

From: [McKelvey, Kevin -FS](#)
To: andrea.ray@noaa.gov; [Guinotte, John](#)
Cc: [Joseph Barsugli - NOAA Affiliate](#)
Subject: RE: Call-in # for wolverine conf call tomorrow at 2pm mountain
Date: Wednesday, November 9, 2016 2:32:32 PM
Attachments: [image005.png](#)
[image006.png](#)
[image007.png](#)
[image008.png](#)
[aubry wolverine distribution.pdf](#)
[bioclimatic envelope of the wolverine.pdf](#)
[McKelvey et al 2011 wolverine climate change.pdf](#)

I don't have much beyond the papers. But if folks had Aubry et al. 2007, Copeland et al. 2009, and McKelvey et al. 2011 handy we could refer to them. K.



Kevin S. McKelvey, PhD
Research Ecologist
Forest Service
Rocky Mountain Research Station, Wildlife and Terrestrial Ecosystems
p: 406-542-4163
f: 406-543-2663
kmckelvey@fs.fed.us
800 East Beckwith
Missoula, MT 59801
www.fs.fed.us
The USDA logo, the Twitter bird icon, and the Facebook 'f' icon are displayed side-by-side.
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From: Andrea Ray - NOAA Federal [mailto:andrea.ray@noaa.gov]
Sent: Wednesday, November 09, 2016 1:35 PM
To: Guinotte, John <john_guinotte@fws.gov>
Cc: Joseph Barsugli - NOAA Affiliate <joseph.barsugli@noaa.gov>; McKelvey, Kevin -FS <kmckelvey@fs.fed.us>
Subject: Call-in # for wolverine conf call tomorrow at 2pm mountain

Hi All, here's the call-in info for tomorrow's meeting. I'm not planning to use the go-to meeting screen, but it gives us the call in number. Kevin, if there's something you'd like to show, let me know.

United States +1 (408) 650-3123; Access Code: 925-942-125

Talk to you tomorrow, Andrea

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

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

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Distribution and Broad-scale Habitat Relations of the Wolverine in the Contiguous United States

KEITH B. AUBRY,¹ *United States Forest Service, Pacific Northwest Research Station, Olympia, WA 98512, USA*

KEVIN S. MCKELVEY, *United States Forest Service, Rocky Mountain Research Station, Missoula, MT 59807, USA*

JEFFREY P. COPELAND, *United States Forest Service, Rocky Mountain Research Station, Missoula, MT 59807, USA*

ABSTRACT Conservation of the wolverine (*Gulo gulo*) at the southern extent of its North American range requires reliable understandings of past and present distribution patterns and broad-scale habitat relations. We compiled 820 verifiable and documented records of wolverine occurrence (specimens, DNA detections, photos, and accounts of wolverines being killed or captured) in the contiguous United States from museums, the literature, and institutional archives. We spatially referenced 729 records with areal precision ≤ 1 township (93.2 km²) and temporal precision ≤ 10 years. Historical records (1827–1960) were located primarily in the western mountains and Great Lakes region. However, our data suggest that the historical distribution of wolverines in the Cascade Range and Sierra Nevada was disjunct, contradicting previous interpretations. Our results indicate that wolverine range in the contiguous United States had contracted substantially by the mid-1900s. Current records (1995–2005) are limited to north-central Washington, northern and central Idaho, western Montana, and northwestern Wyoming. We investigated potential relations between wolverines and alpine vegetation, cold temperatures, and spring snow cover by comparing the distribution of historical wolverine records with Kuchler's potential natural vegetation types, Holdridge's climatic life zones, and EASE snow-cover maps during the latter portion of the wolverine denning period (15 Apr–14 May). In the western mountains, historical wolverine records generally occurred in or near alpine vegetation and climatic conditions, especially at the limits of their distribution in the Cascade Range, Sierra Nevada, and southern Rocky Mountains. However, the only habitat layer that fully accounted for historical distribution patterns was spring snow cover. Causal factors for the extirpation of wolverines from the southern portions of their range in the contiguous United States are unknown, but are likely related to high levels of human-caused mortality and low to nonexistent immigration rates. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2147–2158; 2007)

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KEY WORDS alpine meadows, climate, contiguous United States, distribution, *Gulo gulo*, habitat, Holdridge life zones, Kuchler potential vegetation, snow cover, wolverine.

The wolverine (*Gulo gulo*) is one of the rarest and least-known mammals in North America. It occurs at low densities and is secretive and difficult to observe, even in core areas of its range. Although wolverines are generally found in areas remote from humans and human development, the habitat conditions that influence its distribution and abundance are largely unknown (Banci 1994). Accordingly, published range maps for the wolverine in the contiguous United States vary substantially. Some indicate that wolverines occurred in continuous peninsular extensions southward from Canada into the Cascade Range and Sierra Nevada (hereafter, Pacific Coast mountains), Rocky Mountains, Great Lakes region, and northeastern states (Ashbrook and McMullen 1928, Seton 1929), one depicts islands of occupancy within those regions (Wilson 1982), and others indicate that wolverines occurred in a much larger area encompassing a broad array of habitat conditions (Nowak 1973, Hall 1981, Hash 1987). Because reliable information on wolverine occurrence in much of its potential range was lacking, previous authors either extrapolated the locations of several specimen records to broad areas with similar habitat conditions or simply drew lines around extralimital records. The latter approach is particularly problematic for wide-ranging carnivores capable of long-distance movements because such records may represent extreme dispersal events that are neither indicative of occupied areas nor representative of metapopulation dynamics (McKelvey et al. 2000).

Petitions to list the wolverine in the contiguous United States under the federal Endangered Species Act were submitted in 1994 (Carlton and Steele 1994) and 2000 (Carlton et al. 2000), each claiming that significant range losses had occurred since European settlement. However, subsequent decisions that listing of the wolverine was not warranted cited a lack of reliable information on their distribution in the contiguous United States (U.S. Fish and Wildlife Service 1995, 2003). Thus, obtaining a reliable understanding of the historical distribution of wolverines in the contiguous United States is an essential first step for their conservation. Such information also provides an empirical basis for evaluating broad-scale habitat relations, the extent to which current range differs from historical conditions, and potential causal factors for observed range losses.

The objectives of this study were to 1) develop reliable and spatially explicit understandings of the distribution of wolverines in the contiguous United States during both historical and modern eras, 2) investigate potential relations between wolverine occurrence records and broad-scale ecological and climatic factors, 3) determine if range losses have occurred and, if so, 4) evaluate potential causal factors for observed range losses.

METHODS

Wolverine Occurrence Records in the Contiguous United States

Developing reliable maps of wolverine distribution in the contiguous United States during both past and present eras

¹ E-mail: kaubry@fs.fed.us

requires a large number of records with high spatial resolution, well-distributed in space and time. However, there are <100 museum specimen records for the wolverine in the contiguous United States that are distributed haphazardly (K. B. Aubry, United States Forest Service, unpublished data). Because museum records were inadequate for our purposes, we evaluated other types of occurrence records for use in our study. We concluded that 3 distinct types of occurrence records represent a gradient of decreasing reliability: 1) physical evidence, 2) accounts of wolverines being killed or captured, and 3) sightings of various kinds. Records associated with physical evidence can be independently verified by others, such as specimens in museums and elsewhere, DNA identifications from tissue samples (Riddle et al. 2003), or photographs (hereafter, verifiable records). Accounts of animals being killed or captured lack physical evidence but are typically published or archived records based on information obtained from trappers or hunters who killed a wolverine and examined the carcass (hereafter, documented records). Sighting reports are visual observations of wolverines made at a distance, or reports of tracks and other sign (hereafter, anecdotal records).

We used both verifiable and documented wolverine occurrence records to create distribution maps; we did not consider anecdotal records in any component of our study. Although we cannot be certain that all documented wolverine records are accurate, we believe such records have a high degree of reliability. Most of the occurrence records of furbearing mammals compiled by the United States Biological Survey in the late 1800s and early 1900s were documented records (see archival sources listed in Cox 1986), and many early mammalogists used both verifiable and documented records to describe furbearer distributions in the contiguous United States (e.g., Merriam 1891; Cary 1911; Bailey 1931, 1936; Grinnell et al. 1937). Modern researchers often use these assessments to represent baseline conditions against which potential anthropogenic or natural effects on current species' distributions are evaluated (e.g., Kucera et al. 1995, Krohn et al. 1997, Aubry and Lewis 2003, Zielinski et al. 2005). Conversely, anecdotal records of wolverines and other forest carnivores are inherently unreliable, and can lead to overestimations of species' distributions and faulty conclusions regarding their conservation status (Aubry and Lewis 2003; Aubry and Jagger 2006; K. S. McKelvey and K. B. Aubry, United States Forest Service, unpublished data).

Compiling and Spatially Referencing Wolverine Occurrence Records

To gather available verifiable and documented wolverine records from the contiguous United States, we searched museum collections, the literature, and archival material at numerous state and federal institutions. We contacted 114 museums in the United States and Canada including all those with >10,000 mammal specimens, any museum from which wolverine specimens had been reported, and at least one major museum in each state in which wolverines had

been reported to occur (Hafner et al. 1997). We expended considerable effort searching for records in published and unpublished literature, and in the archives of state wildlife agencies, federal resource management agencies, and the Smithsonian Institution in Washington, D.C. (including archival material from the National Museum of Natural History and the United States Biological Survey). We excluded any record whose authenticity or place of origin was in doubt, including those linked to escaped or intentionally released animals.

We spatially referenced all verifiable and documented wolverine records that had areal precision ≤ 1 township (93.2 km²; United States Public Land Survey System) and temporal precision ≤ 10 years (hereafter, mappable records). We used records that failed to meet these criteria only for assessments at the state level. We chose a minimum mapping unit of about 100 km² because it is small enough to investigate potential broad-scale habitat relations, yet large enough to accommodate the lack of precise location data for many wolverine records. Lastly, we used Terrain Navigator (Maptech, Amesbury, MA) computer software to spatially reference wolverine records. This software package contains digitized and spatially referenced United States Geological Survey (USGS) topographic maps that include township and section boundaries and a search engine for the names of geographic features. Because place names are often the only location data associated with older occurrence records, this feature enabled us to spatially reference many wolverine records that we could not have located otherwise.

For analytical and comparative purposes, we divided resulting wolverine records into 3 time periods representing the geographic distribution of wolverines in the contiguous United States during current (1995–2005), recent (1961–1994), and historical (before 1961) eras. Accurately delineating the distribution of wolverines at a single point in time is not possible without a range-wide survey effort conducted during a relatively short period of time (e.g., McKelvey et al. 1999). Consequently, we used records dating from 1995 to 2005 to describe the current distribution of wolverines in the contiguous United States. We reasoned that a 10-year time-span was short enough that major changes in distribution were unlikely to have occurred, yet long enough to accumulate enough records to provide a reliable estimate of current distribution.

We separated records obtained before 1995 into 2 time periods based on previous speculations that the status and distribution of wolverines in the contiguous United States had changed substantially by the mid-1900s. By that time, evidence of wolverine occurrence in the contiguous United States had become so scarce that many mammalogists believed the species had been extirpated from most or all of its former range (e.g., Wright and Thompson 1935, Grinnell et al. 1937, Allen 1942, Newby and Wright 1955). However, numerous wolverine records in the contiguous United States dating from the 1960s and 1970s suggested that the wolverine was reclaiming portions of its former range during that time (Nowak 1973, Yocom

1974, Johnson 1977). To investigate these hypotheses, we considered wolverine records obtained from 1961 to 1994 separately and restricted our historical dataset to records obtained before 1961.

We also reasoned that restricting our historical dataset to older records was appropriate because it would predate the compilation of spatially referenced wolverine trapping records in Montana, the initiation of radiotelemetry studies of wolverines in the northern Rocky Mountains (Hornocker and Hash 1981), and the era of systematic field surveys using remote cameras and noninvasive genetic sampling (e.g., Foran et al. 1997, Foresman and Pearson 1998). These activities have resulted in the compilation of large numbers of verifiable wolverine records from a few localized areas during the last 30 years or so. Including such records in our historical dataset would reduce the comparability of our data among various portions of the wolverine's potential range.

Relating Historical Wolverine Records to Broad-Scale Habitat Conditions

We limited our investigation of broad-scale habitat relations to mappable records in our historical dataset. We recognize that factors other than wolverine abundance influence the density of such records. Such data do not represent a random sample, and we do not know whether efforts to obtain occurrence data varied among geographic areas or time periods; consequently, it is not appropriate to conduct statistical hypothesis tests using these data. To identify potentially important habitat relations, we overlaid wolverine records on various spatial data layers and evaluated the results visually and with simple descriptive statistics. We chose data layers based on the hypotheses that wolverine occurrence may be associated with alpine vegetation, cold temperatures, or snow cover during the spring denning period (Pasitschniak-Arts and Lariviere 1995; Magoun and Copeland 1998; C. R. Copeland, United States Forest Service, unpublished data; M. Zhang, Northeast Forestry University, People's Republic of China, personal communication). To the extent possible, suitable spatial layers should reflect habitat conditions occurring at the time wolverine records were obtained, and they must be available throughout the area of evaluation. Consequently, we limited spatial data layers to those associated with potential natural vegetation, climatic conditions, topography, and snow cover that encompassed the contiguous United States. We used the following ecological and climatic layers:

Alpine vegetation.—To investigate potential relations between wolverine records and alpine vegetation, we used Kuchler's (1964) potential natural vegetation maps for the contiguous United States, which depict vegetation types that would occur in the absence of major disturbances based on local knowledge and temperature. We constructed a simplified map of Kuchler vegetation types containing 3 strata: 1) Alpine Meadows and Barren (hereafter, Alpine Meadows), 2) Conifer Forest, and 3) Other Vegetation Types. Alpine Meadows is a single Kuchler vegetation type. We created the Conifer Forest stratum by combining all montane and northern conifer forest types; we did not

include Great Basin conifer, northern mixed hardwood and conifer, or southeastern conifer types. We combined these and all other Kuchler vegetation types into the Other Vegetation Types stratum.

Climatic conditions.—To investigate potential relations between wolverine records and alpine climatic conditions, including those that may be poorly represented by Kuchler's Alpine Meadows vegetation type, we constructed a simplified map of Holdridge's (1967) Alpine and Subalpine life zones based on the Altitudinal Zone aggregation developed by Lugo et al. (1999). We chose Holdridge's (1967) system of life-zone classification because it is based on objective environmental criteria (e.g., \bar{x} temp, annual precipitation, frost line), and depicts the climatic conditions for ecosystem function (Lugo et al. 1999).

Topography.—To further investigate these potential relations, we conducted a linear regression of latitude (distance south of latitude 49° N) versus elevation (based on a 1-km Digital Elevation Model) for wolverine records. Vegetation types and climatic zones occur at increasingly higher elevations as one moves south in the northern hemisphere, due to corresponding increases in mean temperature (Arno 1966). Thus, if wolverines are associated with alpine vegetation or climatic conditions, the elevation of occurrence records should increase with decreasing latitude.

Spring snow cover.—To investigate potential relations between wolverine records and spring snow cover, we used the Northern Hemisphere EASE-Grid Weekly Snow Cover and Sea Ice Extent dataset (Armstrong and Brodzik 2005). Researchers collected snow-cover data continuously via satellite throughout the northern hemisphere from 1967 to 2005 and summarized resulting data on a weekly basis. They coded each terrestrial pixel of approximately 625 km² (25 × 25 km) either 1 or 5 if it was snow-covered, 0 otherwise; pixels coded 5 were data holes they recoded as snow-covered based on nearest-neighbor regridding (Armstrong and Brodzik 2005). We chose the time period from 15 April to 14 May to represent snow cover present during the latter portion of the wolverine denning period (Myrberget 1968, Magoun and Copeland 1998). Because the beginning and end dates for weekly snow-cover data vary annually, we included all weeks during which ≥4 days fell within this time period, resulting in 162 weekly records. To estimate the probability of snow cover from 15 April to 14 May, we summed the number of weeks each pixel was snow-covered during these dates and divided by the total number of weeks. We used resulting data to construct maps depicting the snow-cover probability gradient in increments of 25%.

RESULTS

We compiled 901 verifiable or documented records of wolverine occurrence dating from 1801 to 2005 from 24 states in the contiguous United States (Table 1). We found records in the Pacific Coast mountains, Rocky Mountains, north-central Great Plains, Great Lakes region, upper

Midwest, and Northeast. We mapped 729 records dating from 1827 to 2005, including 188 historical (Fig. 1), 319 recent (Fig. 2a), and 222 current records (Fig. 2b).

Distribution of Historical Wolverine Records in the Contiguous United States—1801 to 1960

Pacific Coast mountains.—We found many historical records of wolverine occurrence in the Pacific Coast mountains located almost entirely in Washington (29 records; 4 verifiable) and California (58 records; 10 verifiable); we found 2 documented records in Oregon (Table 1). We mapped 24 records in north-central Washington, 2 in north-central Oregon, and 36 in central California (Fig. 1). The holotype specimen of the southern wolverine (*Gulo gulo luteus*) was collected in California in 1903 (Elliot 1903).

Rocky Mountains.—We found numerous historical records of wolverine occurrence in the Rocky Mountains located primarily in Idaho (25 records; 6 verifiable), Montana (60 records; 26 verifiable), Wyoming (18 records; 4 verifiable), Utah (10 records; 2 verifiable), and Colorado (34 records; 6 verifiable); we found 1 verifiable record in New Mexico (Table 1). We mapped 12 records in northern and central Idaho, 35 in western Montana, 12 in north-western Wyoming, 8 in Utah, and 28 in western Colorado (Fig. 1). Archival records at the National Museum of Natural History indicate that a wolverine skin was obtained in the vicinity of Ft. Burgwin in the Sangre de Cristo Mountains near present-day Taos, New Mexico by J. S. Newberry in 1860 (National Museum of Natural History Skin Catalog 3768). Thus, the southern limit of wolverine distribution in the Rocky Mountains historically may have been northern New Mexico, a conclusion also reached by Frey (2006).

Central Great Plains.—Historical records of wolverine occurrence in the central Great Plains were sparse and uneven in space and time (Table 1). We found 36 records (0 verifiable) in North Dakota, including 1 mappable record in western North Dakota (Fig. 1). The remaining 35 records were trapping reports in the journals of Alexander Henry dating from 1801 to 1806 (Bailey 1926); none were mappable. We mapped one verifiable record in western Nebraska.

Great Lakes region.—We found many historical records of wolverine occurrence in the Great Lakes region located primarily in Minnesota (10 records; 1 verifiable), Wisconsin (14 records; 2 verifiable), and Michigan (12 records; 1 verifiable; Table 1). We mapped 8 records in northern Minnesota, 8 in Wisconsin, and 5 in Michigan (Fig. 1).

Upper Midwest.—Historical records of wolverine occurrence in the upper Midwest states were sparse (Table 1). We mapped 1 verifiable record in eastern Iowa, 2 documented records in northern and southern Indiana, and 1 verifiable record in eastern Ohio (Fig. 1).

Northeast.—Historical records of wolverine occurrence in the Northeast were sparse and haphazard (Table 1). We found 4 records in Pennsylvania (0 verifiable), 3 in New York (1 verifiable), 2 in New Hampshire (0 verifiable), 3 in

Vermont (0 verifiable), and 1 in Maine (0 verifiable). We mapped 1 record in north-central Pennsylvania, 1 in north-central New York, and 2 in northern New Hampshire (Fig. 1).

Distribution of Recent Wolverine Records in the Contiguous United States—1961 to 1994

Pacific Coast mountains.—We found 23 recent records of wolverine occurrence in the Pacific states, including 17 in Washington (11 verifiable) and 6 in Oregon (5 verifiable); we found none in California (Table 1). We mapped all records in both states, including many records located in physiographic provinces that lacked historical records, such as the high plateaus of northeastern Washington, the Columbia River Basin in both states, and the basin and range areas of southeastern Oregon (Fig. 2a).

Rocky Mountains.—Virtually all recent records of wolverine occurrence we found in the Rocky Mountains were in the northern states. We found 41 records in Idaho (31 verifiable), 284 in Montana (282 verifiable), and 1 verifiable record in both Wyoming and Nevada; we found none in Utah or Colorado (Table 1). The 39 records we mapped in Idaho included 16 initial capture locations from a radiotelemetry study in central Idaho (J. P. Copeland, United States Forest Service, unpublished data); all other records were in northern Idaho (Fig. 2a). We mapped 253 records in western Montana, including 240 harvest reports compiled by the state of Montana from 1974 to 1994. We mapped one record in western Wyoming and one in eastern Nevada.

Other regions in the contiguous United States.—We found only 2 recent mappable wolverine records in any region of the contiguous United States east of the Rocky Mountains, including one verifiable record in north-central South Dakota and one documented record in northeastern Minnesota (Fig. 2a).

Distribution of Current Wolverine Records in the Contiguous United States—1995 to 2005

Pacific Coast mountains.—We mapped 7 verifiable records of wolverine occurrence in northern Washington (Table 1; Fig. 2b). We found no current records in Oregon or California, despite concerted efforts to obtain verifiable evidence of wolverine occurrence using remote cameras, bait stations, and helicopter surveys in many areas of the Pacific states (Kucera and Barrett 1993; Aubry and Lewis 2003; Zielinski et al. 2005; K. B. Aubry, unpublished data).

Rocky Mountains.—Current records of wolverine occurrence in the Rocky Mountains were similar in distribution to recent records. We mapped 16 records in Idaho (13 verifiable), 187 in Montana (186 verifiable), and 12 in Wyoming (11 verifiable; Table 1; Fig. 2b). Records in Idaho included 7 initial capture locations from radiotelemetry studies: 3 in central Idaho, 3 in northern Idaho, and 1 in eastern Idaho (R. M. Inman and K. H. Inman, Wildlife Conservation Society, unpublished data; J. P. Copeland, unpublished data). Current records in Montana included 115 trapping reports compiled by the state of Montana from

Table 1. Verifiable and documented records of wolverine occurrence in the contiguous United States by region and state.

