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

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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.

[Traduit par la Rédaction]

Received 17 June 2009. Accepted 20 November 2009. Published on the NRC Research Press Web site at cjj.nrc.ca on 11 February 2010.

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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.

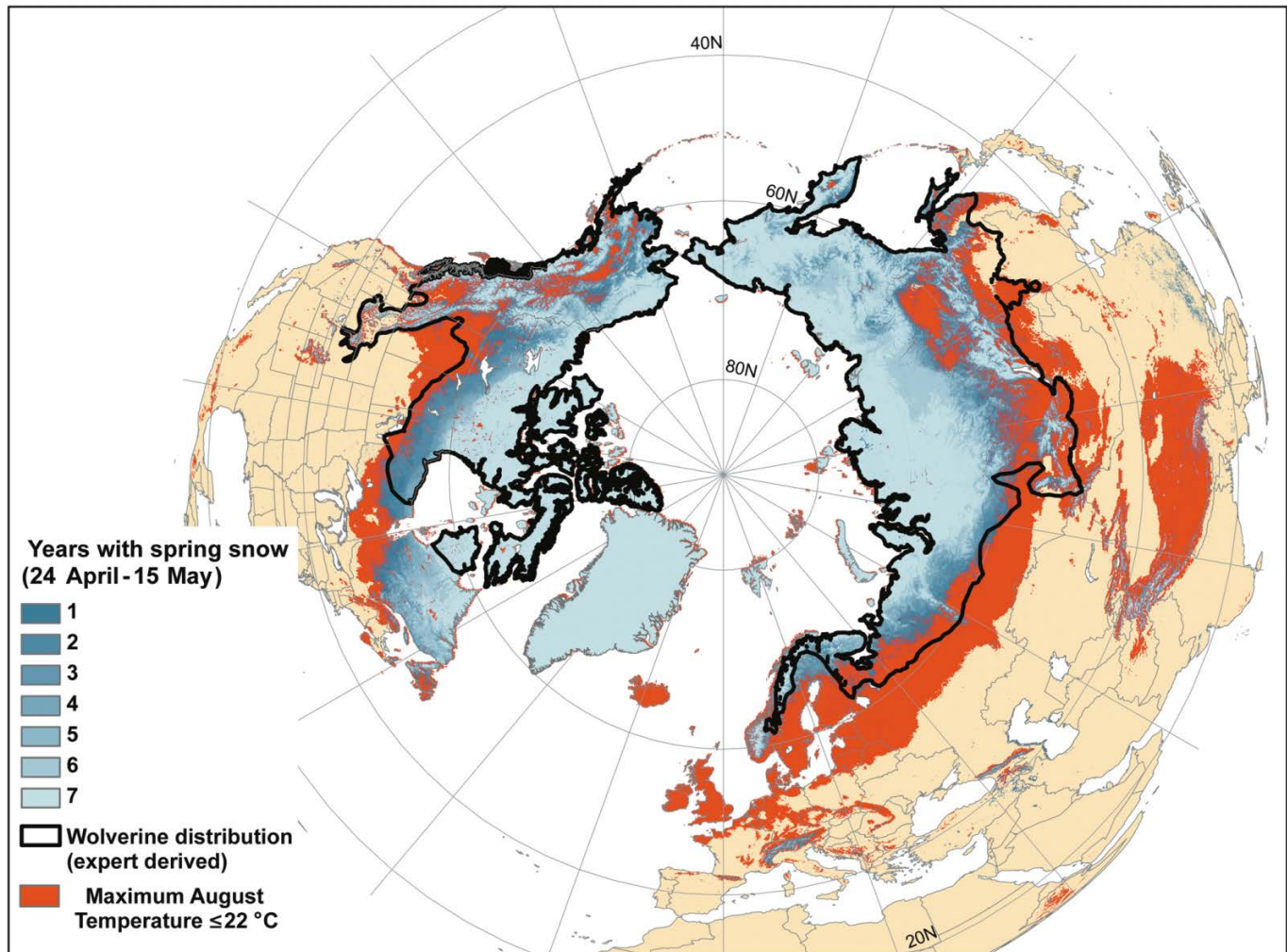
Here, we investigate the hypothesis that wolverine distribution at the broadest spatial scale is constrained within a climatic envelope defined by an obligate association with persistent spring snow cover and by an upper limit of thermoneutrality. We test this hypothesis by comparing and correlating 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.



