to 6°F) for the other seasons (Petersen *et al.* 2017, Appendix A, pp. 2, 6). The winter season projections for RCP 8.5 add an additional 1.67 to 2.22°C (3 to 4°F) by the end of the century (Petersen *et al.* 2017, Appendix A, pp. 2, 6).

Rocky Mountain Region (Colorado)

A report by Lukas *et al.* (2014, entire) presented an assessment of observed and future projections of climate change effects for Colorado. They reported that, statewide, annual average temperatures have increased by 1.1°C (2.0°F) over the past 30 years, and 1.4°C (2.5°F) over the past 50 years (Lukas *et al.* 2014, p. 11). These warming trends have been observed in much of the State (Lukas *et al.* 2014, p. 11). They report no significant long-term trends in annual precipitation (30-, 50-, and 100-year trends) through 2012, but they indicate an observed trend towards more severe soil-moisture drought conditions in Colorado, based on the PDSI, over the past 30 years (Lukas *et al.* 2014, pp. 12, 21).

This report also presents results from climate change modeling using an ensemble of CMIP5 model projections, run with RCP 4.5 and 8.5 scenarios (Lukas *et al.* 2014; Section 5). The results indicate future warming in Colorado for all of the climate model projections (Lukas *et al.* 2014, p. 59). By 2050, for the RCP 4.5 (intermediate) emissions scenario, the statewide average annual temperatures are projected to increase by 1.4 to 2.8°C (2.5 to 5°F) (relative to a 1971–2000 baseline), and increase by 1.9 to 3.6°C (3.5 to 6.5°F) under the RCP 8.5 (high) emissions scenario (Lukas *et al.* 2014, p. 59). For precipitation, they report that climate model projections show less agreement regarding future precipitation change for Colorado, but most projections indicate increasing winter precipitation by 2050 (Lukas *et al.* 2014, p. 59).

Summary

Observed trends and future climate model projections indicate warming temperatures for much of the western United States, including areas within the current range of the wolverine. The degree of future warming varies by region and is dependent upon the future emission scenario used during the modeling process. Future precipitation trends are less certain for many regions, in part, due to naturally high, inter-annual variability; some regions are projected to experience greater winter precipitation. Wolverines have been found to have a wide range in critical temperature depending on season, and undergo seasonal changes in fur insulation to adapt to warmer temperatures in summer. Wolverines also exhibit changes in behavior, such as moving to water bodies or higher elevations in summer months. These physiological and behavioral adaptations allow wolverines to adapt to warming temperatures.

Biotic Factors

In addition to evaluating changes in these abiotic factors, biotic interactions should be considered in evaluating species' response to climate change (reviewed by Post 2013). Although abiotic changes drive ecological processes, the alterations in biotic interactions (e.g., competition among conspecifics, interactions with competitors, resources, and predators) represent the ecological responses that result from those changes (Post 2013, p. 1). Changes in certain abiotic factors, such as snow and ice cover, should also be considered in an ecological context since they represent habitat for many species (Post 2013, p. 11).

Ecological studies evaluating the effects of climate change often evaluate phenology, the timing of life history events and how they vary in space and time, generally at the population or site-specific level, though phenological variation at the individual level may also be important (Post 2013, p. 54). Previous meta-analyses of the rate of phenological advancement have suggested advances of between 2–5 days per decade, across taxa, and between low-mid to mid-high latitudes (Post 2013, p. 59). A more recent meta-analysis from Cohen *et al.* (2017, p. 4) found, on average, significant advancement in the phenology of animals since 1950, advancing by about 2.88 days per decade and 3.08 days per degree Celsius.

Within the Pacific Northwest region, Ford *et al.* 2016 (entire) modeled the timing of growth initiation in coast Douglas-fir trees (*Pseudotsuga menziesii* var. *menziesii*) within the species' range in Washington and Oregon to evaluate its ability to track changes in climate with changes

in phenology. This study found that, for high latitudes and elevations, growth initiation was predicted to occur earlier in the year, which allows trees to track the beginning of favorable growing conditions, without exposure to frost risk (i.e., adaptive phenological response) (Ford *et al.* 2016, pp. 3,718, 3,721). Conversely, their model predicted that at lower latitudes and elevations, growth initiation will lag behind climate change shifts due to reduced chilling with lower productivity, which suggested that coast Douglas-fir has an obligate chilling requirement for height (but not diameter growth initiation) (Ford *et al.* 2016, pp. 3,717–3,719).

Another study reported on the effects of encroachment of woody plants (willows (*Salix* sp.)) in alpine environments to alpine wildflowers and their pollinators due to temporal overlap in flowering phenology, which may result in establishment of plant species with broader environmental tolerance in high alpine ecosystems (Kettenbach *et al.* 2017, p. 6,969). Similarly, in Sweden, Wilson and Nilsson (2009, entire) reported on encroachment of woody vegetation in arctic-mountain habitat, though primarily at lower elevations in response to observed temperature increase of 2.0°C (3.6°F) over 20 years, though this increase in cover was observed primarily at lower elevations (Wilson and Nilsson 2009, p. 1,682).

A high-latitude, North American study evaluated the effect of weather and broad-scale climate variables and vegetation productivity on the timing of spring and fall migrations of migratory caribou herds in northern Québec and Labrador, Canada (Le Corre *et al.* 2017, entire). That study found that, since 2000, except for the spring arrival, migrations occurred earlier, and were affected by resource availability, likely through intraspecific competition factors (Le Corre *et al.* 2017, p. 266).

In addition to phenological changes related to habitat variables or reproduction patterns, the effects of climate change may affect food resources important to wolverine, either directly (e.g., survival) or indirectly (e.g., effects to their habitat). An early study by Wang *et al.* (2002, p. 217) projected a potential increase in ungulate populations in Rocky Mountain National Park (Colorado) under future climate scenarios due to enhanced survival and recruitment of juvenile animals in response to less severe winters. The authors note that their results should be interpreted qualitatively given the uncertainties in applying climate change scenarios based on global models to ecological systems at the local scale (Wang *et al.* 2002, p. 217). In addition, they report that vegetation response (e.g., succession) to climate change effects may result in changes to ungulate habitat (Wang *et al.* 2002, p. 219). Overall, the study concluded that their results were consistent with those reported in other studies that have evaluated the relationships between the effect of weather and density dependence and ungulate population dynamics (Wang *et al.* 2002, p. 219).

Summary

The results presented above indicate biotic effects resulting from climate change, varying from phenological changes to shifts in vegetation and vegetation succession. We are unaware of studies that have directly evaluated these types of effects to the North American wolverine or its habitat. Given the extensive range and varied habitats occupied by wolverines in the contiguous United States, the shifts in vegetation are likely to be relatively narrow in scope and scale. Furthermore, we have no information to suggest that wolverines selectively use any specific

vegetation type and some changes in vegetation may actually be advantageous for wolverine prey.

Climate Change and Potential for Cumulative Effects

Threats can work in concert with one another to cumulatively create conditions that may impact the wolverine or its habitat beyond the scope of each individual threat. Given an expected increase in temperature in the western United States, the best available information indicates that, if there are any cumulative impacts in the future, the most likely to have population level effects on wolverine in the contiguous United States could be: 1) changes in snowpack from the combination of increased temperature and changes in precipitation patterns, or 2) changes in snowpack and increase in wildland fire potential.

Snowpack/Snow Cover

Upper Snake River Watershed (Pacific Northwest region)

The Upper Snake River Tribal Foundation assessment (discussed above) included projected changes in snowpack for three locations in the Upper Snake River watershed, including areas located within our estimated Current Range of the wolverine (from Climate Impacts Group Pacific Northwest (PNW) Hydroclimate Scenarios Project (2860); <http://warm.atmos.washington.edu/2860/products/sites/>). Model results, based on snow water equivalent (SWE) (the water content of snowpack, expressed as depth), indicate a projected loss in April 1st snowpack of 36 percent for the 2030–2059 period and 64 percent for the 2070–2099 period for the *Salmon River at White Bird* location (average of percent change across all models relative to the long-term average for 1916–2006 (“historical period”)). For the *Snow River at Brownlee Dam* location, the projected loss is 37 percent for the 2030–2059 period and 64 percent for the 2070–2099 period (summary presented in Petersen *et al.* 2017, p. 20). These projected changes were found to be consistent with overall changes projected for the Columbia River Basin snowpack in an earlier study. Hamlet *et al.* (2013, p. 404; Figure 7) found that, relative to the long-term average for 1916 to 2006, the April 1st snowpack in the Columbia River Basin is projected to decline by 29% for the 30-year period spanning 2030–2059 and decline by 52% for the period spanning 2070–2099 for the A1B emissions scenario. [Note: the A1B emission scenario represents a more balanced energy portfolio than RCP 8.5, with GHG emissions leveling off by the middle of the 21st century].

Sierra Nevada

Walton *et al.* (2017, entire) developed snow cover projections for the Sierra Nevada region in California, incorporating snow albedo feedback using a hybrid downscaling approach to develop future climate projections. This feedback loop is known to be important for regional climate change (Thackeray and Fletcher 2016, p. 395) and occurs when warming causes snow pack to shrink at margins and the exposed ground absorbs more sunlight than snow, which enhances the warming, resulting in more melting of snow (Walton *et al.* 2017, p. 1,417). This study (using 3 km (1.86 mi) resolution) found that, by the end of the 21st century (2081–2100), warming and loss of snow cover is expected to occur, though the degree varies depending on the GHG

scenario (Walton *et al.* 2017, p. 1,430). Under the RCP 8.5 (high emissions) scenario, the study found that the total area covered by snow during the typical month of April decreases by 48 percent, as compared to historical average (1981–2000) (using ensemble mean) (Walton *et al.* 2017, p. 1,432). Under the RCP 4.5 (moderate emissions) scenario, snow cover losses were projected at about half of those for RCP 8.5 (Walton *et al.* 2017, p. 1,434; Figure 13). The effects of warming were more pronounced at lower elevations and were most severe in May and June (Walton *et al.* 2017, p. 1,431; Figure 12). For the months of March and April, the highest elevations were found to have nearly complete snow cover (measured as snow covered fraction) for all GCM simulations (Walton *et al.* 2017, p. 1,431; Figure 12).

Northern and Southern Rocky Mountains–Glacier and Rocky Mountain National Parks

The effects of climate change on snow persistence has been suggested as an important negative impact on wolverine habitat and populations by the mid-21st century (McKelvey *et al.*, 2011, entire). The Service therefore pursued a refined methodology to provide insights into the potential impacts of climate change on snow persistence.

The Service engaged the National Oceanic and Atmospheric Administration (NOAA) laboratories and University of Colorado in Boulder, Colorado (CU) to evaluate and model fine scale persistence of snow in occupied and potential wolverine habitat in the contiguous United States. Those discussions revealed significant progress in fine scale modeling approaches since the early 2000s. The Service provided funding for an assessment of snow extent and depth to assess the effects of climate change on snow persistence in two areas of the western United States, Rocky Mountain and Glacier National Parks (Ray *et al.* 2017, entire). The primary objective of this study was to refine the spatial and temporal scale of snow modeling efforts and improve the scientific understanding of the extent of spring snow retention currently and into the future under a changing climate (Ray *et al.* 2017, p. 9). The objectives of the study included (Ray *et al.* 2017, p. 10):

- Use of fine-scale models to analyze the topographic effects of snow, including slope and aspect (compass direction that slope faces)
- Use of a range of plausible future climate change scenarios to assess snow persistence
- Analysis of extremes and year-to-year variability by selecting representative wet, dry, and near normal years (using observed conditions) and then modeling changes for those base years under several future climate scenarios
- Assessment of changes in snow persistence by elevation

The study was designed to parallel as much as possible and thereby refine the previous assessment of snow cover persistence in the western United States presented in McKelvey *et al.* (2011). However, an exact replication of the McKelvey *et al.* (2011) study was not possible given the time, funding, and computational constraints needed to develop a fine-scale assessment. The current study was limited to two study areas (approximately 1,500 to 3,000 km² (579 to 1,158 mi²) each) in the northern and southern Rocky Mountains (see **Appendix H** for maps). The two study areas were selected because they encompass the latitude and elevational range of wolverines within the contiguous United States. Glacier National Park (GLAC) is representative of a high latitude and relatively low elevation area currently occupied by wolverines. The Rocky

Mountain National Park region (ROMO) is a lower latitude and higher elevation area within the wolverine's historical range, which was recently occupied by a wolverine from 2009 to at least 2012.

Methods: We provide here a brief summary of the methods used in this study. Additional details are contained in the full report authored by Ray *et al.* (2017). The initial step of the analysis was a review of the observed climate and variability to provide context for trends and year-to-year variability. Next, historical snow cover extent and variability were analyzed using satellite remote sensing (MODIS) data from 2000 to 2016 to calculate a snow disappearance date for each year at each pixel. Summary statistics include total snow covered area (total area covered by snow), representation of snow pack by aspect (percent of land areas covered by snow for each of the 17 years in the historical record by topographic aspect based on compass direction that the slope faces), and elevation dependence for wet, near-normal, and dry years (with median of all years used as reference). Future snow pack projections were then generated using the Distributed Hydrology Soil Vegetation Model (DHSVM), for the historic period 1998-2013, and then validated against SNOTEL observing stations and MODIS satellite data.

Both Ray *et al.* (2017) and McKelvey *et al.* (2011) used the delta method to estimate future snow persistence. The NOAA-DHSVM delta method uses historical observed weather (1998–2013) as the baseline and applies future changes in temperature and precipitation from the chosen GCMs (approximately Year 2055) to estimate future snow persistence on the landscape. Five future scenarios (GCMs) were selected from CMIP5 global climate model projections to capture variability in temperature and precipitation, using the RCP 4.5 (moderate) and RCP 8.5 (high) emissions scenarios. Representative wet, near normal, and dry years were analyzed for the historical simulations and evaluated for the five future scenarios. The number of years (out of 16) with snow depth greater than 0.5 m (20 in) was also analyzed as was the change in Snowcovered Area (SCA) (area with depth greater than 0.5 m (20 in)). This snow depth was selected based on an analysis of the depth of snow at documented wolverine den sites in Glacier National Park (Ray *et al.* 2017; Table 5-2). Results were reported for “light snow cover” (snow depth greater than 1.25 cm (0.5 in)) and “significant” snow (snow depth > 0.5 m (20 in)) for April 15, May 1, and May 15 for previously defined representative years. These dates were selected based on studies indicating den site abandonment generally occurs before May 1 (see Use of Dens and Denning Behavior discussion above in *Reproduction and Growth* section). The term “light snow cover” was incorporated as the most directly comparable parameter to McKelvey *et al.*'s “light” snow cover. The average change in SCA and SWE was analyzed as a function for both study areas of elevation and was overlaid with the elevations of documented wolverine den sites (2003–2007) in GLAC.

Comparison with McKelvey *et al.* (2011): Although the methods used in this study have similarities with those presented in McKelvey *et al.* (2011), there are several key differences. Ray *et al.* (2017) used a finer spatial resolution model (DHSVM) than McKelvey *et al.* (2011) (0.0625 km² vs. 35 km²) that incorporated slope and aspect. The grid cells represented in McKelvey *et al.* (2011) were assumed to be flat (i.e., north-facing slopes treated as identical to south-facing slopes). McKelvey *et al.* (2011) focused on May 1st snow depth as a proxy for May 15th snow disappearance, while Ray *et al.* (2017) focused directly on May 15th snow disappearance and produced results for the presence or absence of deeper snow (nominally

greater than or equal to 0.5 m (20 in) depth) on May 1st and April 15th.⁴ Because of the increased resolution of this study, Ray *et al.* (2017) were able to consider whether any areas of snow with depth greater than 0.5 m (20 in) will persist in these areas. Additional comparisons are outlined below in Table 8 and in Ray *et al.* (2017, p. 6).

Table 8. Comparison of Methods, Ray *et al.* (2017) vs. Copeland *et al.* (2010) and McKelvey *et al.* (2011)

Feature	Ray <i>et al.</i> (2017)	Copeland <i>et al.</i> (2010) and McKelvey <i>et al.</i> (2011)
Spatial Resolution	250 m x 250 m = 62,500 m ² or 0.0625 km ² (0.24 mi ²)	0.125 degrees (~5 km x 7 km; 37 km ² (14.29 mi ²))
Geographic Area	Glacier and Rocky Mountain National Parks, 300 m below treeline and above	Western United States, except California and Great Basin
Topography	Slope, aspect, and shading were used	Slope and aspect were not used
Validation	SNOTEL (in-situ observations) and MODIS (satellite remote sensing)	None specific to the snow dataset used
Future Scenario Method	Delta Method, used to project 2000-2013 conditions out to Year 2055 (average of 2041–2070)	Delta Method (Years: 2045 (2030–2059), 2085 (2070-2099))
Future Scenarios (GCMs)	<i>miroc</i> , <i>giss</i> , <i>fio</i> , <i>cnrm</i> (both study areas); <i>canesm</i> (Glacier National Park only) <i>hadgem2</i> (Rocky Mountain National Park only)	Ensemble mean of 10 GCMs, <i>pcm1</i> , and <i>miroc</i> 3.2
Time-related Results	Long-term means and year-to-year variability (i.e., wet, near normal, and dry years)	Changes in long-term mean snowpack only
Snow Detection and Measurements	Snow presence: 1.25 cm (0.5 in) snow depth threshold on May 15. “Significant snow”: snow depth (0.5 meter (20 in) threshold. Snow depth determined by conversion from Snow Water Equivalent using bulk snow density.	Snow presence (13 cm (5.12 in) snow depth threshold on May 1). Snow depth determined by VIC model.
Number of Years of MODIS Data	17 (2000-2016)	7 (2000-2006)
Snow Model	DHSVM (University of Washington)	VIC (University of Washington)
Snow Cover Dates Analyzed	April 15, May 1, and May 15	May 15 (derived from May 1), May 29 (derived from May 1)

Results: While there are challenges in comparing the results from McKelvey *et al.* (2011) directly to the Ray *et al.* (2017) study due to differences in methodology and focus, the qualitative picture can be summarized as follows: projected warming has a larger effect at lower elevations whereas projected precipitation changes may dominate the springtime snowpack in the high country. We present below a summary of the main results from Ray *et al.* (2017).

⁴ Ray *et al.* (2017) originally focused on May 15th to compare to the McKelvey *et al.* (2011) study, and June 1st to bracket the snowmelt season. However, April 15 and April 30 dates were added to the evaluation of snowcovered areas to align with temporal reproductive patterns of the wolverine (see [Use of Dens and Denning Behavior](#) discussion in *Reproduction and Growth* section above).

MODIS Observed Historic Snowpack Variability Analysis:

- In GLAC, SCA varies considerably by year, 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) (Ray *et al.* 2017, Section 4.3).
- Even in dry years, northeast-facing slopes in GLAC tend to hold more snow and melt later in the season.
- More than 80 percent of the GLAC study area above approximately 2,000 m (6,562 ft) elevation on May 1 has snow cover during dry years, and more than 95 percent has snow cover above approximately 1,200 m (3,937 ft) during wet years.
- In ROMO, the SCA also varies considerably by year.
- The northwest-facing slopes in ROMO 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.

Future Snowpack Projections: The area-wide SCA results include snow cover changes in both forested and above-treeline (alpine) terrain, which may have different implications for wolverine biology.

Glacier National Park (GLAC):

- Projections for April 15th, May 1st, and May 15th SCA and area with snow depth greater than 0.5 m (20 in) show declines on average in all scenarios, compared to the 2000–2013 historic average, except for small increases in the Warm/Wet scenario and for almost all years.
 - For April 15th, light SCA area is reduced by 3–23 percent and significant snow cover (greater than 0.5 m (20 in)) declines by 7–44 percent.
 - For May 15th, light SCA is reduced by 10–36 percent, and the area with significant snow cover declines by 13–50 percent.
- All projections show declines in the number of years with significant snow (equal to or greater than 0.5 m (20 in)), which varies by scenario (e.g., Figure 5-14 in Ray *et al.* 2017). Areas with frequent availability (at least 14 out of 16 years) of significant snow become concentrated in smaller high elevation areas. Lower elevation areas had the largest decreases in the number of years with significant snow cover.
- Most of the known den sites are located between 1,800 m (5,906 ft) and 2,000 m (6,562 ft) in GLAC. Below that elevation band, large snow losses are predicted (40 to 70 percent decrease for two of the scenarios, 16–20 percent for the other three). Above that elevation band, there is little change in SCA for four of the five scenarios (2–8 percent) except in maximum warming scenario (decline of 40 percent (Ray *et al.* 2017; Figure 5-22). In the 1,800–2,000 m (5,906–6,562 ft) band, the snowpack change is sensitive to elevation and to the future climate scenario used.
- For representative wet years, for May 15th, the higher elevations of the study areas experience only 2–7 percent loss of snowpack under the scenarios with “least” change and the “moderate” change, although for the dry years, losses range from 18–57 percent.

- o The implication is that the wet, cold climate of the GLAC study area could act as a “buffer” to change in areas with of 0.5 m (20 in) of deep snow on May 1st, at least for elevations above 1,800 m (5,906 ft).

Rocky Mountain National Park (ROMO):

- Projections of May 15th SCA in ROMO decline on average in all scenarios, except for small increases in the Warm/Wet scenario, and for almost all years.
 - o For April 15th, light SCA (depth $\geq$ 5 mm (0.2 in)) declines by 3–18 percent and significant SCA (depth $>$ 0.5 m (20 in)) changes from –1– +16 percent for the five scenarios considered (compared to the 2000-2013 historical average).
 - o For May 15th, the area with light snow cover declines 8–35 percent and the area with significant snow cover declines 6–38 percent.
- All projections show declines in the number of years with significant snow (equal to or greater than 0.5 (20 in), which varies by scenario (e.g., Figure 5-21 in Ray *et al.* 2017). The areas with frequent availability (at least 14 out of 16 years) of significant snow become concentrated in smaller high elevation areas. In contrast, lower elevation areas had the largest decreases in the number of years with significant snow cover.
- Although no dens have been documented in ROMO, the elevation band for denning, modeled by regression analysis, is estimated at 2,700 to 3,600 m (8,858 to 11,811 ft). On May 1st, modest declines in SWE of about 15 percent and less for areas at 3,400 m (11,155 ft) or above result in losses of only about 10 percent snow cover.
 - o The implication is that the wet, cold climate of the higher parts of the ROMO study area could also act as a “buffer” to change in the area of 0.5 m (20 in) deep snow on May 1st.

Elevation Dependence of Change: In general, and supported by the literature, the snowpack in the higher elevations of both areas is more responsive to precipitation change, while lower elevations are more responsive to temperature change. For GLAC, most of the observed den sites are located within the zone where temperature dominates the future effects of change. For the elevation of den sites in GLAC (i.e., above 1800 m (5,906 ft)), loss of SCA on May 1st spans the range of 5–40 percent, with a 70 percent decrease for the Hot/Wet (*miroc* GCM) scenario. Above 2,200 m (7,218 ft), the losses are less than 5 percent for all but the Hot/Wet scenario.

Current results may be a reasonable estimate for the high mountain ranges within the Rockies that lie between GLAC and ROMO. However, without further study, we cannot reasonably extend these results to say whether or not snow refugia will persist in the Central Rockies below our study elevations (approximately 1,000 m (3,281 ft)). These lower elevations are where McKelvey *et al.* (2011) predicted the greatest losses in snowpack. The NOAA/CU results also cannot be extrapolated to mountain ranges outside of the Rockies (i.e. the Cascade Range) that have different climates (temperature and precipitation). We note here that we have no documented wolverine den sites in the contiguous United States below 1,500 m (4,921 ft) elevation; that is, no documented den locations in the areas where McKelvey *et al.* (2011) predicted the greatest loss in snowpack.

Interpretation and additional analysis relative to wolverine den site scale: The Service was interested in exploring the question, “If snow cover is required for wolverine denning, will there be a sufficient amount of significant snow cover in the future in areas wolverines have historically used for denning in the contiguous United States?” The Service integrated future DHSVM projections (2000–2013 averages) of snow covered area (greater than 0.5 m (20 in) depth) on May 1st for GLAC and ROMO with new information obtained from a spatial analysis of documented den sites in the contiguous United States. This spatial analysis indicated 31 of 34 documented den sites in the contiguous United States were located in areas with slope less than 25 degrees. Avalanche risk increases significantly in areas with slope greater than 25 degrees (Scott 2017, pers. comm.) and wolverines may avoid these areas for denning due to this risk.

Using the projections prepared by Ray *et al.* (2017), we present in Figures 6–13 the spatial distribution of significant snow covered area with slopes less than 25 degrees and within the elevation bands indicated above for three future scenarios in each study area. The three scenarios for GLAC (*miroc*, *cnrm*, and *giss*) and for ROMO (*hadgem2*, *fio*, and *giss*) were chosen to span the range of GCM uncertainty regarding temperature and precipitation, and by extension significant SCA (see Figure 6 and Figure 7). We found that large portions of the study areas meet all three criteria—greater than 0.5 m (20 in) snow depth on May 1st, at elevation 1,514–2,252 m (4,967–7,389 ft) for GLAC or 2,700 to 3,600 m (8,858 to 11,811 ft) for ROMO, and with a slope less than 25 degrees—across both study sites in the future.

The GLAC *miroc* simulation shows the greatest decrease in future snow covered area in the elevation band historically used for denning (orange line in Figure 6). Figure 8 shows the spatial distribution of significant SCA with slope less than 25 degrees and elevation of 1,514–2,252 m (4,967–7,389 ft) for the *miroc* simulation on May 1st (approximately Year 2055). Approximately 494 km² (191 mi²) of area meet the three criteria with an additional 803 km² (310 mi²) of area retaining significant snow covered area, primarily at higher elevations. Moreover, we determined that large tracts of significant SCA are projected in close proximity to documented historical den sites across all three scenarios (Figures 8–10). As shown in Table 9, wolverines would not have to travel far, or at all, relative to either distance or elevation to reach areas with significant snow covered area in the future.