Region and state	Historical records							Recent records			Current records	Most recent verifiable record
	1800s	1901–1910	1911–1920	1921–1930	1931–1940	1941–1950	1951–1960	1961–1970	1971–1980	1981–1994	1995–2005	
Pacific Coast mountains												
WA	17	3	7	0	0	1	1	10	3	4	7	2003
OR	0	0	1	1	0	0	0	2	2	2	0	1992
CA	11	7	9	30	0	0	1	0	0	0	0	1922
Rocky Mountains												
ID	6	5	5	2	0	3	4	5	5	31 ^a	16 ^b	2005
MT	6	1	1	0	4	9	39	14	121 ^c	149 ^d	187 ^e	2005
WY	10	6	1	1	0	0	0	1	0	0	12 ^f	2005
UT	8	0	1	1	0	0	0	0	0	0	0	1921
NV	0	0	0	0	0	0	0	0	1	0	0	1972
CO	22	7	5	0	0	0	0	0	0	0	0	1919
NM	1	0	0	0	0	0	0	0	0	0	0	1860
Central Great Plains												
ND	35	0	1	0	0	0	0	0	0	0	0	None
SD	0	0	0	0	0	0	0	1	0	0	0	1962
NE	1	0	0	0	0	0	0	0	0	0	0	1887
Great Lakes region												
MN	6	0	1	2	1	0	0	1	0	0	0	1899
WI	12	1	0	1	0	0	0	0	0	0	0	1800s ^g
MI	11	0	0	1	0	0	0	0	0	0	0	1868
Upper Midwest												
IA	0	0	0	0	0	0	1	0	0	0	0	1960
IN	2	0	0	0	0	0	0	0	0	0	0	None
OH	0	0	0	0	0	1	0	0	0	0	0	1943
Northeast												
PA	4	0	0	0	0	0	0	0	0	0	0	None
NY	3	0	0	0	0	0	0	0	0	0	0	1811
NH	0	0	2	0	0	0	0	0	0	0	0	None
VT	3	0	0	0	0	0	0	0	0	0	0	None
ME	1	0	0	0	0	0	0	0	0	0	0	None

^a Includes 16 initial capture locations obtained from 1992 to 1994 during a radiotelemetry study.

^b Includes 3 initial capture locations obtained in 1995 during a radiotelemetry study and 4 initial capture locations obtained from 2003 to 2005 during a radiotelemetry study.

^c Includes 94 harvest records from 1974 to 1980 compiled by the MT Department of Fish, Wildlife, and Parks and 24 wolverines that were radiocollared by Hornocker and Hash (1981) in northwestern MT from 1972 to 1977.

^d Includes 146 harvest records from 1981 to 1994 compiled by the MT Department of Fish, Wildlife, and Parks.

^e Includes 115 harvest records from 1995 to 2004 compiled by the MT Department of Fish, Wildlife, and Parks and 49 initial capture locations obtained from 2002 to 2005 during radiotelemetry studies.

^f Includes 9 initial capture locations obtained from 1998 to 2005 during radiotelemetry studies.

^g Jackson (1954) found 2 wolverine specimens in a cave in southwestern WI in 1920 that he estimated had been in the deposit for >50 yr.

1995 to 2004, and 49 initial capture locations from radiotelemetry studies, including 30 in southwestern Montana and 19 in northwestern Montana (J. R. Squires, United States Forest Service, unpublished data; J. P. Copeland, unpublished data; R. M. Inman and K. H. Inman, unpublished data). The 12 records we mapped in Wyoming included 9 initial capture locations from radiotelemetry studies in northwestern Wyoming (J. P. Copeland, unpublished data; and R. M. Inman and K. H. Inman, unpublished data). We found no current records of wolverine occurrence in Utah, Nevada, or Colorado.

Broad-Scale Habitat Relations of Wolverines in the Contiguous United States

Alpine vegetation and climatic conditions.—Overlaying historical wolverine records from the western United States on selected Kuchler potential natural vegetation types (Fig. 3) and Holdridge climatic life zones (Fig. 4), revealed

potential relations with relatively large expanses of alpine vegetation or climatic conditions in many areas. In the Pacific states, such conditions occur primarily in the Cascade Range in Washington, the northern Cascade Range in Oregon, and the central and southern Sierra Nevada in California. Virtually all of the wolverine records we located in the Pacific states were within or near alpine areas (Table 2). In the Rocky Mountain states, we found similar relations between wolverine records and Kuchler's Alpine Meadows vegetation type and Holdridge's Alpine life zones, with the exception of northern Idaho and western Montana, which contained numerous wolverine records but relatively few alpine areas using these classifications. We found additional support for observed habitat relations in our regression analysis; the elevation of wolverine records increased significantly with decreasing latitude and differed substan-

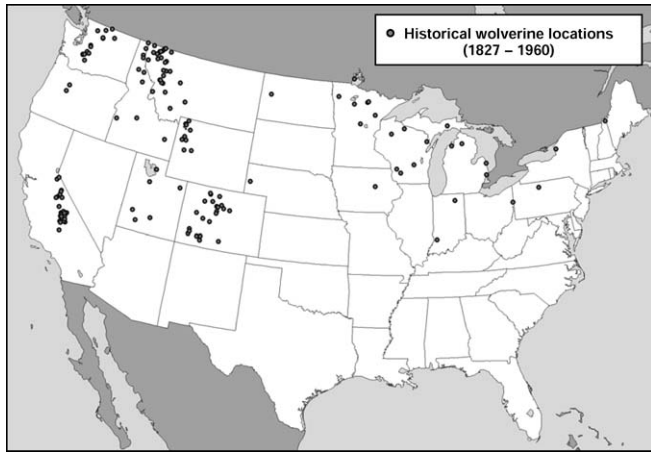


Figure 1. Locations of historical (1827–1960) wolverine records in the contiguous United States with areal precision ≤ 1 township (93.2 km²) and temporal precision ≤ 10 years.

tially from a regression of random locations sampled in the same area (Fig. 5).

No areas in the northeastern United States contain alpine vegetation or climatic conditions using either the Kuchler or Holdridge classification (Fig. 6). The only potential relation we observed by overlaying historical wolverine records from the eastern United States on those habitat layers was the presence of conifer forests in the Kuchler classification (Fig. 6a).

Spring snow cover.—All historical wolverine records in the western United States, and most in the eastern United States, were located in areas with a measurable probability of snow cover persisting through the wolverine denning period during the last 40 years (Fig. 7). All areas with numerous historical wolverine records, including the northern Cascade Range in Washington, the central and southern Sierra Nevada in California, and the Rocky Mountains in northwestern Montana, central Idaho, western Wyoming, northeastern Utah, and western Colorado had $>50\%$ probability

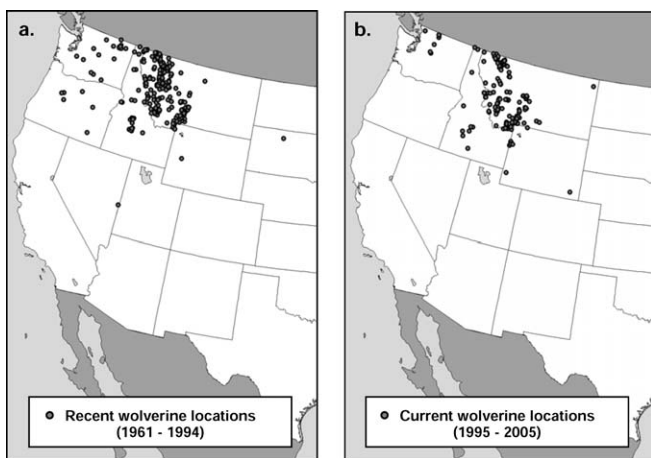


Figure 2. Locations of recent (1961–1994; a) and current (1995–2005; b) wolverine records in the contiguous United States with areal precision ≤ 1 township (93.2 km²) and temporal precision ≤ 10 years. One record in northeastern Minnesota from 1965 is not shown in (a).

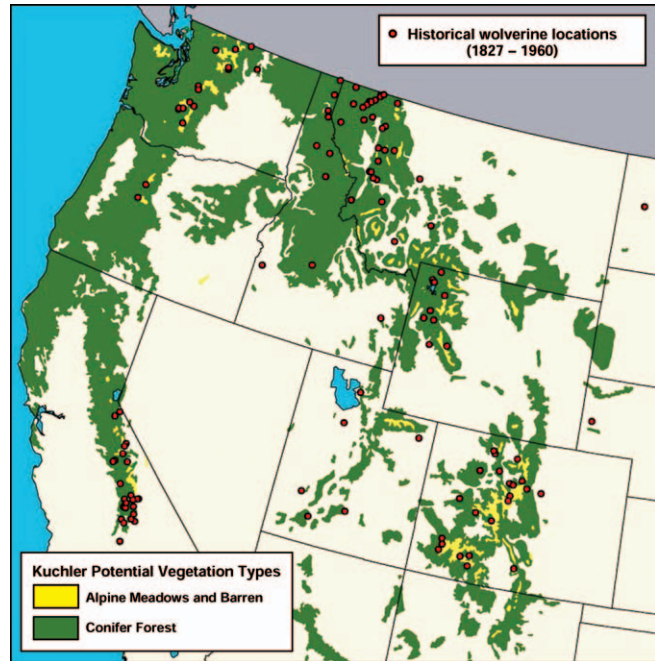


Figure 3. Locations of historical (1827–1960) wolverine records in the western contiguous United States overlaid on a simplified map of Kuchler's (1964) potential natural vegetation types, including Alpine Meadows and Conifer Forests (all montane and northern conifer forest types combined); all other vegetation types are unshaded.

of snow cover. Remaining areas of wolverine occurrence in the Rocky Mountains typically had snow-cover probabilities of 26–50%, and a few records from the Great Lakes, upper Midwest, and Northeast regions were in areas with 1–25% probabilities.

DISCUSSION

Our study provides the first comprehensive and spatially explicit assessment of the geographic distribution of wolverines in the contiguous United States during both historical and modern eras. We found a strong record of wolverine occurrence historically in all portions of the contiguous United States where snow cover typically persists through the spring denning period. Although wolverine records also occurred near alpine vegetation and climatic conditions in many areas, these habitat conditions failed to explain occurrence records in many portions of the northern Rocky Mountains. Thus, we suspect that observed relations with alpine habitat conditions in many areas reflect correlations between those habitat conditions and spring snow cover. Our findings also indicate that the wolverine experienced substantial range losses by the mid-1900s, especially in southern portions of the western mountains and in the Great Lakes region.

Broad-Scale Habitat Relations in the Contiguous United States

Western mountains.—Virtually all historical wolverine records in the western mountains were located in relatively high-elevation montane areas (Fig. 5) and were concentrated in areas containing alpine vegetation (Fig. 3), alpine

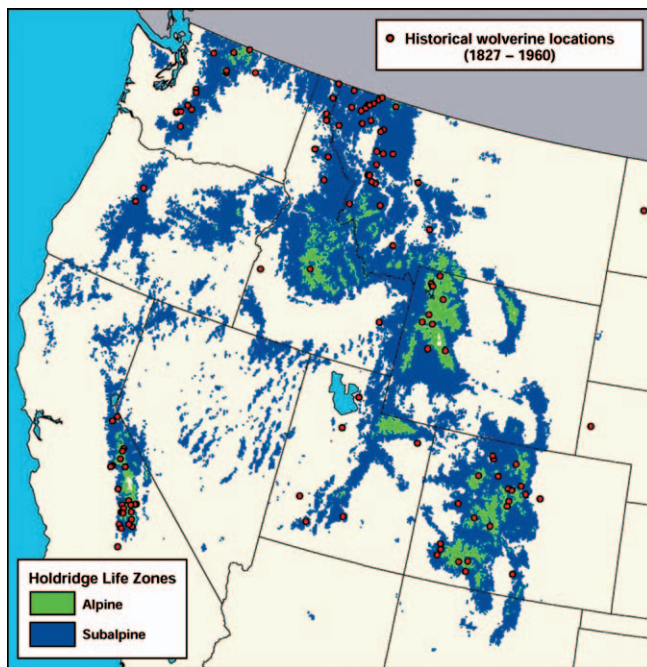


Figure 4. Locations of historical (1827–1960) wolverine records in the western contiguous United States overlaid on Alpine and Subalpine aggregations of Holdridge's (1967) life zones; all other life zones are unshaded.

climatic conditions (Fig. 4), or relatively high probabilities of spring snow cover (Fig. 7). Intervening areas that lacked wolverine records, including southern Oregon, northern California, southern Idaho, southeastern Wyoming, and northwestern Colorado also lacked these environmental conditions. The apparent relation between wolverine records and Kuchler's Alpine Meadows vegetation type is strongest in peripheral portions of their range in the Pacific states and Colorado, where the median distance to Alpine Meadows is ≤ 11 km (Fig. 3; Table 2). This pattern appears to be much weaker in the northern Rocky Mountains, where wolverine records are relatively abundant but alpine vegetation is scarce (median distance = 48 km). We observed a similar pattern with Holdridge's Alpine life zones. Median distances of wolverine records to this stratum were ≤ 1 km in California and Colorado but increased to 51 km in the northern Rocky

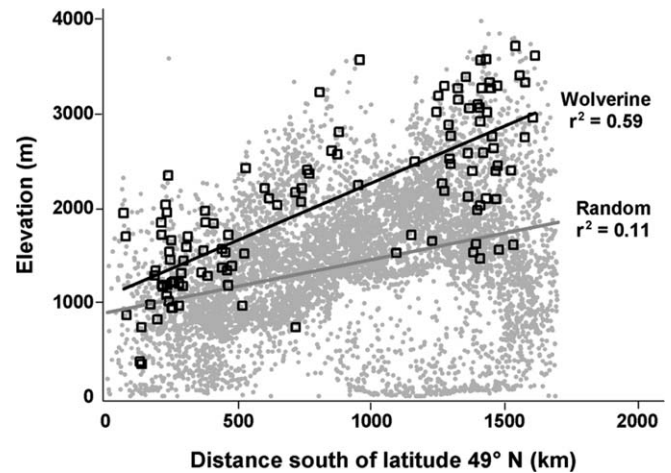


Figure 5. Linear regressions of latitude versus elevation for historical (1827–1960) wolverine records in the western contiguous United States (black squares and regression line), and a random sample of 7,000 locations from the same area (gray dots and regression line).

Mountains (Fig. 4; Table 2). In other geographic areas, observed patterns varied between the 2 habitat layers. Wolverine records in Washington and Oregon appear to be more closely related to Kuchler's Alpine Meadows type (Figs. 3, 4; Table 2) whereas in central Idaho, where Copeland (1996) conducted a radiotelemetry study from 1992 to 1995, Holdridge's Alpine stratum is much more prevalent than Kuchler's (Figs. 2–4; Table 2). Spring snow cover was the only habitat layer that fully accounted for the distribution of historical wolverine records in the western mountains. All areas in the Pacific Coast and Rocky Mountains with numerous wolverine records, including areas that generally lacked alpine vegetation or climatic conditions (e.g., northern ID, northwestern MT, and northern UT; Figs. 3, 4) had $>25\%$ probability of spring snow cover, and most had $>50\%$ probability (Fig. 7).

Snow is generally regarded as an important component of the wolverine's seasonal habitat requirements (Banci 1987, Hatler 1989). Virtually all reported wolverine reproductive dens (sites where kits are born and raised prior to weaning) are relatively long, complex snow tunnels that may or may not be associated with large structures, such as fallen trees or boulders (Pulliainen 1968, Magoun and Copeland 1998).

Table 2. Proportion of mappable historical (1827–1960) wolverine records from the Pacific Coast and Rocky Mountains (USA) that occur in Kuchler's (1964) Alpine Meadows and Conifer Forest potential vegetation types and Holdridge's (1967) Alpine and Subalpine climatic life zones, and the median distances of wolverine records from Kuchler's Alpine Meadows vegetation type and Holdridge's Alpine life zones.

Region and states	Kuchler's potential vegetation types				Holdridge's climatic life zones		
	N	Proportion in	Proportion in	Median distance from	Proportion in	Proportion in	Median distance from
		Alpine Meadows (%)	Conifer Forest (%)	Alpine Meadows (km)			
Pacific Coast mountains							
WA and OR	26	8	88	6	15	50	22
CA	36	17	69	11	58	31	0
Rocky Mountains							
ID, MT, and WY	59	5	76	48	14	81	51
CO	28	25	61	8	46	43	1
UT	8	0	13	113	0	25	78

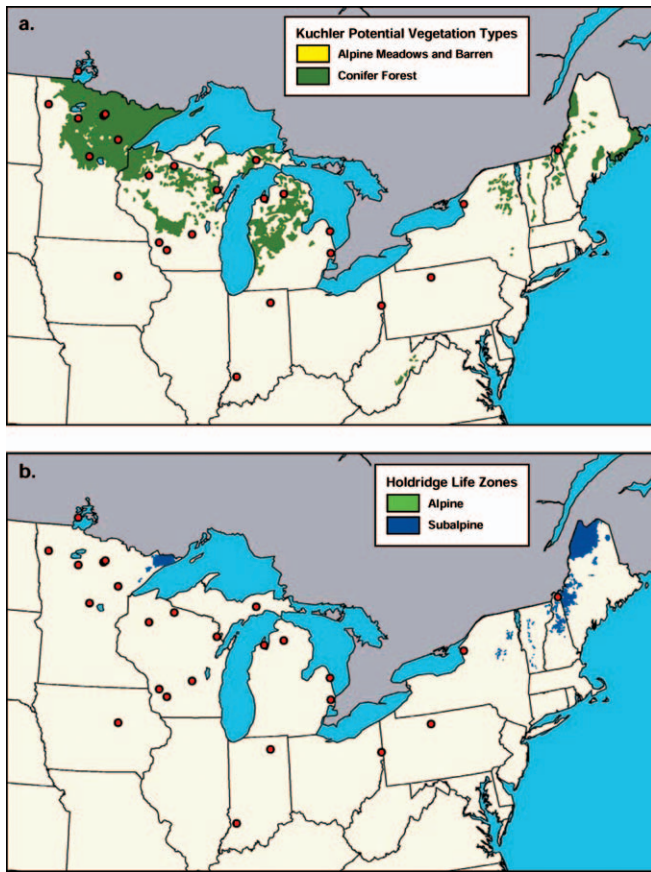


Figure 6. Locations of historical (1827–1960) wolverine records in the eastern contiguous United States overlaid on simplified maps of Kuchler's (1964) potential natural vegetation types, including Alpine Meadows and Conifer Forests (all other vegetation types are unshaded; a); and Alpine and Subalpine aggregations of Holdridge's (1967) life zones (all other life zones are unshaded; b).

Snow dens may aid in kit survival by providing thermal benefits (Pulliainen 1968, Bjärvall et al. 1978), protection from predators (Pulliainen 1968, Krott 1982, Zyryanov 1989), or proximity to high-quality rearing habitat (Magoun and Copeland 1998). The wolverine is well-adapted for life in snowy environments, with moderate foot-loading for traveling efficiently through soft snow (Buskirk et al. 2000) and a relatively large, compact body and thick winter pelage for minimizing heat loss. Telfer and Kelsall's (1984) index of morphological adaptation to snow for the wolverine was similar to indices for both wolves (*Canis lupus*) and coyotes (*C. latrans*), and higher than most North American ungulates; Iversen (1972) estimated that the wolverine's lower threshold of thermoneutrality may be as low as -40°C .

If the persistence of wolverine populations is linked to the availability and quality of relatively deep snow for reproductive den sites, insufficient snow cover during the denning period could play an important role in limiting their distribution. For example, it may explain the apparent absence of wolverines from the Great Plains historically, where predation by wolves and grizzly bears (*Ursus arctos*) on huge herds of American bison (*Bison bison*) would have

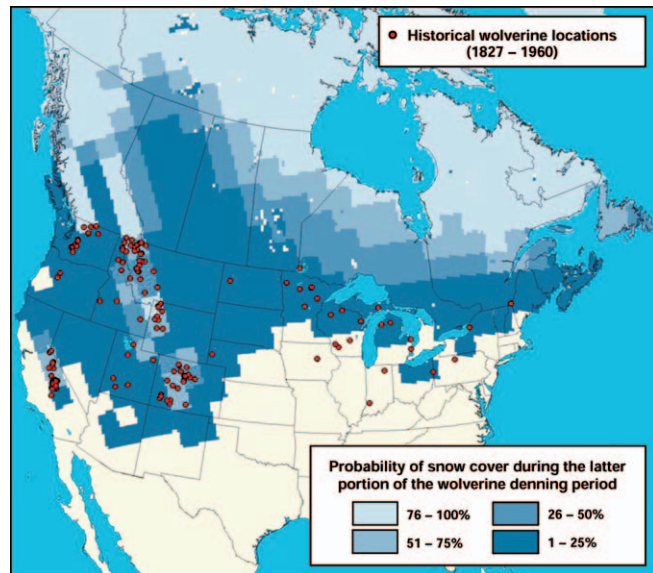


Figure 7. Locations of historical (1827–1960) wolverine records in the contiguous United States overlaid on a map depicting the probability of snow cover during the latter portion of the wolverine denning period (15 Apr–14 May) in increments of 25% based on satellite imagery (EASE-Grid snow cover data) obtained from 1967 to 2005.

provided an abundant food supply for a scavenging species. Wolverines are a common constituent of similarly structured predator–prey communities in subarctic portions of their range. However, snow cover generally persists through the wolverine denning period in those regions, whereas in the Great Plains, it does not (Fig. 7).

Eastern United States.—Most wolverine records in the eastern United States were located in the Great Lakes region, which contains the largest expanses of northern coniferous forest (Table 1; Fig. 6a). Although spring snow cover does not explain the occurrence of wolverines in the Great Lakes states (Fig. 7), our snow data were collected from 1967 to 2005, whereas wolverine records date from 1827 to 1960. According to Salinger (2005), climatic conditions at mid-latitudes in northern continents were substantially cooler in the 1800s than currently, due to gradual warming during the 1900s. During the 1800s, when most wolverine records in the Great Lakes states were obtained, suitable climatic conditions for denning may have occurred farther south in that region than is shown in Figure 7. Supporting evidence for this hypothesis is provided by Dawson (2000), who reported that wolverines occurred throughout Ontario, Canada historically, but the southern limit of their range had receded northward by about 1900. Although increased human activities or habitat changes in southern Ontario may have influenced this northward range shift, almost all wolverine occurrence records from Ontario during the last 25 years were located in portions of the province having $>25\%$ probability of spring snow cover (J. C. Ray, Wildlife Conservation Society Canada, unpublished data; Fig. 7). Thus, as de Vos (1964) suggested, the Great Lakes region probably represented the southern extent of

wolverine distribution in eastern North America prior to European settlement.

Changes in Wolverine Distribution During the 1900s

Historical distribution.—Contrary to most previous interpretations (Seton 1929, Hall 1981, Hash 1987), our findings indicate that the wolverine's historical range was discontinuous in the Pacific states (Fig. 1). We found a similar pattern in the Rocky Mountains; wolverine distribution appears to have been relatively continuous in Idaho, Montana, and Wyoming, but there are substantial gaps in our records in southwestern Wyoming and northwestern Colorado that correspond to gaps in the distribution of both alpine habitat conditions and spring snow cover (Figs. 3, 4, 7). We recognize that the disjunct distribution patterns presented here may reflect sampling error or other limitations of historical data. However, Schwartz et al. (2007) evaluated genetic differences among wolverine populations in various portions of their holarctic range and concluded that California wolverines were isolated from other populations in North America for >2,000 years. Wolverine populations in Colorado and Utah may also have been isolated to some degree, and genetic tests of this hypothesis are in progress (M. K. Schwartz, United States Forest Service, personal communication).

