Distribution and Broadscale Habitat Relations of the Wolverine in the Contiguous United States

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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 $\leq$1 township (93.2 km^2) and temporal precision $\leq$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)

DOI: 10.2193/2006-548

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).

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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

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 km^2; 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 km^2 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 km^2 (25 $\times$ 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 $\geq$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 northwestern 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-

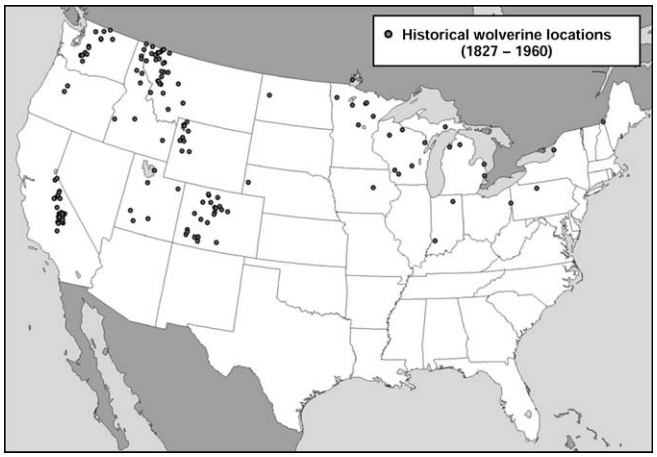

Figure 1. Locations of historical (1827–1960) wolverine records in the contiguous United States with areal precision ≤1 township (93.2 km^2) and temporal precision ≤10 years.

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

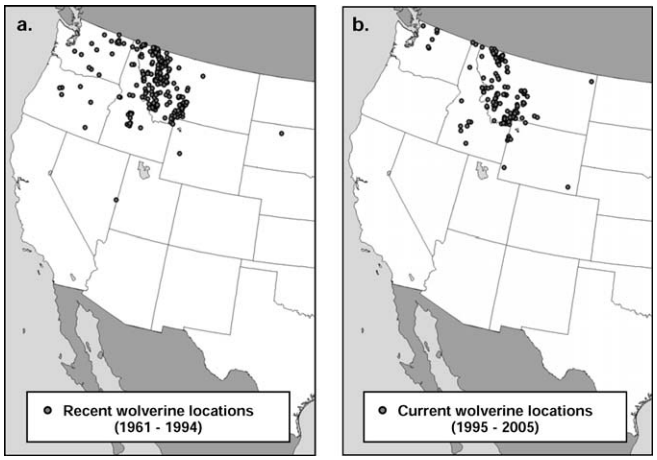

Figure 2. Locations of recent (1961–1994; a) and current (1995–2005; b) wolverine records in the contiguous United States with areal precision ≤1 township (93.2 km^2) and temporal precision ≤10 years. One record in northeastern Minnesota from 1965 is not shown in (a)

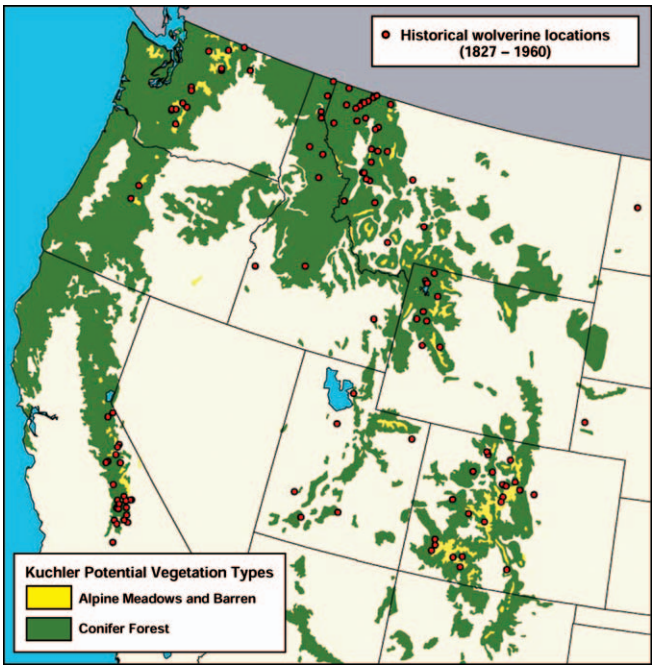

Figure 3. Locations of historical (1827–1960) wolverine records in the western contiguous United States overlaid on a simplified map of Kuchler's (1964) potential natural vegetation types, including Alpine Meadows and Conifer Forests (all montane and northern conifer forest types combined); all other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