A similar analysis was performed for the ROMO study area and the results indicate that large portions of the study area meet all three criteria identified above. The *hadgem2* (Figure 11) and *cnrm* scenarios were found to have the greatest decrease in significant snow covered area of the five scenarios analyzed. Figure 11 (*hadgem2* simulation) shows the spatial distribution of significant SCA (greater than 0.5 m (20 in) depth), elevation of 2,700–3,600 m (8,858–11,811 ft), and slopes less than 25 degrees where denning would be expected to occur. Total area meeting these three criteria was 339 km² (131 mi²) (dark blue in Figure 11), with an additional 446 km² (172 mi²) with snow depth greater than 0.5 m (20 in) (light blue in Figure 11), mostly at higher elevations. Figures 12 (*fio* scenario) and Figure 13 (*giss* scenario) show a similar distribution, albeit larger areas of significant snow retention in the future (see map legends in Figures 12 and 13 for area estimates).

Table 9. Distance of historical GLAC dens (Years 2003–2007) from projected significant snow covered area in the future (approximately Year 2055) (using 2000–2013 average).

A 0 (zero) value indicates the den site location meets all three criteria in the future (greater than 0.5 m (20 in) snow depth on May 1st, at elevation 1,514–2,252 m (4,967–7,389 ft), and with a slope less than 25 degrees).

Den Site	Elevation, m (ft)	Distance from den site to nearest model cell, m (ft)		
		GCM scenario		
		<i>miroc</i>	<i>cnrm</i>	<i>giss</i>
1	2,252 (7,389 ft)	0	0	0
2	2,093 (6,867 ft)	0	0	0
3	1,995 (6,545 ft)	0	0	0
4	1,977 (6,486 ft)	210 (689 ft)	0	0
5	1,973 (6,473 ft)	208 (682 ft)	0	0
6	1,928 (6,326 ft)	0	0	0
7	1,922 (6,306 ft)	9 (29.5 ft)	8 (26 ft)	8 (26 ft)
8	1,912 (6,273 ft)	170 (558 ft)	0	0
9	1,893 (6,211 ft)	110 (361 ft)	0	0
10	1,851 (6,073 ft)	87 (285 ft)	0	0
11	1,843 (6,047 ft)	74 (243 ft)	0	0
12	1,823 (5,981 ft)	56 (184 ft)	0	0
13	1,807 (5,929 ft)	0	0	0
14	1,514 (4,967 ft)	574 (1,883 ft)	571(1,873 ft)	296 (971 ft)

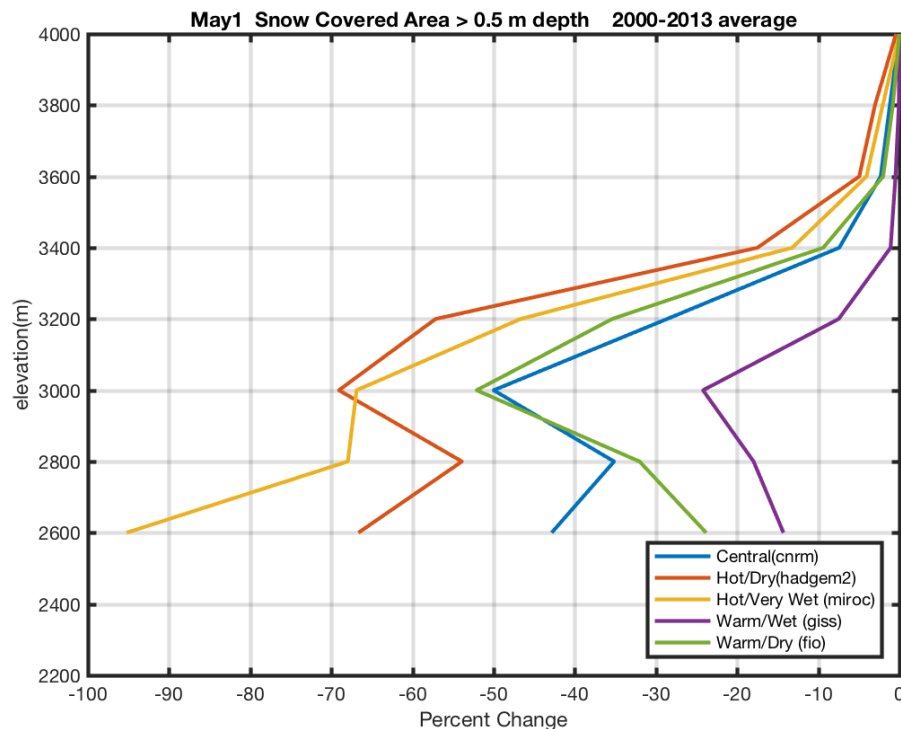


Figure 6. Average Snow Covered Area (depth ≥ 0.5 m (20 in)) percent change at elevation bands for GLAC for five future scenarios on May 1.

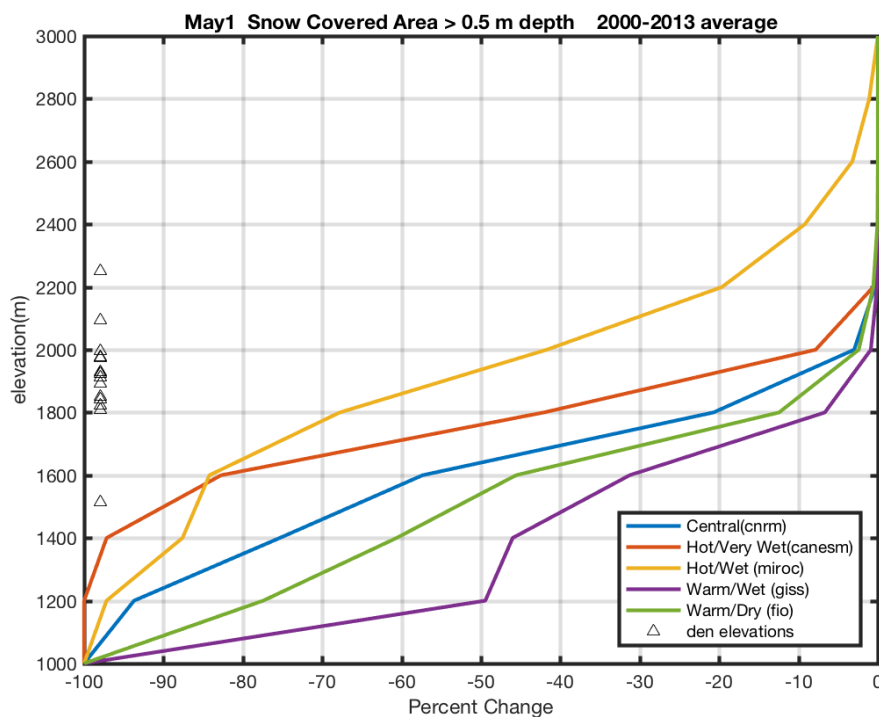


Figure 7. Average Snow Covered Area (depth ≥ 0.5 m (20 in)) percent change at elevation bands for ROMO for five future scenarios on May 1.

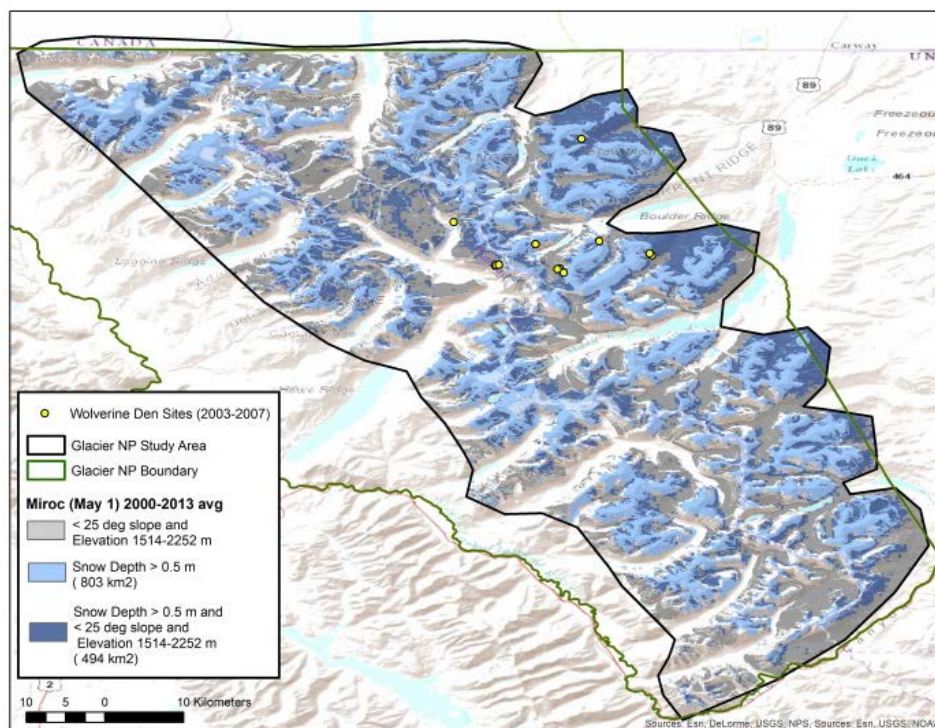


Figure 8. Spatial distribution of averaged (2000-2013) projected snow covered area (depth ≥ 0.5 m (20 in)) for May 1 under the *miroc* (Hot/Wet) scenario in Glacier National Park study area. Map legend shows where slopes are less than 25 degrees and elevations of 1,514–2,252 m (4,968–7,389 ft) (where dens have been documented).

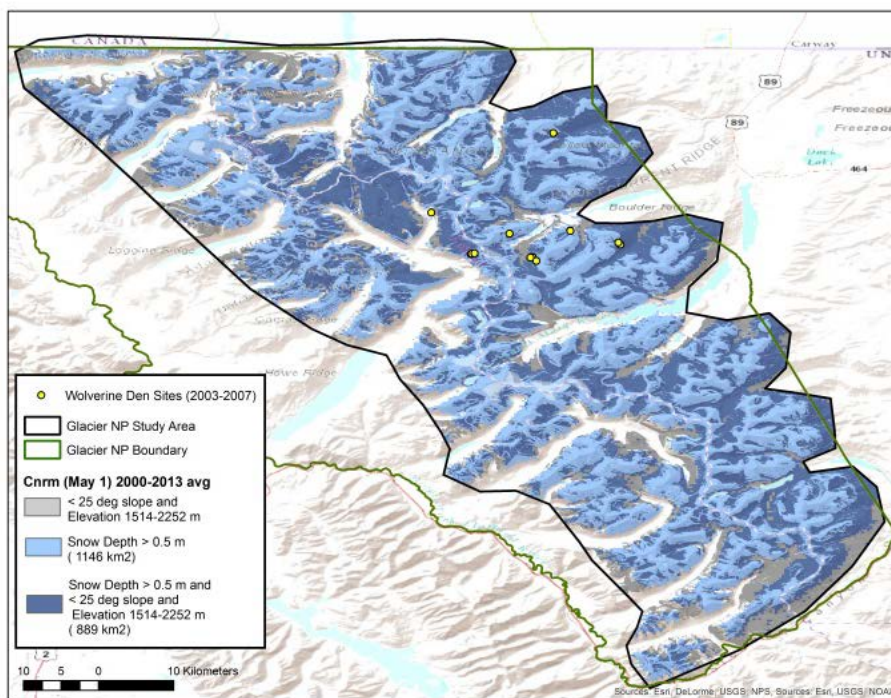


Figure 9. Spatial distribution of averaged (2000-2013) projected snow covered area (depth ≥ 0.5 m (20 in)) for May 1 under the *cnrm* (Central) scenario in Glacier National Park study area. Map legend shows where slopes are less than 25 degrees and elevations 1514–2252 m (4,968–7,389 ft) (where dens have been documented).

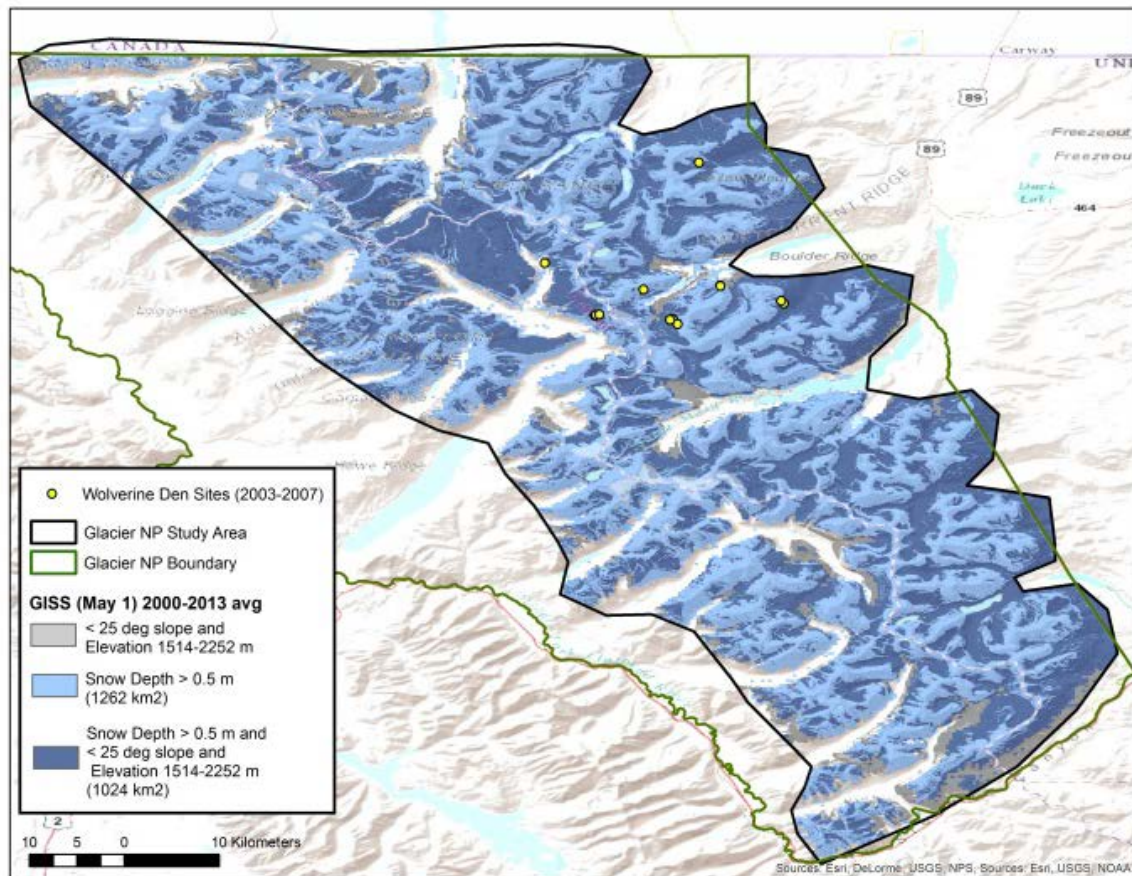


Figure 10. Spatial distribution of averaged (2000-2013) projected snow covered area (depth ≥ 0.5 m (20 in)) for May 1 under the *giss* (Warm/Wet) scenario in Glacier National Park study area. Map legend shows where slopes are less than 25 degrees and elevations 1,514–2,252 m (4,968–7,389 ft) (where dens have been documented).

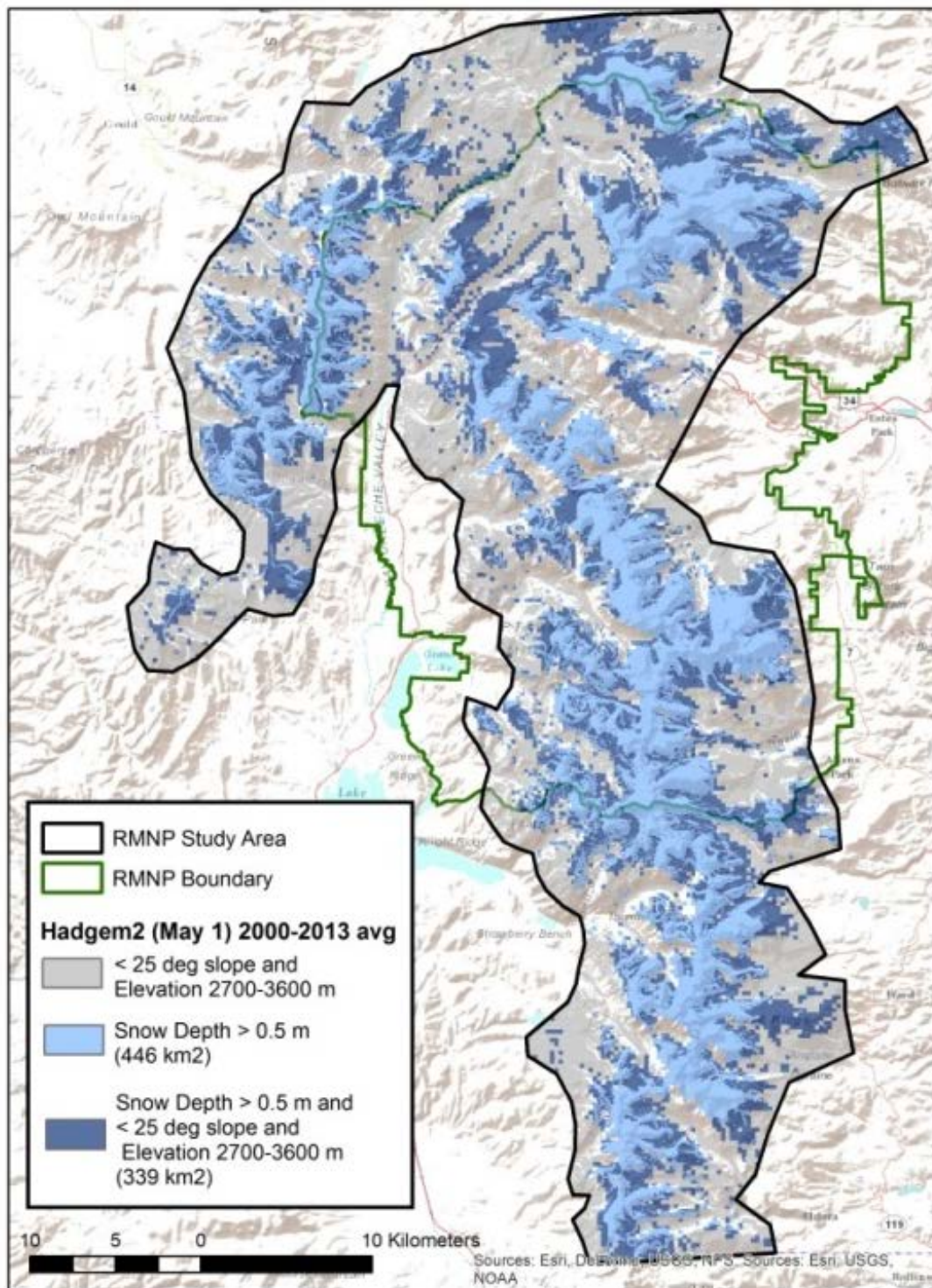


Figure 11. Spatial distribution of averaged (2000-2013) projected snow covered area (depth ≥ 0.5 m (20 in)) for May 1 under the *hadgem2* (Hot/Dry) scenario in Rocky Mountain National Park study area. Map legend shows where slopes are less than 25 degrees and elevations 2,700–3,600 m (8,858–11,811 ft) (inferred elevations where dens would be expected if occupied).

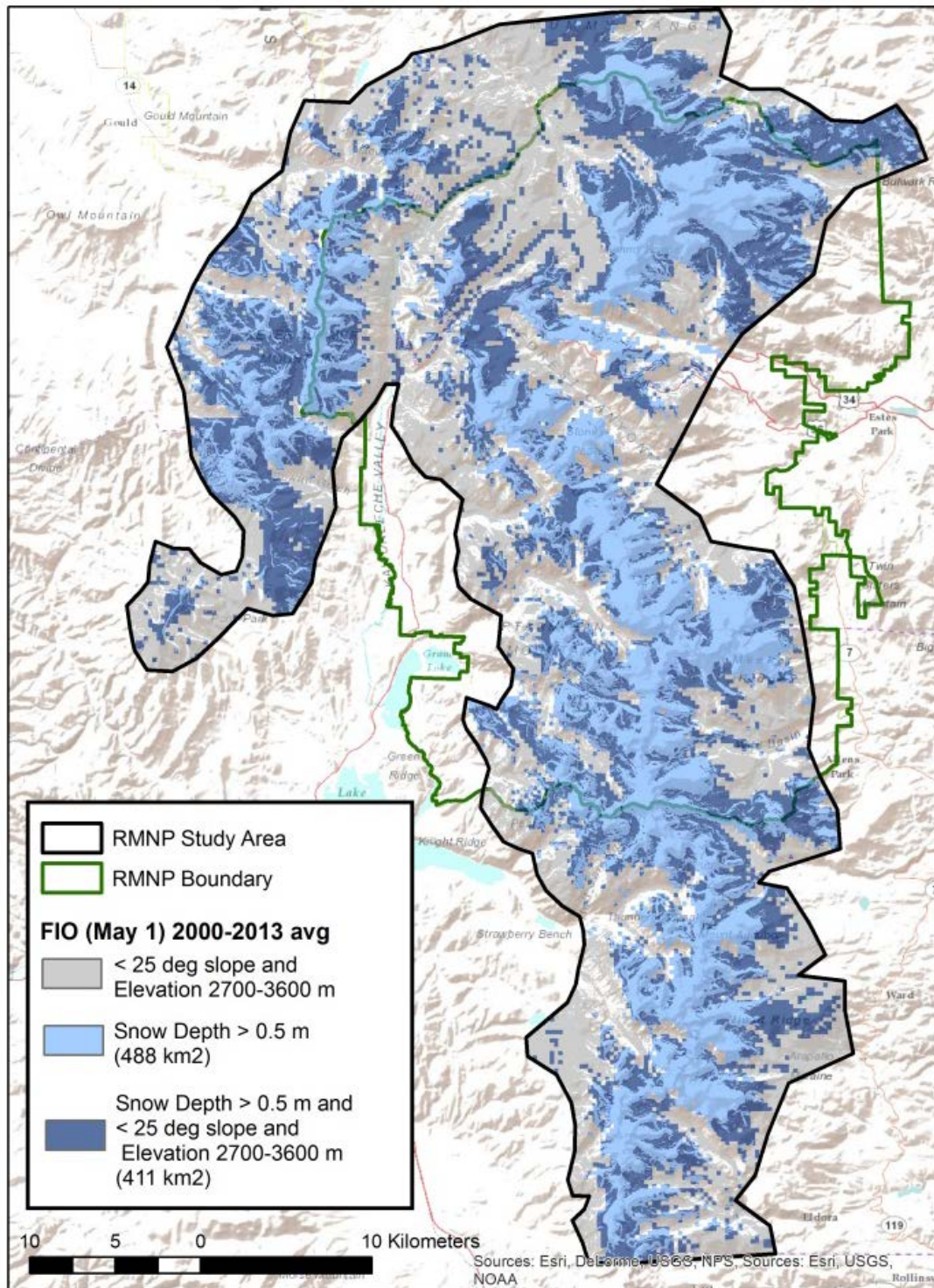


Figure 12. Spatial distribution of averaged (2000-2013) projected snow covered area (depth ≥ 0.5 m (20 in)) for May 1 under the *fio* (Warm/Dry) scenario in Rocky Mountain National Park study area. Map legend shows where slopes are less than 25 degrees and elevations 2,700-3,600 m (8,858–11,811 ft) (inferred elevations where dens would be expected if occupied).