Our results and all published accounts by early naturalists indicate that wolverines were rarely, if ever, encountered in the upper Midwest and Northeast regions of the contiguous United States. Historical records are sparse and haphazard in that area, and the habitat conditions that are associated with wolverine records in the western United States are generally lacking. Additionally, some early wolverine records from the northeastern United States may represent misidentifications. Most wolverine records from that region cannot be verified and, according to several historical accounts from the 1800s, both bobcats (*Lynx rufus*) and Canada lynx (*Lynx canadensis*) were sometimes called wolverines by early settlers (Penobscot 1879, Hough 1893). Thus, available evidence suggests that wolverine records from the northeastern United States probably represent dispersals from populations in other regions. Whether wolverines occurred in that region prior to European settlement is unknown.

Range losses during the 1900s.—Our results support previous assertions that the distribution of wolverines in the contiguous United States had contracted substantially by the mid-1900s (Figs. 1–3; Table 1). Range loss was most apparent in the southern and eastern portions of their historical distribution in California, Utah, Colorado, and the Great Lakes region. The most recent verifiable record of wolverine occurrence in California dates from 1922, in Utah from 1921, in Colorado from 1919, and in Minnesota from 1899; the only documented record from any of these states during either recent (1961–1994) or current (1995–2005) time periods is one from northeastern Minnesota in 1965 (Table 1; Fig. 2). Given the extent to which these areas have been surveyed for wolverines and other forest carnivores (e.g., Halfpenny 1981, Kucera and Barrett 1993, Aubry and

Lewis 2003, Zielinski et al. 2005), and the concerted efforts made by resource management agencies and conservation organizations to compile occurrence records of rare and elusive forest carnivores, the lack of verifiable records in these states for >80 years provides compelling evidence that the wolverine has been extirpated from those portions of its historical range.

Our results also suggest that the wolverine may have experienced significant population declines or local extirpations in the Cascade Range and northern Rocky Mountains during the early 1900s, as previous authors have speculated (Wright and Thompson 1935, Newby and Wright 1955, Newby and McDougal 1964). Between 1921 and 1950, there is only 1 wolverine record from Washington, 1 from Oregon, 5 from Idaho, 13 from Montana, and 1 from Wyoming (Table 1). However, records from these states in subsequent years were relatively numerous, suggesting that wolverine populations may have become reestablished in northwestern regions after a period of range-wide decline (Table 1).

During the 1960s and 1970s, wolverines began appearing in low-elevation, nonforested habitats in eastern Washington and Oregon (Fig. 2a; Table 1). Several authors claimed that these and other verifiable records obtained during this period demonstrated that wolverines were reclaiming broad expanses of their former range (e.g., Nowak 1973, Yocom 1974, Johnson 1977). However, there is no evidence of wolverine occurrence in eastern Washington or Oregon currently (Fig. 2b). It is unclear why wolverines began appearing in previously unoccupied areas during this time period, but we agree with Verts and Carraway (1998) that these records probably represent extreme dispersal events that were not representative of self-sustaining populations. Previous researchers speculated that wolverine populations became reestablished in Montana during the mid-1900s through dispersals from Canada (Newby and Wright 1955) and subsequently expanded their numbers and distribution in the northern Rocky Mountains (Newby and McDougal 1964). Thus, anomalous wolverine records in eastern Washington and Oregon during that time probably represent dispersals from Canada or Montana that failed to establish resident populations.

The distribution of current wolverine records in the contiguous United States is limited to north-central Washington, northern and central Idaho, western Montana, and northwestern Wyoming (Fig. 2b). Causal factors for the apparent extirpation of wolverine populations in the Sierra Nevada and southern Rocky Mountains by the mid-1920s are unknown. However, we believe the most likely explanations for this apparent range loss involve human activities. Both regions have a long history of mining and high-elevation sheep grazing during spring and summer (Fritz 1941, McKelvey and Johnston 1992), and commercial trapping of American marten (*Martes americana*) and other boreal furbearers during winter (Coman 1912, Grinnell et al. 1937, Melchior et al. 1987). Each of these activities

would have increased the likelihood of human encounters with wolverines.

Early settlers and trappers generally viewed wolverines as vermin because they raided trap-lines, stole food from cabins, and ruined remaining food and belongings with musk and urine; at that time, wolverines were also considered to be particularly fierce and dangerous animals (Banci 1994). Consequently, wolverines were often killed when the opportunity arose, and some trappers intentionally poisoned them to prevent the destruction of more valuable furbearers (Moody 1912, Thompson 1929). Additionally, killing large predators with poison baits to protect livestock and game was a common practice among sheep ranchers and federal predator-control agents (Cain 1978, McIntyre 1995); the intentional poisoning of wolverines even occurred in Yellowstone National Park in the late 1800s (Schullery and Whittlesey 1999). Given their scavenging habits, wolverines would have been particularly susceptible to poisoned carcasses. A recent synthesis of wolverine survival rates and mortality sources in North America by Krebs et al. (2004) indicated that wolverine populations with high levels of human-caused mortality cannot be sustained without immigration from neighboring refugia. Given the isolation of wolverine populations in California, and what appears to have been either reduced connectivity or similar isolation of populations in Colorado and Utah, we believe southern populations were extirpated by a combination of unnaturally high mortality rates and nonexistent or very low immigration rates.

Our study provides important new insights into the nature of the wolverine's ecological niche in North America. In many previous assessments, the wolverine was considered to be a habitat generalist, due primarily to its movement capabilities and the latitudinal and ecological breadth of its range, which includes tundra habitats in arctic regions, boreal forests in subarctic regions, and temperate forests at the southernmost extent. However, wolverine distribution in the contiguous United States appears to be closely related to habitat conditions that become increasingly fragmented in more southerly regions. Consequently, there is a much greater potential for wolverine populations in the contiguous United States to become isolated than has been recognized previously. Recent studies support these conclusions; significant population genetic substructuring has been documented in wolverine populations in Idaho (Kyle and Strobeck 2002) and Montana (Cegelski et al. 2003), indicating relatively low migration rates between adjacent mountain ranges.

MANAGEMENT IMPLICATIONS

Given the fragmented nature of suitable habitat conditions for the wolverine at the southern extent of its historical range in North America (Figs. 3, 4, 7), and extensive urban and agricultural development in intervening areas, the reestablishment of southern wolverine populations seems unlikely to occur without human intervention. Because southern wolverine populations appear to have been extirpated by

human-caused mortality factors that no longer pose a significant threat, reintroduction may be an appropriate management strategy. However, the potential effects of increased human activities and disturbance on the reestablishment and persistence of wolverine populations should receive careful consideration during reintroduction planning.

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The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution?

J.P. Copeland, 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. Wilmoth, C.L. Copeland, R.E. Yates, I. Kojola, and R. May

Abstract: We propose a fundamental geographic distribution for the wolverine (*Gulo gulo* (L., 1758)) based on the hypothesis that the occurrence of wolverines is constrained by their obligate association with persistent spring snow cover for successful reproductive denning and by an upper limit of thermoneutrality. To investigate this hypothesis, we developed a composite of MODIS classified satellite images representing persistent snow cover from 24 April to 15 May, which encompasses the end of the wolverine's reproductive denning period. To investigate the wolverine's spatial relationship with average maximum August temperatures, we used interpolated temperature maps. We then compared and correlated these climatic factors with spatially referenced data on wolverine den sites and telemetry locations from North America and Fennoscandia, and our contemporary understanding of the wolverine's circumboreal range. All 562 reproductive dens from Fennoscandia and North America occurred at sites with persistent spring snow cover. Ninety-five percent of summer and 86% of winter telemetry locations were concordant with spring snow coverage. Average maximum August temperature was a less effective predictor of wolverine presence, although wolverines preferred summer temperatures lower than those available. Reductions in spring snow cover associated with climatic warming will likely reduce the extent of wolverine habitat, with an associated loss of connectivity.

Résumé : Nous présentons une répartition géographique fondamentale du glouton (*Gulo gulo* (L., 1758)) basée sur l'hypothèse selon laquelle la présence des gloutons est restreinte par leur association obligatoire à une couverture persistante de neige au printemps nécessaire pour le succès des terriers de reproduction, ainsi que par la limite supérieure de la thermoneutralité. Afin d'examiner cette hypothèse, nous mettons au point un assemblage d'images satellites classifiées MODIS représentant la couverture persistante de neige du 24 avril au 15 mai, ce qui englobe la fin de la période d'utilisation des terriers de reproduction chez les gloutons. Afin d'examiner la relation spatiale du glouton avec les températures maximales moyennes d'août, nous utilisons des cartes de températures interpolées. Ensuite, nous comparons et corrélons ces facteurs climatiques avec des données géographiques spatiales sur les emplacements des terriers de gloutons et les sites de télémétrie en Amérique du Nord et en Fennoscandie, ainsi qu'avec notre compréhension actuelle de l'aire de répartition circumboréale du glouton. Tous les 562 terriers de reproduction de Fennoscandie et d'Amérique du Nord se retrouvent dans des sites à couverture de neige persistante au printemps. Quatre-vingt-quinze pourcent des sites de télémétrie en été et 86 % des sites en hiver concordent avec la couverture de neige du printemps. La température maximale moyenne en août est une variable prédictive moins efficace de la présence des gloutons, bien que les gloutons préfèrent des températures d'été plus fraîches que celles qui sont disponibles. La réduction de la couverture de neige au printemps associée au réchauffement climatique va vraisemblablement réduire l'étendue de l'habitat du glouton, ce qui entraînera une perte de connectivité.

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J.P. Copeland,¹ K.S. McKelvey, J.R. Squires, M.K. Schwartz, and R.E. Yates. U.S. Forest Service, Rocky Mountain Research Station, 800 East Beckwith, Missoula, MT 59801, USA.

K.B. Aubry. U.S. Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512, USA.

A. Landa and R. May. Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway.

J. Persson. Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden.

R.M. Inman. Wildlife Conservation Society, 2023 Stadium Drive, Suite 1A, Bozeman, MT 59715, USA.

J. Krebs. Columbia Basin Fish and Wildlife Compensation Program, 103-333 Victoria Street, Nelson, BC V1L 4K3, Canada.

E. Lofroth. Ministry of Environment, P.O. Box 9338, Victoria, BC V8W 9M1, Canada.

H. Golden. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA.

A. Magoun. Wildlife Research and Management, 3680 Non Road, Fairbanks, AK 99709, USA.

J. Wilmoth. Northern Rockies Conservation Cooperative, P.O. Box 2705, Jackson, WY 83001, USA.

C.L. Copeland. The Wolverine Foundation, 9450 South Black Cat Road, Kuna, ID 83634, USA.

I. Kojola. Finnish Game and Fisheries Research Institute, Tutkijantie 2 E, FI-90570 Oulu, Finland.

¹Corresponding author (e-mail: jpcopeland@fs.fed.us).

Introduction

The extent to which a species' geographic distribution correlates with climatic variables depends on the importance of those variables to the species' fundamental niche (Pearson and Dawson 2003). The influence of climate on the natural distribution of many species (Pearson and Dawson 2003) has led to the development of "bioclimatic envelope" models that relate range limits to sets of climatic conditions within which a species can survive and reproduce (Box 1981; Pearson and Dawson 2003; Thuiller et al. 2005; Lawler et al. 2006). Bioclimatic models consider climatic variables as correlates of a species' current distribution and are often used to predict range shifts that may result from different climate change scenarios (Hijmans and Graham 2006). These correlative approaches are sometimes criticized because they fail to account for interactions with biotic factors (Davis et al. 1998; Pearson and Dawson 2003; Heikkinen et al. 2006; Post et al. 2009) and may not accurately reflect the ecology, behavior, or physiology of the target species (Soberón 2007; Pöyry et al. 2008). Consequently, evaluating an organism's climatic requirements by correlating current range with climatic factors is problematic. However, if researchers possess reliable understandings of both an organism's geographic range and its climatically linked biological requirements, they can evaluate whether current range is consistent with the climatic conditions needed to fulfil those requirements. This is the approach taken here.

The wolverine, *Gulo gulo* (L., 1758), occurs throughout arctic regions and also in subarctic areas and boreal forests of Eurasia and North America. In southern portions of the wolverine's range in western North America, wolverine populations occupy peninsular extensions of boreal forests in montane regions. Our understanding of the wolverine's geographic distribution is informed by a relatively small number of radiotelemetry studies and monitoring programs in North America and Fennoscandia (Landa et al. 1998a; Flagstad et al. 2004; Lofroth and Krebs 2007), but these efforts are often limited in both spatial and temporal extent. Derived understandings of wolverine behavior and habitat use are influenced by the scale at which they are developed; understandings developed from within an individual home range (e.g., second- or third-order selection sensu Johnson 1980) may not be informative concerning factors that limit range at broader spatial scales (e.g., first-order selection sensu Johnson 1980). Only one study has attempted to define the wolverine's niche on a continental scale (Aubry et al. 2007).

Wolverine occurrence has been correlated with remoteness from human development (Banci 1994; Carroll et al. 2001; Rowland et al. 2003; May et al. 2006, 2008). However, historical records for western North America (the only portion of the wolverine's circumboreal range wherein the species' historical distribution has been thoroughly investigated; Aubry et al. 2007) reveal little evidence of wolverine presence outside subalpine habitats (Aubry et al. 2007) and support genetic evidence of long-term isolation in the Sierra Nevada (Schwartz et al. 2007). The only study to look at the wolverine's spatial relationship with human infrastructure (May et al. 2006) found spatial separation occurring at broad spatial scales but little evidence of avoidance at finer scales.

In montane regions, wolverines reportedly shift habitat

use to higher elevations during summer and lower elevations during winter. Moving up in elevation during the summer may provide a thermal advantage to wolverines (Hornocker and Hash 1981) when ambient temperatures are high, or may reflect seasonal variation in prey availability (Gardner 1985; Whitman et al. 1986; Landa et al. 1998b; Copeland et al. 2007; Krebs et al. 2007). However, Banci and Harestad (1990) reported no elevational shift in habitat use by wolverines in Yukon, Canada, hypothesizing that seasonal movements were unnecessary owing to low summer temperatures at low elevations and a scarcity of prey at high elevations. Although it is generally accepted that temperature influences the geographic distribution of animals, there have been few studies of the relationship between range limits and thermal tolerances (Clark 1996).

Snow is regarded as an important component of the wolverine's seasonal habitat requirements (Banci 1987; Magoun and Copeland 1998; Aubry et al. 2007). Well adapted to snow, the wolverine's compact body and large plantigrade feet aid in travel through soft snow, and its dense pelage provides insulation from extreme cold. It has been hypothesized that deep, persistent spring snow cover is an obligate component of wolverine reproductive denning habitat (Magoun and Copeland 1998) because it aids the survival of young by providing a thermal advantage (Pulliainen 1968; Bjärvall et al. 1978) and provides a refuge from predators (Pulliainen 1968; Persson et al. 2003). Reproductive denning begins in early February to mid-March, and post-weaning den abandonment occurs in late April and May (Landa et al. 1998a; Magoun and Copeland 1998; Persson et al. 2003). Reproductive dens may be located under boulders or downed trees buried beneath the snow (Magoun and Copeland 1998) or may be temporary structures within the snow layer itself (Lee and Niptanatiak 1996; Landa et al. 1998a, 1998b; Magoun and Copeland 1998). If persistence of wolverine populations is linked to the availability of suitable reproductive den sites (Banci 1994), snow cover that persists throughout the denning period may be a critical habitat component that limits the wolverine's geographic distribution.

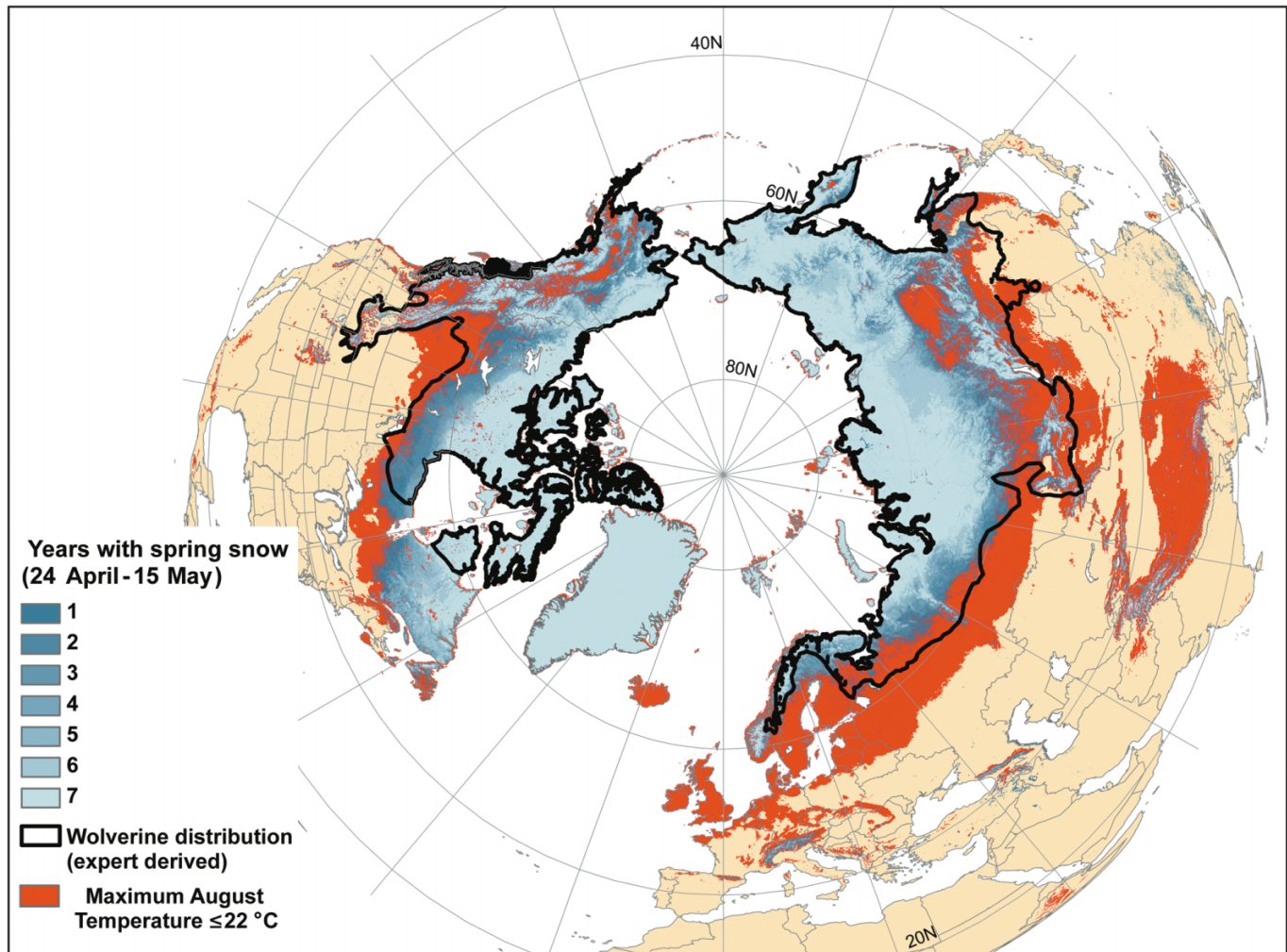
Here, we investigate the hypothesis that wolverine distribution at the broadest spatial scale is constrained within a climatic envelope defined by an obligate association with persistent spring snow cover and by an upper limit of thermoneutrality. We test this hypothesis by comparing and correlating 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. We contrast these findings with a heuristically derived map of the wolverine's current circumboreal range.

Materials and methods

Spring snow cover data

We developed a spatial data layer of spring snow cover in the Northern Hemisphere for a 7-year period from 2000 to 2006 using moderate-resolution imaging spectroradiometer (MODIS) classified daily snow data (500 m spatial resolution) from the Terra satellite (Hall et al. 2006). Terrestrial pixels were classified into four cover classes (snow, bare

Fig. 1. The circumboreal range of the wolverine. The black outline represents the wolverine's putative current geographic distribution developed from existing range maps and local expert knowledge. The wolverine's hypothesized bioclimatic envelope defined by the spring snow coverage (blue gradient) is overlaid on the summer temperature coverage (orange areas). The gradient in the spring snow coverage depicts the number of years out of seven (2000–2006) in which snow cover was present from 24 April to 15 May, and the summer temperature coverage delineates the areas with average maximum August temperatures $\leq 22^{\circ}\text{C}$ from 1950 to 2000.