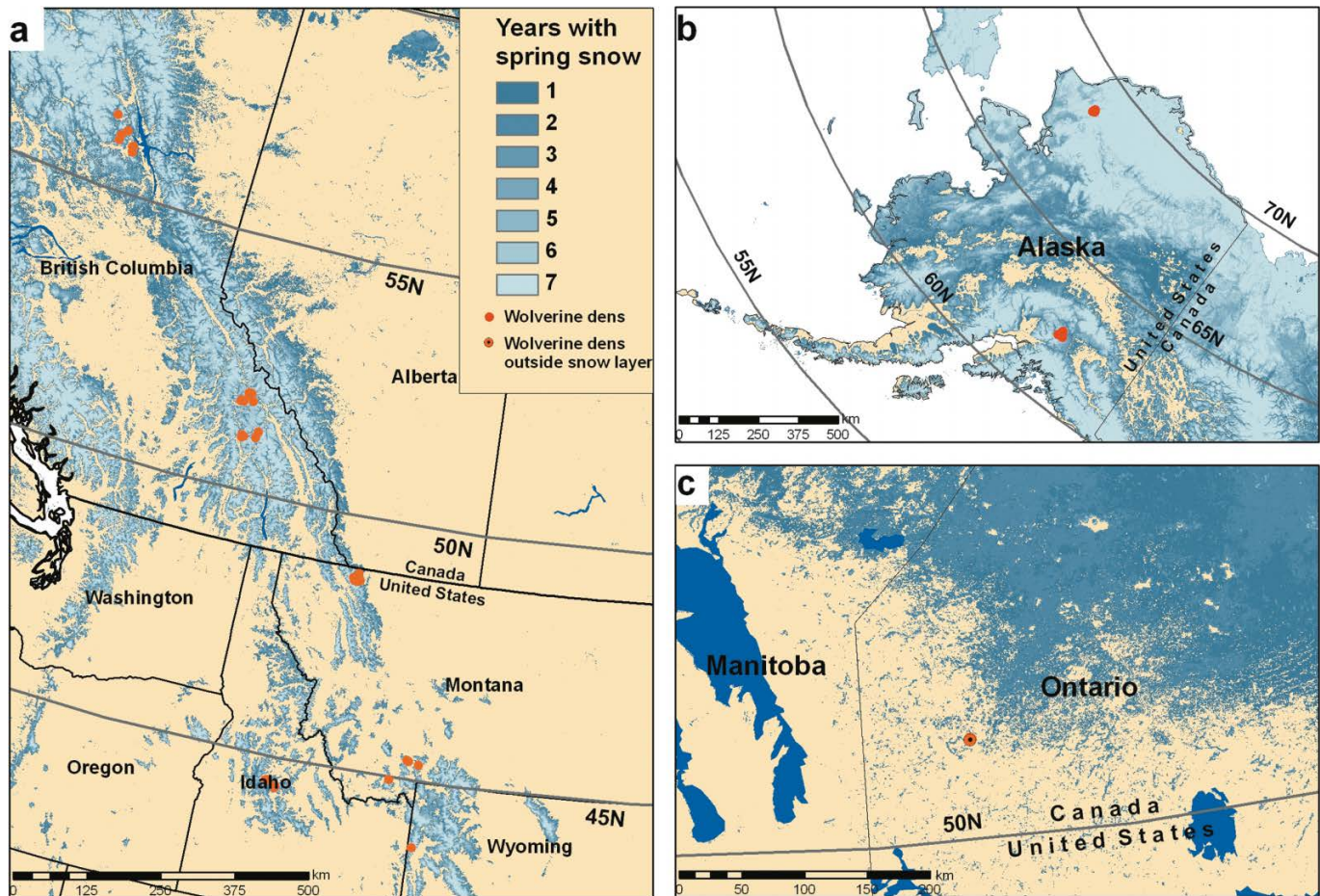
ground, cloud, night) for each of the 7 years (Hall et al. 2006). A portion of each daily MODIS image was typically obscured by clouds or, occasionally, by night. Generating cloud- and night-free images required compositing 21 consecutive daily images from 24 April to 15 May, which generally corresponds 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.