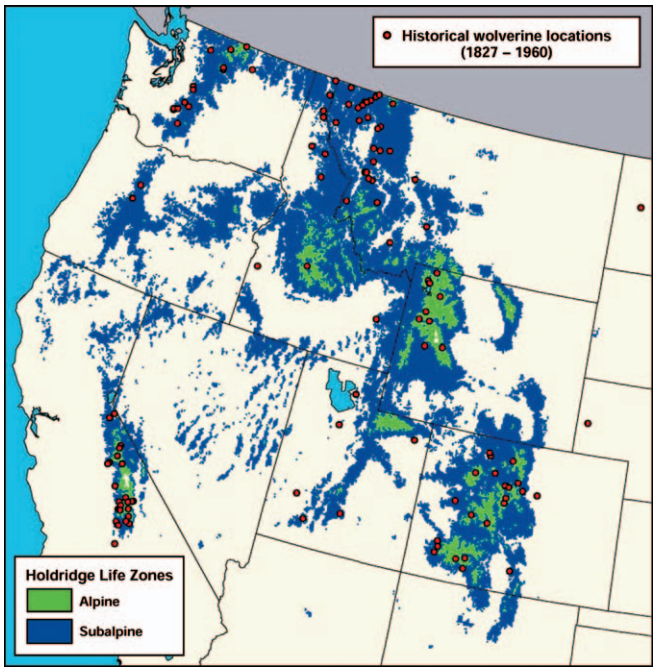

Figure 4. Locations of historical (1827–1960) wolverine records in the western contiguous United States overlaid on Alpine and Subalpine aggregations of Holdridge's (1967) life zones; all other life zones are unshaded.

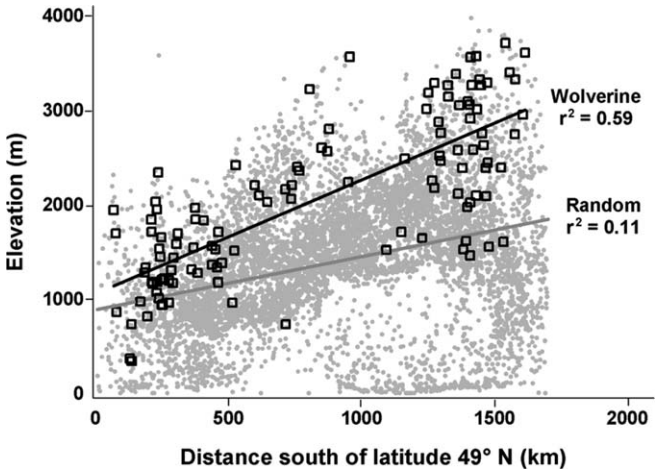

Figure 5. Linear regressions of latitude versus elevation for historical (1827–1960) wolverine records in the western contiguous United States (black squares and regression line), and a random sample of 7,000 locations from the same area (gray dots and regression line).

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 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.

		Kuchler's potential vegetation types			Holdridge's climatic life zones		
Region and states	*N*	Proportion in Alpine Meadows (%)	Proportion in Conifer Forest (%)	Median distance from Alpine Meadows (km)	Proportion in Alpine (%)	Proportion in Subalpine (%)	Median distance from Alpine (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