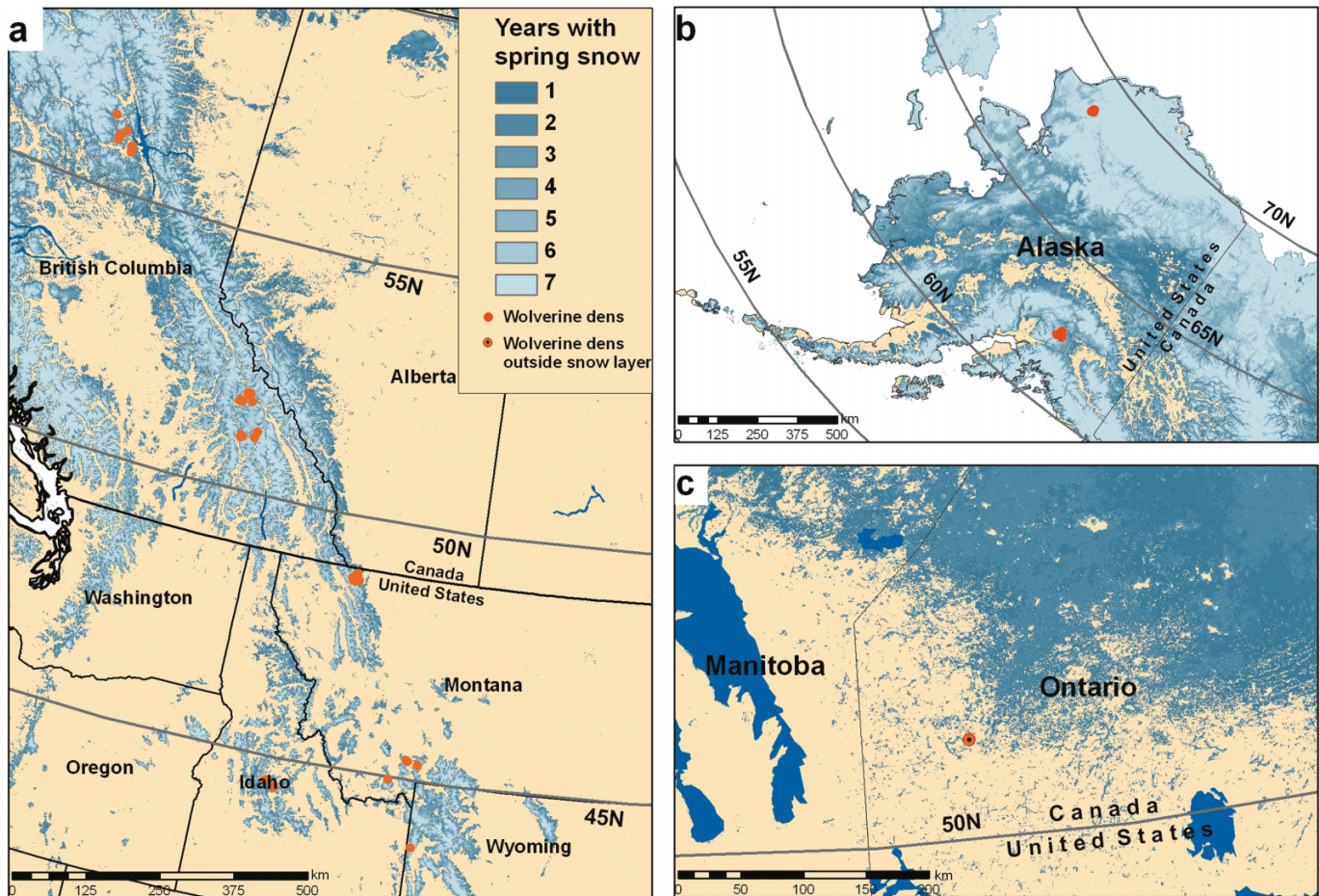
ground, cloud, night) for each of the 7 years (Hall et al. 2006). A portion of each daily MODIS image was typically obscured by clouds or, occasionally, by night. Generating cloud- and night-free images required compositing 21 consecutive daily images from 24 April to 15 May, which generally corresponds to the period of wolverine den abandonment (Magoun and Copeland 1998) and is consistent with the time period used by Aubry et al. (2007) to correlate historical occurrence records with spring snow cover. Compositing images reduced the number of cloud or night pixels during this period to $<3\%$ for all images. To separate areas where snow persisted through 15 May and to avoid confusion due to late ephemeral snow, we coded each pixel as bare ground if, during the 21-day period, the pixel was classified as bare ground at any time. This resulted in annual spring snow cover layers limited to areas with snow cover that persisted through 15 May. We then summed all annual snow layers for the 7-year period to create a coverage that depicted the number of years out of 7 that each pixel was classified as snow (hereafter, the spring snow coverage). We excluded regions of persistent

glaciation (e.g., Greenland) and arctic regions $\geq 80^{\circ}\text{N}$ latitude from the spring snow coverage owing to predictably consistent snow cover during that time of year.

Persistent spring snow cover and wolverine occurrence

To evaluate the concordance of wolverine den sites with the spring snow coverage, we compiled wolverine reproductive den locations having a spatial accuracy ≥ 500 m. For Norway and Sweden, the Scandinavian national wolverine den monitoring program provided precise den locations from the 7 years for which MODIS data were available (Landa et al. 1998a). For Finland and North America, where den data are less common, we included all wolverine dens for which we could obtain coordinates that met or exceeded the spatial resolution of the spring snow coverage; data on those dens extended from 1981 to 2007. We were unable to locate spatially referenced den data for other areas of wolverine occurrence in Eurasia. Wolverine den surveys were well distributed in Norway and Sweden; consequently, for comparisons of use versus availability, we limited the available uni-

Fig. 2. Distribution of wolverine dens in North America overlaid on the spring snow coverage in (a) the Rocky Mountains of British Columbia, Canada, and the western US; (b) Alaska, US, and (c) Ontario, Canada. The gradient in the spring snow coverage represents the number of years out of seven (2000–2006) in which snow cover was present from 24 April to 15 May.



verse for the spring snow coverage to the political boundaries of both countries. We then used χ^2 analyses to test the hypothesis that the distribution of den sites among the seven snow-cover classes (1–7 years of persistent snow) did not differ from availability. If results of χ^2 tests were significant, we used Bonferroni confidence intervals to identify snow-cover classes that differed significantly (Neu et al. 1974). We present these results in the form of selection indices (Manly et al. 1993). For wolverine den sites in North America and Finland, which were not representatively distributed, we simply report the frequency of den-site use among snow-cover classes.

To assess the spatial concordance of year-round habitat use by wolverines with the spring snow coverage, we assembled radiotelemetry data from 10 recent studies conducted in the contiguous United States (US), Canada, and Norway. We restricted our analyses primarily to study areas in mountainous regions in southern portions of current wolverine range because they contain extensive snow-free areas intermixed with areas of persistent spring snow cover. Thus, these areas provided the best opportunity to evaluate selection of habitats occurring within or outside the area delineated by the spring snow coverage. However, the northern Norwegian study area was completely snow-covered through 15 May and was therefore not included in analyses of selection for areas with spring snow.

Data obtained from telemetry studies included wolverine

relocations acquired with VHF (May et al. 2006; Copeland et al. 2007; Krebs et al. 2007), GPS, and ARGOS transmitters. Unpublished data (GPS and ARGOS telemetry points) were screened to avoid serial correlation (May et al. 2006; Copeland et al. 2007) and errors exceeding the spatial resolution of the snow cover data (500 m). For spatial comparison of telemetry points with the spring snow coverage, we delineated our availability areas as the 100% minimum convex polygons (MCPs) around all wolverine telemetry points in each study area. Although kernel estimators and other methods provide more reliable estimates of spatial use patterns, we used 100% MCPs to provide the most conservative estimates of the areas available to wolverines in each study area. We then classified telemetry points as 1 if they fell within pixels classified as snow and 0 if they did not. We evaluated the spatial relationship between telemetry points and the spring snow coverage for each study area using χ^2 tests. To investigate the wolverine's seasonal association with areas having persistent spring snow cover, we pooled data by season (summer, June through November; winter, December through May).

Wolverine distribution and upper thermal limits

We examined the relationship between wolverine distribution and maximum summer temperatures to investigate

Fig. 3. Distribution of wolverine dens in Sweden, Norway, and Finland overlaid on the spring snow coverage. The gradient in the spring snow coverage represents the number of years out of seven (2000–2006) in which snow cover was present from 24 April to 15 May.

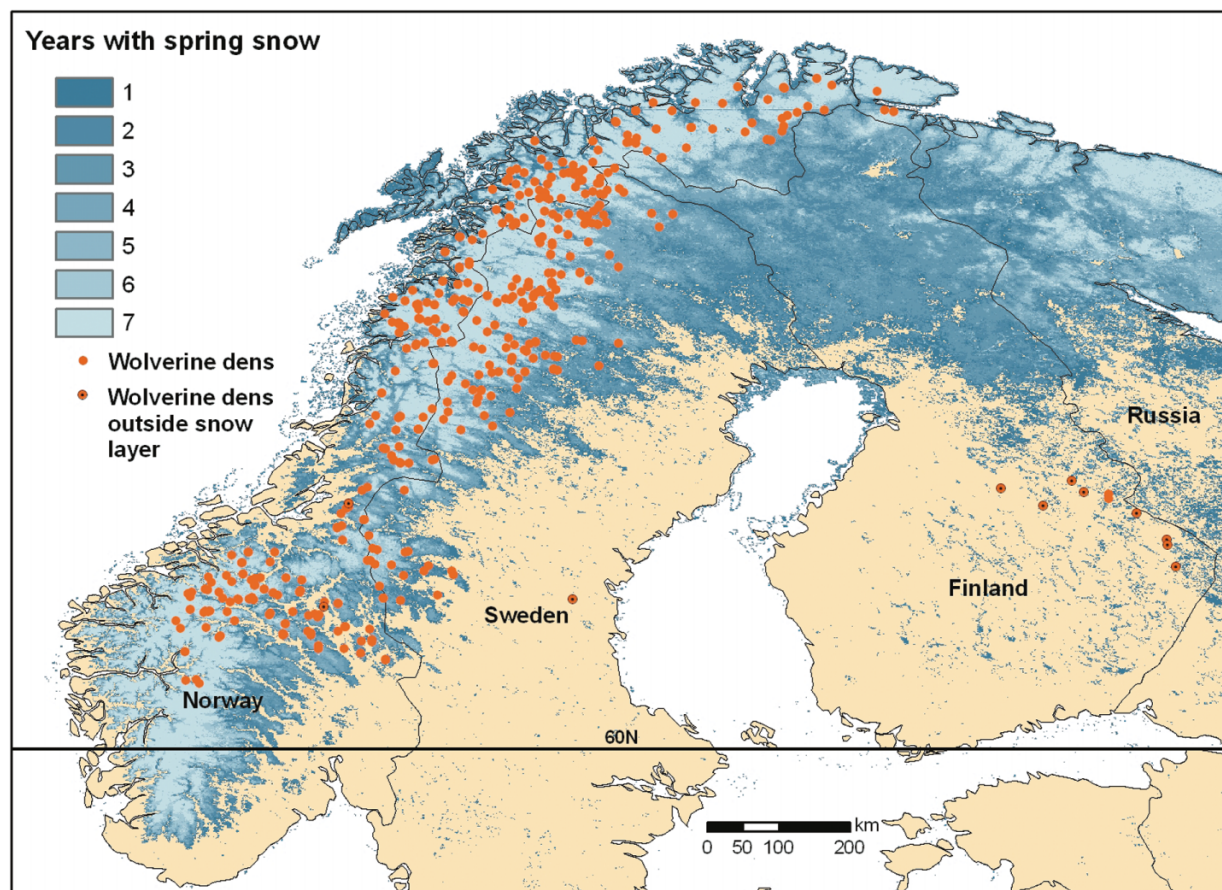
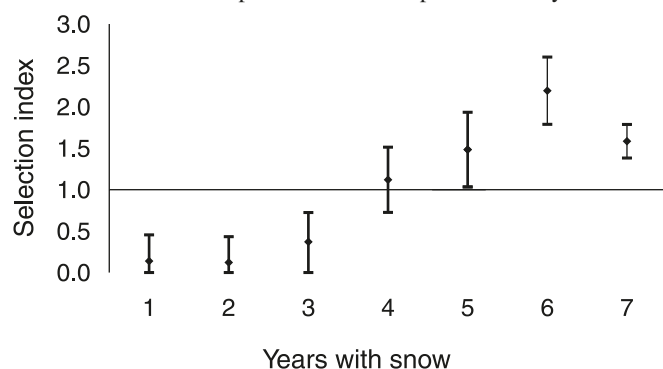


Fig. 4. Selection indices depicting the relation between the spring snow coverage and sites selected by wolverines for reproductive dens in Norway ($n = 327$) and Sweden ($n = 160$). Bars represent 95% Bonferroni-adjusted confidence intervals comparing snow cover values at den sites with proportional availability across Norway and Sweden. Confidence intervals are standardized around 1 to display preference (fully above) or avoidance (fully below). The x-axis represents the number of years out of seven (2000–2006) in which snow cover was present from 24 April to 15 May.

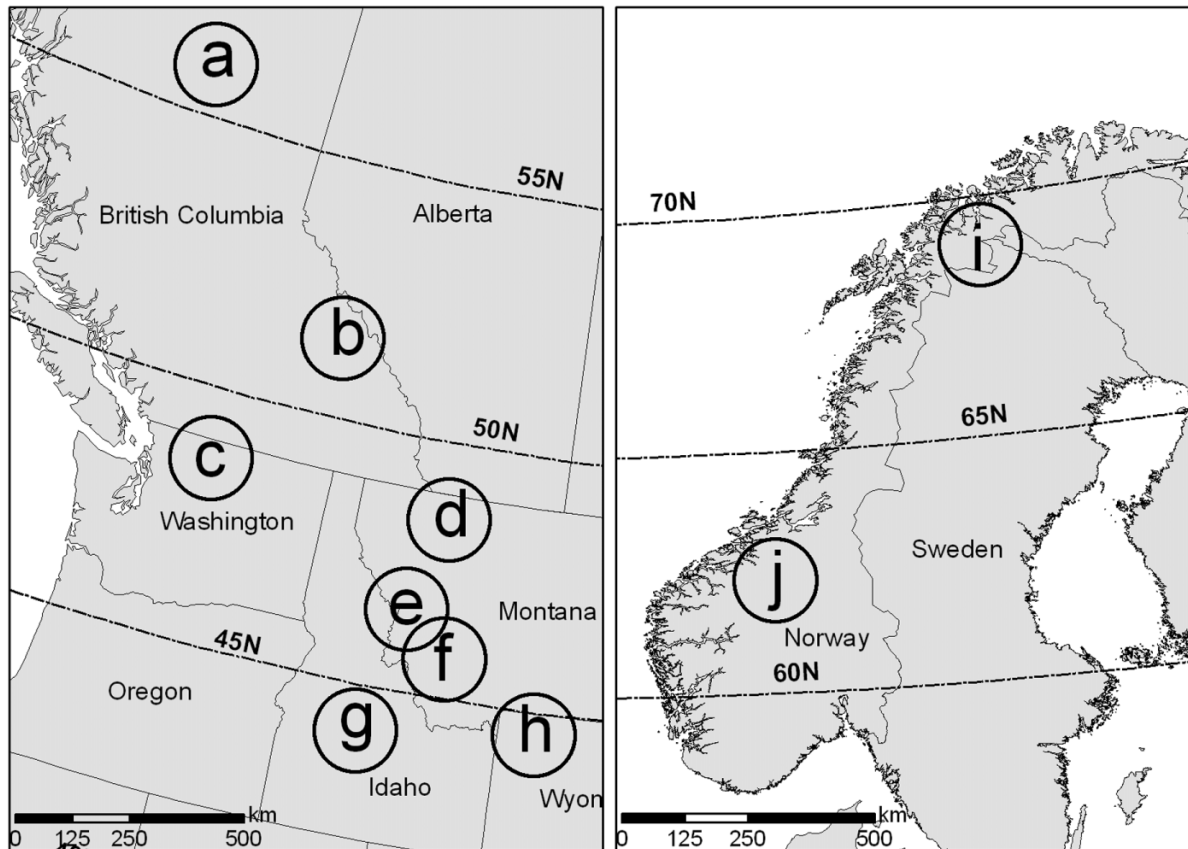


whether wolverine circumboreal range limits are tied to an upper limit of thermal tolerance. We compared published temperature data at 30 arc-seconds (~ 1 km) resolution for average maximum August temperatures for the years 1950–

2000 (Hijmans et al. 2005; hereafter, the summer temperature coverage) with summer wolverine telemetry data sets that represented the latitudinal gradient of wolverine occurrence.

Although the wolverine literature posits seasonal movements upward in elevation to avoid thermal stress, upper thermal limits of wolverines have not been studied (unlike reproductive denning requirements, for which we had a strong a priori hypothesis to test against observed data). Therefore, we fit temperature limits to telemetry data from eight North American and two Norwegian study areas, examined the consistency of the temperature threshold across study areas, and compared derived temperature limits with our contemporary understanding of the wolverine's current range in the Northern Hemisphere. To do so, we extracted temperature values for summer telemetry locations and created cumulative distributions of locations as a function of temperature. We chose, a priori, the 90th percentile of locations as a putative upper thermal limit for wolverines. We then created a coverage representing the spatial distribution of temperatures at or below the 90th percentile temperature value for comparison with the spring snow coverage. In addition, we extracted temperature values associated with random points within the same MCPs used to investigate selection for the spring snow coverage. These values were then used to investigate whether wolverines were selecting for areas with relatively low average summer temperatures.

Fig. 5. Location of wolverine study areas used to compare use (telemetry data) and availability (the spring snow coverage): (a) Omineca Mountains, British Columbia (Krebs et al. 2007, VHF data), (b) Revelstoke, British Columbia (Krebs et al. 2007, VHF data), (c) Northern Cascade Range, Washington (K. Aubry, unpublished ARGOS data), (d) Glacier National Park, Montana (J. Copeland, unpublished VHF and GPS data), (e) Lolo Pass, Montana and Idaho (M. Schwartz, unpublished ARGOS data), (f) Pioneer Mountains, Montana (Squires et al. 2007, VHF data), (g) central Idaho (Copeland et al. 2007, VHF data), (h) Greater Yellowstone Ecosystem, Wyoming, Montana, and Idaho (J. Wilmot and R. Inman, unpublished VHF and GPS data), and (i) northern Norway and (j) south-central Norway (May et al. 2006, VHF data).



Interpretation of current wolverine range

To evaluate the concordance between current wolverine range, spring snow cover, and low summer temperatures, we used a range map created during the 1st International Symposium on Wolverine Research and Management in Jokkmokk, Sweden, in 2005 (Copeland et al. 2005). This map combined information in published range maps (Novikov 1962; Nowak 1973; Wilson 1982; Pasitschniak-Arts and Larivière 1995; Landa et al. 2000; Aubry et al. 2007; Zhang et al. 2007) with local knowledge gathered at the conference (Copeland et al. 2005). Special efforts were made to clarify the geographic distribution of wolverines in areas where occurrence records are particularly sparse (Finland, Russia, China, eastern Canada). Scientists from throughout the Northern Hemisphere were asked to evaluate and refine range boundaries for the geographic areas where they had specific expertise and, where multiple scientists were present, attempts were made to achieve consensus. The resulting range maps were then digitized. Range maps

are broadly delineated and heuristically derived, whereas associations with spring snow cover and maximum summer temperatures were defined for specific time periods and spatial resolutions. Consequently, a statistical analysis of concordance between these distributions was not appropriate; we therefore confined our assessment to a visual evaluation of resulting patterns.

Results

We reclassified over 12 000 MODIS images for the time period of 24 April to 15 May from 2000 to 2006 to produce the spring snow coverage for the Northern Hemisphere (Fig. 1; Figs. S1 and S2).² We compiled spatial information for 562 wolverine reproductive den sites representing all verified dens in North America ($n = 65$) and Finland ($n = 10$) (Figs. 2, 3) and dens from 2000 to 2006 in Norway ($n = 327$) and from 2003 to 2006 in Sweden ($n = 160$) (Fig. 3). When overlaid on the spring snow coverage,

²Supplementary data for this article are available on the journal Web site (<http://cjz.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5338. For more information on obtaining material refer to <http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html>.

Table 1. Spatial concordance between the spring snow coverage and telemetry locations from 10 wolverine study areas in North America and Scandinavia.

Study area ^a	No. of telemetry locations	Area within the spring snow coverage (%)	Telemetry locations within the spring snow coverage (%)	χ^2 critical value	χ^2 P value ^b	Seasonal telemetry locations within the spring snow coverage (%)	
						Summer	Winter
Northern Norway	1819	— ^c	— ^c	— ^c	— ^c	— ^c	— ^c
South-central Norway	455	90.7	98.1	29.7	<0.001	98.5	97.6
Omineca Mountains, British Columbia	1206	77.4	74.4	6.3	(0.011)	85.6	67.5
Revelstoke, British Columbia	2007	85.1	93.6	1919.8	<0.001	89.8	83.3
Northern Cascade Range, Washington	345	73.8	90.7	50.9	<0.001	97.6	79.3
Glacier National Park, Montana	793	81.2	93.1	73.5	<0.001	95.0	92.0
Lolo Pass, Montana and Idaho	44	60.6	79.5	6.6	0.010	83.3	83.0
Pioneer Mountains, Montana	251	46.8	74.9	79.4	<0.001	76.6	71.3
Central Idaho	983	61.4	86.8	267.8	<0.001	91.5	81.7
Greater Yellowstone Ecosystem, Wyoming, Montana, and Idaho	1846	54.6	93.6	1131.0	<0.001	95.2	92.9

^aThe geographic location of each study area is shown in Fig. 5.^bProbability values in parentheses indicate avoidance.^cThe northern Norway study area was entirely snow-covered.

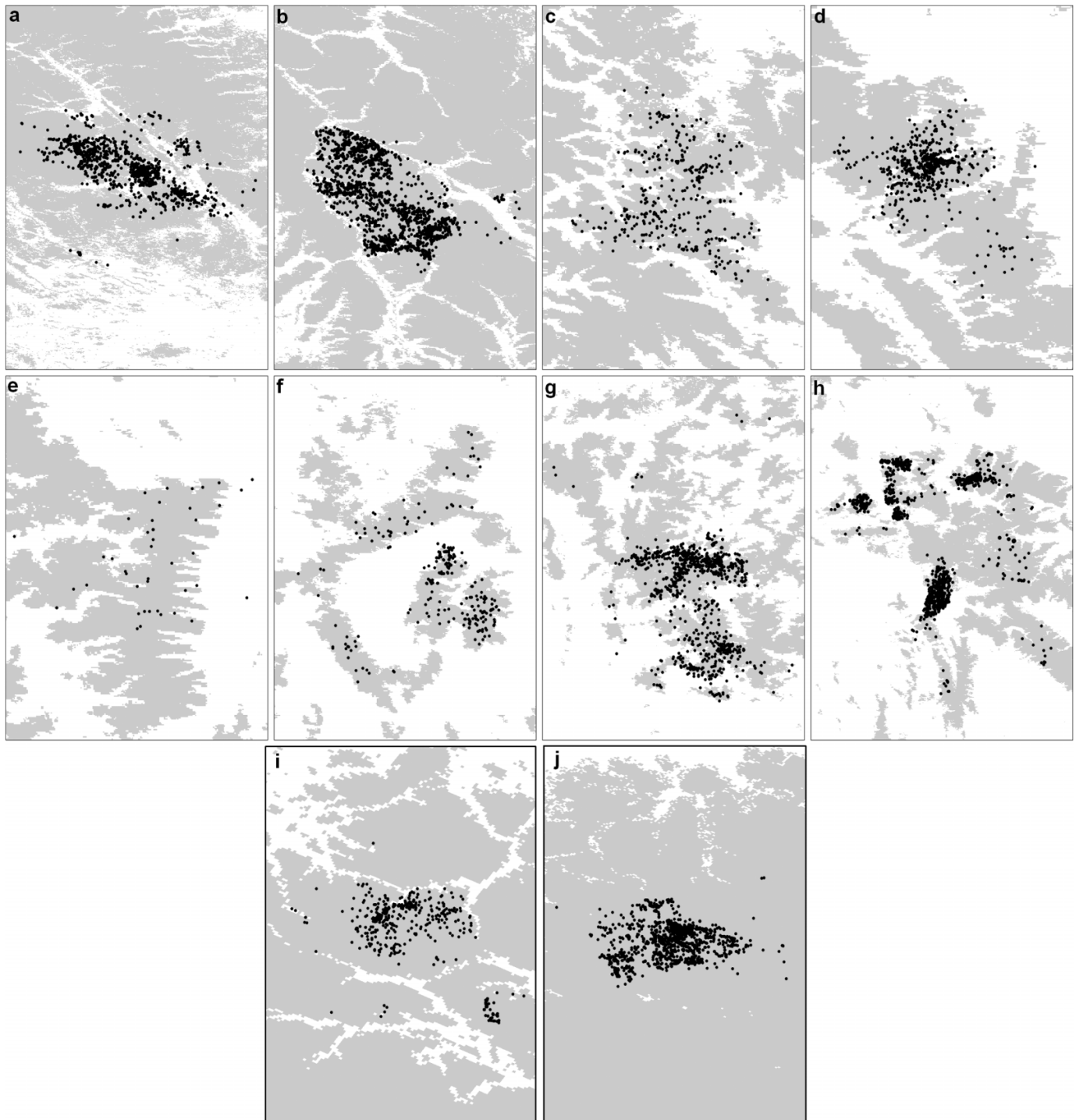
97.9% (550) of the den sites occurred in pixels that were snow-covered in at least 1 of 7 years. Den-site selection relative to years with snow was similar in Norway and Sweden and indicated that Scandinavian wolverines preferred den sites that were snow-covered for 6–7 years ($\chi^2 = 259.63$, $P < 0.0001$) (Fig. 4). North American wolverines also located their dens within the spring snow coverage, and most dens (45/65; 69%) were located in areas that were snow-covered for 6–7 years. Two dens in Norway, one den in Sweden, eight dens in Finland, and one den in Ontario, Canada, fell outside the spring snow coverage. All of these den sites were investigated and determined to be snow dens; they occurred in areas where snow cover was insufficient to classify the 500 m \times 500 m area as persistently snow-covered through 15 May.