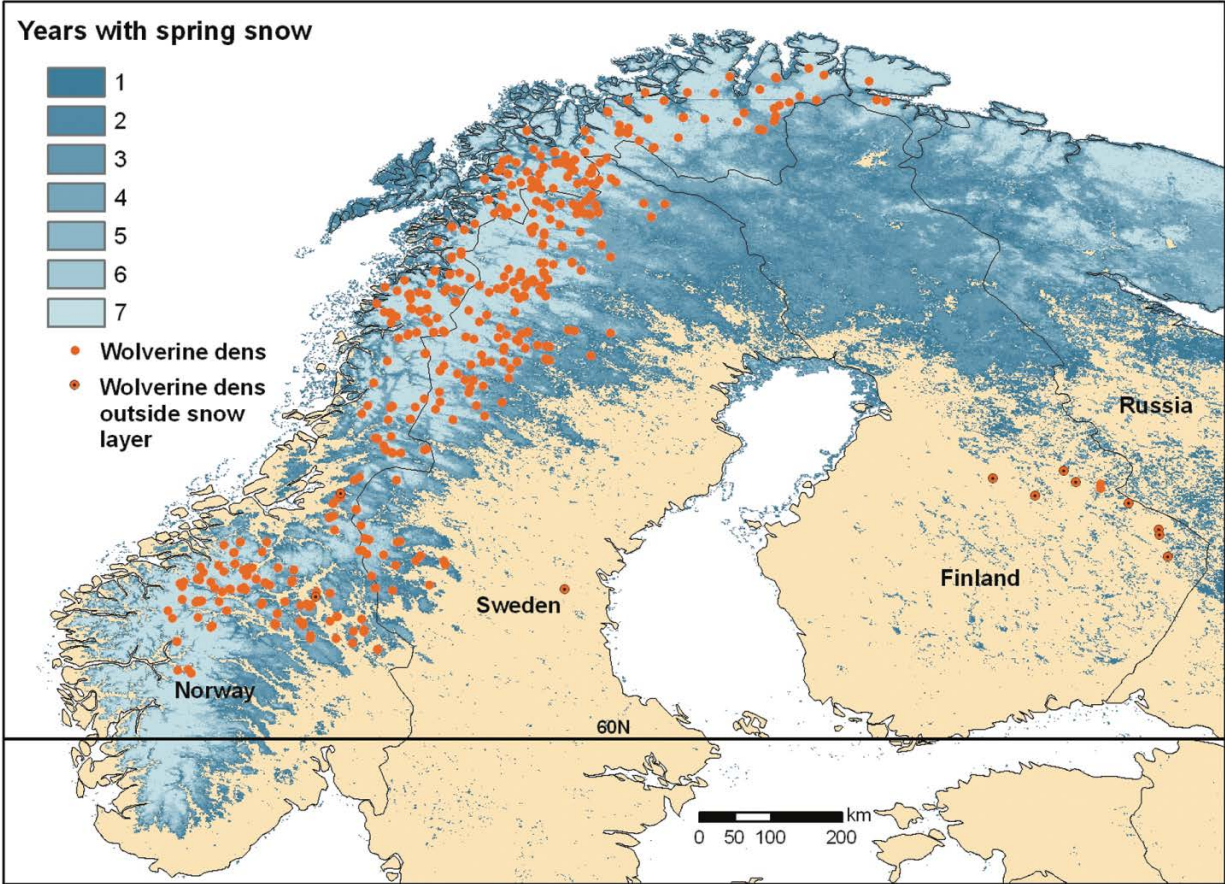
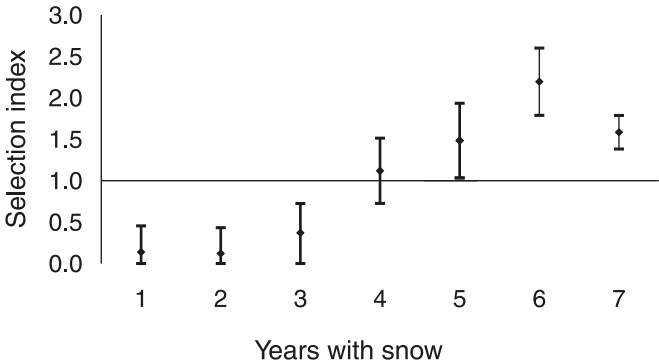


Fig. 4. Selection indices depicting the relation between the spring snow coverage and sites selected by wolverines for reproductive dens in Norway ($n = 327$) and Sweden ($n = 160$). Bars represent 95% Bonferroni-adjusted confidence intervals comparing snow cover values at den sites with proportional 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.