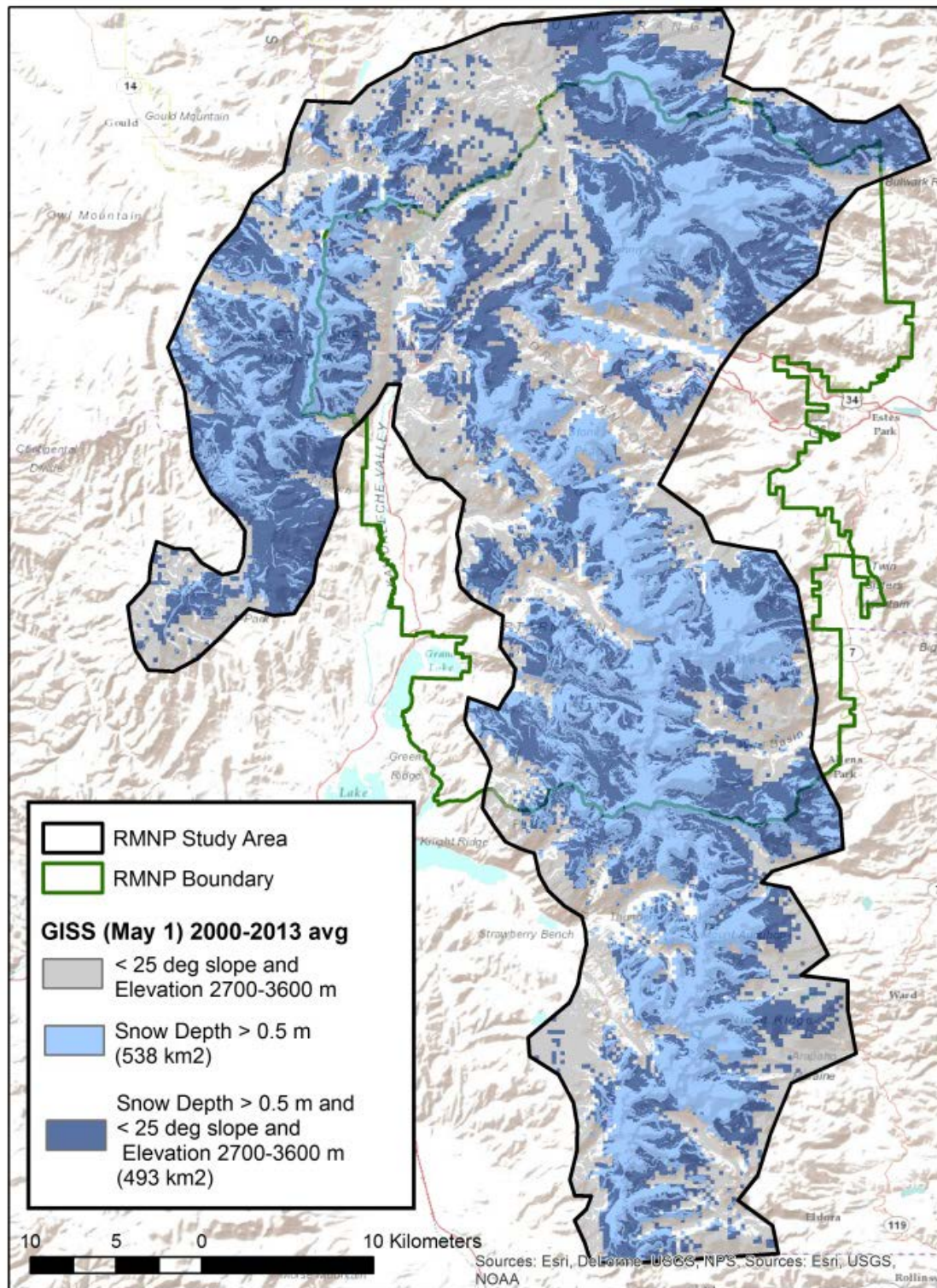


Figure 13. Spatial distribution of averaged (2000-2013) projected snow covered area (depth ≥ 0.5 m (20 in)) for May 1 under the *giss* (Warm/Wet) scenario in Rocky Mountain National Park study area. Map legend shows where slopes are less than 25 degrees and elevations 2,700-3,600 m (8,858–11,811 ft) (inferred elevations where dens would be expected if occupied).

Montana Climate Assessment

Another recent assessment of snowpack was conducted for the State of Montana (Whitlock *et al.* 2017, no page number). The report analyzed recent climate trends in Montana and assessed how climate is projected to change in the future (2040–2069). The study found that snowpack that accumulates at high elevations tends to be more stable and persists longer than at low elevations, due largely to the colder temperatures at high elevations. The largest projected changes in snowpack appear to be in areas located west of the Continental Divide, given their exposure to relatively warm Pacific air masses. Overall, the assessment found that declines in snowpack volume are likely in the future in the basins studied.

Wildland Fire

California

Keeley and Syphard (2016, entire) analyzed fire-climate relationships relative to predicting future fire regimes in California. Their review concluded that: (1) Climate is not a major determinant of fire activity across all landscapes; (2) hotter and drier conditions for areas at lower elevations and lower latitude were found to have little or no increase in fire activity as vegetation types in these regions are ignition limited; (3) increasing annual temperatures by themselves are not good predictors of increased fire activity; seasonality, especially spring and summer temperatures, are more important; and (4) fire-climate models need to be scaled to vegetation types; broad-scale models may produce over-predictions of the total increase in future fire regimes (Keeley and Syphard 2016, pp. 1, 10). Additionally, drought is a key factor in defining fire regimes and annual precipitation is the primary driver of drought variability (Williams *et al.* 2015, p. 6,819), but, at the present time, it is difficult to separate current droughts in California from natural cycles of drought (Keeley and Syphard 2016, p. 6).

Pacific Northwest

Sheehan *et al.* (2015, entire) used downscaled CMIP5 projections to model vegetation and fire changes, with and without fire suppression, within three subregions of the Pacific Northwest. Emission scenarios RCP 4.5 and 8.5 were used for future climate projections (2011–2100). The resulting trends varied by geographic region. In the Western Northwest subregion (from the crest of the Cascade Mountains west), the mean fire interval (MFI) averaged over all climate projections decreased by up to 48 percent, an increase in annual percent area burned (PAB), and the predominant conifer forest is replaced by mixed forest under future climate under both RCP scenarios, with and without fire suppression; thus, climate, rather than fire was found to be the primary influence in this subregion (Sheehan *et al.* 2015, pp. 22–26). In the Eastern Northwest Mountains (ENWM) subregion (mountainous areas east of the Cascade Mountains), the MFI (averaged across all climate projections) decreased by up to 81 percent, there was a projected increase in mean annual PAB, and, while subalpine communities are projected to be lost, conifer forests were projected to continue to dominate this subregion (Sheehan *et al.* 2015, pp. 22–24). When modeled using a without fire suppression regime, the future projections for ENWM indicated a lower MFI and higher mean annual PAB as compared to the with fire suppression regime (Sheehan *et al.* 2015, p. 22; Table 5). However, the eastern portion of the ENWM

subregion was found to show a differing response based on elevation; that is, higher elevations were found to have a *higher* MFI and a *lower* mean annual PAB during the 20th century as compared to lower elevations (Sheehan *et al.* 2015, p. 23).

Gergel *et al.* (2017, entire) evaluated the effects of climate change on snowpack, and soil moisture and fuel moisture (fire potential) in the western United States. This study used a statistical downscaling approach, using an ensemble of 10 GCMs across several mountainous regions known to be occupied by wolverines, with a 6.25 km (3.88 mi) spatial resolution hydrologic model. Simulations were run for three future periods: 2020s (2010–2039), 2050s (2040–2069), and 2080s (2070–2099) (Gergel *et al.* 2017, p. 291). The authors report significant declines in snowpack (measured as SWE) in all mountain ranges for all future scenarios (using RCPs 4.5 and 8.5) and GCMs (Gergel *et al.* 2017, p. 295). This study found that spring snowpack in mountains along the Pacific Coast is quite sensitive to warmer temperatures, but in the continental mountain ranges (Northern and Southern Rocky Mountains) spring snowpack is more sensitive to changes in precipitation (Gergel *et al.* 2017, p. 295). Differences were observed based on elevation (Gergel *et al.* 2017, p. 292). The study reported on future projected declines of summer soil moisture in forested areas (e.g., Northern Rockies) and the likelihood of increased risk of drought and therefore an increase in wildland fire risk for forested areas (e.g., Northern Rocky Mountains), though they recognize there is significant uncertainty in these future projections in high-elevation areas (Gergel *et al.* 2017, pp. 295–296).

In summary, based on these projections, wildland fire risk is likely to increase across the western United States, but future patterns and trends of wildland fire are dependent on several factors (e.g., degree of warming and drought conditions, fuel and soil moisture, wildland fire management practices, elevation) and geographic region.

Other Cumulative Effects

Finally, we note here that the effects of climate change on snowpack are projected to negatively affect the season lengths for winter recreational activities, such as skiing and snowmobiling (Wobus *et al.* 2017, entire), thus, potentially reducing this stressor to the wolverine in the future. Wobus *et al.* (2017) modeled potential changes in snowpack at locations across the contiguous United States using output from five GCMs, two representative pathways (RCPs) that represent a future scenario with continued high emissions growth with limited efforts to reduce GHGs (RCP 8.5) and a future scenario with global GHG mitigation (RCP 4.5), and two future time periods (2050 and 2090) (Wobus *et al.* 2017, pp. 2, 5). Although there was some inter-annual variability in 2050 for some model projections, in general, the Rocky Mountains and Sierra Nevada regions had smaller reductions in season length than other locations due to higher elevation, though for the RCP 8.5 scenario coupled with the 2090 future time period, the smallest projected reduction in season length was 15 percent (Wobus *et al.* 2017, p. 9).

Summary of Future Conditions

Models represent tools to describe basic physical and biological behaviors using the best available science, and, by presenting a range of plausible future outcomes, they can help generate hypotheses while also identifying knowledge gaps where greater accuracy is needed (Batchelet *et*

al. 2016, p. 23). Detecting a species' response to climate change in a single population, and sometimes multiple populations, may not always indicate the response throughout its range given the variation in annual mean surface temperatures over the past century (Post 2013, p. 5). In addition, inter-annual variability in temperature can be as important to a species' ecological needs as the actual temperature itself (Post 2013, p. 7).

Climate change model projections for the range of the wolverine within the contiguous United States indicate increases in temperature by the mid-21st century as compared to early to mid-20th century values. Precipitation patterns into the future are less clear as the climate models show significant disagreement in their many regional projections. Although drought conditions in the western United States are not unusual, drought duration and intensity have the potential to be exacerbated by projected temperature increases. Projected temperature and precipitation changes will affect future snow cover and the persistence of snow on the landscape.

Snow cover is projected to decline in response to warming temperatures and changing precipitation patterns, but this varies by elevation, topography, and by geographic region. Simulations of natural snow accumulation at winter recreation locations have found that, overall, higher elevation areas (e.g., Rocky Mountains, Sierra Nevada Mountains) are more resilient to projected changes in temperature and precipitation as compared to lower elevations (Wobus *et al.* 2017, p. 12). In general, models indicate higher elevations will retain more snow cover than lower elevations, particularly in early spring (April 30/May1). We present results (above) from several recent climate models projecting snowpack declines in the western United States. More specifically, we reviewed a new analysis from NOAA/CU that modeled future snow persistence for Glacier and Rocky Mountain National Parks (areas that encompass the latitudinal and elevational range of the wolverine in the contiguous United States) at high spatial resolution (Ray *et al.* 2017, entire). Their results indicate significant areas (several hundred square kilometers (miles) for each site) of future snow (greater than 0.5 m (20 in) in depth) will persist on May 1st at elevations currently used by wolverines for denning. This is true, on average, across the range of climate models used out to approximately Year 2055.

Although it has been assumed that wolverines have an obligate relationship with snow for natal denning, the key variables or combination of variables, that defined this relationship have not been empirically analyzed. As discussed above (**Box 1**), depth of snow cover and its duration increases with elevation; even minor elevation differences are noticeable (Formozov 1963, p. 123). The spotty distribution of snow cover is also affected by unequal distribution of snow precipitation on slopes with different exposures, transport of snow by wind, melting of snow on sun-exposed slopes, avalanche or rolling down of snow from steeper areas, and vegetation (Formozov 1963, p. 123). As discussed above (Denning Habitat), wolverines select den sites for differing characteristics depending on location, and wolverine (natal) dens have been observed outside of the boundary of the snow model presented in Copeland *et al.* (2010). In addition, very few studies to date have evaluated the importance of denning habitat to reproductive success, or the key physiological and ecological characteristics, including avoidance and/or protection from predators, prey availability, availability of food caching habitat, that define denning behavior and den site selection.

We also considered temperature and precipitation projections from climate change models in conjunction with wildland fire risk. This risk is likely to increase across the western United States, but patterns and trends are dependent on several factors (e.g., degree of warming and drought conditions, fuel and soil moisture) and geographic region.

As described above (see *Life History and Ecology* section), across their North American range, wolverines are found in a number of habitats, and exhibit wide-ranging movements. In conjunction with behavioral responses (e.g., dispersal over great distances, prey switching), physiological adaptations, including observed seasonal changes in the insulative capacity of fur, allow wolverines to occupy a variety of habitats throughout the year. Physiological adaptations at the cellular and biochemical level are also important in adapting to projected increases in temperature due to climate changes, though we are unaware of studies evaluating these types of responses in wolverines.

Overall Assessment

The wolverine's current range extends across the west-northwestern United States, large areas of Canada, and Alaska. In the contiguous United States, potentially suitable habitat (i.e., primary habitat), as determined by the physical and ecological features and the ecological needs of the wolverine, has been estimated at 164,125 km² (63,369 mi²) (Inman *et al.* 2013, p. 281). The species is found in a variety of habitats, but generally occurs in remote locations.

In the contiguous United States, the structure of the wolverine population is represented as a metapopulation, although its genetic structure relative to its entire North American range has not been comprehensively evaluated. Wolverine populations in Alaska are considered to be continuous with populations in the Yukon and British Columbia provinces of Canada based on genetic studies (COSEWIC 2014, p. 37). Similarly, studies of wolverines in the North Cascades region have documented movement of wolverines from Washington into British Columbia (Aubry *et al.* 2016, pp. 16, 20).

Based on the best available information, wolverines select den sites for different characteristics depending on location. Dens located under snow cover may be related to wolverine distribution based on other life history traits, including morphological, demographic, and behavioral adaptations that allow them to successfully compete for food resources (Inman 2013, pers. comm.). Structure (e.g., uprooted trees, boulders and talus fields) appears to be essential for natal den sites. However, reproductive success of wolverines has not been evaluated relative to the depth and persistence of snow cover, or in combination with these or other important characteristics, including prey availability and predator avoidance. Recent studies of wolverine populations and distribution in Sweden have observed wolverine populations and reproductive den sites outside areas with persistent spring snow cover (Aronsson and Persson 2016; Persson 2017, pers. comm.).

We identified several potential stressors that may be affecting the species' and its habitat currently or in the future, including impacts associated with climate change effects. We recognize there is limited information available for the wolverine, including population estimates and abundance trends. Based on the best available information, demographic risks to the species

from either known or most likely potential stressors (i.e., effects from roads, disturbance due to winter recreational activities, effects of wildland fire, and overutilization) are low based on our evaluation of the best available information as it applies to current and potential future conditions for the wolverine and in the context of the attributes that affect the needs of the species.

Climate change model projections for the range of the wolverine within the contiguous United States indicate increases in temperature by the mid-21st century as compared to early to mid-20th century values. Our evaluation of climate change indicates that snow cover is projected to decline in response to warming temperatures and changing precipitation patterns, but this varies by elevation, topography, and by geographic region. In general, models indicate higher elevations will retain more snow cover than lower elevations, particularly in early spring (April 30/May1). Although the persistence of spring snow has not yet been evaluated as critical to wolverine survival in North America, our review of projected snow persistence (to approximately Year 2055) within the Northern and Southern Rocky Mountains, indicates that several hundred kilometers (miles) of deep snow will persist on May 1st at elevations used by the wolverine for denning.

Legal protections include State listing in California and Oregon (as threatened), endangered in Colorado, as a candidate species in Washington, and protection as a non-game species in Idaho and Wyoming. In Canada, provincial designations range from endangered to threatened in eastern provinces, and sensitive/special concern to no ranking in other provinces. Legal trapping or hunting of wolverines is currently prohibited in the contiguous United States. Trapping effort along the U.S.–Canada border does not represent a significant barrier to wolverine movement and dispersal along the international border.

Approximately 96 percent of modeled wolverine primary habitat in the contiguous United States is located on Federal lands, with 41 percent located in designated wilderness areas. Management actions for conservation of the wolverine and its habitat are included within State Wildlife Action Plans, the Idaho Wolverine Conservation Plan, and USDA Forest Service Land and Resource Management Plans (see **Appendix G**). Various provisions of these plans include, but are not limited to, winter road closures, fire management, and land acquisition or conservation easements. These management measures, currently and in the future, will alleviate effects associated with potential impacts related to stressors discussed in this report.

Based on our review of available relevant literature for similar species, we identified the physical and ecological needs of the species as follows: large territories in remote landscapes; at high elevation (1,800 to 3,500 meters (5,906 to 11,483 feet)) within the contiguous United States; access to a variety of food resources, that varies with seasons; and reproductive behavior linked to both temporal and physical features. These needs are currently met for wolverines in the contiguous United States and are expected to be met in the future.

Risk Assessment

In order to characterize a species' viability and demographic risks, we consider the concepts of resilience, representation, and redundancy. We also consider known and potential stressors that may negatively impact the physical and biological features that the species needs for survival and

reproduction. Stressors are expressed as risks to its demographic features such as abundance, population and spatial structure, and genetic or ecological diversity. We consider the level of impact a stressor may have on a species along with the consideration of demographic factors (e.g., whether a species has stable, increasing, or decreasing trends in abundance, population growth rates, diversity of populations, and loss or degradation of habitat).

Wolverine populations in much of North America are still recovering from large losses of individuals from intensively hunting and persecution pressures in the late 1880s into the mid-20th century. Surveys conducted in the winter of 2015, and 2016–2017 continue to document its presence across its range in the contiguous United States. These surveys have recorded 85 observations, including in locations where they have not been recently detected (e.g., south of Interstate 90 in Washington, Teton Mountain Range/Grand Teton National Park). Thus, based on the best available information, wolverines continue to be detected across suitable habitat within the contiguous United States. Redundancy, the ability to withstand catastrophic events, can be characterized by the distribution and connectivity of populations. In considering wolverine in the contiguous United States, individuals are spread across a wide range of locations and connected habitats, affording protection to withstand catastrophic events. Additionally, wolverines in the contiguous United States appear to be connected to wolverine populations in Canada, also contributing to current and future redundancy.

Resiliency, the ability to withstand stochastic events, can be characterized by numbers of individuals and abundance trends. As indicated above, population size, growth rate, and current population trends are unknown for the wolverine due to the lack of abundance information. The range of the wolverine occurs within a large area of northern North America (see Figure 3). The most recent estimate for Canada indicates over 10,000 adult wolverines, as well as expansion of wolverines into historically occupied areas in both Canada and the contiguous United States with movement across both international borders. The 2014 COSEWIC report concluded that a climate-driven decline in wolverine populations in North America is not evident at this time in much of its range (COSEWIC 2014, p. 22). Wolverine populations in Canada are considered stable. Density estimates indicate no declining trend in wolverine populations in Alaska. We recognize that there is limited information on population sizes for the wolverine in the contiguous United States, and no comprehensive studies to indicate what a viable (or minimal) wolverine population size should be across its North American range. However, the best available information does not indicate either increasing or declining numbers of the wolverine in North America, including the contiguous United States. Further, at this time, the best available information does not indicate that the species' abundance is significantly impacted by human-caused stressors and this is unlikely to change in the future, supporting current and future resiliency.

As discussed above (Status–Future Conditions), both direct and cumulative effects of climate change (e.g., higher temperatures, loss of snow cover, wildland fire) may affect the resilience of the wolverine by creating an environment that is less favorable to its physiological and ecological needs. We are unaware of studies of the wolverine that have formally evaluated the species' responses (e.g., reproductive success) to warming temperatures or other climate change effects. However, a recent evaluation of behavioral plasticity, as an adaptive response to climate change effects, was presented for another mammal considered to be sensitive to climate change

effects—the American pika (*Ochotona princeps*; pika) (Beever *et al.* 2017, entire). As with the wolverine, this species is known to use several behavioral responses to variability in climate including changes in foraging strategies, use of habitat, and thermoregulation (Beever *et al.* 2017, p. 302). The pika was recently detected in heavily shaded rainforest habitat adjacent to talus patches at lower elevation (Columbia River Gorge) not typical of the talus-type habitats commonly used in many alpine areas of the western United States (Beever *et al.* 2017, p. 302). The authors suggest that, in the Columbia River Gorge region, this species is selecting microclimates in nearby shaded forests that provide insulation from warm summer temperatures (Beever *et al.* 2017, p. 302). This study also included results from a review of available literature related to behavior as a response to changing environmental conditions for several taxonomic groups. They found that behavioral responses to climate change effects were most commonly observed in longer-lived species, and the most common response, across all taxa, was a change in reproductive behavior, followed by dispersal or migration (Beever *et al.* 2017, p. 300). Most of the studies they evaluated identified temperature as the climate metric that was responsible for, or correlated with, changes in behavior; however, about 14 percent of the examined literature included responses to indirect (biotic) factors, such as changes in food resources (Beever *et al.* 2017, p. 300).

The authors also note that there are tradeoffs (e.g., reduction in time for foraging due to sheltering) that may impact long-term persistence and population viability (Beever *et al.* 2017, pp. 301–302), and the pika’s flexibility in habitat selection has not been observed in populations in the Great Basin (Beever *et al.* 2017, p. 302), where some populations have been extirpated (Beever *et al.* 2016, p. 1,498; Table 1). A recent study concluded that the pika has been extirpated from an interior portion of its geographic distribution in the Sierra Nevada region (California) due to climate effects (i.e., increase in temperature, decline in snowpack), and although sites surrounding this core area still harbor the species, the net effect has been fragmentation of habitat and species distribution (Stewart *et al.*, 2017, entire).

However, the pika continues to be found at sites that are outside of areas contained within bioclimatic envelop models (Jeffress *et al.* p. 253). The study found previously undocumented extant populations of the American pika in a region of the Great Basin (northwestern Nevada) that has been described as extirpated (Jeffress *et al.* 2017, entire). Relative to wolverine, the authors note that these results highlight the need for monitoring programs, particularly at remote and isolated locations, and the importance of evaluating occupancy at multiple scales (Jeffress *et al.* 2017, p. 266). In addition, the study noted the inconsistency of modeled climate factors in explaining occupied/unoccupied sites, and the likely importance of the pika’s talus (micro) habitat as well as the scale in which environmental variables are examined (Jeffress *et al.* 2017, p. 264). Resilience of pika populations is therefore likely related to these types of landforms, which act to decouple surface temperatures, with the talus rock habitat providing cool refugia (Jeffress *et al.* 2017, pp. 253, 264–265), but additional microsite data is needed as well as analyses of physiological variables to develop predictions of persistence (Jeffress *et al.* 2017, pp. 265–266). In sum, these studies indicate that small mammals exhibit adaptive responses to changing climate provided that refugia are available to support life history requirements. These studies also highlight the importance of continued monitoring and surveillance for difficult to study animals such as the wolverine, who are found in remote areas in naturally low densities, as

well as the potential for geographical variation and habitat structure in adaptation to climate change effects.

As described in this SSA Report, the best available information indicates confirmed observations of wolverines denning in areas with patchy snow cover in Alaska, Canada, and Scandinavia. Given their high rate of movement, large dispersal, and other observed life history traits (e.g., behavioral plasticity) observed in wolverines, we do not predict a significant loss of individual and population resiliency to the species in the future within its North America range, including the contiguous United States.

Currently, we are unaware of any documented specific risks for the wolverine related to a substantial change or loss of diversity in life history traits, population demographics, morphology, behavior, or genetic characteristics which can be used to characterize species representation (the ability to adapt to change). Rates of dispersal or gene flow are not known to have changed. Additionally, there is no currently available information to indicate that the current abundance of the wolverine across its current range is at a level that is causing inbreeding depression or loss of genetic variation that would affect representation. Nor is there any information to indicate that this species is unable to adapt or adjust to changing conditions (e.g., potential reduction in snow cover). We do not expect a reduction in representation of the wolverines in the contiguous United States in the future.

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[Add reviewer names, agency, Tribal Nations]

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California State Agency

Washington State Agency

Oregon State Agency

Idaho State Agency

Montana State Agency

Wyoming State Agency

Tribal Nations

[Add peer reviewer names]

References Cited

- [AAAS] American Association for the Advancement of Sciences. 2014. What We Know: The Reality, Risks and Response to Climate Change. The AAAS Climate Science Panel. 28 pp.
- Abatzoglou, J.T., K.T. Redmond, and L.M. Edwards. 2009. Classification of regional climate variability in the State of California. *Journal of Applied Meteorology and Climatology* 48:1527–1541.
- Abatzoglou, J.T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology* 33:121–131.
- Abramov, A.V. 2016. *Gulo gulo*. The IUCN Red List of Threatened Species 2016: e.T9561A45198537. Available at: <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T9561A45198537.en>. Last accessed January 25, 2017.
- [ADF&G] Alaska Department of Fish and Game. 2012. Trapper Questionnaire Statewide Annual Report, 1 July 2010–30 June 2011. Wildlife Management Report ADF&G/DWC/WMR-2012-2. Juneau, Alaska.
- _____. 2013a. Trapper Questionnaire Statewide Annual Report, 1 July 2011–30 June 2012. Wildlife Management Report ADF&G/DWC/WMR-2013-4. Juneau, Alaska.
- _____. 2013b. Trapper Questionnaire Statewide Annual Report, 1 July 2012–30 June 2013. Wildlife Management Report ADF&G/DWC/WMR-2013-5. Juneau, Alaska.
- _____. 2013c. *Rabies in Wildlife: Frequently Asked Questions for Alaska*. Dated May 2013. Available at: http://www.adfg.alaska.gov/static/home/news/pdfs/rabies_faq.pdf
- _____. 2015a. Susitna-Watana Hydroelectric Project (FERC No. 14241), Wolverine Distribution, Abundance, and Habitat Occupancy Study Plan Section 10.9, Study Completion Report. Prepared for Alaska Energy Authority. Dated October 2015. 18 pp.
- _____. 2015b. Federal Aid and Annual Research Performance Report for *Wildlife Health and Disease Surveillance in Alaska* Project. Reporting period July 1, 2014–June 30, 2015. Juneau, Alaska.
- _____. 2017a. Wolverine Species Profile. Available at: <http://www.adfg.alaska.gov/index.cfm?adfg=wolverine.main> Last accessed July 12, 2017.
- _____. 2017b. 2017-2018 Alaska Hunting Regulations, Effective July 1, 2017 through June 30, 2018. Anchorage, Alaska.