For the nine telemetry study areas included in analyses of snow-cover selection (Fig. 5, excluding *i*), the spring snow coverage included 89% of the telemetry points but only 72% of the total area within MCPs (Table 1, Fig. 6). Ninety-five percent of summer locations and 86% of winter locations fell within the spring snow coverage (Table 1). In seven of eight North American study areas and in southern Norway, wolverines selected for areas within the spring snow coverage during winter, summer, and when seasons were pooled. In the Omineca Mountains study area in British Columbia (Fig. 5), wolverines avoided the spring snow coverage in winter and when seasons were pooled (Table 1), but selected for it during the summer months.

The 90% cumulative temperature value varied by 10.3 °C across the 24° of latitude encompassed by the 10 study areas (Table 2). In the more northerly study areas, higher temperatures were less available and wolverine use generally mirrored availability, although lower temperatures were preferred within most study areas (Table 2, Fig. 7). Temperature use diverged from availability between 56°N and 52°N latitude (Fig. 7). At southerly latitudes in North America, wolverines selected for cooler habitats in the summer (Table 2, Fig. 7), with 90% of telemetry locations occurring in areas with average maximum August temperatures ≤ 22 °C (averaged across all study areas south of 56°N latitude). Areas in this temperature range were much more concordant with the spring snow coverage at southerly latitudes (Table 2, Fig. 1). In North America, the spring snow coverage and maximum summer temperature models diverged from each other at about 54°N latitude, just south of the Omineca Mountains study area (Fig. 8).

The wolverine's southern range limits generally extended slightly beyond the spring snow coverage, particularly in areas with low topographic relief (Fig. 1). Areas where current range limits were not consistent with persistent spring snow cover included areas of recent extirpation (southern portions of Norway, Sweden, and Finland; Quebec, Canada; California and Colorado, US) and Eurasian regions where the historical presence of wolverines is largely unknown. These include southern montane regions, such as the Alps and the Carpathian Mountains in Europe and the Himalayas in southern Asia (Fig. S2).² The summer temperature coverage extends far south of both the current range of wolverines and the spring snow coverage, including coastal areas where maritime influences keep temperatures low (Fig. 1).

Fig. 6. Wolverine telemetry locations obtained during all seasons of the year from eight study areas in western North America overlaid on the spring snow coverage (see caption in Fig. 5 for details on data sources).



Discussion

Reproductive dens and persistent spring snow cover

The association between wolverine reproductive denning and snow cover has been documented previously (Magoun and Copeland 1998), though sample sizes were small (5 females, 15 dens). However, neither the generality of this association nor its potential influence on range limits had been explored. Virtually all wolverine reproductive dens we con-

sidered occurred within the spring snow coverage. Those that fell outside (Figs. 2c, 3) occurred on the periphery of the wolverine's current range. The extralimital den in Sweden is believed to be associated with a subpopulation that recently colonized lowland forests, but the viability of this population is unknown (Hedmark and Ellegren 2007). Documentation of Eurasian wolverine reproductive dens outside Fennoscandia is virtually nonexistent; most documented den sites are in Sweden and Norway. Pulliainen (1968) described

Table 2. Spatial concordance between the summer temperature coverage (Hijmans et al. 2005) and summer telemetry locations from 10 wolverine study areas in North America and Scandinavia.

Study area ^a	Latitude (decimal degrees)	No. of summer ^b telemetry locations	Average maximum August temperature (°C)		χ^2 critical value for observed vs. expected	χ^2 P value	Spatial concordance of the summer temperature and spring snow coverages (%)
			90% cumulative use	Range of availability			
Northern Norway	68.00	1233	13.6	7.6–14.7	124.7	<0.001	— ^c
South-central Norway	62.00	203	14.0	6.2–18.0	17.5	0.129	— ^c
Omineca Mountains, British Columbia	56.03	459	19.8	13.2–21.0	128.9	<0.001	— ^c
Revelstoke, British Columbia	51.54	935	20.5	9.2–24.6	357.7	<0.001	89.5
Glacier National Park, Montana	48.77	278	22.6	15.3–26.2	111.5	<0.001	78.2
Northern Cascade Range, Washington	48.61	84	20.5	12.6–29.1	41.9	<0.001	86.2
Lolo Pass, Montana and Idaho	46.31	5	22.3 ^d	— ^e	— ^e	— ^e	55.9
Pioneer Mountains, Montana	45.72	141	22.8	16.8–26.6	47.1	<0.001	86.1
Central Idaho	44.05	508	23.9	18.5–30.5	256.8	<0.001	69.2
Greater Yellowstone Ecosystem, Wyoming, Montana, and Idaho	44.26	547	21.7	11.8–28.3	602.5	<0.001	87.4

^aThe geographic location of each study area is shown in Fig. 5.

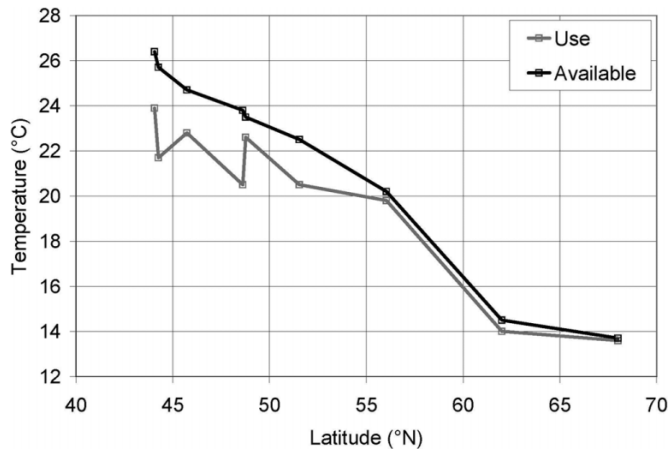
^bSummer: 1 June to 30 November based on presence or absence of snow.

^cSummer temperatures did not reach 22 °C.

^dRepresents average rather than 90% cumulative.

^eSample sizes were inadequate for analysis.

Fig. 7. Latitude vs. average maximum August temperature from 1950 to 2000 for each of nine wolverine study areas (14° of latitude) for data on use (90% of summer wolverine telemetry locations) and availability (5000 random locations).



an additional 31 dens from Finland. Although these dens lacked precise locality data, they appear to have been in an area that is consistent with the spring snow coverage (compare Pulliainen's Fig. 1 with our Fig. 3), and Pulliainen (1968) also concluded that snow plays an important role in the breeding biology of the wolverine. Similarly, wolverines occur in the central Canadian provinces of Alberta, Saskatchewan, Manitoba, and Ontario at the southern extent of the spring snow coverage (Fig. 1). However, wolverines are believed to be declining in Alberta and are considered rare outside the northern extremes of the other south-central provinces (Slough 2007). The Ontario den and the Finland dens represent populations at the extreme southern extent of current wolverine range in Ontario (Magoun et al. 2007) and Finland. Their presence outside the spring snow coverage probably reflects accelerated spring snow melt characteristic of a topographically flat landscape (Ohara and Kavvas 2006). These and all other dens that occurred outside the spring snow coverage were located at sites containing adequate snow cover for establishing a reproductive den. Thus, there may be areas classified as snow-free at the southern extent of the spring snow coverage (at the 500 m resolution) that contain enough drifted snow for reproductive dens. This may also be true in portions of interior Alaska that are not included within the spring snow coverage. Although Alaskan wolverine dens occurred well within the spring snow coverage (Fig. 2b), they were always associated with either drifted snow or the presence of structures beneath a shallow snow layer (Magoun and Copeland 1998). However, there is no evidence of wolverine populations occurring in areas far removed from those with persistent spring snow cover, either currently or historically.

Thermal limits to wolverine distribution

The similarity in temperature limits that encompass 90% of summer telemetry locations from southern study areas and the divergence of those limits from available temperatures (Table 2, Fig. 8) suggests that high summer temperatures may limit the wolverine's geographic distribution. However, spatial concordance between the spring snow and summer temperature coverages indicates that maximum

summer temperatures may covary with other environmental and ecological variables limiting wolverine range. Preferences for lower summer temperatures across all latitudes (Table 2) may be more indicative of elevational or habitat preferences than a response to high summer temperatures. For example, the wolverine's spatial affinity to high-elevation denning areas may influence its year-round habitat use. In addition, lack of spatial concordance between the spring snow and summer temperature coverages (Table 2) may reflect local variation in climate. Specifically, warm, wet areas in the western US produce deep, persistent snow. It was the presence of historical wolverine records in these areas that led Aubry et al. (2007) to conclude that spring snow cover was a better predictor of historical range limits than either alpine vegetation or alpine climatic zones.

As Aubry et al. (2007) noted, in southern portions of the wolverine's historical range, the geographic extents of spring snow cover, alpine vegetation, and low temperatures all begin to converge, both with each other and with wolverine occurrences. Thus, at southerly latitudes, the relative importance of these factors for limiting wolverine range becomes increasingly difficult to assess. Johnston and Bennett (1996) argued that everything an organism does is influenced by and dependent on its thermal condition. While considerable literature addresses thermoregulation in mustelid carnivores (see review in Knudsen and Kilgore 1990), most studies have investigated only lower limits of thermoneutrality. Iversen (1972) estimated that the lower threshold of thermoneutrality for the wolverine in winter pelage may be as low as -40°C , whereas Casey et al. (1979) suggested that -8 to 5°C encompasses the lower thermal limit for wolverines in summer pelage. In contrast, estimates for upper thermal limits are sparse. The estimated upper critical temperature range of 26 – 28°C for the arctic fox (*Alopex lagopus* (L., 1758)) (Klir and Heath 1992), which is sympatric to the wolverine over much of its range, is consistent with our findings for the wolverine.

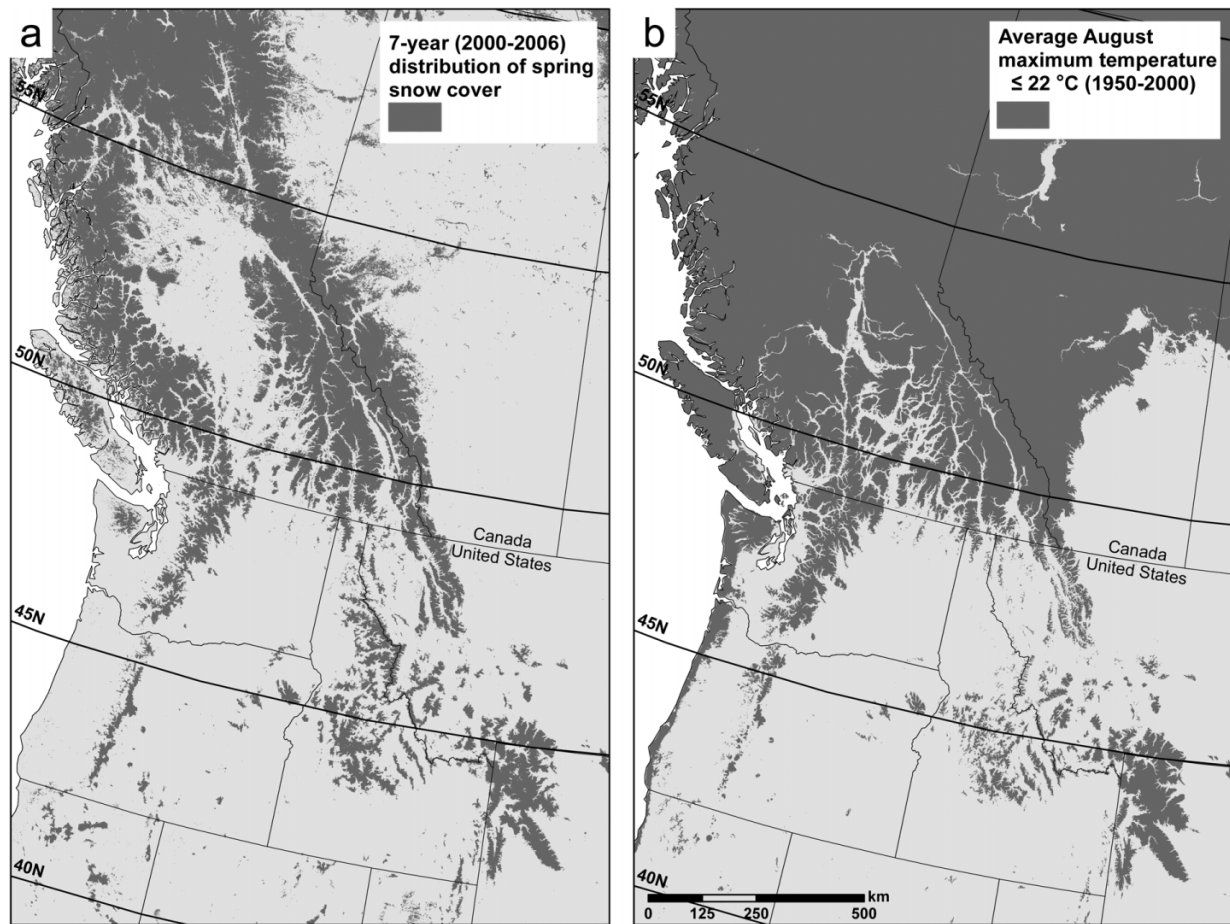
A warming climate may represent a paradoxical threat for the wolverine. Warmth provided by deep, persistent snow surrounding reproductive dens may diminish with earlier spring snow melt, while increasing summer temperatures may reduce the availability of summer habitat. Physiological investigations into critical temperatures for the wolverine could be important for understanding and anticipating the potential impacts of climate change on wolverine distribution and population persistence.

Year-round habitat use

In southern portions of the wolverine's circumboreal range, avoidance of high summer temperatures would force wolverines to higher elevations and may result in habitat-use patterns concordant with the spring snow coverage. However, for more northerly populations, there appear to be no temperature-based constraints on habitat use by wolverines; additionally, the spring snow cover needed for reproductive dens becomes ubiquitous. Consequently, in northern regions that are well within the wolverine's climatic constraints, seasonal shifts in elevation likely reflect a response to prey availability, not high temperatures (Gardner 1985; Whitman et al. 1986; Landa et al. 1998b; Krebs et al. 2007).

In montane habitats at southerly latitudes, wolverines re-

Fig. 8. Geographic distribution of the spring snow coverage (a) and geographic distribution of average maximum August temperatures $\leq 22^{\circ}\text{C}$ (b) in western North America.



main at high elevations throughout the year, avoiding lower elevation habitats with xeric conditions. Low-elevation areas also provide the most suitable conditions for human settlement, which has led some to conclude that spatial separation between wolverines and people is a causal relationship (Carroll et al. 2001; Rowland et al. 2003; May et al. 2006). As noted above, there is no question that the wolverine's range has been affected by human persecution and that wolverine numbers can be reduced by trapping (Krebs et al. 2007; Lofroth and Krebs 2007; Squires et al. 2007), but the specific relationships explored in this paper are unlikely to have anthropogenic explanations. Across the wolverine's range, areas identified as associated with persistent snow, which enclose wolverine use and den sites, are generally not proximal to areas with human habitation or high levels of human use. Evidence for the avoidance of low-elevation areas regardless of human presence has been reported for western North America and Norway (May et al. 2006; Copeland et al. 2007). Low-elevation, xeric habitats in the western US that provided winter range for ungulates were avoided by radio-marked wolverines, even though they contained an abundant food source (Copeland et al. 2007). Unlike populations across much of the wolverine's range in northern North America and Fennoscandia, wolverines in Idaho, Washington, and Wyoming are not trapped or hunted, and incidental mortality is extremely low (see Aubry et al. 2007

for an account of historical mortalities). Thus there is no potential for human avoidance or human-caused mortality to generate observed patterns of habitat use. Similarly, in western North America neither historical nor genetic data provide any indication that wolverine populations ever occurred far from high-elevation subalpine and alpine habitats (Aubry et al. 2007; Schwartz et al. 2007). Although prey or carrion availability may limit spatial use by individual wolverines (Krebs et al. 2007), it does not explain their geographic distribution at broader spatial scales. Extensive low-elevation areas that once supported abundant ungulate populations, such as the Great Plains of the central US and Canada (Sampson and Knopf 1994), have no record of wolverine occurrence historically (Aubry et al. 2007).

The wolverine's circumboreal range

Comparative biogeographic studies commonly rely on generalized range maps that contain errors in precision and accuracy that can confound interpretations (Brown et al. 1996; Hurlbert and White 2005). Previous range maps for the wolverine often resulted from the extrapolation of a few observational or specimen records to similar habitats in other regions, or were generated by drawing range boundaries around extralimital records with little regard to the habitat conditions they encompassed (Aubry et al. 2007). The reliability of such descriptions often goes unchallenged. For

species such as the wolverine, in which dispersing individuals are capable of moving long distances, spatial boundaries between metapopulations and extralimital movements can become difficult to distinguish (McKelvey et al. 2000). Wolverines were once considered to be continuously distributed throughout montane regions in the western US, but Aubry et al. (2007) found substantial gaps in the distribution of verifiable records of wolverine occurrence historically that corresponded to gaps in the distribution of alpine habitats and areas with persistent spring snow cover. Available evidence also indicates that connectivity among wolverine populations is essential for maintaining viability in fragmented portions of their range (Flagstad et al. 2004; Cegelski et al. 2003, 2006; Schwartz et al. 2007). Schwartz et al. (2009) found that restricting wolverine dispersal paths to areas defined by the presence of persistent spring snow cover improved correlations to patterns of genetic structure, indicating that successful dispersal was largely limited to paths within these areas. Therefore, at least in the western US, historical and current distribution; den sites; habitat use across sexes, ages, and seasons; and dispersals that lead to gene flow all occur within this bioclimatic envelope.

At the circumboreal scale, the spring snow coverage accords fairly well with the expert-derived range map (Fig. 1). Current wolverine range in North America differs from the area delineated by the spring snow coverage, primarily in regions where wolverines occurred historically but were extirpated during the 20th century, such as California, Colorado (Aubry et al. 2007), and Quebec (Slough 2007). In Eurasia, the species' current and historical ranges are less clearly understood. In some portions of the wolverine's putative historical range in Eurasia, habitat loss resulting from climatic changes in the past may have contributed to extirpations. This is particularly true before the mid-1800s, when average temperatures in the northern hemisphere were much lower (Salinger 2005). Both the Alps and the Carpathian Mountains contain areas with persistent spring snow cover and maximum summer temperatures consistent with wolverine climatic requirements (Fig. S2), suggesting that these montane systems may have supported wolverine populations historically. However, we lack reliable information on the wolverine's historical range in Europe or Asia. Consequently, montane areas at the southern extent of the spring snow coverage in Russia, Mongolia, and China represent high-priority areas for investigating both current and historical wolverine distributions, verifying wolverine use of snow for reproductive dens, and documenting seasonal shifts in elevation.

It is also important to recognize that the spring snow and summer temperature coverages are spatial models that incorporate interpolated and averaged data. In addition, the time period we used for the spring snow coverage (24 April – 15 May) was based on that used by Aubry et al. (2007). Although 15 May represents the approximate end of denning, the actual date likely varies geographically. We made no attempt to fit the snow coverage to either the collected data or the heuristically derived range map, but recognize that slight shifts in the analysis period result in significant changes in areal snow cover. For example, when we lengthened the time period by 1 week on either end (15 April – 28 May), the extent of the coverage declined by 3% in portions

of the western US. Thus, the spring snow coverage should be viewed as an approximation of underlying bioclimatic requirements.

Creating range boundaries heuristically incorporates errors of precision, accuracy, and interpretation (Brown et al. 1996; McKelvey et al. 2000; Hurlbert and White 2005). As an alternative, we refined the wolverine's circumboreal range using climatic conditions as explanatory variables for reproductive den site selection and year-round habitat use. The strong concordance of wolverine den sites with the spring snow coverage clearly reflects an obligatory relationship with snow cover for reproductive dens. The spatial concordance of wolverine telemetry locations with the summer temperature coverage supports the hypothesis that wolverines redistribute to cooler environments during hot summer months in southern portions of their range. The ubiquitous distribution of wolverines at northern latitudes, where temperatures remain low in the summer, provides additional support for this hypothesis. Consequently, we believe that the denning requirements of the wolverine primarily determine the limits of its circumboreal range, whereas temperature likely plays an important role in habitat selection occurring at finer spatial scales. In northern areas where these climatic factors represent less important limits, other more proximal factors such as prey or carrion availability and human persecution likely determine wolverine presence and habitat use.

If wolverine distribution in southern regions can be delineated reliably by persistent spring snow cover, climate-driven reductions in the size and connectivity of these areas may signal associated range losses for the wolverine. Significant reductions in spring snow cover associated with climatic warming have already occurred in some portions of the wolverine's range in the contiguous US (Mote et al. 2005). If these trends continue, habitat conditions for the wolverine along the southern extent of its circumboreal range will likely be diminished through reductions in the size of habitat patches and an associated loss of connectivity, leading to a reduction of occupied habitat in a significant portion of the species range.