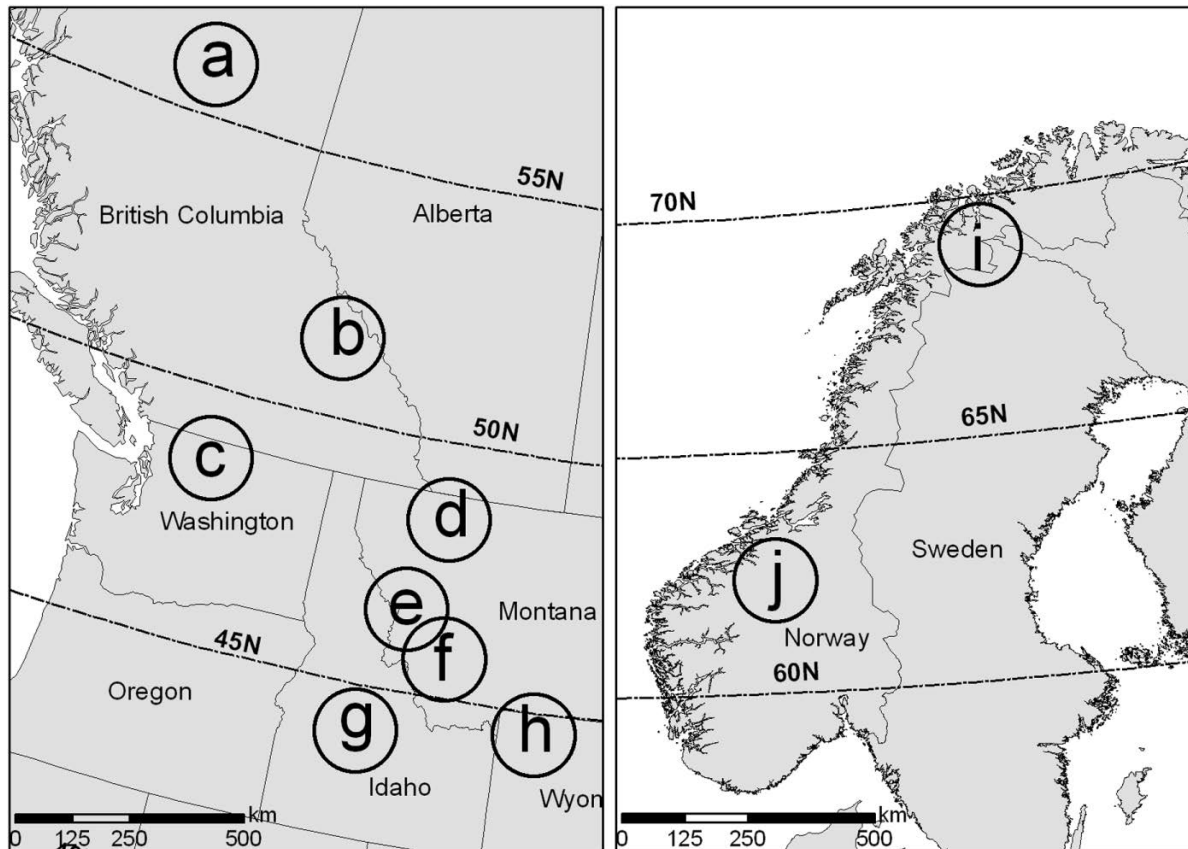


whether wolverine circumboreal range limits are tied to an upper limit of thermal tolerance. We compared published temperature data at 30 arc-seconds (~ 1 km) resolution for average maximum August temperatures for the years 1950–

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.