- Ahmad, I., D. Tang, T. Wang, M. Wang, and B. Wagan. 2015. Precipitation trends over time using Mann-Kendall and Spearman's rho tests in Swat River Basin, Pakistan. *Advances in Meteorology*, Volume 2015, Article ID 431860. 15 pp.
<http://dx.doi.org/10.1155/2015/431860>
- Allen, M. E. and D. E. Ullrey. 2004. Relationships among nutrition and reproduction and relevance for wild animals. *Zoo Biology* 23:475–487.
- Anderson, E. 1977. Pleistocene mustelidae (Mammalia, Carnivora) from Fairbanks, Alaska. *Bulletin of the Museum of Comparative Zoology* 148:1–121.
- Anderson, N.J. and K.E. Aune. 2008. Fecundity of female wolverine in Montana. *Intermountain Journal of Sciences* 14(1–3):17–30.
- Andrén, H., J. Persson, J. Mattisson, and A.C. Danell. 2011. Modelling the combined effect of an obligate predator and a facultative predator on a common prey: lynx *Lynx lynx* and wolverine *Gulo gulo* predation on reindeer *Rangifer tarandus*. *Wildlife Biology* 17:33–43.
- Aronsson, M. 2017. 'O Neighbour, Where Art Thou? Doctoral Thesis No. 2017:24. Swedish University of Agricultural Sciences, Department of Ecology; Uppsala, Sweden.
- Aronsson, M. and J. Persson. 2016. Mismatch between goals and the scale of actions constrains adaptive carnivore management: the case of the wolverine in Sweden. *Animal Conservation* 20:261–269. [first published online, October 2016]
- Aronsson, M., M. Low, H. Andrén, A. Ordiz, P. Segerström, and J. Persson. 2017. The link between local territorial dynamics and dispersal patterns for female wolverines. Manuscript.
- Araújo, M.B. and A. Townsend Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93(7): 1527–539. <http://www.jstor.org/stable/23225219>
- Aubry, K.B., K.S., McKelvey, and J.P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71(7):2147–2158.
- Aubry, K.B., J. Rohrer, C.M. Raley, and S. Fitkin. 2016. Wolverine distribution and ecology in the North Cascades ecosystem. Final Progress Report, dated February 9, 2016.
- Awan, M. and G. Szor. 2012. Wolverine (*Gulo gulo*) carcass collection and harvest monitoring in Nunavut: Summary Report. Department of Environment, Government of Nunavut, Canada.

- Baltar, M., J.E. Keeley, and F.P. Schoenberg. 2014. County-level analysis of the impact of temperature and population increases on California wildfire data. *Environmetrics* 25:397–405.
- Banci, V. 1982. The wolverine in British Columbia: distribution, methods of determining age and status of *Gulo gulo vancouverensis*. British Columbia Ministries of Environment and Forests; Victoria, British Columbia, Canada.
- Banci, V. 1987. Ecology and behaviour of wolverine in Yukon. M.S. Thesis, Simon Fraser University; Burnaby, British Columbia, Canada.
- Banci, V. 1994. Wolverine. Pp. 99–127 in *The Scientific Basis for Conserving Forest Carnivores: American marten, fisher, lynx, and wolverine in the western United States*. [L.F. Ruggiero *et al.* (tech. eds.)]. General Technical Report RM-254. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; Fort Collins, CO. 184 pp.
- Banci, V. and A. Harestad. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Annales Zoologici Fennici* 25:265–270.
- Banci, V. and G. Proulx. 1999. Resiliency of furbearers to trapping in Canada. Pp. 175–204 in *Mammal Trapping* [G. Proulx (ed.)]. Alpha Wildlife Research and Management, Ltd.; Sherwood Park, Alberta, Canada.
- Barnett, S.A. and L.E. Mount. Resistance to cold in mammals. Pp. 411–477 in *Thermobiology* [A.H. Rose (ed.)]. Academic Press Inc.; New York, New York.
- Bachelet, D., K. Ferschweiler, T. Sheehan, and J. Strittholt. 2016. Climate change effects on southern California deserts. *Journal of Arid Environments* 127:17–29.
- Beasom, S.L., E.P. Wiggers, J.R. Giardino. 1983. A technique for assessing land surface ruggedness. *Journal of Wildlife Management* 47:1163–1166.
- Beever, E.A., J.D. Perrine, T. Rickman, M. Flores, J.P. Clark, C. Waters, S.S. Weber, B. Yardley, D. Thoma, T. Chesley-Preston, K.E. Goehring, M. Magnuson, N. Nordensten, M. Nelson, and G.H. Collins. 2016. Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. *Journal of Mammalogy* 97(6):1495–1511.
- Beever, E.A., L.E. Hall, J. Varner, A.E. Loosen, J.B. Dunham, M.K. Gahl, F.A. Smith, and J.J. Lawler. 2017. Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and Environment* 15(6):299–308.
- Berg, N., and A. Hall. 2017. Anthropogenic warming impacts on California snowpack during drought. *Geophysical Research Letters* 44:2511–2518. doi:[10.1002/2016GL072104](https://doi.org/10.1002/2016GL072104).

- Bevanger, K. 1992. Report on the Norwegian wolverine (*Gulo gulo* L.). Small Carnivore Conservation 6:8–10.
- Bischof, R., E.R. Gregersen, H. Brøseth, H. Ellegren, and Ø. Flagstad. 2016. Noninvasive genetic sampling reveals intrasex territoriality in wolverines. *Ecology and Evolution* 6(5): 1527–1536. doi: 10.1002/ece3.1983.
- Björvall, A. 1982. A study of the wolverine female during the denning period. *Transactions of the International Congress of Game Biology* 14:315–322.
- Bjornlie, N., L. Tafelmeyer, and Z. Walker. 2017. Wolverine (*Gulo gulo*) distribution and occupancy in western Wyoming. Project Report, for period November 1, 2015 to May 31, 2016.
- [BLM] Bureau of Land Management. 2005. Land Use Planning Handbook. BLM Handbook H-1601-1. Prepared by the U.S. Bureau of Land Management. March 11, 2005.
- Bowman, J., J.C. Ray, A.J. Magoun, D. S. Johnson, and F.N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Canadian Journal of Zoology* 88:454–467.
- Bozinovic, F., P. Calosi, and J.I. Spicer. 2011. Physiological correlates of geographic range in animals. *Annual Review of Ecology, Evolution, and Systematics* 42:155–179.
- Bryant, H.N. 1987. Wolverine from the Pleistocene of the Yukon: evolutionary trends and taxonomy of *Gulo* (Carnivora: Mustelidae). *Canadian Journal of Earth Science* 24:654–663.
- Burkholder, B.L. 1962. Observations concerning wolverine. *Journal of Mammalogy* 43:263–264.
- Canadian Boreal Forest Agreement Secretariat. 2015. Boreal Priority Species–Wolverine: Additional Considerations for Conservation Planning. CBFA Secretariat; Ottawa, Canada. 18 pp.
- Cardinal, N. 2004. Aboriginal Traditional Knowledge COSEWIC Status Report on Wolverine *Gulo gulo* Oavvik. Prepared for Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ontario; Canada. ix + 40 pp.
- Carroll R., C. Augspurger, A. Dobson, J. Franklin, G. Orians, W. Reid, R. Tracy, D. Wilcover, and J. Wilson. 1996. Strengthening the use of science in achieving the goals of the endangered species act: an assessment by the Ecological Society of America. *Ecological Applications* 6:1–11.
- Carroll, C., R.F. Noss, and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* 11(4): 961–980.

- Casey, T.M., P.C. Withers, and K.K. Casey. 1979. Metabolic and respiratory responses of Arctic mammals to ambient temperature during the summer. *Comparative Biochemistry and Physiology* 64A:331–341.
- Cathcart, S. 2014. Manitoba Winter: Snow Activity Program. Revised from J. Pattimore, 1981. Manitoba Parks; Manitoba, Canada.
- [CDFG] California Department of Fish and Game. 2011. California Wolverine Population Augmentation Considerations, Briefing Document. Prepared by Daniel Applebee (lead), Esther Burkett, Richard Callas, Dr. Deana Clifford, Greg Gerstenberg, Canh Nguyen, Dr. Tom Stephenson, Chris Stermer, Dr. David Wright, Joseph Vondracek, and Dr. Eric Loft. Dated November 7, 2011.
- [CDFW] California Department of Fish and Wildlife. 2015. California State Wildlife Action Plan, 2015 Update: A Conservation Legacy for Californians. Edited by Armand G. Gonzales and Junko Hoshi, PhD. Prepared with assistance from Ascent Environmental, Inc., Sacramento, California.
- _____. 2017a. State and Federally Listed Endangered and Threatened Animals of California. Biogeographic Data Branch California Natural Diversity Database. Dated July 2017.
- _____. 2017b. California Endangered Species Act (CESA) Permits. Available at: <https://www.wildlife.ca.gov/Conservation/CESA> Last accessed August 29, 2017.
- Cegelski, C.C., L.P. Waits, and N.J. Anderson. 2003. Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-based approaches. *Molecular Ecology* 12:2907–2918.
- Cegelski, C.C., L.P. Waits, N.J. Anderson, O. Flagstad, C. Strobeck, and C.J. Kyle. 2006. Genetic diversity and population structure of wolverine (*Gulo gulo*) populations at the southern edge of their current distribution in North America with implications for genetic viability. *Conservation Genetics* 7:197–211.
- Channell, R. and M.V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. *Nature* 403:84–86.
- Chappell, D.E., R.A. Van Den Bussche, J. Krizan, and B. Patterson. 2004. Contrasting levels of genetic differentiation among populations of wolverines (*Gulo gulo*) for northern Canada revealed by nuclear and mitochondrial DNA. *Conservation Genetics* 5:759–767.
- Clevenger, A.P., G. Mowat, M. Barrueto, and J.T. Fisher. 2016. Mapping the wolverine way: understanding landscape and human effects on wolverine abundance, distribution, and connectivity in the Canadian Crown of the Continent (CCoC) ecosystem. 2016 Summary Report. June 2016.

- Clevenger, A.P., G. Mowat, and M. Barrueto. 2017. Mapping the wolverine way: identifying conservation corridors and linkages in the Canadian Crown of the Continent ecosystem. Final report to the Wilburforce Foundation. April 2017.
- Coggins, G.C., C.F. Wilkinson, and J.D. Leshy. 2002. Modern National Forest Management. Pp. 720–737 in *Federal Public Land and Resources Law* (5th ed). Foundation Press; New York, New York.
- Cohen, J., M. Lajeunesse, and J.R. Rohr. 2017. A global synthesis of phenological responses to climate change. bioRxiv preprint online version, July 18, 2017. Available at doi: <https://doi.org/10.1101/164806>
- Colorado Parks and Wildlife. 2015a. Chapter 10, Nongame Wildlife Index. Dated July 9, 2015. Available at: <http://cpw.state.co.us/Documents/RulesRegs/Regulations/Ch10.pdf> Last accessed August 29, 2017.
- Colorado Parks and Wildlife. 2015b. Colorado's State Wildlife Action Plan.
- Committee of Scientists. 1999. Sustaining the People's Lands: Recommendations for Stewardship of the National Forests and Grasslands into the Next Century. USDA Forest Service; Washington, D.C. March 15, 1999. Available at <https://www.fs.fed.us/emc/nfma/includes/cosreport/Committee%20of%20Scientists%20Report.htm>
- Copeland, J.P. 1996. Biology of the wolverine in central Idaho. MS Thesis, University of Idaho; Moscow, Idaho.
- Copeland, J.P. and R.E. Yates. 2008. Wolverine population assessment in Glacier National Park: comprehensive summary update. USDA Forest Service, Rocky Mountain Research Station; Missoula, Montana. Dated January 2008.
- Copeland, J.P., J.M. Peek, C.R. Groves, W.E. Melquist, K.S. McKelvey, G. W. McDaniel, C.D. Long, and C.E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. *Journal of Wildlife Management* 71(7):2201–2212.
- Copeland, J.P., K.S. McKelvey, K.B. Aubry, A. Landa, J. Persson, R.M. Inman, J. Krebs, E. Lofroth, H. Golden, J.R. Squires, A. Magoun, M.K. Schwartz, J. Wilmot, C.L. Copeland, R.E. Yates, I. Kojola, and R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88:233–246.
- Coues. E. 1877. *Fur-Bearing Animals: A Monograph of North American Mustelidae*. Miscellaneous Publications No. 8. Department of Interior, U.S. Geological Survey. Government Printing Office; Washington, D.C.

- [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2014. COSEWIC Assessment and Status Report on the Wolverine (*Gulo gulo*) in Canada. Ottawa, Canada. vi + 41 pp.
- Dalerum, F., K. Kunkel, A. Angerbjörn, and B.S. Shults. 2009. Diet of wolverines (*Gulo gulo*) in the western Brooks Range, Alaska. *Polar Research* 28:246–253.
- Dawson, F.N., A.J. Magoun, J. Bowman, and J.C Ray. 2010. Wolverine, *Gulo gulo*, home range size and denning habitat in lowland boreal forest in Ontario. *Canadian Field-Naturalist* 124(2): 139–144.
- Dawson, F.N., A.J. Magoun, J. Bowman, and J.C. Ray, unpubl. data. 2013. Ontario Ministry of Natural Resources, RR#1, Thunder Bay, Ontario, Wildlife Research and Management (WRAM), Fairbanks, Alaska, and Wildlife Conservation Society Canada, Toronto, Ontario. [not seen, cited according to COSEWIC 2014]
- Degerbøl, M. 1935. Report of the mammals collected by the fifth Thule Expedition to Arctic North America 1921–24; Zoology. I. Mammals; Vol. 2, No 4–5]. Part I. Systematic Notes. 1976 reprint. Originally published by Gyldendalske; Copenhagen. Reprinted in 1976 by AMS Press; New York, New York.
- De Puyjalon, H. 1900. Histoire naturelle à l’usage des chasseurs canadiens et des éleveurs d’animaux à fourrures. Imprimerie du Soleil, Québec. 428 pp.
- Derrickson, E.M. 1992. Comparative reproductive strategies of altricial and precocial eutherian mammals. *Functional Ecology* 6:57–65.
- Dorendorf, R. 2016. Fine-scale habitat selection by wolverines on Alaska’s North Slope. Pp. 6–7 in *The Alaskan Wildlifer*. Newsletter of the Alaska Chapter of the Wildlife Society. September 2016.
- Dulkeit, G. D. 1953. Znachenie rysi i rosomakhi kak khishchnikov v pridrodnom kpmlekse Altaiskoi taiga. In: *Sbornik Preobrazovanie fauny pozvonochnykh nashei strany* [A. A. Nasimovich, ed.]. Moskva: MOIP [not seen, cited according to Novikov 1962].
- [EPA] U.S. EPA Office of Research and Development, National Health and Environmental Effects Research Laboratory. 2010 NA_CEC_Eco_Level2. Available at: <http://www.epa.gov/wed/pages/ecoregions.htm>
- Ellerman, J.R. and T.C.S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian Mammals, 1758 to 1946. British Museum Natural History; London, United Kingdom.
- _____. 1966. Checklist of Palaearctic and Indian Mammals, 1758 to 1946 (2nd ed.). British Museum Natural History; London, United Kingdom.

- Erickson, A.B. 1946. Incidence of worm parasites in Minnesota Mustelidae and host lists and keys to North American species. *American Midland Naturalist* 36:494–509.
- Fisher, J.T., S. Bradbury, B. Anholt, L. Nolan, L. Roy, J.P. Volpe, and M. Wheatley. 2013. Wolverines (*Gulo gulo luscus*) on the Rocky Mountain slopes: natural heterogeneity and landscape alternation as predictors of distribution. *Canadian Journal of Zoology* 91:706–716.
- Flagstad, Ø., E. Hedmark, A. Landa, H. Brøseth, J. Persson, R. Andersen, P. Segerström, and H. Ellegren. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18(3): 676–688.
- Folk, G.E., Jr., M.A. Folk, and D. Craighead. 1977. A comparison of body temperatures of least weasels and wolverines. *Comparative Biochemistry and Physiology* 58A:229–234.
- Ford, K.R., C.A. Harrington, S. Bansal, P.J. Gould, and B. St. Clair. 2016. Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir. *Global Change Biology* 22:3712–3723.
- [Forest Service] U.S. Department of Agriculture. 2009. Beaverhead-Deerlodge National Forest Land and Resource Management Plan. January 2009.
- _____. 2013. Sierra Nevada Forest Plan Amendment, Final Supplemental Environmental Impact Statement. Pacific Southwest Region, R5-MB-262. August 2013
- _____. 2015. Kootenai National Forest Land Management Plan, 2015 Revision. Missoula, Montana.
- _____. 2016a. Flathead National Forest, Draft Environmental Impact Statement, Volumes 1 and 2, Revised Forest Plan. Kalispell, Montana.
- _____. 2016b. Flathead National Forest, Draft Revised Forest Plan. Kalispell, Montana.
- Formozov, A.N. 1961. The significance of snow cover in the ecology and geographical distribution of mammals and birds. *In* The Role of Snow Cover in Natural Processes [W.A. Fuller (ed.)]. Institute of Geography; Moscow, USSR. Translated by E. Issakoff.
- Formozov, A.N. 1963. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Originally published in 1946 in Materials for Fauna and Flora of the USSR New Series 5:1–152 by Moscow Society of Naturalists, Moscow, USSR. English translation by W. Prychodko and W. O. Pruitt, Jr. Published 1963 as Occasional Paper Number 1, Boreal Institute, University of Alberta, Edmonton; Alberta, Canada.

- Fortin, C., V. Banci, J. Brazil, M. Crête, J. Huot, M. Huot, R. Lafond, P. Paré, J. Shaefer, and D. Vandal. 2005. National recovery plan for the wolverine (*Gulo gulo*) [Eastern Population]. National Recovery Plan No. 26. Recovery of Nationally Endangered Wildlife (RENEW). Ottawa, Ontario. 33 pp.
- 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. Appendix B in Associations and movement patterns of reproductive female wolverines (*Gulo gulo luscus*) on the Southeast Alaska Mainland, prepared by Magoun *et al.* 2010. Final Report 2010; Submitted to The Wolverine Foundation, Inc.
- Frankham, R., C.J.A. Bradshaw, and B.W. Brook. 2014. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria, and population viability analyses. *Biological Conservation* 170:56–63.
- Franklin, I.R. 1980. Evolutionary change in small populations. Pp. 135–149 in *Conservation Biology: An Evolutionary-Ecological Perspective* [M. Soulé and B. Wilcox (eds.)]. Sinauer Associates; Sunderland, Massachusetts.
- Freuchen, P. 1935 (1976 reprint). Part II. Field Notes and Biological Observations; Report of the Fifth Thule Expedition 1921–24; Vol. 2, No 4–5. Originally published by Gyldendalske; Copenhagen. Reprinted in 1976 by AMS Press; New York, New York.
- Frey, J.K. 2006. Inferring species distributions in the absence of occurrence records: an example considering wolverine (*Gulo gulo*) and Canada lynx (*Lynx canadensis*) in New Mexico. *Biological Conservation* 130:16–24.
- Gardner, C. L. 1985. The ecology of wolverines in southcentral Alaska. M.S. Thesis, University of Alaska; Fairbanks, Alaska. 82 pp.
- Gardner, C.L., W. B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. *Journal of Mammalogy* 67:603.
- Gardner, C.L., J.P. Lawler, J.M. Ver Hoef, A.J. Magoun, and K.A. Kellie. 2010. Coarse-scale distribution surveys and occurrence probability modeling for wolverine in interior Alaska. *Journal of Wildlife Management* 74:1894–1903.
- Gergel, D.R., B. Nijssen, J.T. Abatzoglou, D.P. Lettenmaier, and M.R. Stumbaugh. 2017. Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change* 141:287–299.
- Glick, P., B.A. Stein, and N.A. Edelson (eds.). 2011. *Scanning the Conservation Horizon: A Guide to Climate Change Vulnerability Assessment*. National Wildlife Federation; Washington, DC. 168 pp.

- Goethe, F. 1964. Das Verhalten der Musteliden. *Hanbuch der Zoologie* 8(10):1–80. [not seen cited according to Rieger 1979]
- Griffin, D. and K. J. Anchukaitis. 2014. How unusual is the 2012–2014 California drought? *Geophysical Research Letters* 41:9017–9023. doi:10.1002/2014GL062433.
- Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1937. *Fur-bearing Mammals of California*. Volume I. University of California Press; Berkeley, California. 375 pp.
- Guilday, J.E. 1971. The Pleistocene history of the Appalachian mammal fauna. Pp. 233–262 in *The distributional history of the biota of the southern Appalachians*. Part III: Vertebrates [P.C. Holt (ed.)] Research Division Monograph 4. Virginia Polytechnic Institute and State University; Blacksburg, Virginia.
- Gustine, D.D., K.L. Parker, R.J. Lay, M.P. Gillingham, and D.C. Heard. 2006. Calf survival of woodland caribou in a multipredator ecosystem. *Wildlife Monographs* 165:1–32.
- Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. [De stora rovdjurens vintervanor, I.] *Viltrevy* 4(3):81–310.
- Halfpenny, J.C., R.W. Thompson, S.C. Morse, T. Holden, and P. Rezendes. 1995. Snow tracking. Pp. 91–163 (Chapter 5) in *American marten, fisher, lynx, and wolverine: survey methods for their detection*. [W.J. Zielinski and T.E. Kucera (technical eds.)]. General Technical Report PSW-GTR-157. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; Albany, California. 163 pp.
- Hall, E.R. 1981. *The Mammals of North America*. Volume II. (2nd ed.). John Wiley & Sons; New York, New York.
- Hall, D.K. and G.A. Riggs. 2016. MODIS/Terra Snow Cover 8-Day L3 Global 500m Grid, Version 6. Boulder, Colorado, USA. Release data May 27, 2016. NASA National Snow and Ice Data Center Distributed Active Archive Center. doi: <http://dx.doi.org/10.5067/MODIS/MOD10A2.006>. Last accessed June 22, 2017.
- Hamlet, A.F., M.M. Elsner, G.S. Mauger, S. Lee, I. Tohver, and R.A. Norheim. 2013. An overview of the Columbia Basin Climate Change Scenarios Project: approach, methods, and summary of key results. *Atmosphere-Ocean* 51(4):392–415. doi: 10.1080/07055900.2013.819555.
- Hanski, I. and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pp. 5–26 in *Metapopulation Biology: Ecology, Genetics, and Evolution* [I.A. Hanski and M.E. Gilpin, eds.]. Academic Press; San Diego, California.

- Hansson, A. 1947. The physiology of reproduction in mink (*Mustela vison* Schreb.) with special reference to delayed implantation. *Acta Zoologica* 28:1–136.
- Hardy, T.M. P. 1948. Wolverine fur frosting. *The Journal of Wildlife Management* 12(3):331–332.
- Hart, J.S. 1956. Seasonal changes in insulation of the fur. *Canadian Journal of Zoology* 34:53–57.
- Hash, H.S. 1987. Wolverine. Pp. 575–585 in *Wild furbearer management and conservation in North America* [M. Novak, J.A. Baker, and M.E. Obbard (eds.)]. Ontario Ministry of Natural Resources; Toronto, Canada.
- Hedmark, E., J. Persson, P. Segerstrom, A. Landa, and H. Ellergen. 2007. Paternity and mating system in wolverines *Gulo gulo*. *Wildlife Biology* 13(13(sp2):13–30.
- Heinemeyer, K. and J. Squires. 2013. Wolverine–Winter Recreation Research Project: Investigating the Interactions between Wolverines and Winter Recreation. 2013 Progress Report. Dated November 16, 2013. Available at www.roundriver.org/wolverine
- Heinemeyer, K. and J. Squires. 2015. Wolverine–Winter Recreation Research Project: Investigating the Interactions between Wolverines and Winter Recreation. 2015 Progress Report. Dated December 30, 2015. Available at www.roundriver.org/wolverine.
- Henshaw, R.E. 1970. Insulative advantage in arctic wolves, wolverines, and huskies. Abstract #276. *Abstracts. American Zoologist* 10(4): 473–559. Available at <http://www.jstor.org/stable/3881598>
- Hipel, K.W. and A.I. McLeod. 2005. *Time Series Modelling of Water Resources and Environmental Systems*. Electronic reprint of book originally published in 1994. Available online at <http://www.stats.uwo.ca/faculty/aim/1994Book/>
- Hoffman, A.A., S.M. Sgrò, and T.N. Kristensen. 2017. Revisiting adaptive potential, population size, and conservation. *Trends in Ecology & Evolution* 32:506–517. doi:<http://dx.doi.org/10.1016/j.tree.2017.03.012>
- Hope, A.G., N. Takebayashi, K.E. Galbreath, S.L. Talbot, and J.A. Cook. 2013. Temporal, spatial and ecological dynamics of speciation among amphi-Beringian small mammals. *Journal of Biogeography* 40:415–429.
- Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology* 59:1286–1301.
- Hutchings, M. R. and P.C.L. White. 2000. Mustelid scent-marking in managed ecosystems: implications for population management. *Mammal Review* 30:157–169. doi:10.1046/j.1365-2907.2000.00065.x

- [IDFG] Idaho Department of Fish and Game. 2014. Management Plan for the Conservation of Wolverines in Idaho. Boise, Idaho. 52 pp.
- _____. 2017a. Road and Salvage Highway Mortality Reports. Retrieved from:
https://idfg.idaho.gov/species/roadkill/list?highway=&species_id=17557&salvage=All®ion_id=All&county_id=All&gmu_id=All&date%5Bmin%5D%5Bdate%5D=&date%5Bmax%5D%5Bdate%5D=&items_per_page=25
- _____. 2017b. Idaho State Wildlife Action Plan, 2015. Boise (ID): Idaho Department of Fish and Game. Grant No.: F14AF01068 Amendment #1. Available from:
<http://fishandgame.idaho.gov/>.
- Inman, R.M., K.M. Inman, A.J. McCue, and M.L. Packila. 2007. Wolverine harvest in Montana: survival rates and spatial considerations for harvest management. Chapter 5 in Greater Yellowstone Wolverine Study, Cumulative Progress Report. Dated May 2007. Wildlife Conservation Society, North America Program, General Technical Report; Bozeman, Montana.
- Inman, R.M., M.L. Packila, K.H. Inman, A.J. McCue, G.C. White, J. Persson, B.C. Aber, M.L. Orme, K.L. Alt, S.L. Cain, J.A. Fredrick, B.J. Oakleaf, and S.S. Sartorius. 2012a. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76(4):778–792.
- Inman, R.M., A.J. Magoun, J. Persson, and J. Mattisson. 2012b. The wolverine’s niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93(3):634–644.
- Inman, R.M., B.L. Brock, K.H. Inman, S.S. Sartorius, B.C. Aber, B. Giddings, S.L. Cain, M.L. Orme, J.A. Fredrick, B.J. Oakleaf, K.L. Alt, E. Odell, and G. Chapron. 2013. Developing priorities for metapopulation conservation at the landscape scale: wolverines in the Western United States. *Biological Conservation* 166:276–286.
- Inman, R., M. Riley, Z. Walker, B. Lanka, and G. White. 2015. Distribution of female wolverines in Wyoming, Progress Report – August 2015. The Wolverine Initiative; Ennis, Montana.
- [IPCC] International Panel on Climate Change. 2000. IPCC Special Report: Emissions Scenarios. Summary For Policymakers; A Special Report of IPCC Working Group III of the Intergovernmental Panel on Climate Change. 27 pp.