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Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors

KEVIN S. MCKELVEY,^{1,5} JEFFREY P. COPELAND,¹ MICHAEL K. SCHWARTZ,¹ JEREMY S. LITTELL,² KEITH B. AUBRY,³
JOHN R. SQUIRES,¹ SEAN A. PARKS,⁴ MARKETA M. ELSNER,² AND GUILLAUME S. MAUGER²

¹USDA Forest Service, Rocky Mountain Research Station, 800 East Beckwith, Missoula, Montana 59801 USA

²University of Washington Climate Impacts Group, 3737 Brooklyn Avenue NE, Seattle, Washington 98105 USA

³USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, Washington 98512 USA

⁴USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute, 790 East Beckwith, Missoula, Montana 59801 USA

Abstract. Boreal species sensitive to the timing and duration of snow cover are particularly vulnerable to global climate change. Recent work has shown a link between wolverine (*Gulo gulo*) habitat and persistent spring snow cover through 15 May, the approximate end of the wolverine's reproductive denning period. We modeled the distribution of snow cover within the Columbia, Upper Missouri, and Upper Colorado River Basins using a downscaled ensemble climate model. The ensemble model was based on the arithmetic mean of 10 global climate models (GCMs) that best fit historical climate trends and patterns within these three basins. Snow cover was estimated from resulting downscaled temperature and precipitation patterns using a hydrologic model. We bracketed our ensemble model predictions by analyzing warm (miroc 3.2) and cool (pcml) downscaled GCMs. Because Moderate-Resolution Imaging Spectroradiometer (MODIS)-based snow cover relationships were analyzed at much finer grain than downscaled GCM output, we conducted a second analysis based on MODIS-based snow cover that persisted through 29 May, simulating the onset of spring two weeks earlier in the year. Based on the downscaled ensemble model, 67% of predicted spring snow cover will persist within the study area through 2030–2059, and 37% through 2070–2099. Estimated snow cover for the ensemble model during the period 2070–2099 was similar to persistent MODIS snow cover through 29 May. Losses in snow cover were greatest at the southern periphery of the study area (Oregon, Utah, and New Mexico, USA) and least in British Columbia, Canada. Contiguous areas of spring snow cover become smaller and more isolated over time, but large (>1000 km²) contiguous areas of wolverine habitat are predicted to persist within the study area throughout the 21st century for all projections. Areas that retain snow cover throughout the 21st century are British Columbia, north-central Washington, northwestern Montana, and the Greater Yellowstone Area. By the late 21st century, dispersal modeling indicates that habitat isolation at or above levels associated with genetic isolation of wolverine populations becomes widespread. Overall, we expect wolverine habitat to persist throughout the species range at least for the first half of the 21st century, but populations will likely become smaller and more isolated.

Key words: climate change; corridor; downscale; ensemble model; fragmentation; *Gulo gulo*; habitat; hydrologic modeling; snow; wolverine.

INTRODUCTION

Boreal species that are adapted to cold, snowy environments are particularly susceptible to the impacts of predicted warming trends on snowpack. Not only do they display many specific adaptations to seasonal snow (e.g., enlarged feet and seasonally white pelage), but shifts in both temperature and precipitation are predicted to increase in magnitude toward the poles (IPCC 2007). Additionally, vast areas of boreal forest and tundra are relatively flat and will provide few higher elevation refuges should climates become unsuitable for

boreal species (Loarie et al. 2009). For these reasons, the likelihood of boreal species persisting in montane areas at middle latitudes under global warming is of significant interest to conservation.

The wolverine (*Gulo gulo*) is a boreal species that may be particularly vulnerable to current trends in climatic warming (see Plate 1). It was once considered to be a habitat generalist whose geographic distribution was dictated more by the avoidance of humans than with specific habitat needs. However, recent research findings have substantially altered that perspective. Consistent with field observations indicating that all wolverine reproductive dens are located in areas that retain snow in the spring (Magoun and Copeland 1998), Aubry et al. (2007) concluded that the distribution of persistent

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⁵ E-mail: kmckelvey@fs.fed.us

spring snow cover was congruent with the wolverine's historical distribution in the contiguous United States. This relationship was further supported by the findings of Schwartz et al. (2007) that showed historical wolverine populations in the southern Sierra Nevada of California, which occupied a geographically isolated area of persistent spring snow cover, were genetically isolated from northern populations.

More recently, Copeland et al. (2010) compiled most of the extant spatial data on wolverine denning and habitat use to test the hypotheses that wolverines require snow cover for reproductive dens (Magoun and Copeland 1998), and that their geographic range is limited to areas with persistent spring snow cover (Aubry et al. 2007). Although Aubry et al.'s (2007) analysis covered only North America and used relatively coarse EASE-Grid Weekly Snow Cover and Sea Ice Extent data (Armstrong and Brodzik 2005), Copeland et al. (2010) confirmed these relationships with finer scale snow data (0.5-km pixels) obtained throughout the Northern Hemisphere from the Moderate-Resolution Imaging Spectroradiometer (MODIS) instrument on the Terra satellite (Hall et al. 2006). Specifically, Copeland et al. (2010) compiled and evaluated the locations of 562 reproductive dens in North America and Scandinavia in relation to spring snow. All dens were located in snow and 97.9% were in areas identified as being persistently snow covered through the end of the wolverine's reproductive denning period (15 May; Aubry et al. 2007) based on MODIS imagery. Additionally, Copeland et al. (2010) found that areas characterized by persistent spring snow cover contained 89% of all telemetry locations from throughout the year in nine study areas at the southern extent of current wolverine range. Excluding areas where wolverines were known to have been extirpated recently, persistent spring snow cover provided a good fit to current understandings of the wolverine's circumboreal range (Copeland et al. 2010). Moreover, Schwartz et al. (2009) found that the genetic structure of wolverine populations in the Rocky Mountains was consistent with dispersal within areas identified as being snow covered in spring, and strong avoidance of other areas. Thus, the areas with spring snow cover that supported reproduction (Magoun and Copeland 1998) could also be used to predict year-round habitat use, dispersal pathways, and both historical (Aubry et al. 2007) and current ranges (Copeland et al. 2010).

The reasons that wolverines of both sexes remain in areas with persistent spring snow cover throughout the year is not well understood. Summer use of these areas may be due to avoidance of summer heat (Hornocker and Hash 1981, Copeland et al. 2010), prey availability in avalanche chutes and at timberline (Krebs et al. 2007), or perhaps a combination of both. Whatever the cause, evidence suggests that wolverines occurring at the southern periphery of their range remain within a relatively narrow elevation zone throughout the year

(Copeland et al. 2007). There is no evidence, either currently or historically, that wolverine populations can persist in other areas. For these reasons, Copeland et al. (2010) argued that the bioclimatic niche of the wolverine can be defined by the areal extent of persistent spring snow cover.

The wolverine was recently evaluated for listing under the Endangered Species Act of 1973 (16 U.S.C. 1531-1544, 87 Stat. 884) and received "Candidate" status in 2010 (USFWS 2010). If, as Copeland et al. (2010) and Aubry et al. (2007) argue, the extent of persistent spring snow cover has constrained current and historical distributions, then it is reasonable to assume that it will also constrain the wolverine's future distribution. Consequently, for conservation planning, predicting the future extent and distribution of persistent spring snow cover can help identify likely areas of range loss and persistence, and resulting patterns of connectivity.

Regional snow modeling

Choosing a global climate model.—To link future climate projections to current and historical patterns of wolverine habitat use requires modeling snow conditions into the future, and relating modeled snow to the MODIS-derived snow cover layer that Copeland et al. (2010) and Schwartz et al. (2009) correlated with patterns of wolverine habitat use and gene flow. Generally, future climatic conditions are estimated using global climate models (GCMs). There are >20 GCMs of varying structural complexity and greenhouse gas sensitivity, each of which can be forced with a variety of greenhouse gas emission scenarios. Recently, the Intergovernmental Panel on Climate Change (IPCC) argued that ensemble-averaging more faithfully reproduced existing patterns of climate change than any single model (IPCC 2007: Chapters 8 and 10). The IPCC used 23 GCMs, regardless of their bias or "skill levels" (IPCC 2007: Chapter 8). For finer scale regional modeling efforts, however, it may be more useful to generate an ensemble model based on the skill-weighted scenarios or subset of GCMs that best model historical trends for those regions (Macadam et al. 2010). For example, Mote and Salathé (2010) built a weighted composite model for the Pacific Northwest that emphasized those models that best fit local historical climate data.

Choosing an emission scenario.—Future climate will ultimately depend on future carbon emissions; accurate predictive modeling hinges on assumptions about future patterns of fossil fuel use. Unlike models that can be compared based on their abilities to simulate historical climate patterns, the likelihood of future emission scenarios is unknown. The IPCC developed a total of 40 emission scenarios (Special Report on Emissions Scenarios [SRES]; IPCC 2007, Nakicenovic et al. 2000), but only a few are widely used for simulation modeling: A2, representing heavy use of fossil fuels; A1B, reflecting a rapidly growing economy but with significant movement toward renewable power sources; and B1 or B2,

which represent more conservative scenarios associated with organized efforts to reduce emissions worldwide. Although these scenarios result in highly divergent climatic conditions over the long term, they cluster tightly together in the short term; during the 21st century in the Pacific Northwest (PNW), model-to-model variability greatly exceeds within-model differences due to different emission scenarios until at least the mid-21st century (Mote and Salathé 2010).

Downscaling.—Because GCMs are based primarily on mathematical models of the general circulation of the Earth's atmosphere, output grids are coarse in scale (~100–300 km, or 1–5 degrees latitude/longitude) and the underlying topography is greatly simplified. Processes such as the buildup of snowpack at higher elevations cannot be assessed at this scale. Therefore, if GCM output is to be used to simulate snowpack, results need to be downscaled. There are a variety of downscaling methods, but two primary approaches have been used: regional modeling, in which a finer grain circulation model is applied (GCMs provide boundary conditions; see Salathé et al. [2010] for an example in the Pacific Northwest), and statistical downscaling in which additional data such as topography and historical precipitation patterns are used to adjust GCM outputs to reflect local conditions (see Elsner et al. [2010] for an example in the Pacific Northwest). Fowler et al. (2007) provide a review of downscaling methods in the context of hydrological modeling which, in western North America, requires accurate estimation of snowpack.

Modeling snow.—Aubry et al. (2007), Schwartz et al. (2009), and Copeland et al. (2010) related wolverine habitat use and movements to persistent spring snow cover. For a pixel to be considered snow covered by Copeland et al. (2010), it had to be consistently covered with snow during a 21-day period ending on 15 May. The 21-day window had two purposes: It allowed cloud-free observation of each pixel, and it eliminated areas that were ephemerally snow covered but lacked residual snowpack. Although downscaled GCMs do not provide precise estimates that correspond to MODIS-based snow cover data, snowpack has been modeled by transforming downscaled GCM output using hydrologic models designed to work with interpolated weather station data. Wood et al. (2004) used the variable infiltration capacity (VIC) hydrologic model (Liang et al. 1994, Hamlet and Lettenmaier 2005) to test various downscaling approaches in the Pacific Northwest. VIC, which is designed to use interpolated weather data such as Historical Climate Network (e.g., Menne et al. 2010) or PRISM output (Daly et al. 1994, 2008), produces variables of hydrological interest including snow water equivalent (SWE) and snow depth.

In this paper, we modeled future patterns of persistent spring snow cover within the Columbia, Upper Colorado, and Upper Missouri River Basins using downscaled GCM temperature and precipitation data transformed into snow by the VIC hydrologic model.

Using understandings of the wolverine's bioclimatic niche derived by Copeland et al. (2010) we transformed these snow projections into predicted wolverine habitat and, using approaches developed by Schwartz et al. (2009), evaluated future changes in connectivity between areas of wolverine habitat.

METHODS

Ensemble model selection, downscaling, and hydrologic modeling

We used a future climate projection derived from an ensemble mean of 10 GCMs under a single intermediate emission scenario (A1B; Elsner et al. 2010, Littell et al. 2010, Mote and Salathé 2010) to produce climate projections in the Columbia, Upper Missouri, and Upper Colorado River Basins (Fig. 1). Starting with the IPCC Fourth Assessment Report's (AR4) suite of models (IPCC 2007), we eliminated models with poor cumulative performance or that routinely performed the worst in one or more categories, leaving an ensemble of the following 10 GCMs: bccr, cnrm_cm3, csiro_3_5, echam5, echo_g, hadcm, hadgem1, miroc_3.2, miroc_3_2_hi, and pcm1 (Meehl et al. 2007, Littell et al. 2010).

We derived historical climate following methods in Hamlet and Lettenmaier (2005) as implemented for the Columbia River Basin by Elsner et al. (2010). We generated data sets similar to those used by Elsner et al. (2010) for the Upper Colorado and Missouri River Basins. We interpolated local climate from historical weather station data at 1/16 degree (latitude/longitude; ~6 km at 45° N) using PRISM (Daly et al. 1994, 2002; see Elsner et al. [2010] for details). We inferred future local climate patterns from each of the 10 GCMs by downscaling to this resolution using the "delta" method (e.g., Elsner et al. 2010), which assumes that local relationships, such as relative shifts in temperature and precipitation associated with elevation and prevalent weather patterns, remain constant. In the delta method, a GCM grid cell mean is fit to interpolated historical weather data. Projections are then forecast for a future period based on an expected emission scenario, and differences in cell values between the historical fit and the future projection are calculated. Downscaling is accomplished by adding these differences (deltas) to each cell in a fine-scale interpolated grid based on historical data, combined with topographic influences on temperature and precipitation. We averaged deltas derived from the 10 GCMs to produce an ensemble model. From these data, we developed spatially explicit future temperature and precipitation deltas for each cell in the model grid for the years 2030–2059 and 2070–2099 under emission scenario A1B following methods similar to Elsner et al. (2010; see Littell et al. [2010] for details). In addition to the ensemble means, we produced similar climate surfaces for relatively cool (pcm1) and warm (miroc 3.2) models (based on evaluation of the Columbia and Upper Missouri domain; see Littell et al. [2010] for details) to produce a pseudo-range of

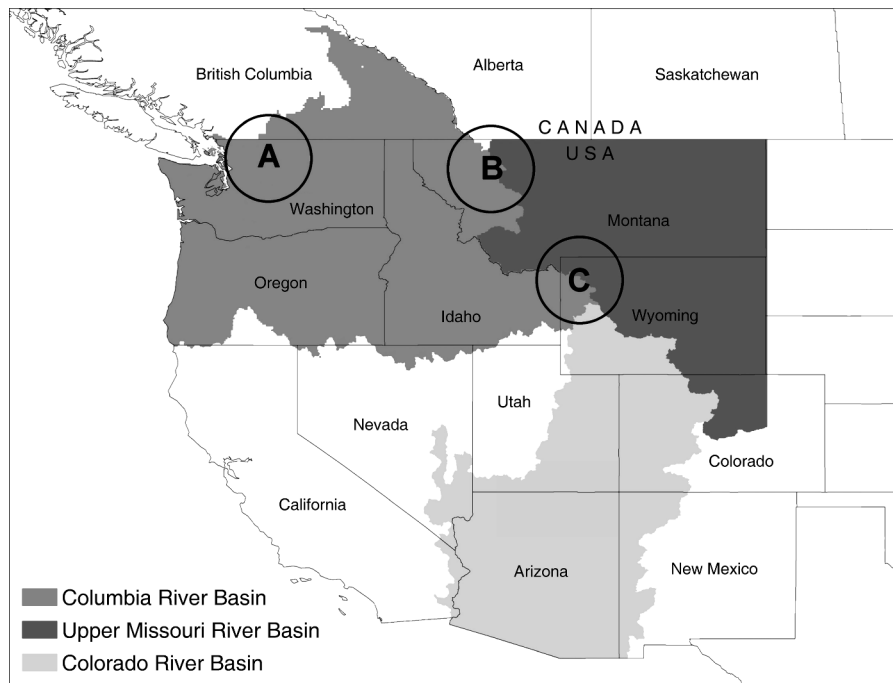


FIG. 1. The study area (shaded), including the Columbia, Upper Missouri, and Upper Colorado River Basins. Geographic or administrative areas referred to in the text include (A) the North Cascades in Washington and British Columbia, (B) Glacier National Park and Bob Marshall Wilderness in Montana, and (C) the Greater Yellowstone Area in Montana, Idaho, and Wyoming.

potential future climatic conditions. Following methods in Elsner et al. (2010), we used the 6-km regional precipitation and temperature estimates derived from the historical interpolated data, GCM ensemble, pcm1, and miroc 3.2 to drive a hydrologic model that we used to predict patterns of snow water equivalent (SWE) and snow depth.

Following Elsner et al. (2010), we used the VIC hydrologic model to transform temperature and precipitation into a suite of hydrological variables including snow depth and SWE. VIC is a validated and continuously maintained model that has been used widely in the Pacific Northwest to estimate snowpack volume, runoff, and streamflow (e.g., Elsner et al. 2010).

*Historical Reconstruction: cross-walking between
downscaled GCM and MODIS*

Schwartz et al. (2009) and Copeland et al. (2010) used persistent snow cover through 15 May derived from daily 0.5-km MODIS data to infer relationships between snow cover and wolverine denning, habitat use, and dispersal. Interpolated historical temperature and precipitation were input into VIC to model average snow depth and SWE for the 1st of each month at 1/16-degree resolution. Pixel-level correlations between modeled SWE and snow depth were $>99.5\%$; we chose snow depth on 1 May as the metric to match to MODIS-derived persistent spring snow cover. MODIS snow

cover data were binary (snow covered or not); to convert VIC snow depth data to a binary cover variable, we established a threshold snow depth, whereby pixel values greater than the threshold were classified as snow covered. To produce the optimal fit, we searched for a threshold that maximized the agreement between MODIS 15 May snow cover and modeled snow depth, and minimized areas of disagreement. Because snow depth was evaluated for pixels 1/16 degree in size, whereas MODIS data were at 0.5-km resolution (about $140\times$ as large), we resampled the VIC-generated snow depth to 0.5-km scale while maintaining its alignment with the MODIS coverage. We then optimized the ratio of agreement to disagreement based on comparing the resampled coverage to MODIS-derived snow cover through 15 May (hereafter, the optimal fit between snow depth and MODIS snow cover is referred to as the Historical Reconstruction).

*Simulating the onset of spring snow melt two weeks
earlier in the year*

To validate our GCM analysis, we conducted a second analysis looking at MODIS snow cover data later in the year. Many have argued that a variety of biological and physical attributes are occurring earlier in the year than they did in the early- to mid-20th century. Specifically, snow melt occurs earlier than it did 50–100 years ago (Mote et al. 2005, Knowles et al. 2006, Stewart



PLATE 1. The wolverine (*Gulo gulo*), which is one of the largest terrestrial members of the weasel family, persists at extremely low population densities across alpine habitats of the Northern Hemisphere. The wolverine's obligate association with persistent snow cover for successful reproduction denning leaves the species vulnerable to decreasing habitat and population connectivity due to global warming. Photo credit: Dale Pedersen.

2009), consistent with the earlier onset of spring conditions. Based on plant and animal phenology, Menzel et al. (2006) estimated that the onset of spring/summer has progressed at a rate of 2.5 days per decade. Consequently, we determined how wolverine distribution and connectivity would change if it were based on persistent snow cover through 29 May rather than 15 May, thereby forcing spring snow melt two weeks earlier. This approach does not account for changes in winter temperature and precipitation patterns (i.e., it does not predict future climates), but it is based on the same data as previous analyses of wolverine habitat use and dispersal (Schwartz et al. 2009, Copeland et al. 2010). Thus, errors associated with localizing and downscaling GCMs, transforming temperature and precipitation data into snow cover through VIC (Liang et al. 1994, Hamlet and Lettenmaier 2005), and cross-walking GCM-based snow depth to MODIS-based snow cover are eliminated.

Predicting future snow cover and its influence on patterns of wolverine habitat use and dispersal

Schwartz et al. (2009) used methods in which landscape features were transformed into putative movement costs that were used to derive matrices of least-cost paths among individuals. Associated costs were then correlated with matrices of genetic relatedness among individuals (Manel et al. 2003, Coulon et al. 2006, Cushman et al. 2006, 2009). Using these methods, genetic patterns best fit snow-covered landscapes when the costs associated with traveling within areas of snow

cover were 1/20 the costs of movements outside those areas. Schwartz et al. (2009) found that indications of genetic isolation in the Little Belt and Crazy Mountains in Montana correlated with higher movement costs to and from those areas. Because map boundaries differed, we repeated the analyses in Schwartz et al. (2009) and, assuming the same 1/20 cost ratio for traveling within rather than outside snow-covered areas, applied these methods to the Historical Reconstruction. We used the average costs associated with the Little Belt and Crazy Mountains derived from MODIS-based snow cover through 15 May and the Historical Reconstruction to infer areas of genetic isolation associated with MODIS-based snow cover through 29 May and GCM-based projections, respectively.

RESULTS

GCM model selection, downscaling, and performance

Seven GCMs (bccr, echam5, echo_g, hadcm, hadgem1, miroc3.2, and pcm1) performed consistently well in most metrics (e.g., annual precipitation and temperature trend) for all three river basins. The models fgoals1_0_g, gfdl_cm2_1, giss_aom, and ipsl_cm4 were less consistent across metrics and basins, and no models routinely performed best in all metrics. Other models (e.g., ccsmb3, both cgcmb models, giss_er) performed well in some indicators (e.g., average annual precipitation) and not in others (e.g., 20th-century trend in temperature). For example, giss_er performed well in all categories except the North Pacific index, for which it ranks lowest of all

TABLE 1. Confusion matrix for cross-walk between persistent spring snow cover based on 0.5-km Moderate Resolution Imaging Spectroradiometer (MODIS) data (Copeland et al. 2010) and historical 1 May snow depth based on 1/16-degree (latitude/longitude) resolution variable infiltration capacity (VIC) hydrologic modeling (Historical Reconstruction).

	MODIS	
	Snow	No snow
Historical Reconstruction		
Snow	1 160 771	503 389
No snow	222 488	9 655 150

Note: The 1/16-degree pixels were rescaled to match the 0.5-km MODIS data, and numbers in the cells indicate the number of 0.5×0.5 km areas where the projections agreed or disagreed.

models (Mote and Salathé 2010). For each model, regional rankings are relatively consistent among the three river basins (see Littell et al. [2010] for details).