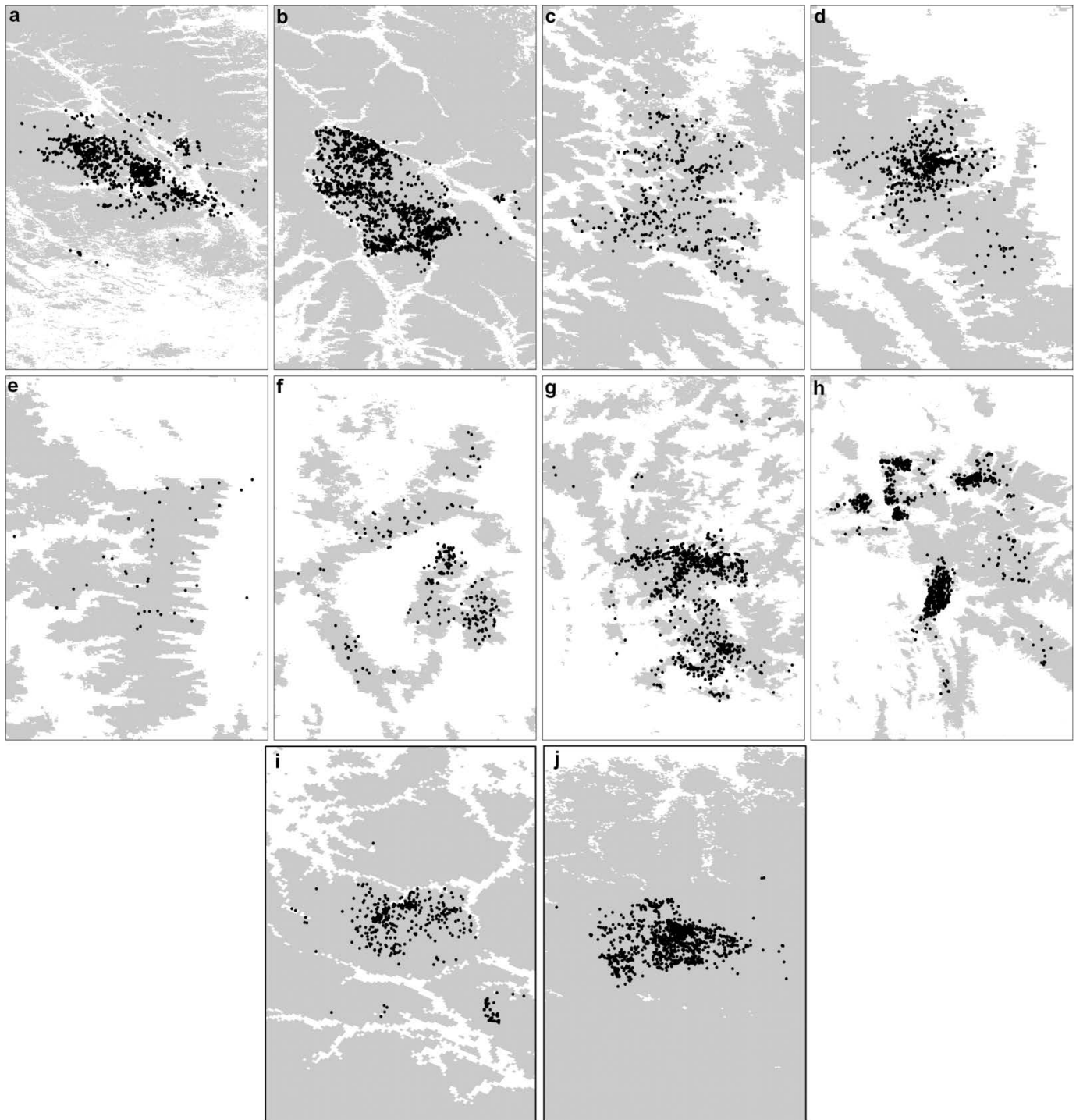
97.9% (550) of the den sites occurred in pixels that were snow-covered in at least 1 of 7 years. Den-site selection relative to years with snow was similar in Norway and Sweden and indicated that Scandinavian wolverines preferred den sites that were snow-covered for 6–7 years ($\chi^2 = 259.63$, $P < 0.0001$) (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.

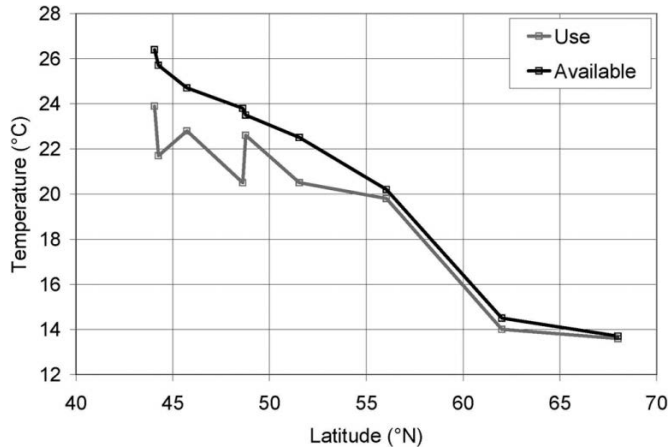
^bSummer: 1 June to 30 November based on presence or absence of snow.