- _____. 2013a. Annex III: Glossary [Planton, S. (ed.)]. *In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 20 pp.
- _____. 2013b. Summary for Policymakers. *In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA. 33 pp.
- _____. 2013c. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA. 1535 pp.
- _____. 2014. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Summary for Policymakers*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 44 pp. Available at: http://ipcc-wg2.gov/AR5/images/uploads/IPCC_WG2AR5_SPM_Approved.pdf
- Irving, L., H. Krog, and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. *Physiological Zoölogy* 28(3):173–185.
- Irving, L. 1972. *Arctic Life of Birds and Mammals, Including Man*. Springer-Verlag; Berlin Heidelberg, Germany.
- Iversen, J.A. 1972a. Basal energy metabolism of mustelids. *Journal of Comparative Physiology* 81:341–344.
- Iversen, J.A. 1972b. Basal metabolic rate of wolverines during growth. *Norwegian Journal of Zoology* 20:317–322.
- Jackson, H.H.T. 1961. *Mammals of Wisconsin*. University of Wisconsin Press; Madison, Wisconsin. 504 pp.
- Jamieson, I.G. and F.W. Allendorf. 2012. How does the 50/500 rule apply to MVPs? *Trends in Ecology & Evolution* 27: 578–584.
- Jeffress, M.R., K.J. Van Gunst, and C.I. Millar. 2017. A surprising discovery of American pika sites in the northwestern Great Basin. *Western North American Naturalist* 77(2):252–268.

- Johnson, C.J., M.S. Boyce, R.L. Case, H.D. Cluff, R.J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects on human developments on Arctic wildlife. *Wildlife Monographs* 160:1-36.
- Jones, Jr., J.K., R.S. Hoffman, D.W. Rice, C. Jones, R.J. Baker, M.D. Engstrom. 1992. Revised checklist of North American mammals north of Mexico, 1991. *Occasional Papers The Museum Texas Tech University* 146:1–23.
- Jung, T. S. and P.M. Kukka. 2013. Wolverine carcass collection program: 2013 progress report. Yukon Fish and Wildlife Branch Report PR-13-04. Whitehorse; Yukon, Canada.
- Keeley, J.E. and A.D. Syphard. 2016. Climate change and future fire regimes: examples from California. *Geosciences* 6:37. 14 pp. doi:10.3390/geosciences6030037.
- Kettenbach, J.A, N. Miller-Struttmann, Z. Moffett, and C. Galen. 2017. How shrub encroachment under climate change could threaten pollination services for alpine wildflowers: a case study using the alpine skypilot, *Polemonium viscosum*. *Ecology and Evolution* 7:6963–6971.
- Khalil, H., M. Pasanen-Mortensen, and B. Elmhagen. 2014. The relationship between wolverines and larger predators, lynx and wolf, in a historical ecosystem context. *Oecologia* 175:625–637.
- Klein, D.R. 1982. Fire, lichens, and caribou. *Journal of Range Management* 35(3):390–395.
- Knorre, E.P. 1959. Ecology of the elk. *In* Transactions of the Pechora-Ilych Game Preserve, Issue VII [G.A. Novikov (ed.)]. Translated by the Canadian Wildlife Service, 1966; Document Number 3895. 324 pp.
- Kociolek, A., L. Craighead, B. Brock, and A. Craighead. 2016. Evaluating Wildlife Mortality Hotspots, Habitat Connectivity and Potential Accommodation along US 287 and MT 87 in the Madison Valley, Montana. Final Report. Prepared for Montana Department of Transportation: Helena, Montana. Dated November 2016.
- Koehler, G.M. and M.G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. *The Journal of Wildlife Management* 41(3):500–505.
- Koskela, A. 2013. Wolverine habitat selection, diet, and conservation genetics. Academic dissertation, Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu; Oulu, Finland.
- Koskela, A., I. Kojola, J. Aspi, and M. Hyvärinen. 2013a. Effect of reproductive status on the diet composition of wolverines (*Gulo gulo*) in boreal forests of eastern Finland. *Annales Zoologici Fennici* 50:100–106.

- Koskela, A., S. Kaartinen, J. Aspi, I. Kojola, P. Helle, and S. Rytönen. 2013b. Does grey wolf presence affect habitat selection of wolverines. *Annales Zoologici Fennici* 50:216–224.
- Krebs, J., E. Lofroth, J. Copeland, V. Banci, D. Cooley, H. Golden, A. Magoun, R. Mulders, and B. Shults. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management* 68(3):493–502.
- Krebs, J., E.C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7):2180–2192.
- Krott, P. 1958. *Demons of the North*. Alfred A. Knopf; New York, New York. 260 pp. Translated from German.
- Krott, P. 1960. Ways of the wolverine. *Natural History* 69:16–29.
- Kurtén, B. and R. Rausch. 1959. A comparison between Alaskan and Fennoscandian wolverine (*Gulo gulo* Linnaeus). *Acta Arctica* 11:5–20.
- Kyle, C.J. and C. Strobeck. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. *Molecular Ecology* 10: 337–347.
- Kyle, C.J. and C. Strobeck. 2002. Connectivity of peripheral and core populations of North American wolverines. *Journal of Mammalogy* 83:1141–1150.
- Laikre, I., F. Olsson, E. Jansson, O. Hössjer, and N. Ryman. 2016. Metapopulation effective size and conservation genetic goals for the Fennoscandian wolf (*Canis lupus*) population. *Heredity* 117: 279–289.
- Laliberte, A.S. and W.J. Ripple. 2004. Range contraction of North American carnivores and ungulates. *Bioscience* 54:123–138.
- Landa, A., O. Strand, J.E. Swenson, and T. Skogland. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology* 75:1292–1299.
- Landa, A., O. Strand, J.D.C. Linnell, and T. Skogland. 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology* 76:448–457.
- Larsen, J.A. 1980. *The Boreal Ecosystem*. Academic Press, Inc.; New York, New York. 500 pp.
- Le Corre, M., C. Dussault, and S.D.Côté. 2017. Weather conditions and variation in timing of spring and fall migrations of migratory caribou. *Journal of Mammalogy* 98:260–271.

- Lofroth, E.C. 2001. Northern Wolverine Project 2000/01 Year End Report. Wolverine Ecology in Plateau and Foothill Landscapes, 1996-2001. Prepared in partnership with Forest Renewal BC, Ministry Of Environment, Lands & Parks, and the Ministry Of Environment, Lands & Parks. British Columbia, Canada.
- Luck, K., B. Wagner, J. Schurer, R. Sharma, J. Harms, T. Jung, P. Kukka, B. Elkin, R. Mulders, M. Branigan, J. Pongracz, and E. Jenkins. 2016. Parasites of wolverines (*Gulo gulo*) from northwestern Canada. Abstract. Presented at 65th Annual International Conference of the Wildlife Disease Association, July 31–August 5, 2016; Cortland, New York.
- Luensmann, S. 2008. *Gulo gulo*. In Fire Effects Information System [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available at: <http://www.fs.fed.us/database/feis/animals/mammal/gugu/all.html> Last accessed August 2, 2017.
- Lukas, J., J.J. Barsugli, N. Doesken, I. Rangwala, and K.E. Wolter. 2014. *Climate Change in Colorado: A Synthesis to Support Water Resources Management and Adaptation* (2nd edition). Report by the Western Water Assessment for the Colorado Water Conservation Board. 108 pp. Available at: <http://www.colorado.edu/climate/co2014report/>
- Lyon, L.J., E.S. Telfer, and D.S. Schreiner. 2000. Direct effects of fire and animal responses. Pp. 17–24 (Chapter 3) in *Wildland fire in ecosystems: effects of fire on fauna* [J.K. Smith (ed.)]. General Technical Report RMRS-GTR-42-Volume 1. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station; Ogden, Utah. 83 pp.
- Magoun, A.J. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. PhD Thesis, University of Alaska; Fairbanks, Alaska.
- Magoun, A.J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in Arctic Alaska. *Canadian Field-Naturalist* 101:392–397.
- Magoun, A.J. and J.P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *The Journal of Wildlife Management* 62(4):1313–1320.
- Magoun, A.J., P. Valkenburg and R. E. Lowell. 2008. Habitat associations and movement patterns of reproductive female wolverines (*Gulo gulo luscus*) on the Southeast Alaska Mainland. Wildlife Research Annual Progress Report. Alaska Department of Fish and Game. Petersburg, Alaska. 29 pp.
- Magoun, A. J., C.D. Clinton, M.K. Schwartz, K.L. Pilgrim, R.E. Lowell, and P. Valkenburg. 2011. Integrating motion-detection cameras and hair snags for wolverine identification. *Journal of Wildlife Management* 75:731–739.
- Magoun, A.J., M.D. Robards, M.L. Packila, and T.W. Glass. 2017. Detecting snow at the den-site scale in wolverine denning habitat. *Wildlife Society Bulletin* 41(2):381–387.

- Makkonen, T. 2015. Den site characteristics of female wolverine (*Gulo gulo*) in Scandinavian forest landscape. Master's Thesis. University of Oulu; Oulu, Finland.
- Malyarchuk, B.A., M.V. Derenko, and G.A. Denisova. 2015. Mitochondrial genome variability in the wolverine (*Gulo gulo*). Russian Journal of Genetics 51(11):1113–1118.
- Manly, B.F.J., L.L. McDonald, D.L. Thomas, T. L. McDonald, and W.P. Erickson. 2002. Resource Selection by Animals (2nd ed.). Kluwer Academic Publishers: Dordrecht, The Netherlands.
- Marmi, J., J.F. López-Giráldez, and X. Domingo-Roura. 2004. Phylogeny, evolutionary history and taxonomy of the Mustelidae based on sequences of the cytochrome *b* gene and a complex repetitive flanking region. Zoologica Scripta 33(6):481–499.
- Mattisson, J., J. Persson, H. Andrén, and P. Segerström. 2011a. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Canadian Journal of Zoology 89:79–89.
- Mattisson, J., H. Andrén, J. Persson, and P. Segerström. 2011b. Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. Journal of Mammalogy 92(6):1321–1330.
- Mattisson, J., G.R. Rauset, J. Odden, H. Andrén, J.D.C. Linnell, and J. Persson. 2016. Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine. Ecosphere 7(8):e01407. doi:10.1002/ecs2.1407.
- May, R., L. Gorini, J. van Dijk, H. Brøseth, J.D.C. Linnell, and A. Landa. 2012. Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. Journal of Zoology 287:195–204.
- McLeod, A.I. 2011. Package 'Kendall,' Kendall rank correlation and Mann-Kendall trend test. Version 2.2. Dated May 16, 2011.
- McCue, A.J., R.M. Inman, K.H. Inman, and M.L. Packila. 2007. Diel winter activity of wolverines in Greater Yellowstone. Chapter 6 in Greater Yellowstone Wolverine Study, Cumulative Progress Report. Dated May 2007. Wildlife Conservation Society, North America Program, General Technical Report; Bozeman, Montana.
- McKelvey, K.S., J.P. Copeland, M.K. Schwartz, J.S. Littell, K.B. Aubry, J.R. Squires, S.A. Parks, M.M. Elsner, and G.S. Mauger. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. Ecological Applications 21(8):2882–2897.

- McKelvey, K.S., K.B. Aubry, N.J. Anderson, A.P. Clevenger, J.P. Copeland, K.S. Heinemeyer, R.M. Inman, J.R. Squires, J.S. Waller, K.L. Pilgrim, M.K. Swartz. 2014. Recovery of wolverines in the western United States: recent extirpation and recolonization or range retraction and expansion? *The Journal of Wildlife Management* 78(2):325–334.
- McLeod, A.I. 2011. Package ‘Kendall.’ Kendall rank correlation and Mann-Kendall trend test. Version 2.2 (dated May 18, 2011). Available at: <http://www.stats.uwo.ca/faculty/aim>.
- Mead, R.A., M. Bowles, G. Strypan, and M. Jones. 1993. Evidence for pseudopregnancy and induced ovulation in captive wolverines (*Gulo gulo*). *Zoo Biology* 12:353–358.
- Mehrer, C.F. 1976. Gestation period in the wolverine, *Gulo gulo*. *Journal of Mammalogy* 57:570.
- Melillo, J.M., T.C. Richmond, and G.W. Yohe (eds.). 2014. Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program. 841 pp.
- Michalak, J.L., J.C. Whitey, J.L. Lawler, and M.J. Case. 2017. Future climate vulnerability – evaluating multiple lines of evidence. *Frontiers in Ecology and Environment* 15(7): 367–376.
- Moeller, K. 2017. *Wildlife Services says cyanide that killed dog, hurt boy isn’t ‘bomb,’ it’s pesticide*. The Idaho Statesman, July 26, 2017. Retrieved July 27, 2017 from: <http://www.idahostatesman.com/news/local/community/boise/article163783578.html>
- Montana Fish, Wildlife & Parks. 2015. Montana’s State Wildlife Action Plan. Montana Fish, Wildlife & Parks; Helena, Montana. 441 pp.
- Montana Natural Heritage Program and Montana Fish, Wildlife & Parks. 2017. Wolverine — *Gulo gulo*. Available at: <http://FieldGuide.mt.gov/speciesDetail.aspx?elcode=AMAJF03010> Last accessed July 31, 2017.
- Moriarty, K.M., W.J. Zielinski, A.G. Gonzales, T.E. Dawson, K.M. Boatner, C.A. Wilson, F.V. Schlexer, K.L. Pilgrim, J.P. Copeland, and M.K. Schwartz. 2009. Wolverine confirmation in California after nearly a century: native or long-distance immigrant? *Northwest Science* 83(2):154–162.
- Myhr, T-M. 2015. Movement pattern of wolverine females around the den during the denning period. BSc. Swedish University of Agricultural Sciences (SLU) (in Swedish). Translated by Ann Olsson.
- Myhre, R. and S. Myrberget. 1975. Diet of wolverines (*Gulo gulo*) in Norway. *Journal of Mammalogy* 56:752–757.

- [NPS] National Park Service. 2017. Superintendent's Compendium, Grand Teton National Park & John D. Rockefeller, Jr. Memorial Parkway. Dated May 19, 2017. Available at: <https://www.nps.gov/grte/learn/management/upload/2017-Superintendent-s-Compendium-FINAL-For-Web.pdf> Last accessed August 17, 2017.
- [NRC] National Research Council. 2013. Abrupt impacts of climate change: anticipating surprises. Committee on Understanding and Monitoring Abrupt Climate Change and Its Impacts; Board on Atmospheric Sciences and Climate; Division on Earth and Life Studies. The National Academies Press; Washington, D.C. 250 pp.
- [NWS] National Oceanic and Atmospheric Administration, National Weather Service. 2015. Introduction to Teleconnection, Northern Hemisphere Teleconnection Patterns. Available at: <http://www.cpc.ncep.noaa.gov/data/teledoc/teleintro.shtml>. Last accessed August 17, 2015.
- Nead, D.M., J.C. Halfpenny, and S. Bissell. 1985. The status of wolverines in Colorado. *Northwest Science* 8(4):286–289.
- Novikov, G.A. 1962. Carnivorous mammals of the fauna of the USSR. Translation of the Russian book, Keys to the fauna of the USSR published by the Zoological Institute of the Academy of Sciences of the USSR, No.62 (1956) (translated by A. Birron and Z.S. Cole). Israel Program for Scientific Translations, Ltd.; Jerusalem, Israel.
- Oftedal, O. T. and J. L. Gittleman. 1989. Patterns of energy output during reproduction in carnivores. Pp. 355–378 in *Carnivore Behaviour, Ecology, and Evolution*, Volume 1 [J. L. Gittleman (ed.)]. Cornell University Press; Ithaca, New York.
- Olsson, F., Laikre, L., Hössjer, O. and Ryman, N. 2017. GESP: A computer program for modelling genetic effective population size, inbreeding and divergence in substructured populations. *Molecular Ecology Resources* 00:1–7. <https://doi.org/10.1111/1755-0998.12673>
- [ODFW] Oregon Department of Fish and Wildlife. 2016. Oregon Conservation Strategy. Available online at: <http://www.oregonconservationstrategy.org/> Last accessed July 31, 2017.
- _____. 2017. Oregon Wildlife Species: Wolverine. Available online at: http://www.dfw.state.or.us/species/mammals/weasels_skunks_badgers_otters.asp Last accessed July 31, 2017.
- Packila, M.L., R.M. Inman, K.H. Inman, and A.J. McCue. 2007. Wolverine road crossings in western Greater Yellowstone. Chapter 7 in *Greater Yellowstone Wolverine Study, Cumulative Progress Report*. Dated May 2007. Wildlife Conservation Society, North America Program, General Technical Report; Bozeman, Montana.

- Parr, B.L. 2016. 2015 Alaska Trapper Report: 1 July 2015–30 June 2016. Alaska Department of Fish and Game, Division of Wildlife Conservation, Wildlife Management Report ADF&G/DWC/WMR-2016-1. Juneau, Alaska.
- Pasitschniak-Arts, M. and S. Larivière. 1995. *Gulo gulo*, Mammalian Species. The American Society of Mammalogists 499:1–10.
- Persson, J., T. Willebrand, A. Landa, R. Andersen, and P. Segerström. 2003. The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. *Wildlife Biology* 9:21–28.
- Persson, J., A. Landa, R. Andersen, and P. Segerström. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87(1):75–79.
- Persson, J., G. Ericsson, and P. Segerström. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142:325–331.
- Persson, J., P. Wedholm, and P. Segerstrom. 2010. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife Research* 56:49–57.
- Persson, J., M. Aronsson, H. Andrén, and M. Low. 2017. Reproductive timing and denning behaviour of female wolverines in relation to resource availability and population monitoring. Submitted manuscript.
- Petersen, S., J. Bell, S. Hauser, H. Morgan, M. Krosby, D. Rudd, D. Sharp, K. Dello, and L. Whitley Binder. 2017. Upper Snake River Climate Change Vulnerability Assessment. Upper Snake River Tribes Foundation and Member Tribes. Available at: <http://www.uppersnakerivertribes.org/climate/>
- Pierce, D.W., T. Das, D.R. Cayan, E.P. Maurer, N.L. Miller, Y. Bao, M. Kanamitsu, K. Yoshimura, M.A. Snyder, L.C. Sloan, G. Franco, and M. Tyree. 2013. Probabilistic estimates of future changes in California temperature and precipitation using statistical and dynamical downscaling. *Climate Dynamics* 40:839–856.
- Post, E. 2013. *Ecology of Climate Change: The Importance of Biotic Interactions*. Princeton University Press; Princeton, New Jersey.
- Pruitt, W.O., Jr. 1959. Snow as a factor in the winter ecology of the barren ground caribou (*Rangifer arcticus*). *Arctic* 12(3):158–179. <http://www.jstor.org/stable/40506822>.
- Pruitt, W.O., Jr. 2005. Why and how to study a snowcover. *Canadian Field Naturalist* 119(1): 118–128.
- Pulliainen, F. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. *Annales Zoologici Fennici* 5(4):338–344.

- Pulliainen, E. and P. Ovaskainen. 1975. Territory marking by a wolverine (*Gulo gulo*) in northeastern Lapland. *Annales Zoologici Fennici* 12(4):268–270.
- Quick, H. F. 1952. Some characteristics of wolverine fur. *Journal of Mammalogy* 33(4): 492–493.
- R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Version 3.1.2. URL: <http://www.R-project.org>.
- Rausch, R. 1953. On the status of some Arctic mammals. *Arctic* 6(2):91–148.
- Rausch, R.L. 1959. Studies on the helminth fauna of Alaska. XXXVI. Parasites of the wolverine, *Gulo gulo* L., with observations on the biology of *Taenia twitchelli* Schwartz, 1924. Faculty Publications from the Harold W. Manter Laboratory of Parasitology. Paper 583. Available at <http://digitalcommons.unl.edu/parasitologyfacpubs/583>
- Rausch, R. 1959. Studies on the helminth fauna of Alaska, Volume 36, Parasites of the wolverine *Gulo gulo* L., with observations on the biology of *Taenia twitchelli* Schwartz, 1924. *Journal of Parasitology* 45:465–484.
- Rausch, R.A and A.M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon Territory. *Journal of Wildlife Management* 36:249–268.
- Rauset, G.R., M. Low, and J. Persson. 2015. Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology* 96:3153–3164.
- Ray, A.L., J.J. Barsugli, B. Livneh, C.F. Dewes, I. Rangwala, A. Heldmyer, and J. Stewart. 2017. Future Snow Persistence in Rocky Mountain and Glacier National Parks: An Analysis to Inform the USFWS Wolverine Species Status Assessment. Prepared by NOAA/ESRL/Physical Sciences Division, CU/Cooperative Institute for Research in Environmental Sciences (CIRES) and CU Civil, Environmental & Architectural Engineering. Dated September 7, 2017.
- Regehr, H. and D. Lacroix. 2016. Unexpectedly high detections of wolverine (*Gulo gulo*) in southwestern British Columbia. *Northwestern Naturalist* 97:246–251.
- Rico, Y., J.Morris-Pocock, J. Zigouris, J.J. Nocera, and C.J. Kyle. 2015. Lack of spatial immunogenetic structure among wolverine (*Gulo gulo*) populations suggestive of broad scale balancing selection. *PLoS ONE* 10(10):e0140170.
- Rieger, I. 1979. Scent rubbing in carnivores. *Carnivore* 2(1):17–25.

- Robert, A., V. H. Paiva, M. Bolton, F. Jiguet, and J. Bried. 2012. The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. *Ecology* 93:1944–1952.
- Rogers, R.A., L.A. Rogers, R.S. Hoffman, and L.D. Martin. 1991. Native American biological diversity and the biogeographic influence of Ice Age refugia. *Journal of Biogeography* 18:623–630.
- Rogers, L.A., and D.E. Schindler. 2011. Scale and the detection of climatic influences on the productivity of salmon populations. *Global Change Biology* 17:2546–2558.
- Røskoft, E. 1990. Jerven. Pp. 152–164 in *Norges Dyr. Pattedyren I* [A. Semb-Johansson and E. Frislid (eds.)]. Cappelen, Oslo. [not seen, cited according to Bevanger 1992]
- Rowland, M.M., M.J. Wisdom, D.H. Johnson, B.C. Wales, J.P. Copeland, and F.B. Edelman. 2003. Evaluation of landscape models for wolverines in the interior Northwest, United States of America. *Journal of Mammalogy* 84(1):92–105.
- Royle, J.A., A.J. Magoun, B. Gardner, P. Valkenburg, and R.E. Lowell. 2011. Density estimation in a wolverine population using spatial capture–recapture models. *The Journal of Wildlife Management* 75(3):604–611. doi: 10.1002/jwmg.79.
- Ruggiero, L.F., W.J. Zielinski, K.B. Aubry, S.W. Buskirk, and L. J. Lyon. 1994. A conservation assessment framework for forest carnivores. Pp. 1–6 in *The Scientific Basis for Conserving Forest Carnivores: American marten, fisher, lynx, and wolverine in the western United States*. [L.F. Ruggiero et al. (tech. eds.)]. General Technical Report RM-254. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; Fort Collins, Colorado. 184 pp.
- Rupp, D.E., J.T. Abatzoglou, and P.W. Mote. 2016. Projections of 21st century climate of the Columbia River Basin. *Climate Dynamics* 49:1783–1799.
- Ruth, F.S. 1954. Wolverine seen in Squaw Valley, California. *Journal of Mammalogy* 35(4):594–595.
- Sadleir, R.M.F.S. 1984. Ecological consequences of lactation. *Acta Zoologica Fennica* 171:179–182.
- Sæther, B.-E., S. Engen, J. Persson, H. Broseth, A. Landa, and T. Willebrand. 2005. Management strategies for the wolverine in Scandinavia. *Journal of Wildlife Management* 69:1001–1014.
- Scholander, P.F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950a. Heat regulation in some Arctic and tropical mammals and birds. *The Biological Bulletin* 99(2):237–258.