Based on the ensemble projections, increases in average annual temperature for 2030–2059 are predicted for all three river basins: $+2.1^{\circ}\text{C}$ for the Columbia Basin (pcm1, $+1.8^{\circ}\text{C}$; and miroc 3.2, $+2.7^{\circ}\text{C}$), $+2.3^{\circ}\text{C}$ for the Upper Missouri Basin (pcm1, $+1.7^{\circ}\text{C}$; and miroc 3.2, $+3.1^{\circ}\text{C}$), and $+2.4^{\circ}\text{C}$ for the Upper Colorado Basin (pcm1, $+1.7^{\circ}\text{C}$; and miroc 3.2, $+3.3^{\circ}\text{C}$), with 0%, 3%, and 2% increases in annual precipitation, respectively. For 2070–2099, predicted increases are $+3.8^{\circ}\text{C}$ for the Columbia Basin (pcm1, $+2.7^{\circ}\text{C}$; and miroc 3.2, $+4.6^{\circ}\text{C}$), $+4.1^{\circ}\text{C}$ for the Upper Missouri Basin (pcm1, $+2.6^{\circ}\text{C}$; and miroc 3.2, $+5.3^{\circ}\text{C}$), and $+4.3^{\circ}\text{C}$ for the Upper Colorado Basin (pcm1, $+2.6^{\circ}\text{C}$; and miroc 3.2, $+5.7^{\circ}\text{C}$), with 2%, 7%, and 5% increases in annual precipitation, respectively. The variation in precipitation among GCMs in the ensemble is large and differs among regions and seasons, but predictions for the ensemble mean winter (December/January/February) precipitation increase in all three basins (4–8% for 2030–2059; 9–

13% for 2070–2099). However, in the spring (March/April/May), precipitation increases in the Columbia (4% for 2030–2059; 7% for 2070–2099) and Upper Missouri (5% in 2030–2059; 11% for 2070–2099) Basins, but decreases in the Upper Colorado Basin (-4% for 2030–2059; -7% for 2070–2099).

Cross-walk between MODIS and the ensemble climate model

The best fit between snow depth based on the Historical Reconstruction and the MODIS-based snow cover layer through 15 May (hereafter, 15 May MODIS) occurred when 1/16-degree pixels with average snow depth values >13 cm were considered snow covered and those with <13 cm were not. Rescaling the 1/16-degree map to 0.5-km pixels to match the MODIS data resulted in the correct classification of 93.7% of pixels (Table 1). Spatial patterns were also similar (Fig. 2). Because fitting was done by maximizing the ratio of correctly classified snow pixels to misclassifications, more snow cover was generated in the Historical Reconstruction than in 15 May MODIS (Table 2). Most of the additional areas classified as snow covered in the Historical Reconstruction were in the Columbia River Basin (Table 2, Fig. 2A). Some areas, such as the northern Cascade Range in Washington and British Columbia, had more snow area in the Historical Reconstruction. Overall, the Upper Missouri and Upper Colorado River Basins contained slightly less snow-covered area in the Historical Reconstruction than in 15 May MODIS.

Future predictions based on ensemble means

Spring snow cover projections based on the ensemble mean climate for 2030–2059 (hereafter, Ensemble 2045) retained 66.8% of spring snow cover depicted in the Historical Reconstruction (Table 2). Predicted losses in

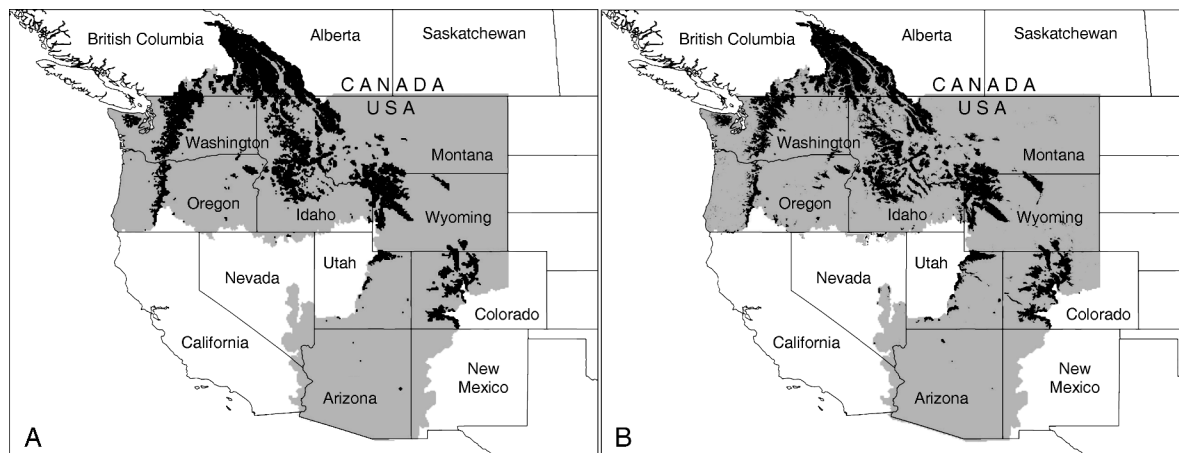


FIG. 2. Comparison between the (A) 1/16-degree Historical Reconstruction of snow cover and (B) Moderate Resolution Imaging Spectroradiometer (MODIS)-based snow cover through 15 May (Copeland et al. 2010). The study area is shown in gray, and snow cover is black. Historical Reconstruction refers to the optimal fit between snow depth and MODIS snow cover. In the Historical Reconstruction, we classified 1/16-degree pixels as wolverine habitat if snow depth exceeded 13 cm.

TABLE 2. Areal extent of persistent spring snow cover in river basins, states, and provinces analyzed using MODIS and three downscaled climate projections (Ensemble, miroc 3.2, and pcm1).

Location	Snow cover, by model type (km ²)						
	15 May MODIS	29 May MODIS	Historical Reconstruction	Ensemble 2045	Ensemble 2085	miroc 3.2, 2070–2099	pcm1, 2070–2099
River basin							
Columbia	92 332	40 285	127 302	83 237	43 211	17 311	50 672
Upper Missouri	42 601	16 996	40 484	30 814	19 837	7566	26 660
Upper Colorado	32 334	8681	30 029	18 240	10 364	2285	12 619
Total	167 268	65 962	197 815	132 290	73 411	27 163	89 952
State/province							
British Columbia	60 176	43 081	76 263	67 382	57 831	48 725	59 026
Washington	21 883	12 214	33 891	24 594	14 744	10 326	16 933
Oregon	10 122	2660	12 716	6281	2589	1417	3949
Idaho	35 206	12 919	44 769	25 724	9977	1433	13 928
Montana	35 727	16 490	45 914	33 506	20 163	6937	23 431
Wyoming	31 588	14 005	31 264	23 556	14 437	3995	17 570
Nevada	1000	27	288	72	0	0	0
Utah	9588	2476	5820	2956	1438	0	1586
Colorado	27 702	6681	27 409	18 525	11 756	3203	14 506
New Mexico	261	1	281	40	0	0	40
Total†	173 077	67 472	202 353	135 253	75 104	27 310	91 941

Notes: Ensemble 2045 and Ensemble 2085 refer to snow cover projections based on downscaled ensemble global climate modeling (GCM) for the periods 2030–2059 and 2070–2099, respectively. Models pcm1 and miroc 3.2 refer to snow cover projections for the period 2070–2099 based on downscaling of the National Center for Atmospheric Research (NCAR)'s Parallel Climate Model and the medium resolution Model for Interdisciplinary Research on Climate collectively created by the Center for Climate System Research (University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change, Japan (see Littell et al. [2011] for details).

† Totals for the state/province analysis vary slightly from those for the basins because the basin polygons clip the edges of pixels that are not clipped by state boundaries; therefore, the state/province totals always are slightly larger than those for the basins.



FIG. 3. Ensemble model projections for the period 2030–2059 (Ensemble 2045). Ensemble 2045 refers to snow cover projections based on downscaled ensemble global climate models (GCM) and hydrologic modeling for the period 2030–2059. The study area is shown in gray, and snow cover is black.

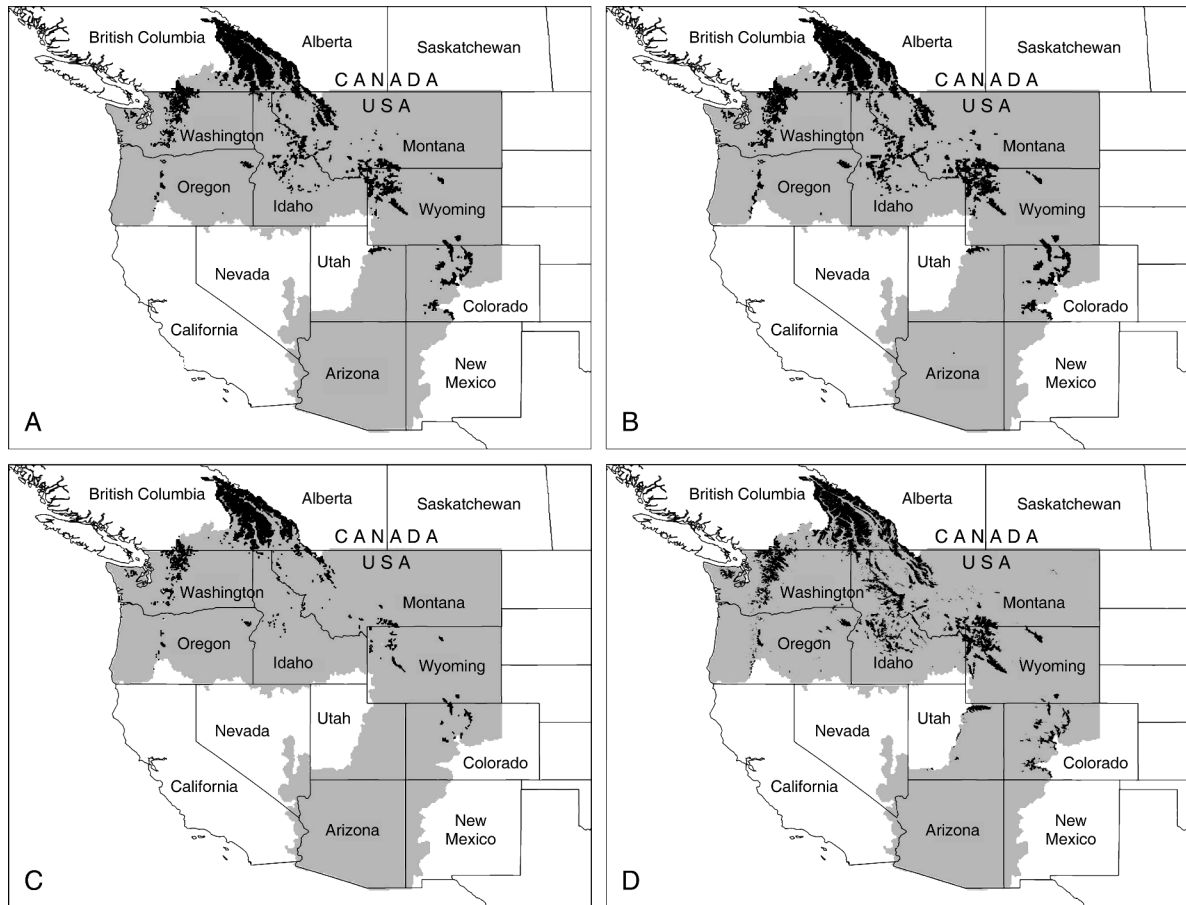


FIG. 4. Comparisons among three model projections, (A) Ensemble, (B) pcm1, and (C) miroc 3.2 for the period 2070–2099, and (D) MODIS-based snow cover through 29 May. Ensemble 2045 and Ensemble 2085 refer to snow cover projections based on downscaled ensemble GCM and hydrologic modeling for the periods 2030–2059 and 2070–2099, respectively. Models pcm1 and miroc 3.2 refer to snow cover projections for the period 2070–2099 based on downscaling of the National Center for Atmospheric Research's Parallel Climate Model and the medium resolution Model for Interdisciplinary Research on Climate collectively created by the Center for Climate System Research (University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change, Japan (see Littell et al. [2011] for details). The study area is shown in gray, and snow cover is black.

snow-covered areas were greatest at the southern periphery of our study area; i.e., New Mexico, Nevada, and Oregon will lose most (50.6–85.9%) of their spring snow cover, whereas Idaho is predicted to lose only 42.5% of its current snow cover. Losses were smallest in those areas currently characterized by extensive areas of spring snow cover: British Columbia, the northern Cascade Range in Washington, Glacier National Park and Bob Marshall Wilderness in western Montana, and the Greater Yellowstone Area in Montana, Idaho, and Wyoming (Figs. 1 and 3).

Spring snow cover projections based on ensemble mean climate for 2070–2099 (hereafter, Ensemble 2085) show continued declines in spring snow cover across the study area, with only 37.1% of spring snow cover remaining overall (Table 2). Only British Columbia retains most of its spring snow cover (75.8%). The states

of Washington, Montana, Wyoming, and Colorado all retain >40% of their snow cover. Oregon, Idaho, and Utah lose 75.3–79.6% of their spring snow cover. Snow cover is eliminated in those portions of Nevada and New Mexico that are included in the Columbia and Upper Colorado River Basins (Table 2, Fig. 4A).

29 May MODIS

MODIS-based persistent snow cover through 29 May (hereafter, 29 May MODIS) retained 39.0% of snow-covered areas compared to 15 May MODIS (Table 2). By 29 May, large declines in snow cover are predicted in central Idaho, but snow cover is largely retained in British Columbia. Both the Glacier National Park/Bob Marshall Wilderness and the Greater Yellowstone Area maintain spring snow cover, but become more fragmented (Figs. 1 and 4D).

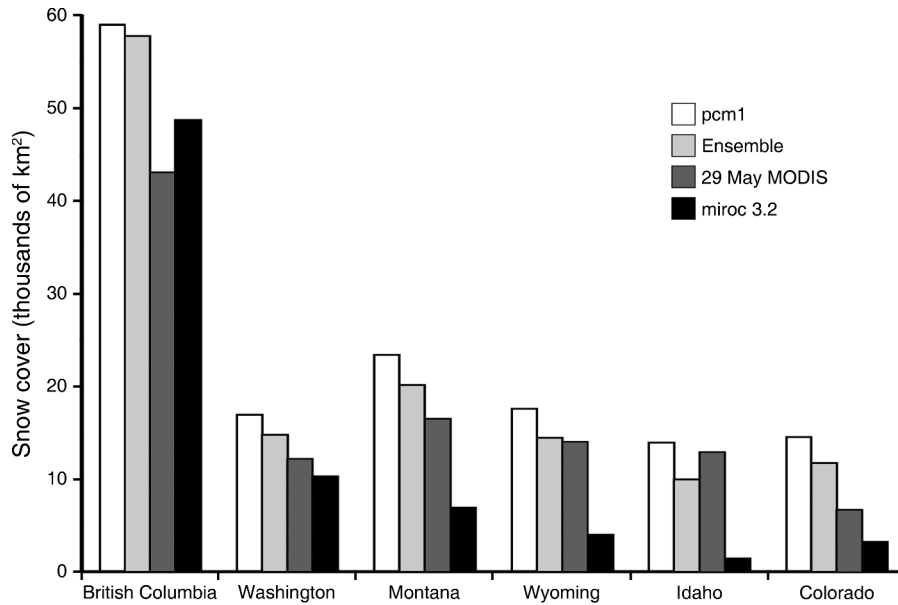


FIG. 5. Comparisons of the areal extent of persistent spring snow cover among three downscaled climate models (pcm1, Ensemble, miroc 3.2) and MODIS data extending the snow-cover period through 29 May. All model projections are for the period 2070–2099.

Comparisons between GCM projections for 2070–2099 and 29 May MODIS

Of the three alternative GCM projections (ensemble, miroc 3.2, and pcm1), spring snow cover in 29 May MODIS is most similar to Ensemble 2085 projections (Table 2, compare Fig. 4A with Fig. 4D). As expected, by 2070–2099, pcm1 has the most spring snow cover and

miroc 3.2 has the least. Of the three alternative projections, Ensemble 2085 is most divergent from miroc 3.2 (compare Fig. 4A with Fig. 4C). In terms of spatial patterns, Ensemble 2085 is most consistent with pcm1, but in most areas, pcm1 results in slightly more snow cover (Fig. 5, Table 2). Models are most convergent in British Columbia (Fig. 6), where most

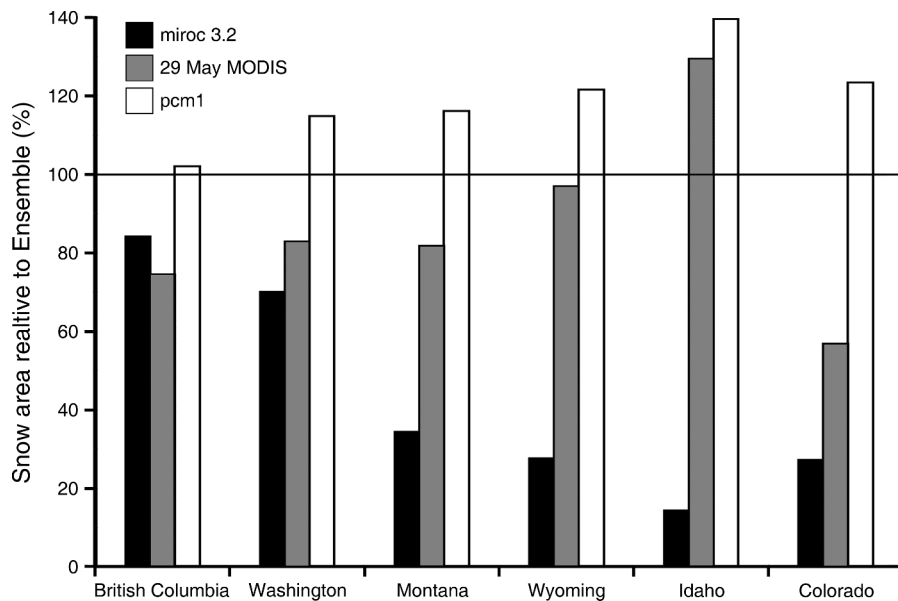


FIG. 6. Comparison of spring snow distributions between the ensemble-averaged GCM projection (Ensemble 2085), the cool (pcm1), and warm (miroc 3.2) projections, and MODIS snow cover extended through 29 May. All model projections are for the period 2070–2099.

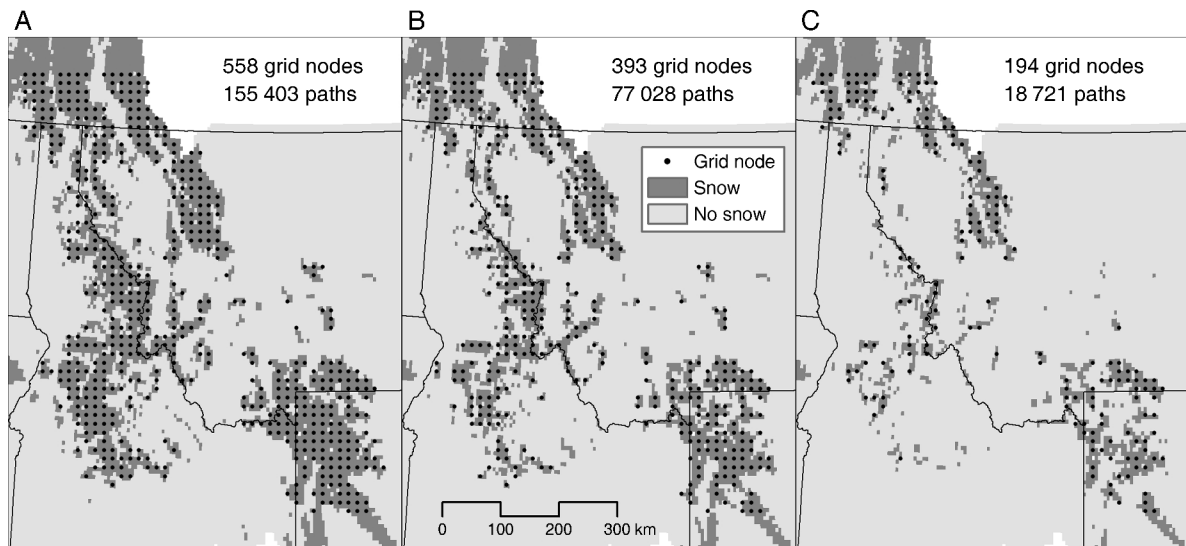


FIG. 7. Source and destination “grid nodes” for each period of analysis: the (A) Historical Reconstruction, and ensemble projections for (B) the periods 2030–2059 (Ensemble 2045) and (C) for 2070–2099 (Ensemble 2085). We located snow points by placing points at 15-km intervals and keeping only those points that overlapped with a snowpack patch at least 225 km² in size (see Schwarz et al. [2009] for details). “Paths” refer to the total number of pairwise least-cost paths possible given the number of nodes.

spring snow cover is retained in all projections (Table 2), and most divergent in Idaho, which is the only area where 29 May MODIS shows more snow-covered areas than Ensemble 2085 (Fig. 6).

Modeling the future connectivity of wolverine populations

Ensemble projections.—Each point where a wolverine could originate requires a contiguous snow area larger than 15×15 km (225 km²), which is the approximate home range size for female wolverines (Schwartz et al.

2009). Thus, the number of potential pairwise paths drops quadratically as snow-covered areas >225 km² in size are lost. The number of potential start locations decreases from 558 in the Historical Reconstruction to 194 in Ensemble 2085 and this decrease, in turn, leads to an order-of-magnitude reduction in the number of pairwise least-cost paths (Fig. 7). Due to the loss of spring snow cover in Idaho (Table 2) predicted by Ensemble 2085, the most important corridors connecting Glacier National Park and the Bob Marshall

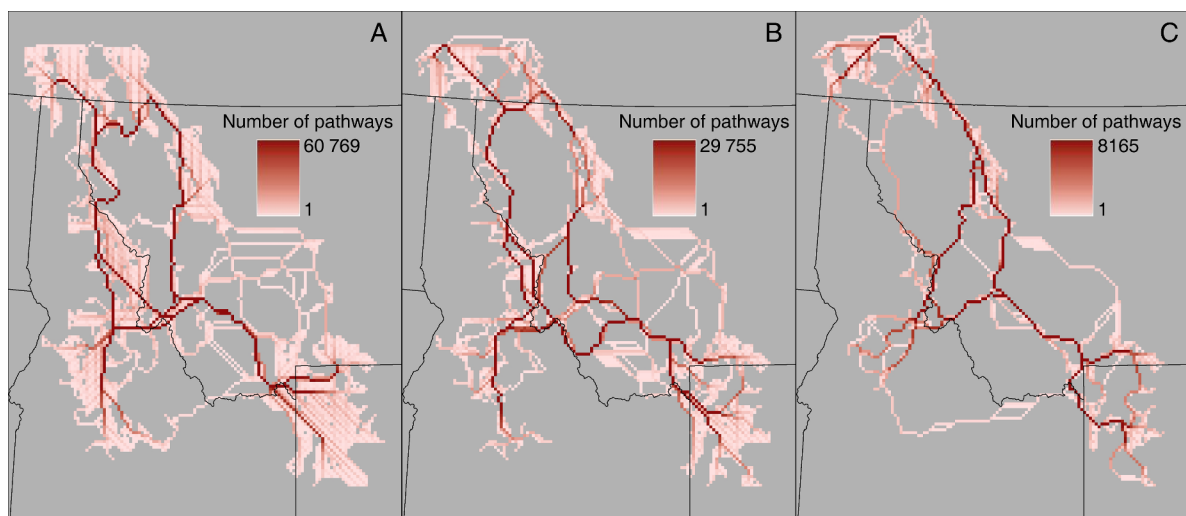


FIG. 8. Cumulative cost paths for all pairs of snow points for the (A) Historical Reconstruction, and ensemble projections for (B) the periods 2030–2059 (Ensemble 2045) and (C) 2070–2099 (Ensemble 2085). Coloring has been scaled to the total number of pairwise least-cost paths that cross each pixel (see Schwartz et al. [2009] for details), which declines over time due to decreased habitat.