^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.

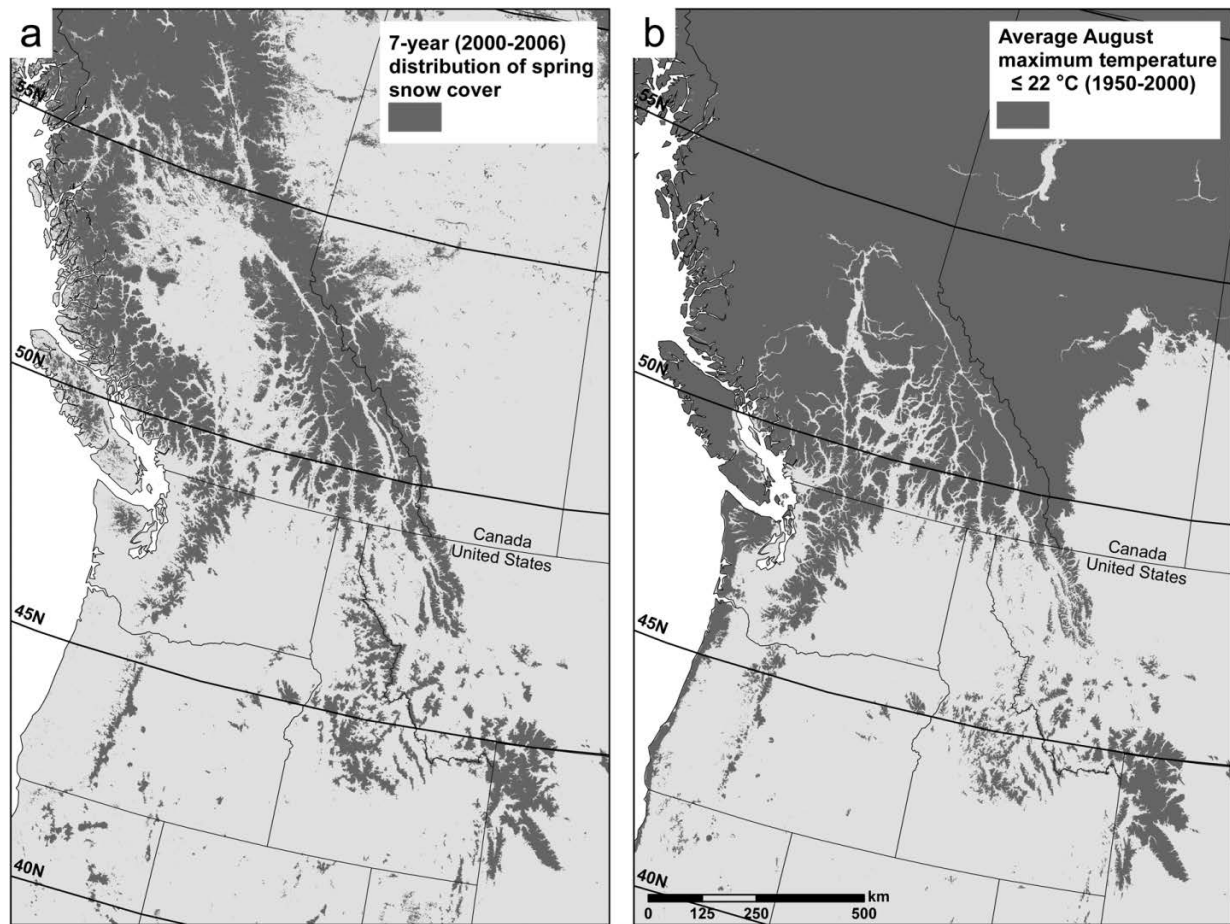
A warming climate may represent a paradoxical threat for the wolverine. Warmth provided by deep, persistent snow surrounding reproductive dens may diminish with earlier spring snow melt, while increasing summer temperatures may reduce the availability of summer habitat. Physiological investigations into 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.

Acknowledgements

M. Young and M. Johnson provided helpful comments on manuscript drafts. A. Taaheri contributed invaluable assistance with MODIS image analysis. We thank M. Copeland for long hours downloading, organizing, and manipulating MODIS satellite images, and the many individuals from field crews across all contributing studies.

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