- Scholander, P.F., V. Walters, R. Hock, and L. Irving. 1950b. Body insulation of some Arctic and tropical mammals and birds. *The Biological Bulletin* 99(2):225–236. doi:10.2307/1538740.
- Schwartz, M.K., K.B. Aubry, K.S. McKelvey, K.L. Pilgrim, J.P. Copeland, J.R. Squires, R.M. Inman, S.M. Wisely, and L.F. Ruggiero. 2007. Inferring geographic isolation in wolverines in California using historical DNA. *Journal of Wildlife Management* 71(7):2170–2179.
- Schwartz, M.K., J.P. Copeland, N.J. Anderson, J.R. Squires, R.M. Inman, K.S. McKelvey, K.L. Pilgrim, L.P. Waits, and S.A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90(11):3222–3232.
- Scrafford, M.A., T. Avgar, B. Abercrombie, J. Tigner, and M.S. Boyce. 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. *Forest Ecology and Management* 395:27–36. <http://dx.doi.org/10.1016/j.foreco.2017.03.029>
- Seton, E.T. 1909. *Life-Histories of Northern Animals: An Account of the Mammals of Manitoba. Volume II. Flesheaters.* Charles Scribner's Sons; New York, New York.
- Sheehan, T., D. Bachelet, and K. Ferschweiler. 2015. Projected major fire and vegetation changes in the Pacific Northwest of the conterminous United States under selected CMIP5 climate futures. *Ecological Modelling* 317:16–29.
- Shilo, R.A. and M.A. Tamarovskaya. 1981. The growth and development of wolverines (*Gulo gulo*) at Novosibirsk Zoo. *International Zoo Yearbook* 21:146–147. doi:10.1111/j.1748-1090.1981.tb01969.x
- Shukla, S., M. Safeeq, A. AghaKouchak, K. Guan, and C. Funk. 2015. Temperature impacts on the water year 2014 drought in California. *Geophysical Research Letters* 42:4384–4393. doi:10.1002/2015GL063666.
- Sieck, M., P.L. Ibisch, K.A. Moloney, and F. Jeltsch. 2011. Current models broadly neglect specific needs of biodiversity conservation in protected areas under climate change. *BMC Ecology* 22:1–12. <http://www.biomedcentral.com/1472-6785/11/12>
- Slough, B.G. and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. *The Journal of Wildlife Management* 60(4):946–961.
- Slough, B.G., R.H. Jessup, D.I. McKay, and A.B. Stephenson. 1987. Wild furbearer management in western and northern Canada. Pp. 1,062–1,076 in *Wild Furbearer Management and Conservation in North America* [M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch (eds.)]. Ontario Trappers Association; North Bay, Ontario.

- Stewart, F.E.C., N.A. Heim, A.P. Clevenger, J. Paczkowski, J.P. Volpe, and J.T. Fisher. 2016. Wolverine behavior varies spatially with anthropogenic footprint: implications for conservation and inferences about declines. *Ecology and Evolution* 6(5):1493–1503. doi:10.002/ece3.1921.
- Stewart, J.A.E, D.H. Wright, and K.A. Heckman. 2017. Apparent climate-mediated loss and fragmentation of core habitat of the American pika in the Northern Sierra Nevada, California, USA. *PLoS ONE* 12(8): e0181834. <https://doi.org/10.1371/journal.pone.0181834>
- Stocker, T.F., D. Qin, G-K Plattner, L.V. Alexander, S.K. Allen, N.L. Bindoff, F-M. Bréon, J.A. Church, U. Cubasch, S. Emori, P. Forster, P. Friedlingstein, N. Gillett, J.M. Gregory, D.L. Hartmann, E. Jansen, B. Kirtman, R. Knutti, K. Krishna Kumar, P. Lemke, J. Marotzke, V. Masson-Delmotte, G.A. Meehl, I.I. Mokhov, S. Piao, V. Ramaswamy, D. Randall, M. Rhein, M. Rojas, C. Sabine, D. Shindell, L.D. Talley, D.G. Vaughan, and S-P. Xie. 2013. Technical Summary. *In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA. 84 pp.
- Sullivan, T.P. 1986. Influence of wolverine (*Gulo gulo*) odor on feeding behavior of snowshoe hares (*Lepus americanus*). *Journal of Mammology* 67(2):385–388.
- Sullivan, T.P., L.O. Nordstrom, and D.S. Sullivan. 1985. Use of predator odors as repellents to reduce feeding damage by herbivores II. Black-tailed deer. *Journal of Chemical Ecology* 11(7):921–934.
- Telfer, E. S. and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology* 65:1828–1834.
- Thackeray, C.W. and C.G. Fletcher. 2016. Snow albedo feedback: current knowledge, importance, outstanding issues and future directions. *Progress in Physical Geography* 40(3):392–408.
- Tomasik, E. and J.A. Cook. 2005. Mitochondrial phylogeography and conservation genetics of wolverine (*Gulo gulo*) of northwestern North America. *Journal of Mammology* 86(2):386–396.
- Townsend, C.W (editor). 1911. Captain Cartwright and His Labrador Journal. Dana Estes & Company; Printed by the Colonial Press; Boston, Massachusetts.

- Utah Wildlife Action Plan Joint Team. 2015. Utah Wildlife Action Plan: A plan for managing native wildlife species and their habitats to help prevent listing under the Endangered Species Act. Publication number 15-14. Utah Division of Wildlife Resources, Salt Lake City, Utah.
- Vangen, K.M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79(9):1641–1649.
- van Zyll de Jong, C.G. 1975. The distribution and abundance of the wolverine (*Gulo gulo*) in Canada. *Canadian Field-Naturalist* 89(4):431–437.
- [WAFWA] Western Association of Fish & Wildlife Agencies. 2017. Wolverine Conservation in the Western United States. The Western States Wolverine Working Group. Presented at WAFWA meeting, July 2017.
- Walsh, J., D. Wuebbles, K. Hayhoe, J. Kossin, K. Kunkel, G. Stephens, P. Thorne, R. Vose, M. Wehner, J. Willis, D. Anderson, S. Doney, R. Feely, P. Hennon, V. Kharin, T. Knutson, F. Landerer, T. Lenton, J. Kennedy, and R. Somerville. 2014. Chapter 2 in Melillo, J.M., T.C. Richmond, and G.W. Yohe (eds.), *Our Changing Climate*. Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program.
- Walton, D.B., A. Hall, N. Berg, M. Schwartz, and F. Sun. 2017. Incorporating snow albedo feedback into downscaled temperature and snow cover projections for California's Sierra Nevada. *Journal of Climate* 30(4):1417–1438.
- Wang, G., N. Thompson Hobbs, F. J. Singer, D. S. Ojima, and B. C. Lubow. 2002. Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, U.S.A. *Climate Change* 54:205–223.
- Wang, J., E. Santiago, and A. Caballero. 2016. Prediction and estimation of effective population size. *Heredity* 117:193–206.
- Waples, R.S. 2016. Making sense of genetic estimates of effective population size. *Molecular Ecology* 25(19):4689–4691.
- [WDFW] Washington Department of Fish and Wildlife. 2013. Threatened and Endangered Wildlife in Washington: 2012 Annual Report. Listing and Recovery Section, Wildlife Program, Washington Department of Fish and Wildlife; Olympia, Washington. 251 pp.
- _____. 2015. Washington's State Wildlife Action Plan: 2015 Update. Washington Department of Fish and Wildlife; Olympia, Washington.
- Webb, S.M., R. B. Anderson, D.L. Manzer, B. Abercrombie, B. Bildson, M.A. Scrafford, and M.S. Boyce. 2016. Distribution of female wolverines relative to snow cover, Alberta, Canada. *The Journal of Wildlife Management* 80(8):1461–1470.

doi:10.1002/jwmg.21137.

[WGFD] Wyoming Game and Fish Department. 2017. Wyoming State Wildlife Action Plan–2017.

White, J. A, H. G. McDonald, E. Anderson, and J. M. Soiset. 1984. Lava blisters and carnivore traps. Pp. 241–256 in *Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday* [H.H. Genoways and M.R. Dawson (eds.)], Special Publication of the Carnegie Museum of Natural History Number 8; Pittsburgh, PA.

White, K.S., H.N. Golden, K.J. Hundertmark, and G.R. Lee. 2002. Predation of wolves, *Canis lupis*, on wolverines, *Gulo gulo*, and an American marten, *Martes americana*, in Alaska. *Canadian Field-Naturalist* 116(1):132–134.

Whitlock, C., W. Cross, B. Maxwell, N. Silverman , and A.A. Wade AA. 2017. 2017 Montana Climate Assessment. Bozeman and Missoula Montana; Montana State University and University of Montana, Montana Institute on Ecosystems. 318 p. Available at <http://montanaclimate.org/chapter/title-page>. doi:10.15788/m2ww8w.

Williams, A.P., R. Seager, J.T. Abatzoglou, B.I. Cook, J.E. Smerdon, and E.R. Cook. 2015. Contribution of anthropogenic warming to California drought during 2012–2014. *Geophysical Research Letters* 42:6819–6828.

Wilson, D.E. 1982. Wolverine (*Gulo gulo*). Pp. 644–652 in *Wild Mammals of North America, Biology, Ecology, and Management* [J.A. Chapman and G.A. Feldhamer (eds.)]. The Johns Hopkins University Press; Baltimore, Maryland.

Wilson, S.D. and C. Nilsson. 2009. Arctic alpine vegetation change over 20 years. *Global Change Biology* 15:1676–1684. doi:10.1111/j.1365-2486.2009.01896.x

Wobus, C., E.E. Small, H. Hosterman, D. Mills, J. Stein, M. Rissing, R. Jones, M. Duckworth, R. Hall, M. Kolian, J. Creason, and J. Martinich. 2017. Projected climate change impacts on skiing and snowmobiling: a case study of the United States. *Global Environmental Change* 45:1–14.

Wolf, S., B. Hartl, C. Carroll, M.C. Neel, and D.N. Greenwald. 2015. Beyond PVA: why recovery under the Endangered Species Act is more than population viability. *Bioscience* 65:200–207.

Wolverine Science Panel. 2014. Wolverine Science Panel Workshop Report. April 3–4, 2014. Spokane, Washington.

Woodford, R. 2014. *Wolverines: Behind the Myth*. Alaska Fish and Wildlife News. December 2014. Published by Alaska Department of Fish and Game. Available at: http://www.adfg.alaska.gov/index.cfm?adfg=wildlifefews.view_article&articles_id=692 Last accessed February 3, 2017.

- Woodford, R. and K. Beckham. 2012. *Rabies in Alaska: Rabid Wolverine Found on North Slope*. Alaska Fish and Wildlife News. December 2012. Published by Alaska Department of Fish and Game. Available at: http://www.adfg.alaska.gov/index.cfm?adfg=wildlifeneews.view_article&articles_id=582 Last accessed July 26, 2017.
- Wozencraft, W.C. 2008. Species—*Gulo gulo*. Wilson & Reeder's Mammal Species of the World (3rd ed.). Smithsonian National Museum of Natural History. Online publication date June 1, 2008.
- [WRCC] Western Regional Climate Center. 2017. California Climate Tracker Reports, Northeast Region, California. Available at http://www.wrcc.dri.edu/monitor/cal-mon/frames_version.html. Downloaded July 20, 2017.
- Wright, J.D. and J. Ernst. 2004a. Effects of mid-winter snow depth on stand selection by wolverines, *Gulo gulo luscus*, in the boreal forest. Canadian Field-Naturalist 118(1):56–60.
- Wright, J.D. and J. Ernst. 2004b. Wolverine, *Gulo gulo luscus*, resting sites and caching behavior in the boreal forest. Canadian Field-Naturalist 118(1):64–64.
- Yates, R. E. and J.P. Copeland. Food habits of wolverines in Glacier National Park, Montana. *In prep* manuscript.
- Young, J.K., B. Hudgens, and D.K. Garcelon. 2012. Estimates of Energy and Prey Requirements of Wolverines. USDA National Wildlife Research Center – Staff Publications. Paper 1219. http://digitalcommons.unl.edu/icwdm_usdanwrc/1219.
- Zigouris, J., F.N. Dawson, J. Bowman, R.M. Gillett, J.A. Schaefer, and C.J. Kyle. 2012. Genetic isolation of wolverine (*Gulo gulo*) populations at the eastern periphery of their North American distribution. Conservation Genetics 13:1543–1559.
- Zigouris, J., J.A. Schaefer, C. Fortin, and C.J. Kyle. 2013. Phylogeography and post-glacial recolonization in wolverines (*Gulo gulo*) from across their circumpolar distribution. PLoS ONE 8(12): e83837. doi:10.1371/journal.pone.0083837.
- Zigouris, J. 2014. Spatial and temporal genetic structure of wolverine populations. PhD Dissertation. Trent University; Peterborough, Ontario, Canada.

Federal Register Publications

- 77 FR 21162. April 9, 2012. National Forest System Land Management Planning; Final rule and record of decision. Forest Service, U.S. Department of Agriculture.

78 FR 7864. February 4, 2013. Endangered and Threatened Wildlife and Plants; Threatened Status for the Distinct Population Segment of the North American Wolverine Occurring in the Contiguous United States; Proposed Rule. Fish and Wildlife Service, Interior.

79 FR 47522. August 13, 2014. 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 Population of the North American Wolverine in Colorado, Wyoming, and New Mexico. Proposed Rules; Withdrawal. Fish and Wildlife Service, Interior.

81 FR 71670. October 16, 2016. Endangered and Threatened Wildlife and Plants; Proposed Rule for the North American Wolverine; Proposed rule; reopening of comment period. Fish and Wildlife Service, Interior.

Personal Communications

Anglin, R. 2013. Letter received from Ron Anglin, Wildlife Division Administrator, Oregon Department of Fish and Wildlife, in response to proposed rule to list the North American wolverine (78 FR 7864; February 4, 2013). May 6, 2013.

Broscheid, B.D. 2016. Letter received from Bob Broscheid, Director, Colorado Parks and Wildlife, in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 17, 2016.

Buell Environmental. 2016. Letter received from Buell Environmental LLC (Oak Creek Colorado), in response in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 15, 2016.

Burkett, E. 2017. Electronic mail message from Esther Burkett, Senior Environmental Scientist, California Department of Fish and Wildlife, re wolverine permitting, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. July 28, 2017.

Copeland, J.P. 2017. Telephone conversation between Jeff Copeland re wolverine biology to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. January 13, 2017.

Davis, C. 2017. Electronic mail message from Cory Davis, SWCC Coordinator, University of Montana, with notes from Meso-Carnivore Monitoring Workshop (April 5-7, 2017), to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. August 16, 2017.

Dewey, S. 2017. Electronic mail message from Sarah Dewey, Wildlife Biologist, Grand Teton National Park, National Park Service, re wolverine detections, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. August 17, 2017.

- Edmo, B. 2016. Letter received from Blaine Edmo, Chairman, Shoshone-Bannock Tribes, (submitted on behalf of the Fort Hall Business Council) in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 2, 2016.
- Golden, H. 2017. Electronic mail message from Chris Krenz, Wildlife Science Coordinator, Alaska Department of Fish & Game, with wolverine density estimate information from Howard Golden, Region 2 Supervisor, Division of Wildlife Conservation, Alaska Department of Fish & Game, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. April 6, 2017.
- Harrower, B. 2017. Electronic mail message from Bill Harrower, Lead Biologist, High-Country Wildlife Ltd., re wolverine population structure in Canada, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. October 5, 2017.
- Heinemeyer, K. 2016. Letter and reports received from Kim Heinemeyer, Lead Conservation Scientist, Round River Conservation Studies, in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 16, 2016.
- Hersey, K. 2017. Electronic mail message from Kim Hersey, Utah Division of Wildlife, regarding wolverine road mortality in Utah, to Ed Turner, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. April 5, 2017.
- Idaho Department of Fish and Game. 2013. Letter received from Idaho Department of Fish and Game in response to proposed rule to list the North American Wolverine Distinct Population Segment as threatened under the Endangered Species Act (78 FR 7864; February 4, 2013). May 6, 2013.
- Idaho Department of Fish and Game. 2016. Letter received from Idaho Department of Fish and Game in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 17, 2016.
- Inman, R.M. 2012. Electronic mail message from Robert Inman, Director, Greater Yellowstone Wolverine Program, Wildlife Conservation Society, re trapping of female wolverine (F421) in Wyoming, to Shawn Sartorius, U.S. Fish and Wildlife Service, Montana Field Office, Helena, Montana. December 4, 2012.
- Inman, R.M. 2013. Peer review comments submitted by Robert Inman on proposed rule to list the North American wolverine (78 FR 7864; February 4, 2013). May 2013.

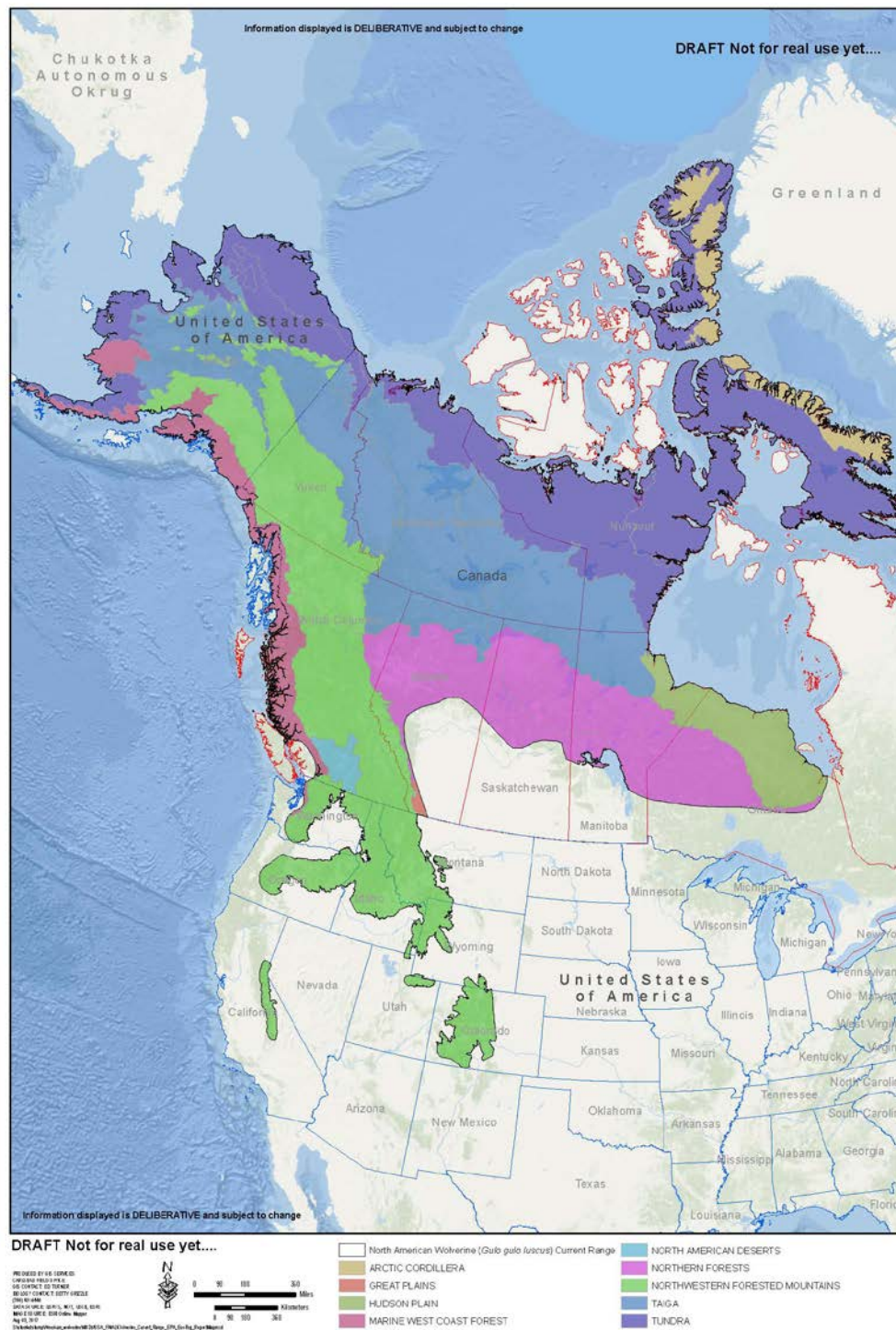
- Inman, R.M. 2017a. Electronic mail message from Robert Inman, Carnivore-Furbearer Coordinator, Montana Fish, Wildlife & Parks, re wolverine road mortalities, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. June 29, 2017.
- Inman, R.M. 2017b. Electronic mail message from Robert Inman, Carnivore-Furbearer Coordinator, Montana Fish, Wildlife & Parks re wolverine detections and summary of winter survey results, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. August 14, 2017.
- Inman, R.M. 2017c. Electronic mail message from Robert Inman, Carnivore-Furbearer Coordinator, Montana Fish, Wildlife & Parks re incidental trapping of wolverines in Montana, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. October 23, 2017.
- Kuennen, R. 2017. Electronic mail message from M. Reed Kuennen, Wildlife Biologist, USDA Forest Service, Flathead National Forest, re clarifications in Final EIS, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. September 11, 2017.
- Mack, D. 2017a. Electronic mail message from Diane Evans Mack, Regional Wildlife Diversity Biologist, Idaho Department of Fish and Game re wolverine detections in Idaho, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. September 7 and September 13, 2017.
- Mack, D. 2017b. Electronic mail message from Diane Evans Mack, Regional Wildlife Diversity Biologist, Idaho Department of Fish and Game re wolverine locations, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. September 13, 2017.
- Magoun, A.J. 2013. Peer review comments (including attachments) submitted by Audrey J. Magoun on proposed rule to list the North American wolverine (78 FR 7864; February 4, 2013). May 2013.
- Magoun, A. J. 2017. Telephone conversation between Audrey Magoun, re wolverine behavior and life history, with Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. January 26, 2017.
- Mead, M.H. 2013. Letter received from Matthew H. Mead, Governor, State of Wyoming, in response to proposed rule to proposed rule to list the North American Wolverine Distinct Population Segment as threatened under the Endangered Species Act (78 FR 7864; February 4, 2013). May 6, 2013.
- Miles, M.J. 2017. Letter received from Mary Jane Miles, Chairman, Nez Perce Tribe, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. January 27, 2017.

- Montana Fish, Wildlife, & Parks. 2016. Letter and documents received from Montana Fish, Wildlife, & Parks, in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 15, 2016.
- Parr, B. 2017. Electronic mail message from Brynn Parr, Permitting Biologist, Alaska Department of Fish & Game, re wolverine population estimates in Alaska, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. October 6, 2017.
- Persson, J. 2017. Electronic mail message from Jens Persson, Associate Professor, Swedish University of Agricultural Sciences, re wolverine den locations in Sweden, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. May 10, 2017.
- Shufelberger, A. 2017. Electronic mail message from Amanda Shufelberger, Wildlife Biologist, Sierra Pacific Industries, re detection of wolverine in Sierra region in 2017, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. October 13, 2017.
- Scott, D. 2017. Telephone conversation between Douglas Scott, AvalancheMapping.org, Boulder, Colorado, re slope and avalanche risk, and John Guinotte, U.S. Fish and Wildlife Service, Rocky Mountain Regional Office, Lakewood, Colorado. January 16, 2017.
- Southwestern Crown of the Continent Working Group. 2016. Letter and summary report received by email from Cory Davis (Coordinator Southwestern Crown of the Continent Collaborative), Southwestern Crown of the Continent Working Group to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. December 9, 2016.
- Stermer, C. 2017. Electronic mail message from Chris Stermer, Nongame Wildlife Program, California Department of Fish and Wildlife, re wolverine status in California, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. February 6, 2017.
- Walker, Z. Electronic mail message from Zack Walker, Statewide Nongame Bird and Mammal Program Supervisor, Wyoming Game and Fish Department, re wolverine observations, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. August 16, 2017.
- Webb, S. 2017. Electronic mail message from Shevenell Webb, Wildlife Biologist, Alberta Conservation Association, re wolverine trapping information, to John Guinotte, Mountain Prairie Regional Office, U.S. Fish and Wildlife Service, cc to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. March 24, 2017.

- Weir, R. 2017. Electronic mail message from Rich Weir, Carnivore Conservation Specialist, Ministry of Environment, British Columbia, Canada, re wolverine population genetics project, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. March 9, 2017.
- Weir, R. 2017b. Electronic mail message from Rich Weir, Carnivore Conservation Specialist, Ministry of Environment, British Columbia, Canada, re wolverine trapping by region, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. October 6, 2017
- Weir, R. 2017c. Electronic mail message from Rich Weir, Carnivore Conservation Specialist, Ministry of Environment, British Columbia, Canada, re wolverine trapping, to Betty Grizzle, U.S. Fish and Wildlife Service, Carlsbad Fish and Wildlife Office. October 10, 2017
- [WGFD] Wyoming Game and Fish Department. 2016. Letter received from Wyoming Game and Fish Department in response to proposed rule reopening of comment period and request for information for North American wolverine (81 FR 71670; October 18, 2016). November 3, 2016.