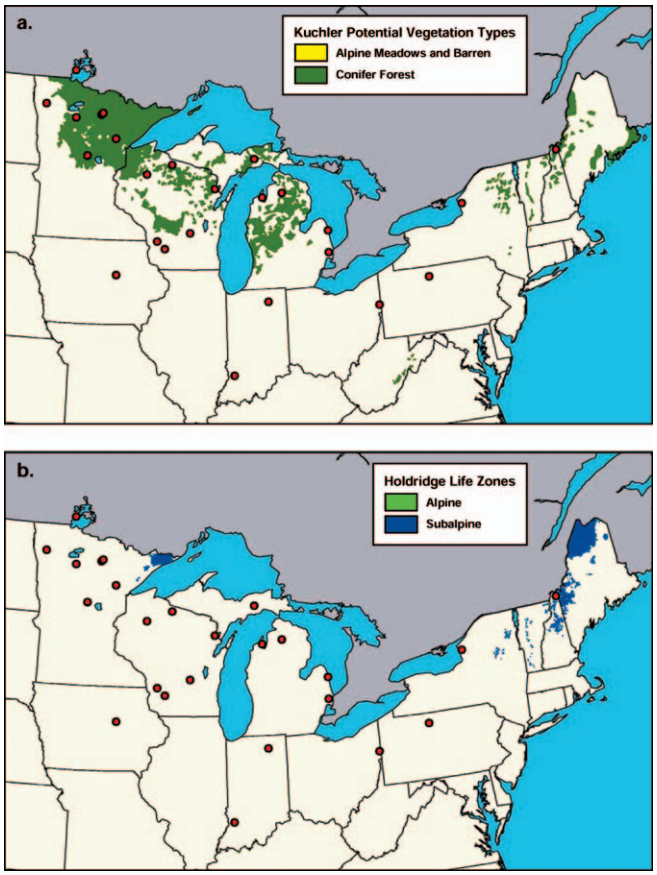

Figure 6. Locations of historical (1827–1960) wolverine records in the eastern contiguous United States overlaid on simplified maps of Kuchler's (1964) potential natural vegetation types, including Alpine Meadows and Conifer Forests (all other vegetation types are unshaded; a); and Alpine and Subalpine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

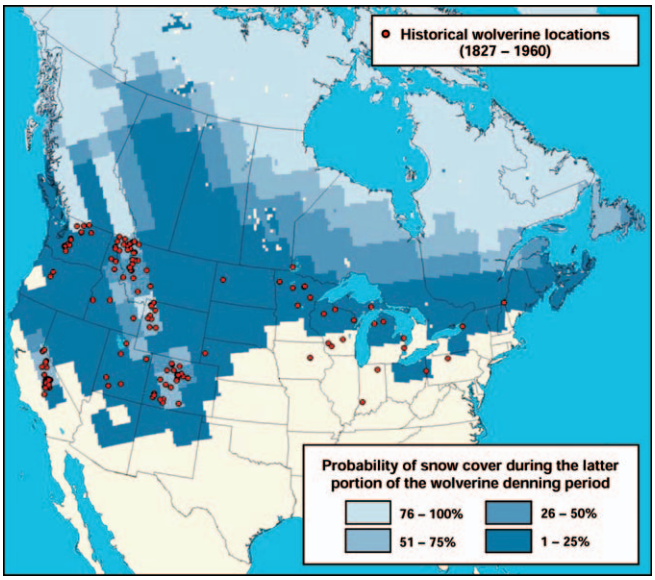

Figure 7. Locations of historical (1827–1960) wolverine records in the contiguous United States overlaid on a map depicting the probability of snow cover during the latter portion of the wolverine denning period (15 Apr–14 May) in increments of 25% based on satellite imagery (EASE-Grid snow cover data)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

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 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.

ACKNOWLEDGMENTS

We thank C. Copeland for assistance with Geographic Information System analyses and the preparation of figures, and P. Rivera, D. Kline, C. Raley, and D. Munzing for assistance with data compilation and analyses. R. Fisher of the National Museum of Natural History generously provided access to archival material in the Division of Mammals. B. Giddings of the Montana Department of Fish, Wildlife and Parks provided spatially referenced wolverine harvest records compiled from 1974 to 2004, and R. Inman and K. Inman of the Wildlife Conservation Society and J. Squires of the United States Forest Service, Rocky Mountain Research Station provided data on initial capture locations for study animals during radiotelemetry studies in Montana, Idaho, and Wyoming. E. Lofroth, A. Magoun, C. Raley, T. Max, P. Cunningham, R. King, H. Beyer, R. Powell, and 2 anonymous reviewers provided helpful comments on previous drafts of this manuscript. This study was funded by the United States Forest Service, Pacific Northwest and Rocky Mountain Research Stations. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the United States Department of Agriculture of any product or service.

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Associate Editor: Powell.