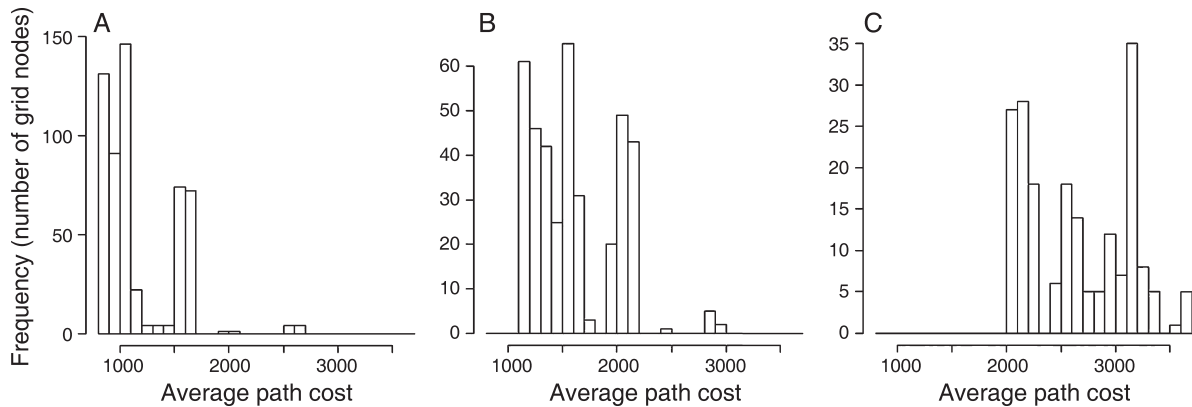


FIG. 9. Frequency distribution depicting the average path cost from each snow point to all other snow points for the (A) Historical Reconstruction, and ensemble projections for (B) the period 2030–2059 (Ensemble 2045) and (C) for 2070–2099 (Ensemble 2085). The average path cost units are arbitrary and are computed as the sum costs associated with all pairwise least-cost paths between a given node and all other nodes divided by the total number of paths.

Wilderness to the Greater Yellowstone Area shift eastward, favoring more direct north–south connections (compare Fig. 8A with Fig. 8C). With the decline in snow-covered area, average movement cost between locations increases (Fig. 9). Movement cost values at or higher than those associated with currently observed genetic isolation (Schwartz et al. 2009) occur between all locations based on Ensemble 2085 predictions (Figs. 9 and 10).

29 May MODIS.—Because 29 May MODIS is based on the same data source and therefore is at the same resolution as the analyses conducted by Schwartz et al. (2009), connectivity maps generated by Schwartz et al. (2009) can be directly compared with those in 29 May MODIS (Fig. 11). Comparing spring snow cover in 29

May MODIS with that in 15 May MODIS, western pathways become less important and direct north–south connections more so, but the shift is not as dramatic as in connectivity maps for Ensemble 2085 (compare Figs. 8 and 11). Increases in average movement cost when comparing 29 May MODIS least-cost paths with those in 15 May MODIS (Fig. 12; Schwartz et al. 2009) suggest changes in connectivity similar to those predicted in Ensemble 2085 (compare Figs. 9 and 12), in which average movement costs associated with genetic isolation become widespread.

DISCUSSION

The ensemble of 10 GCMs selected for our analyses produced mean annual and seasonal projections that

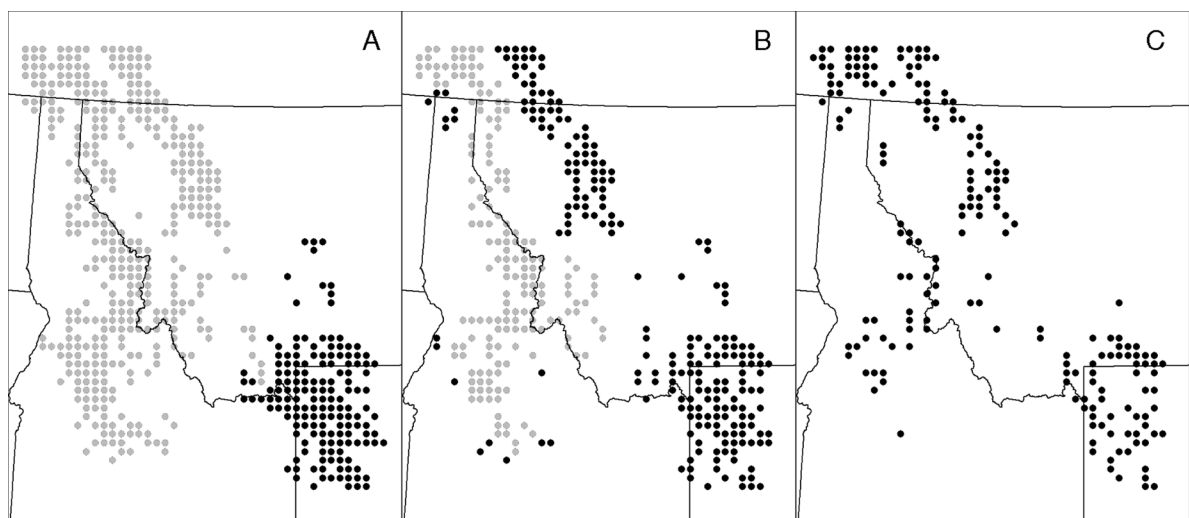


FIG. 10. Maps depicting whether snow points in the northern Rocky Mountains were genetically isolated (black circles) or not (gray circles), based on least-cost connectivity pathways and thresholds of isolation developed by Schwartz et al. (2009). (A) Current patterns of genetic isolation (Schwartz et al. 2009) are compared with predicted patterns of isolation for (B) the periods 2030–2059 (Ensemble 2045) and (C) for 2070–2099 (Ensemble 2085).

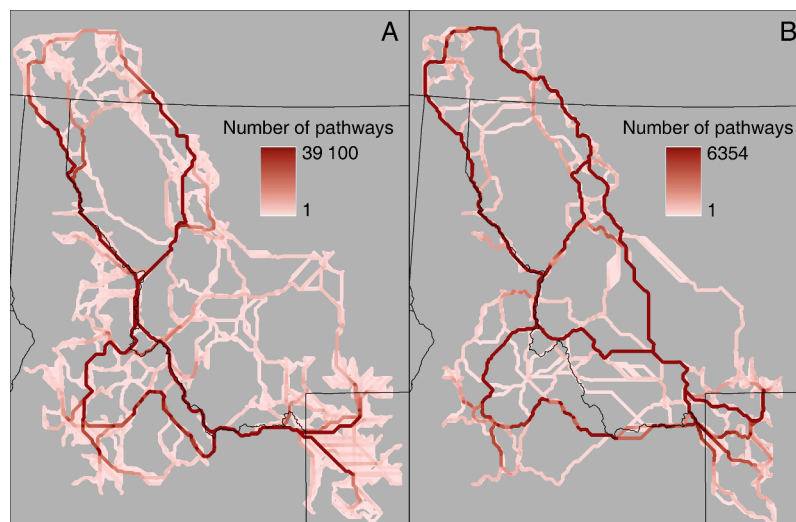


FIG. 11. Wolverine connectivity pathways based on (A) persistent snow cover through 15 May and (B) persistent snow cover through 29 May. Panel (A) is similar to Fig. 4 in Schwartz et al. (2009) and shows putative wolverine paths based on conformity with observed patterns of genetic structure. Panel (B) uses the same model to predict wolverine paths with an additional two weeks of snowmelt. Coloring has been scaled to the total number of pairwise least-cost paths that cross each pixel (see Schwartz et al. [2009] for details), which declines over time due to decreased habitat.

generally agree with the ensemble of 20 GCMs using the A1B emission scenario analyzed by Mote and Salathé (2010) for the Pacific Northwest. However, there are regional differences in the projections: Slightly more warming is predicted in the Upper Colorado River Basin than in the Upper Missouri Basin, which in turn, is slightly greater than in the Columbia Basin. The Pacific Northwest is characterized by large amounts of winter precipitation at temperatures near freezing. Thus, modest increases in temperature cause precipitation to fall as rain rather than snow, making its snowpack highly vulnerable to climatic warming (e.g., Elsner et al.

2010, Mantua et al. 2010). However, perhaps because historical snowpack is so deep and extensive in the Pacific Northwest, estimated May snow cover in that region is not as highly impacted by climate change as are interior areas, such as Idaho (Table 2).

Given a warming trend, spring snow cover is expected to decline and snow-covered areas are expected to become more fragmented and isolated. However, the ensemble model was more consistent with pcml (the cool extreme of the applied models) than with miroc 3.2 (the warmest model). For this reason, most snow cover (66.9%) is retained in Ensemble 2045. Additionally,

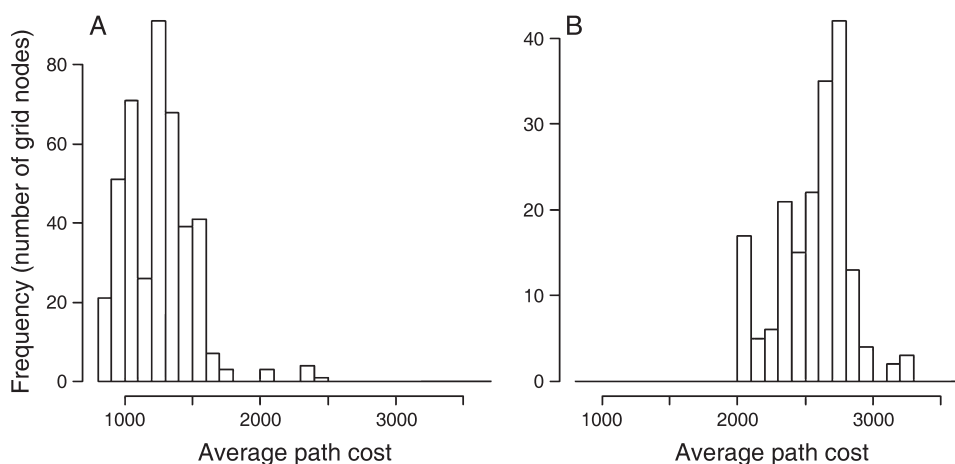


FIG. 12. Frequency distributions depicting the average path cost from each snow point to all other snow points comparing least-cost pathways based on (A) 15 May MODIS and (B) 29 May MODIS snow cover. Note that the y-axes are scaled differently for each date; see Fig. 9 for clarification of average path cost.

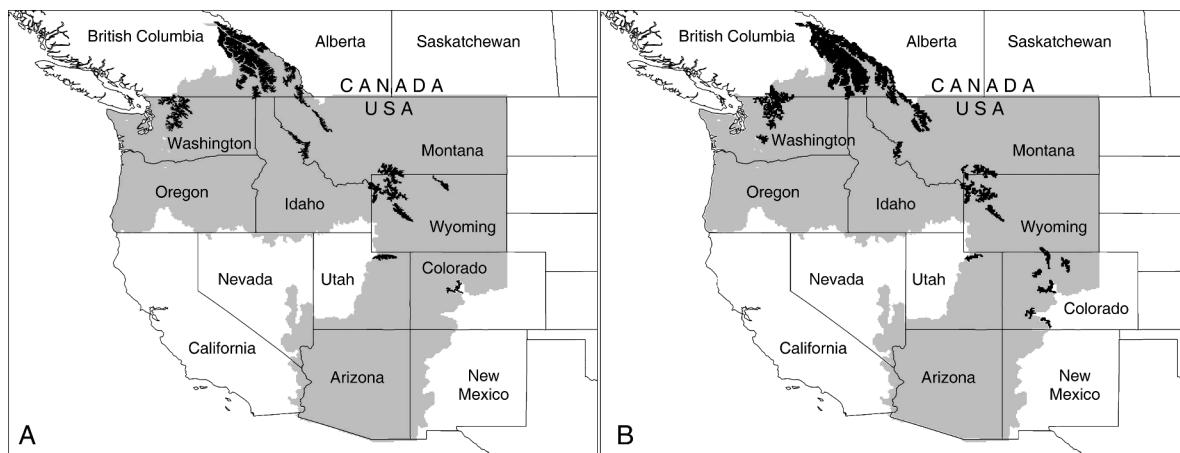


FIG. 13. Contiguous areas of persistent spring snow cover $>1000 \text{ km}^2$ based on (A) MODIS snow cover shifted two weeks later in the year (29 May MODIS) and (B) the ensemble climate projection for the period 2070–2099 (Ensemble 2085). The study area is shown in gray, and snow cover is black.

states in the contiguous United States where wolverines currently occur (Washington, Idaho, Montana, and Wyoming) retain 75.3% of their spring snow cover based on Ensemble 2045. For Ensemble 2045, Montana and Idaho maintain some connected areas in the mid-21st century (Fig. 10), but many of the potential movement paths have much higher costs. Higher costs, coupled with decreased denning habitat, will likely lead to fewer successful wolverine dispersals. Therefore, as wolverine habitat shrinks during the 21st century, large contiguous areas of habitat where local extirpation is less likely to occur will become increasingly important for the conservation of wolverines in the western United States.

Continued warming trends may create many small and isolated populations that would be subject to high levels of demographic and genetic stochasticity. Wolverine populations are at risk from isolation (Krebs et al. 2004); their extirpation in Colorado and California likely resulted from a combination of high human-caused mortality and very low immigration rates (Aubry et al. 2007, Schwartz et al. 2007). Currently, many of the areas containing wolverines in the western United States support relatively small populations. For example, Squires et al. (2007) estimated that four mountain ranges in southwestern Montana collectively contained about 13 wolverines (12.8, 95% CI = 9.9–15.7). Clearly, such population densities are too low for long-term persistence without connectivity to other populations. Schwartz et al.'s (2009) analysis assumed a well-distributed population of wolverines with all larger areas of habitat occupied. This is consistent with current understandings (see Aubry et al. 2007), but may not be in the future if decreased connectivity results in the loss of wolverine populations in many of the smaller mountain ranges. Meta-population theory predicts that decreased connectivity will shift the balance between colonization and extinction, leading to decreased patch

occupancy (Levins 1969, 1970). Additionally, the predicted responses of meta-populations to reductions in occupied area are nonlinear and characterized by extinction thresholds (e.g., Lande 1987). Therefore, like the statistical downscaling of GCMs, the changes in connectivity predicted in our analyses should be considered conservative (see section on *Limitations and caveats* below); if most of the wolverine habitat was unoccupied, average movement costs would be much higher than indicated.

Although areas of wolverine habitat will likely be greatly reduced and isolated by the late 21st century, relatively large islands of spring snow cover are predicted to persist. Contiguous areas of snow cover $>1000 \text{ km}^2$ in size, which are large enough to support small breeding populations of wolverines and presumably large enough for short-term population persistence, are retained in both the Ensemble 2085 and 29 May MODIS projections. In particular, British Columbia contains extensive areas of spring snow cover that are connected to snow-covered areas in northwestern Montana. Additionally, large snow-covered areas exist in northern Washington, along the Montana–Idaho border, and in the Greater Yellowstone Area (Fig. 13). Colorado appears to provide habitat for wolverines in the late 21st century based on Ensemble 2085, but not in 29 May MODIS (Fig. 13).

Qualitatively, Ensemble 2085 and 29 May MODIS are similar because topographic patterns strongly constrain both projections. Both projections identify most of the same large areas of retained snow cover, which may provide potential refuges for wolverines: British Columbia, northern Washington, northwestern Montana, and the Greater Yellowstone Area (compare Fig. 4A with Fig. 4D). Ensemble 2085, however, predicts significantly more snow in Colorado than would be expected if the only process we modeled was accelerated spring snow

melt. Colorado has virtually identical snow-covered areas in both the Historical Reconstruction and 15 May MODIS (Table 2). Although there is 10.2% less snow overall in 29 May MODIS compared to Ensemble 2085, there is 176% more snow-covered area in Colorado. This divergence does not indicate differences related to scale (see section on *Limitations and caveats* below). Rather, it is likely due to altered patterns of combined seasonal temperature and precipitation projected by the climate models; climate models are predicting more winter snow in this area by the end of the 21st century. Conversely, the large degree of uncertainty associated with future snow conditions in Idaho (Fig. 6) may be due, at least in part, to the interaction between snow cover and spatial scale. In Idaho, spring snow cover is highly fragmented and follows narrow ridges in many areas (Fig. 2B). However, even in Idaho, where projections are most divergent, the overall results from comparing 29 May MODIS with Ensemble 2085 are similar: Idaho loses proportionately more of its snow cover than either Montana or Wyoming (Table 2). Additionally, even though connectivity modeling is sensitive to fine-grained changes in snow cover, the qualitative shifts in connectivity associated with losing Idaho as a population source are also very similar in both the Ensemble 2085 and MODIS 29 May projections (compare Figs. 8C and 11B).

Limitations and caveats

Throughout our analyses, we made many assumptions about constancy. We have assumed, for example, that observed relationships between the habitat use and movement patterns of wolverines and areas with persistent spring snow cover will remain constant if climatic conditions change. In downscaling climate models, we have assumed that small-scale climatic relationships will also remain constant. Any attempt to project climate patterns into the future will, by necessity, involve these kinds of assumptions. Thus, it is important to understand that the validity of our analyses will ultimately depend on the validity of such assumptions.

The downscaling approach used here assumes that relationships between local and regional climate will remain constant in the future. This assumption can lead to underestimations of local climate change. For example, using a regional climate model, Salathé et al. (2010) show that some montane areas in the PNW may warm faster than expected based on statistical downscaling due to decreased albedo associated with snow loss. These types of process-based feedbacks are not captured through statistical downscaling. However, Salathé et al. (2010) found that differences in regional projections were still dominated by the GCMs used to set boundary conditions, rather than by the scale of regional models used.

Additional areas of uncertainty are associated with possible changes in the nature of storm tracks, which may affect the future accumulation and distribution of

snowpack (Salathé 2006), and therefore, the degree to which GCMs and their ensemble averages capture potential change. For these reasons, the use of ensemble means and the delta method for downscaling likely underestimate local climate changes that would impact wolverine habitat; changes in spring snow cover predicted by our analyses should be considered conservative.

Although wolverine distribution is closely tied to persistent spring snow cover (Copeland et al. 2010), we do not know how fine-scale changes in snow patterns within wolverine home ranges may affect population persistence. Wolverines den in the snow column itself or under snow-covered logs and boulders (Magoun and Copeland 1998, Landa et al. 1998); thus, we assume that decreasing spring snow cover within wolverine home ranges will reduce the availability of reproductive den sites. However, there are a variety of local factors that determine both where wolverines den and the quality of den sites. For example, reproductive dens are often associated with avalanche chutes (Lofroth and Krebs 2007), and wolverines of both sexes are associated with these features throughout the year (Krebs et al. 2007). Avalanche chutes provide both subnivean debris piles for denning (Lofroth and Krebs 2007) and food sources, including ungulate carrion in the winter and rodents in the summer (Krebs et al. 2007). Consequently, as the amount and timing of snowfall changes, associated changes in avalanche frequency and other small-scale phenomena could have significant effects on wolverine habitat quality.

Cross-walking the historical temperature and precipitation data to MODIS-based snow cover has a number of limitations. The first is that modeled snow depth (or SWE) is not an exact surrogate for persistent spring snow cover. However, these two metrics are highly correlated because the areas where snow cover persists into the spring are often those that support the deep snowpacks needed for wolverine denning. Arguably, snow depth may have a greater influence on wolverine denning than spring snow cover; Copeland et al. (2010) used snow cover because of the ability to obtain these data with precise spatial and temporal resolution. Thus, the MODIS snow cover is a proxy for the biological needs of the wolverine, but appears to be a very good one. Cross-walking to VIC-derived snow depth at much coarser resolution weakens this proxy association. In the modeled snow distributions, pixels are about 140× larger than they are in the 0.5-km MODIS coverage. Given the complex topographic patterns in the western mountains of the contiguous United States, there are few areas where all 140 MODIS-scale pixels contained in a 1/16-degree area will be persistently snow covered in mid-May. Similarly, the average snow depth modeled across a 1/16-degree pixel will, in most cases, be an average between areas with deep persistent snow cover and areas that are generally bare. When statistically fitting the MODIS snow coverage to VIC-derived snow depth, the

size and shape of snow-covered areas will therefore influence the local quality of the fit. Generally, in areas where snow is extensive and contiguous, the best fit will consistently lead to an increase in snow area with increased pixel size; most areas will be snow-covered and small, bare areas will be eliminated. Conversely, in areas where snow is highly fragmented or limited to linear areas along ridgelines, the best fit will produce larger pixels that are consistently classified as snow free. The excess (when compared to MODIS) snow cover in the Historical Reconstruction in areas such as northern Washington and British Columbia, and the lack of snow in areas such as Idaho, is at least partially due to these scaling issues and is unavoidable. Also, the time periods for the MODIS data and Historical Reconstruction are different. Data for the Historical Reconstruction were compiled for most of the 20th century, whereas MODIS data were limited to the first seven years of the 21st century (2000–2006).

Lastly, these analyses are constrained by the geographic extent of the river basins analyzed. States such as Oregon, which contain areas exterior to the three analyzed basins, likely contain more wolverine habitat, both currently and in the future, than is indicated in the figures and Table 2. Thus, there are probably areas in the contiguous United States that could provide future wolverine habitat, but are beyond the geographic scope of our analyses. Importantly, the potential contribution of the southern Sierra Nevada in California, which provided wolverine habitat historically (Aubry et al. 2007) and currently contains extensive areas of persistent spring snow cover (Copeland et al. 2010) was not considered here.

CONCLUSIONS

We expect that the geographic extent and connectivity of suitable wolverine habitat in western North America will decline with continued global warming. Under some scenarios, such as miroc 3.2, western North America heats up rapidly and snowpack is quickly eroded. However, the ensemble model does not behave like miroc 3.2; rather, it is much more similar to pcm1. If these scenarios are valid, then conservation efforts should focus on maintaining wolverine populations in the largest remaining areas of contiguous habitat and, to the extent possible, facilitating connectivity among habitat patches.

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