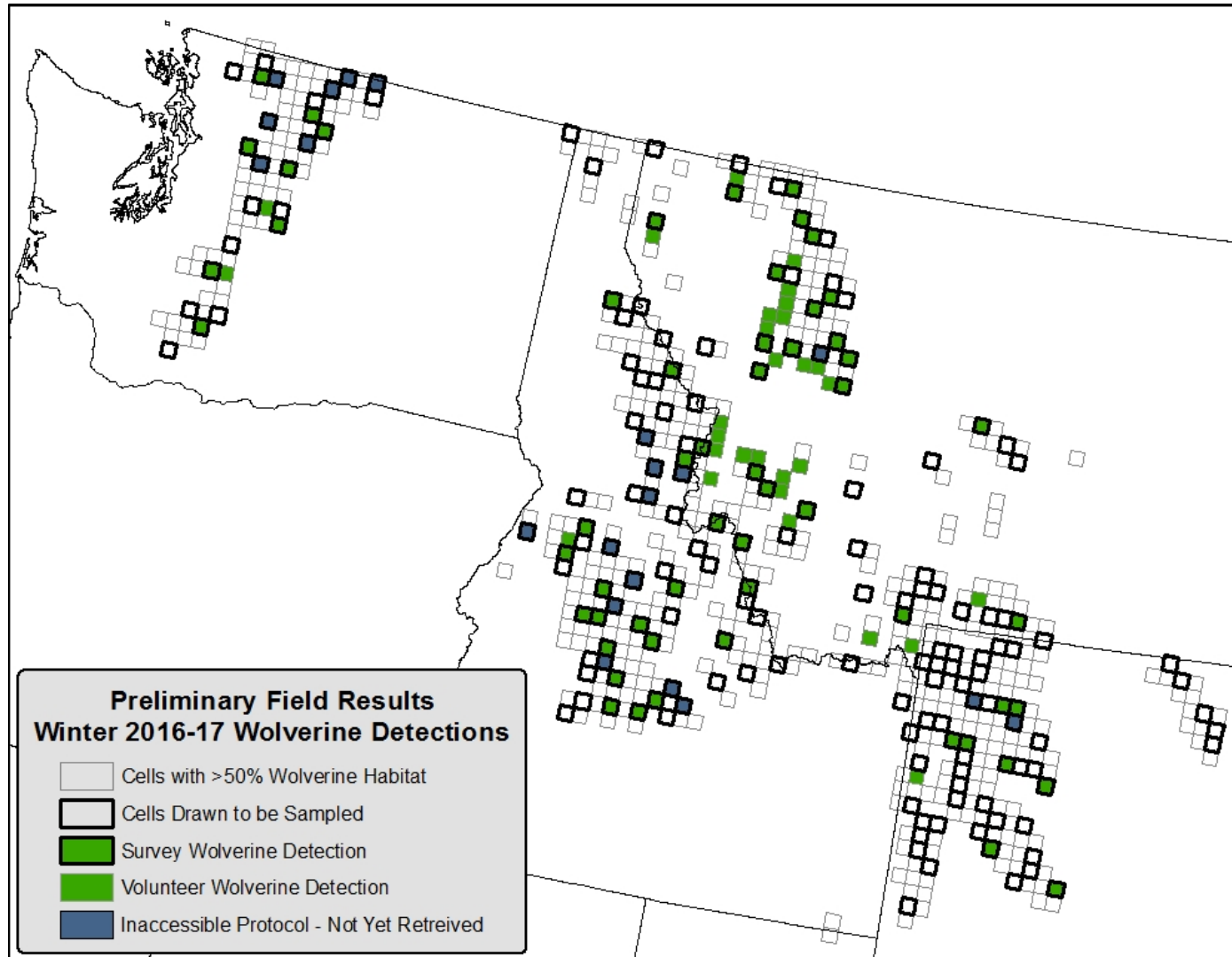
Appendices

Appendix A – Ecoregions of North American within Estimated Current Range of North American Wolverine
(Adapted from EPA 2010)



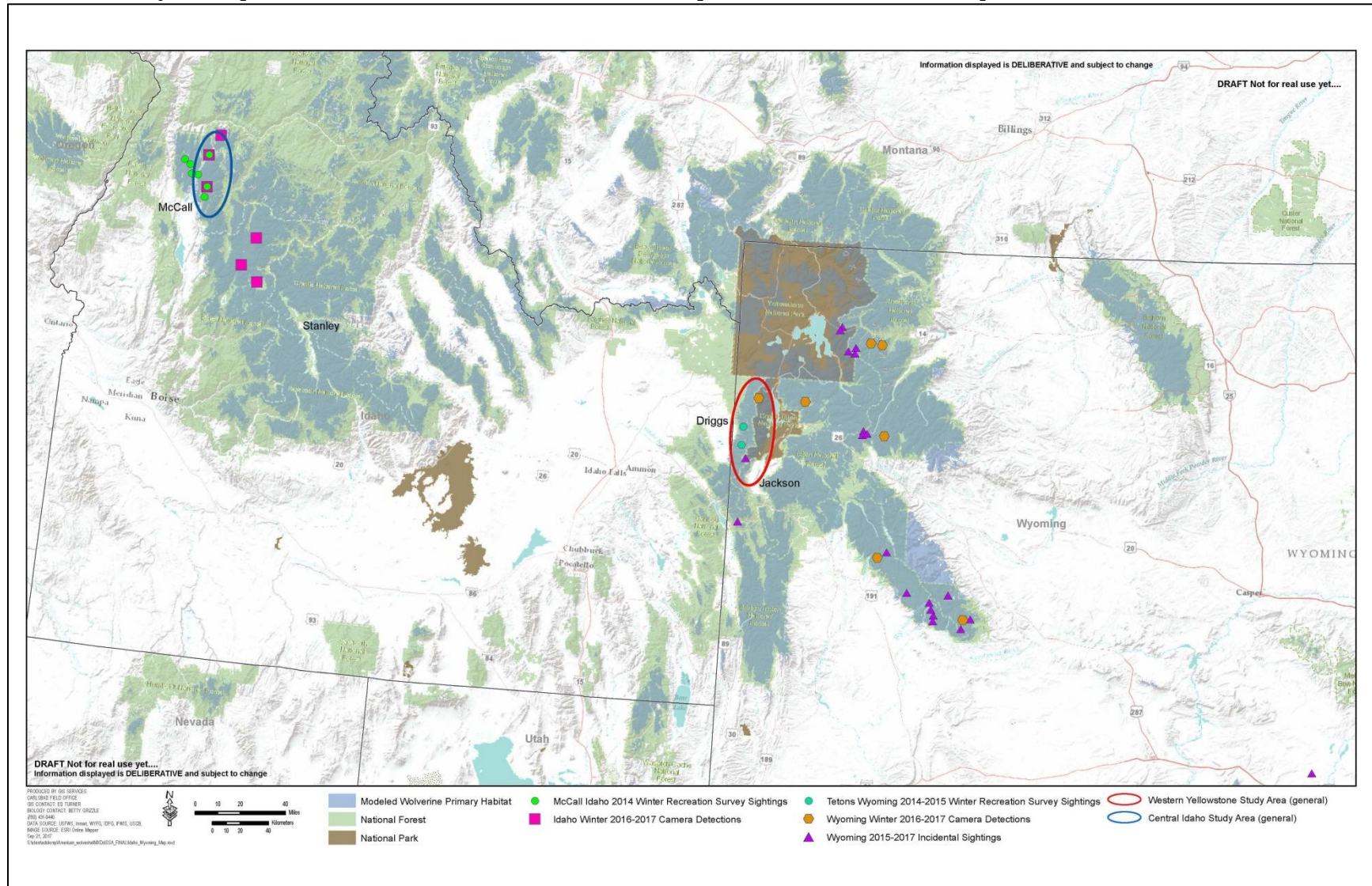
Appendix B – Wolverine Detections, Winter 2016–2017 (as of July 2017)

Source: Inman 2017b, pers. comm.



Appendix C – Recent Wolverine Detections, Idaho and Wyoming

Sources: Dewey 2017, pers. comm.; Evans Mack 2017a and 2017b, pers. comm.; Walker 2017, pers. comm.



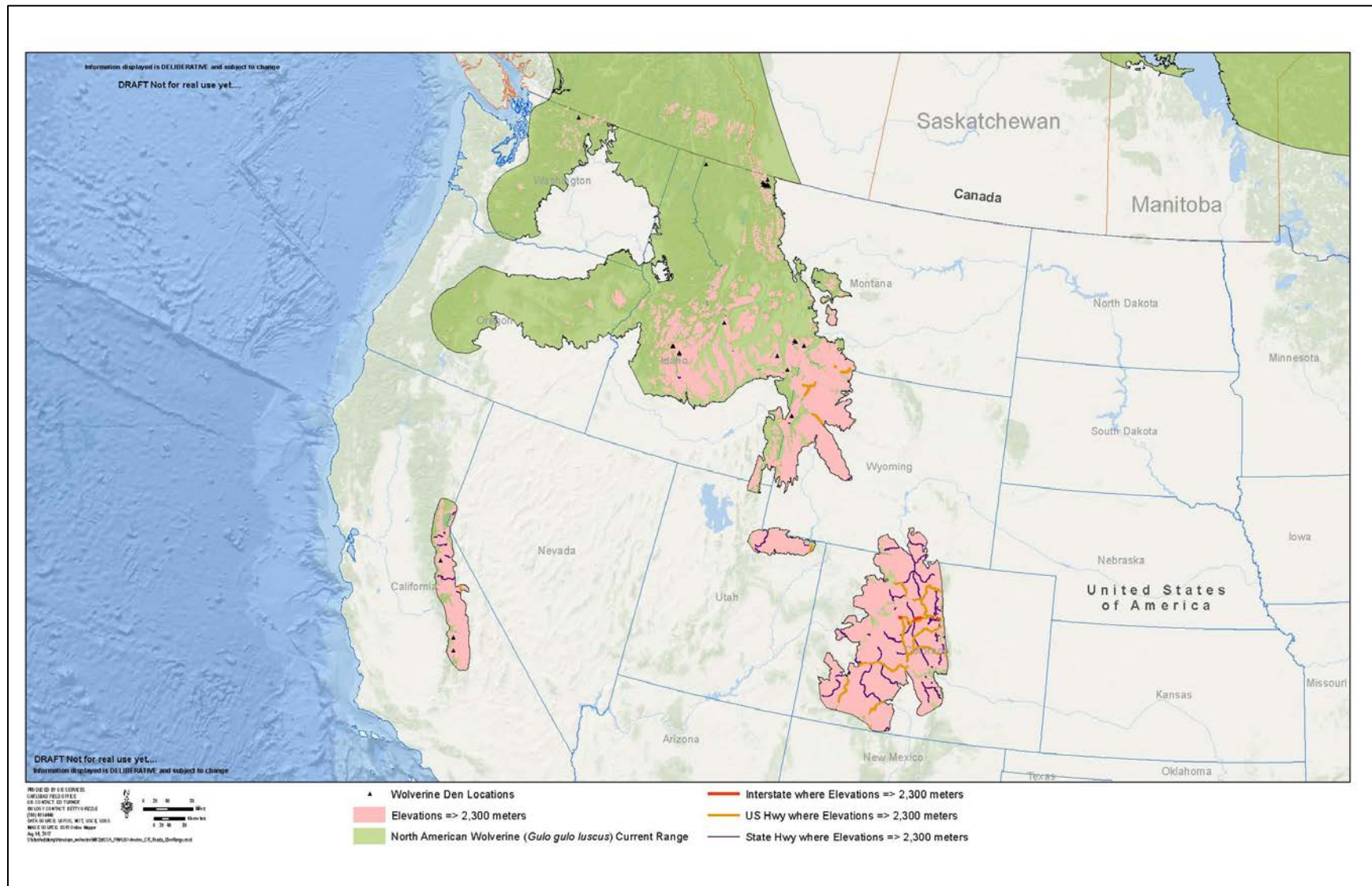
Appendix D – Land Ownership of Modeled Wolverine Primary Habitat in Contiguous United States

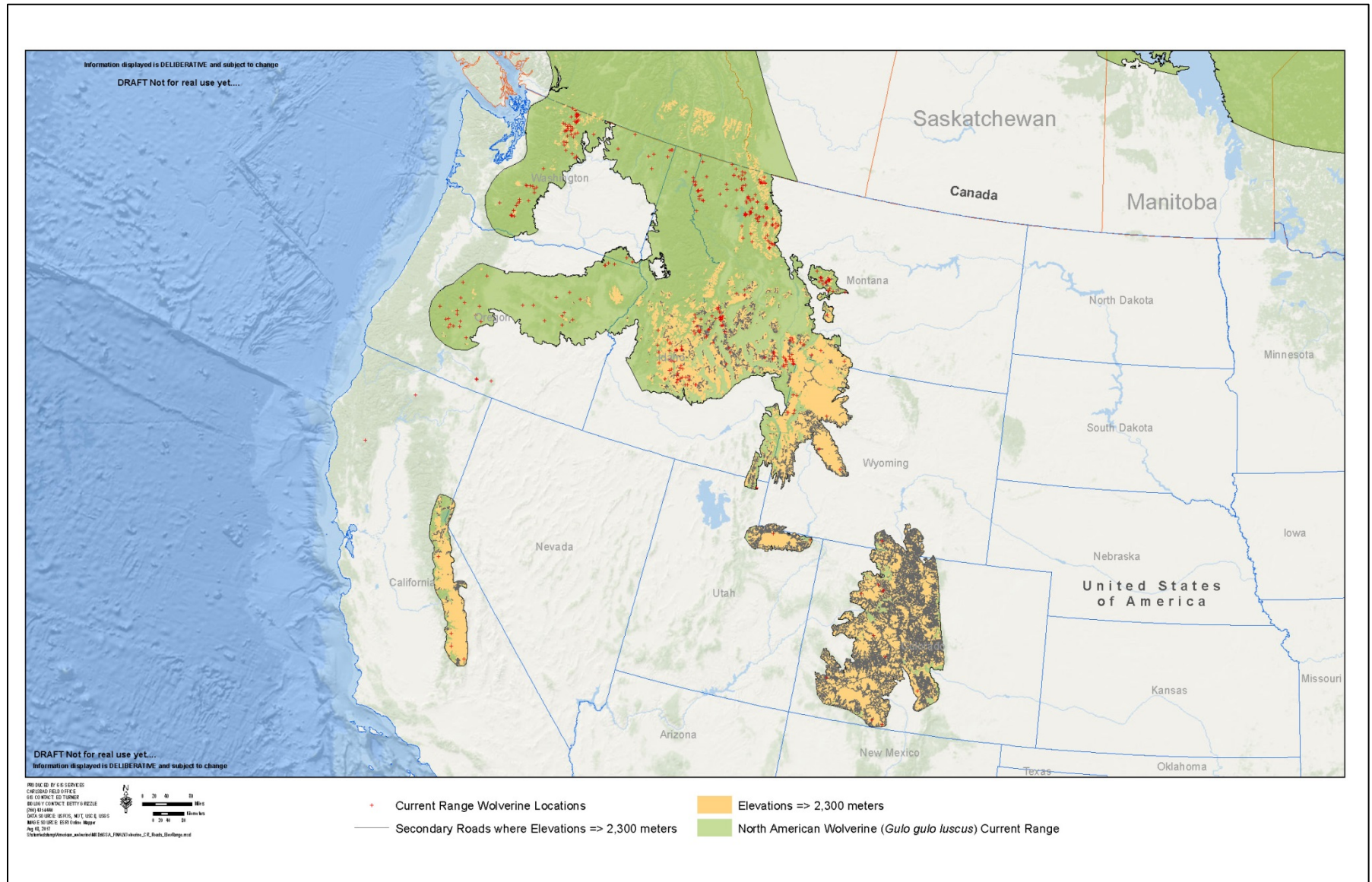
(based on model from Inman *et al.* 2013)

Ownership (% of total)	Agency or other Entity	Total (acres)	Total (hectares)
Federal Lands	Bureau of Indian Affairs	453,866	183,673
	Bureau of Land Management	498,977	201,929
	Bureau of Reclamation	1,868	756
	Forest Service	34,331,515	13,893,471
	U.S. Fish and Wildlife Service	5,528	2,237
	National Park Service	3,791,491	1,534,362
	Other U.S. Department of Agriculture	13,312	5,387
	Other Federal	0.05	0.02
Total Federal (96.4%)		39,096,557	15,821,815
State Lands (0.68%)	Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming	277,181	112,171
Local Government (0.12%)		49,464	20,017
Private Lands (2.63%)		1,064,858	430,933
No Code (“99”) (0.15%)		60,380	24,435
Undetermined (0.02%)		7,598	3,075
Total (100%)		40,556,038	16,412,446

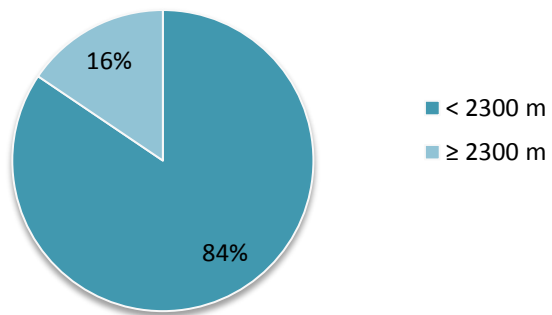
Note: Numbers may not total to 100 percent due to rounding.

Appendix E – Results from Spatial Analysis of Roads within Current Range of Wolverine

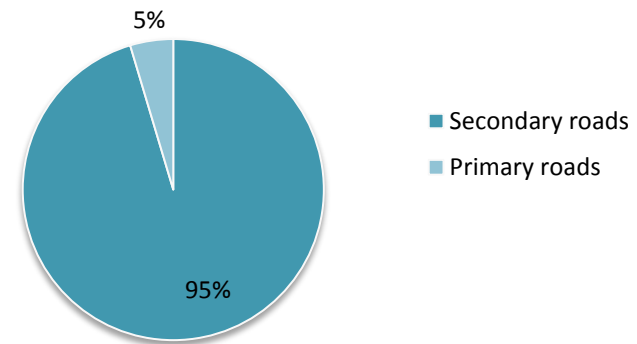




**Percent of Roads by Elevation
within Current Range**



**Percent of Roads by Type in
Current Range ≥ 2300 meters**



Appendix F – Road Closure Map, Grand Teton National Park

Retrieved from: <https://2v9usu38jb9t3l8big1alsn-wpengine.netdna-ssl.com/wp-content/uploads/2015/11/GTNP-closure-map.pdf>



Appendix G – Existing Regulatory Mechanisms and Voluntary Conservation Measures

Federal Mechanisms

Organic Administration Act of 1897 and the Multiple–Use, Sustained–Yield Act of 1960

The USFS Organic Act of 1897 (16 U.S.C. § 475–482) established general guidelines for administration of timber on USFS lands, which was followed by the Multiple–Use, Sustained–Yield Act (MUSY) of 1960 (16 U.S.C. § 528–531), which broadened the management of USFS lands to include outdoor recreation, range, watershed, and wildlife and fish purposes.

National Forest Management Act

The National Forest Management Act (NFMA) (16 U.S.C. § 1600 *et seq.*) requires the Forest Service to develop a planning rule under the principles of the MUSY of 1960 (16 U.S.C. § 528–531). The NFMA outlines the process for the development and revision of the land management plans and their guidelines and standards (16 U.S.C. § 1604(g)).

A new National Forest System (NFS) land management planning rule (Planning Rule) was adopted by the U.S. Department of Agriculture Forest Service (Forest Service) in 2012 (77 FR 21162; April 9, 2012). The new Planning Rule guides the development, amendment, and revision of land management plans for all units of the NFS to maintain and restore NFS land and water ecosystems while providing for ecosystem services and multiple uses. Land management plans (also called Forest Plans) are designed to: (1) Provide for the sustainability of ecosystems and resources; (2) meet the need for forest restoration and conservation, watershed protection, and species diversity and conservation; and (3) assist the Forest Service in providing a sustainable flow of benefits, services, and uses of NFS lands that provide jobs and contribute to the economic and social sustainability of communities (77 FR 21261, April 9, 2012). A land management plan does not authorize projects or activities, but projects and activities must be consistent with the plan (77 FR 21261; April 9, 2012). The plan must provide for the diversity of plant and animal communities including species-specific plan components in which a determination is made as to whether the plan provides the “ecological conditions necessary to...contribute to the recovery of federally listed threatened and endangered species...” (77 FR 21265; April 9, 2012).

The Record of Decision for the final Planning Rule was based on the analyses presented in the *Final Programmatic Environmental Impact Statement, National Forest System Land Management Planning* (77 FR 21162–21276; April 9, 2012), which was prepared in accordance with the requirements of the National Environmental Policy Act (NEPA) (discussed below). In addition, the NFMA requires land management plans to be developed in accordance with the procedural requirements of NEPA, with a similar effect as zoning requirements or regulations as these plans control activities on the national forests and are judicially enforceable until properly revised (Coggins *et al.* 2001, p. 720).

A Species of Conservation Concern (SCC) is defined in the 2012 Planning Rule and in regulation (36 CFR 219.9(c)), as “a species, other than federally recognized threatened,

endangered, proposed, or candidate species, that is known to occur in the plan area and for which the regional forester has determined that the best available scientific information indicates substantial concern about the species' capability to persist over the long-term in the plan area.” The 2012 Planning Rule requires Regional Foresters to identify SCC for plan revision, and, when identified for a National Forest, monitoring plans are changed as needed (77 FR 21250, 21267; April 9, 2012). Wolverine is considered a SCC in the Rocky Mountain Region (Region 2). It is considered a Sensitive Species in the Intermountain Region (Region 4) and Northern Region (Region 1).

Within our estimated Current Range of the wolverine (see Figure 3), we identified 49 National Forests or Scenic Recreation Areas in the contiguous United States, and 2 within the State of Alaska. These areas are contained within 6 Forest Service Regions across the western United States and Alaska.

National Forest Land Management Plans (Forest Plans)

We reviewed several Forest Plans or related planning documents in an effort to describe how these plans provide conservation management for the wolverine and its habitat, including wildland fire management practices. The sections below are, in most cases, taken directly from relevant documents. However, this discussion is not intended to be inclusive of all NFS management strategies and activities across the entire Current Range of the wolverine in the contiguous United States.

Sierra Nevada Forest Plan Implementation

The 2004 Sierra Nevada Forest Plan Amendment (referred to as the Sierra Nevada Framework) amended the Land and Resource Management Plans (LRMP) for the eleven National Forests in the Sierra Nevada range to improve protection of old forests, wildlife habitats, watersheds and communities in the Sierra Nevada Mountains and Modoc Plateau. This amendment applies to the Tahoe National Forest, which has been occupied by a single male wolverine since at least 2008 (Moriarty *et al.* 2009, p. 150). The emphasis of the 2004 Sierra Nevada Framework is to adopt an integrated strategy for vegetation management that is aggressive enough to reduce the risk of wildfire to communities in the wildland urban interface, while modifying fire behavior over the broader landscape. Direction is provided as management goals and strategies, desired conditions, management intents and objectives, and management standards and guidelines. The 2004 Framework addressed five problem areas: old forest ecosystems and associated species; aquatic, riparian and meadow ecosystems and associated species; fire and fuels management; noxious weeds; and lower west side hardwood ecosystems (Forest Service 2013, p. 2–3).

Kootenai National Forest

The Kootenai National Forest is located in the northwest corner of Montana along the Canadian border and includes about 2.2 million acres of public land (Forest Service 2015, p. 7). The Forest Service published a Revised Land Management Plan for the Kootenai National Forest in 2015 that identifies forestwide direction, including goals, desired conditions, objectives, standards, and guidelines for physical and biological elements including wildlife such as management activities

that promote connectivity and avoiding or minimizing disturbance at known active denning sites for sensitive, proposed, threatened, or endangered species not covered under other forestwide guidelines. It also outlines objectives and guidelines related to the use of fire to maintain or improve habitat and maintaining unlogged conditions in some portions of areas burned by wildfires for 5 years post-fire (Forest Service 2015, pp. 28–32).

The Kootenai National Forest Land Management Plan also identifies *proposed or possible* actions for wildlife management that includes establishing and maintaining the vegetation diversity necessary to provide food, cover, and security for wildlife species native to the Kootenai National Forest in cooperation with federal, state, and other organizations. For wolverine, those management activities might include maintaining, managing, and protecting lands known or suspected to contribute to landscape linkages for wolverine (and other carnivores) in order to promote genetic dispersal and healthy populations (Forest Service 2015, p. 128).

Beaverhead-Deerlodge National Forest

The Beaverhead-Deerlodge National Forest covers 3.38 million acres in southwest Montana (Forest Service 2009, p. 2). The Beaverhead-Deerlodge National Forest Land and Resource Management Plan identifies goals, objectives, and standards for wildlife management (Forest Service 2009, pp. 45–49). Of relevance to the wolverine, wildlife security management goals include securing areas and connectivity for ungulates and large carnivores and managing the density of open motorized roads and trails by landscape region (Forest Service 2009, p. 45). Objectives include management of habitat conditions for elk security and winter habitat integrity for wolverine and mountain goat relative to changes in abundance of these Management Indicator Species (Forest Service 2009, p. 47). Monitoring elements are defined in the Land and Resource Management Plan that link goals and objectives to elements of the National Monitoring and Evaluation Framework (Forest Service 2009, pp. 273–280). For wildlife security, three performance measures relative to determining whether management activities are effectively protecting high elevation winter habitats for wolverines and mountain goats are defined: (1) presence or absence of wolverines in high elevation habitats, (2) populations of mountain goats (from Montana Fish Wildlife & Parks), and (3) number of snowmobile entries into non-motorized high elevation units protected for wolverines and mountain goats (Forest Service 2009, p. 277). In addition, in order to evaluate objectives related to road and trail densities, a performance measure related to changes in open motorized road and trail density for both seasons by landscape is included (Forest Service 2009, p. 277).

The Forest Service is monitoring the Mount Jefferson Recommended Wilderness boundary for illegal snowmobile intrusions into the wolverine habitat closure; that is, illegal use will be monitored and recorded (number and distance of intrusions) during the period open to snowmobiles December 2 to May 15 and any other time of the year snow conditions make snowmobiling possible (Forest Service 2009, p. 277). A reassessment of the decision to allow snowmobile use will be triggered if: (1) illegal intrusions are documented throughout the closure period; (2) illegal intrusions into the closed area, or (3) illegal intrusions that extend as far as the Bureau of Land Management (BLM) Wilderness Study Area (Forest Service 2009, p. 277).

Flathead National Forest

The Flathead National Forest is located in the northern Rocky Mountains in western Montana and includes approximately 2.4 million acres of public land (Forest Service 2016a, p. 3). This National Forest is surrounded by the Kootenai, Lewis and Clark, and Lolo National Forests, Glacier National Park, and Canada and includes large areas of designated wilderness (e.g., Bob Marshall Wilderness Complex, Mission Mountains Wilderness), Crown of the Continent Ecosystem, and wild and scenic river systems (Forest Service 2016a, pp. 3–4).

A Draft Revised Forest Plan was prepared for the Flathead National Forest in 2016 (Forest Service 2016b, entire). The Draft Revised Forest Plan identifies components to guide future projects and activities and the plan monitoring program, though these components are not commitments or final decisions approving projects or activities (Forest Service 2016b, p. 3). These components include desired conditions, objectives, standards, guidelines, suitability, and monitoring questions and monitoring indicators (Forest Service 2016b, p. 3). [A *desired condition* is a description of specific social, economic, and/or ecological characteristics of the plan area, or a portion of the plan area, toward which management of the land and resources should be directed, while an *objective* a concise, measurable, and time-specific statement of a desired rate of progress toward a desired condition or conditions (Forest Service 2016b, p. 4). A *standard* is a mandatory constraint on project and activity decision making, established to help achieve or maintain the desired condition or conditions, and a *guideline* is a constraint on project and activity decision-making that allows for departure from its terms, and are established to help achieve or maintain a desired condition or conditions, to avoid or mitigate undesirable effects, or to meet applicable legal requirements (Forest Service 2016b, pp. 4–5).]

Relative to wolverine, plan components for the revised forest plan include two guidelines that are protective of wolverine habitat; one that would protect modeled wolverine maternal denning habitat with respect to new projects or activity authorizations involving helicopter use and one that stipulates no net increase in the percentage of modeled wolverine maternal denning habitat where motorized over-snow vehicle use would be suitable on National Forest System lands. Additionally, as described in the Final EIS, management area allocations for Alternatives A, B modified and C include recommended wilderness areas that would add to existing wilderness. Desired conditions related to maintaining connectivity for wolverine and other wildlife are also identified within several geographic areas (Kuennen 2017, pers. comm.).

Federal Land Policy and Management Act (FLPMA) of 1976

FLMPA (43 U.S.C. 1711-1712) represents the BLM’s “organic act” for public lands management under the principles of multiple use and sustained yield. Its implementing regulations give BLM regulatory authority over activities for protection of the environment, including mining claims. Under FLPMA and BLM policy, public lands must be managed so as to protect the quality of scientific, scenic, historical, ecological, environmental, air and atmospheric, water resource, and archaeological values (BLM 2005, p. 1).

Land Use and Resource Management Plans

BLM land use planning requirements are established by Sections 201 and 202 of FLMPA and regulations at 43 CFR 1600 (BLM 2005, p. 1). A *Land Use Planning Handbook* (BLM 2005, entire) provides guidance for implementing land use planning requirements established under FLMPA and implementing regulations. Land use plans prepared by BLM include resource management plans (RMPs) and management framework plans (BLM 2005, p. 1). The RMPs establish the basis for actions and approved uses on the public lands and are prepared for areas of public lands, called planning areas (BLM 2005, pp. 1, 14). These plans are periodically evaluated and revised in response to changed conditions and resource demands (BLM 2005, pp. 33–34).

National Environmental Policy Act (NEPA)

All Federal agencies are required to adhere to the NEPA of 1970 (42 U.S.C. 4321 et seq.) for projects they fund, authorize, or carry out. Prior to implementation of such projects with a Federal nexus, NEPA requires the agency to analyze the project for potential impacts to the human environment, including natural resources. The Council on Environmental Quality's regulations for implementing NEPA state that agencies shall include a discussion on the environmental impacts of the various project alternatives (including the proposed action), any adverse environmental effects that cannot be avoided, and any irreversible or irretrievable commitments of resources involved (40 CFR part 1502). The public notice provisions of NEPA provide an opportunity for the Service and other interested parties to review proposed actions and provide recommendations to the implementing agency. NEPA does not impose substantive environmental obligations on Federal agencies—it merely prohibits an uninformed agency action. However, if an Environmental Impact Statement is prepared for an agency action, the agency must take a “hard look” at the consequences of this action and must consider all potentially significant environmental impacts. Federal agencies may include mitigation measures in the final Environmental Impact Statement as a result of the NEPA process that may help to conserve the wolverine and its habitat.

Although NEPA requires full evaluation and disclosure of information regarding the effects of contemplated Federal actions on sensitive species and their habitats, it does not by itself regulate activities that might affect the wolverine; that is, effects to the subspecies and its habitat would receive the same scrutiny as other plant and wildlife resources during the NEPA process and associated analyses of a project's potential impacts to the human environment. The Service receives notification letters for Draft and Final Environmental Impact Statements prepared by the Forest Service, BLM and other Federal agencies pursuant to NEPA for specific proposed projects including those within National Forests or National Parks, and preparation of Forest Service Land and Resource Management Plans, as discussed above.

Wilderness Act

The Wilderness Act of 1964 (16 U.S.C. 1131–1136) provides protection of habitat from most forms of development, though no single agency is responsible for administration of lands provided this designation, which are designated (or modified) by Congress. The Wilderness Act prohibits commercial enterprises and permanent roads within wilderness area and restricts temporary roads, motorized and mechanical transport, and structures, but does not prohibit all commercial uses (e.g., grazing). Within the portion of our estimated Current Range of the

wolverine in the contiguous United States and Alaska, approximately 15 percent is designated as wilderness areas under the Wilderness Act. We also evaluated wilderness contained within modeled wolverine primary habitat from Inman *et al.* (2013). We found 41 percent of this suitable habitat was designated as wilderness areas.

State Mechanisms

California

As noted above, the wolverine is a threatened species under the California Endangered Species Act or CESA, which prohibits the take of any species of wildlife designated by the California Fish and Game Commission as endangered, threatened, or candidate species (CDFW 2017b). CDFW may authorize the take of any such species if certain conditions are met through the issuance of permits (e.g., Incidental Take Permits) (CDFW 2017b). The wolverine is also a Species of Greatest Conservation Need (SGCN) in the State's Wildlife Action Plan⁵ and is a focal species of conservation strategies for conservation targets in the Southern Cascades and Sierra Nevada Ecoregions, and in the Mono Ecoregion of the Deserts Province section (Big Sagebrush Scrub (CDFW 2015, pp. 5.2-16, 5.4-23, 5.6-19).

In 2011, the CDFW (formerly California Department of Fish and Game) prepared an assessment/briefing document, *California Wolverine Population Augmentation Considerations*, in response to a *Feasibility Assessment and Implementation Plan for Population Augmentation of Wolverines in California* (November 2010) submitted to the Department by the Institute for Wildlife Studies (California Department of Fish and Game (CDFG) 2011). As of August 2017, no action has been taken by CDFW toward implementation of augmentation of wolverines in California.

Oregon

The wolverine has been listed as threatened species in Oregon since 1975, under the Oregon Endangered Species Act, and is fully protected under management authority of the ODFW (Anglin 2013, pers. comm.).

A Conservation Strategy for conserving the State's fish and wildlife has been prepared by the ODFW. The Conservation Strategy identifies 294 Strategy Species, which are Oregon's SGCN, (including wolverine) and are defined as those species having small or declining populations, are at-risk, and/or are of management concern (ODFW 2016). For each of the Strategy Species, the Conservation Strategy identifies information on the special needs, limiting factors, data gaps, and conservation actions. For wolverine, conservation actions include management of recreational use to avoid impacts to the species (ODFW 2016). Other Strategy Species identified in the

⁵ The U.S. Congress created the State Wildlife Grant (SWG) funding program in 2000 (Title IX, Public Law 106-553 and Title 1, Public Law 107-63). SWG funds are to be used "...for the planning and implementation of [States and territories] wildlife conservation and restoration program and wildlife conservation strategy, including wildlife conservation, wildlife conservation education, and wildlife-associated recreation projects." Congress stipulated that each State or territory applying for this funding program must develop a wildlife conservation strategy (**State Wildlife Action Plan** (SWAP)) by October 1, 2005. All 56 states and territories submitted SWAPs by 2005 and made commitments to review and/or revise their SWAP at least every 10 years.

State's Conservation Strategy are prey species important to wolverine, including the Rocky Mountain bighorn sheep and Columbian white-tailed deer (ODFW 2016).

Washington

The wolverine is a candidate species for listing in the State of Washington and, since 2006, the Washington Department of Fish and Wildlife (WDFW) has been collaborating with wolverine researchers in the Cascades of northern Washington and southern British Columbia to better understand the status, distribution, and general ecology of wolverines in this region (WDFW 2013). It is also considered a SGCN, and is identified as a species whose population is in critical condition (WDFW 2013, pp. 3-7).

Washington's State Wildlife Action Plan (updated in 2015) identifies several major conservation strategies to address the conservation of fish and wildlife habitat and biodiversity in Washington, on both public and private lands (WDFW 2015, pp. 2-12–2-28). The wolverine is included in several identified ecological systems of concern such as alpine scrub, forb meadow, and grassland vegetation, cliff, scree and rock vegetation, and temperate forests (WDFW 2015, pp. 4-19, 4-27, 4-98). The State's *Wildlife Action Plan* identifies major stressors and key actions needed to maintain habitat quality for each of these ecological systems.

Of relevance to wolverine, the WDFW and its partners have been targeting land acquisition and conservation easements with high habitat or biodiversity values such as mixed-conifer forests as well as areas that support winter range and connectivity for wolverine and other carnivores (e.g., Methow River and Okanogan River Watersheds projects) (WDFW 2015, pp. 2-15–2-17). Other landscape conservation efforts highlighted in the State's *Wildlife Action Plan* include a Federal-State partnership with Washington's Department of Transportation to implement the Interstate-90 Snoqualmie Pass East Project to enhance wildlife connectivity that includes wildlife underpasses under the highway along creeks and rivers and two 150-foot wide wildlife bridges over the highway (WDFW 2015, p. 2-26).

Idaho

In Idaho, the wolverine is a protected nongame species and SGCN in Idaho (IDFG 2014). The *Idaho State Wildlife Action Plan, 2015* is a statewide plan for conserving and managing Idaho's fish and wildlife and their habitats, and provides a framework for conserving Idaho's 205 SGCN and their habitats, which includes the wolverine (IDFG 2017b, pp. xv–xviii). The wolverine is identified as a Tier 1 SGCN, which indicates it represents a species of most critical conservation need (IDFG 2017b, p. xvi). The statewide plan presents a species assessment for each SGCN and ecological section plans. Each of the ecological section plans presents a conservation target (e.g., habitat, species assemblage) that summarizes its viability as well as prioritized threats and strategies (IDFG 2017b, p. xv). A section outlining species designation, planning, and monitoring is also provided. The wolverine is included in three of the defined conservation targets—forested lowlands, subalpine-high montane conifer forest, and low density forest carnivores (IDFG 2017b, p. 76). Along with objectives and strategies, these summaries identify actions for the SGCNs included in the defined conservation targets. Examples include: develop and implement a long-term multi-taxa monitoring program; determine high risk areas for wildlife

crossings; construct highway over- and underpasses; promote and/or facilitate the use of prescribed fire as a habitat restoration tool, on both public and private lands where appropriate; determine best management practices to maintain cool microsites and benefit cool air associated species; and implement strategies to minimize disturbance from winter recreation activities as outlined in the *Management Plan for the Conservation of Wolverines in Idaho, 2014–2019* (IDFG 2017b, pp. 79, 80, 91, 94, 110).

The *Management Plan for the Conservation of Wolverines in Idaho, 2014–2019* (Management Plan) (IDFG 2014, entire) represents a framework for proactive efforts to ensure the long-term persistence and viability of wolverine populations in Idaho (IDFG 2016, pers. comm.). The Management Plan is described as a voluntary guidance document to lead conservation efforts at the State and local level, as well as to facilitate communication and collaboration efforts among wildlife and land managers (IDFG 2014, p. v).

Conservation issues and management actions are described in the Management Plan and the appropriate section plans of the *Idaho State Wildlife Action Plan*. The recommended strategies include development of finer-scale climate projections, research regarding wolverine-snow relationships, characterizing wolverine response to recreational activities, developing predictions of the potential overlap of wolverine and high levels of snow-sports recreation, and educating trappers to minimize incidental trapping of nontarget species, including the wolverine (IDFG 2014, pp. 32–39; IDFG 2017b, p. 1058). Seven conservation and management objectives are outlined in the Management Plan (IDFG 2014, pp. 32–39) and, as outlined in a November 2016 response letter, there has been progress on all of these objectives (IDFG 2016, pers. comm.). As an example, the agency (under the Multi-species Baseline Initiative) has developed and implemented a baseline micro-climate monitoring protocol for collecting environmental parameters in an effort to identify areas that serve as cool-air refugia (IDFG 2016, pers. comm.). As described above (*Overutilization for Commercial, Recreational, Scientific, or Educational Purposes*), the IDFG has prepared educational materials to promote best management practices for minimizing non-target wolverine captures and continues to educate trappers under a legislative mandate passed in 2016 (State of Idaho House Bill 378) (IDFG 2016, pers. comm.).

In addition, management of prey species important to the wolverine diet is outlined in the Idaho Elk Management Plan 2014-2024 (IDFG 2014a), the Mule Deer Management Plan 2008-2017 (2008) and the Bighorn Sheep Management Plan (2010).

Montana

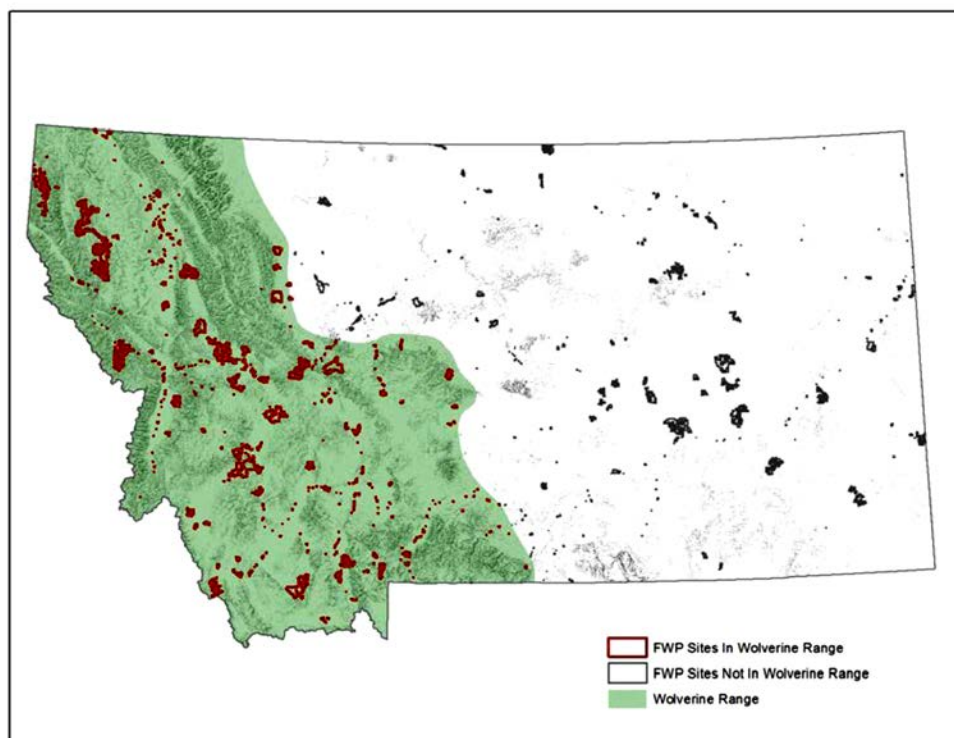
In the State of Montana, the wolverine is classified as a furbearer and species of concern. Since 2013, there has been a zero quota for trapping or harvest of wolverine and trappers that capture a wolverine must notify a designated Montana FWP employee within the relevant trapping district within 24 hours for collection if the animal cannot be released uninjured (Montana FWP 2016, pers. comm.).

There are two broad-scale wildlife conservation efforts that provide conservation benefits to the wolverine. *Montana's State Wildlife Action Plan* (updated and revised in 2015) identifies the wolverine as one of 128 SGCN (Montana FWP 2015, Appendix N). The State's Wildlife Action

Plan identifies priority community types, focal Areas, and species to help informing Montana FWP's priorities and decisions and to assist other agencies and organizations in making decisions as to where to focus their conservation efforts (Montana FWP 2015, p. 2). Community types and focal areas are designed to identify and direct attention to specific geographical areas in the State that have the greatest conservation need (Montana FWP 2015, p. 5). For the wolverine, *Montana's State Wildlife Action Plan* identifies wolverine habitats in seven community types, all designate Tier I (or those with greatest conservation need), and in all focal areas (also Tier I) within those community types (Montana FWP 2016, pers. comm.). For each community type, impacts, threats, and corresponding conservation actions are identified, as well as specific impacts and threats such as habitat fragmentation (e.g., prioritize land acquisition, provide wildlife under- and overpasses), land management (e.g., management to address altered fire regimes), recreation (e.g., consider seasonal closures during breeding season), and climate change (e.g., collection of baseline data to document shifting range limits of SGCN and Community Types of Greatest Conservation Need) (Montana FWP 2015, pp. 59–63).

The second conservation effort in the State of Montana is a Crucial Area Assessment to identify crucial areas and fish and wildlife corridors, and development of a Crucial Areas Planning System (URL: <http://fwp.mt.gov/fishAndWildlife/conservationInAction/crucialAreas.html>). This is a Montana FWP mapping application and planning tool designed to assist in future planning of development and conservation (Montana FWP 2016, pers. comm.).

The State of Montana is also conserving wildlife habitat through land acquisition and conservation easements (Montana FWP 2016, pers. comm.). In western Montana, including areas known to be occupied by the wolverine, 425 properties for a total 310,523 ha (767,320 ac) have been either acquired (e.g., State Parks, Wildlife Management Areas) or protected by conservation easements, as of November 2016, as shown in figure below (Montana FWP 2016, pers. comm.).



Wyoming

The wolverine is a protected animal and SGCN in Wyoming (WGFD 2017). The *Wyoming Game and Fish Department State Wildlife Action Plan* directs the activities of the WGFD and serves to guide in conserving Wyoming's SGCN through the combined efforts of government agencies, conservation organizations, academia, tribes, and others (WGFD 2017, p. I-1-1). As noted above, the wolverine is identified as a SGCN, a designation intended to identify species whose conservation status warrants increased management attention and funding, and consideration in conservation, land use, and development planning in the State (WGFD 2017, p. IV- i-1). The *State Wildlife Action Plan* incorporates the wolverine as a SGCN in several terrestrial habitat types or ecological systems, including cliffs, canyons, and rock outcrops, montane and subalpine forests, and mountain grasslands and alpine tundra (WGFD 2017, pp. III-2-5, III-5-7, III-6-5).

In 2015, Wyoming funded a pilot project (through The Wolverine Initiative) to evaluate wolverine detection and monitoring of the species in the State and is a contributing collaborator in the Multistate Wolverine Working Group implementing a monitoring strategy (the WSWCP) in the winter of 2016–2017 across four western states (WGFD 2017, p. IV-5-357). Results of those studies (e.g., Inman *et al.* 2015) are summarized above (*Population Abundance and Distribution*). The WSWCP is also updating and refining connectivity models for the wolverine in an effort to focus and prioritize habitat conservation and management (WGFD 2016, pers. comm.).

Colorado

The wolverine is a state-endangered species in Colorado (Colorado Parks and Wildlife 2015a); however, there is no known current resident or reproducing wolverine population.

The *Colorado State Action Plan* (Colorado Parks and Wildlife 2015b) provides a blueprint for a collaborative effort to conserve Colorado's at-risk wildlife and their habitats, with a primary goal for securing wildlife populations in order to avoid protections implemented so that they do not require protection via federal or state listing regulations (Colorado Parks and Wildlife 2015b, p. 1). The wolverine is designated as a Tier 1 (highest conservation priority; up from Tier 2) SGCN (Colorado Parks and Wildlife 2015b, p. 19). The primary conservation action for wolverine described in the 2015 State Action Plan is to continue discussions among wildlife managers, conservation partners and stakeholders of the social and political aspects regarding reintroduction of wolverine populations into the southern Rocky Mountains (Colorado Parks and Wildlife 2015b, p. 186). The State has not yet prepared a potential restoration program for the species (Broscheid 2016, pers. comm.).

Other Conservation Mechanisms

Tribes

Nez Perce Tribe

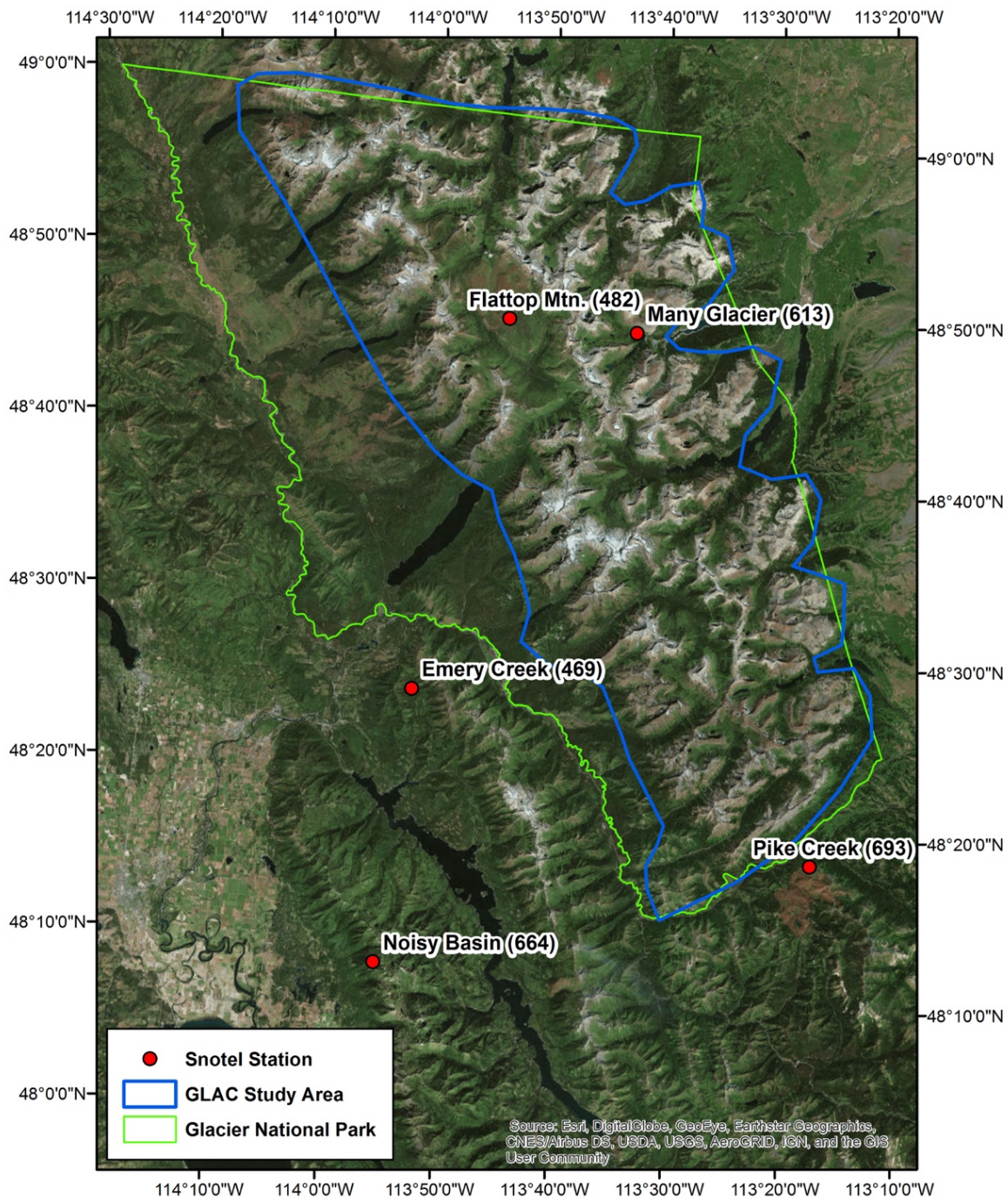
Wolverines are found within the aboriginal territory of the Nez Perce Tribe in north-central Idaho, and conservation and restoration of the species within the Nez Perce homeland is important to the Nez Perce Tribe (Miles 2017, pers. comm.). The Nez Perce Tribe is currently preparing an Integrated Resource Management Plan (IRMP), a Plant and Wildlife Conservation Strategy, and a Forest Management plan with the wolverine defined as a species of conservation concern in all three draft plans (Miles 2017, pers. comm.). The planning area for the IRMP, which is being prepared in partnership with the Bureau of Indian Affairs, incorporates the approximately 311,608 ha (770,000 ac) Nez Perce Reservation, located within portions of Nez Perce, Lewis, Clearwater, Latah, and Idaho Counties in north-central Idaho (<http://www.nezperce.org/irmp/>; accessed August 24, 2017). The preparation of the IRMP is currently at the scoping stage in the NEPA process for development of a Programmatic Environmental Impact Statement (<http://www.nezperce.org/irmp/>; accessed August 24, 2017).

The Shoshone-Bannock Tribes

The Shoshone-Bannock Tribes are currently conducting climate change modeling for the Northern Rocky Mountains as part of its preparation of a Climate Change Adaptation Plan (Edmo 2016, pers. comm.). The Upper Snake River Tribes Foundation (USRT), which is comprised of four member tribes—the Burns Paiute Tribe, Fort McDermitt Paiute-Shoshone Tribe, Shoshone-Bannock Tribes of the Fort Hall Reservation, and Shoshone-Paiute Tribes of the Duck Valley Reservation—within the Upper Snake River Watershed region, prepared a *Climate Change Vulnerability Assessment* in February 2017 (Petersen *et al.* 2017, entire). The assessment is the first of three steps the USRT and its member tribes plan activities over the next several years as part of a comprehensive climate change effort, and will include an Adaptation Plan (expected to be completed in 2017–2018), and, depending on future funding, a process for development of Implementing Adaptation Actions and Monitoring (Petersen *et al.* 2017, p. 7).

*Appendix H—NOAA/CU Study Areas Used to Evaluate Future Snow Persistence
(from Ray et al., 2017)*

Glacier National Park Study Area



Rocky Mountain National Park Study Area

