2014

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The Journal of Wildlife Management 78(2):325–334; 2014; DOI: 10.1002/jwmg.649

Management and Conservation

Recovery of Wolverines in the Western United States: Recent Extirpation and Recolonization or Range Retraction and Expansion?

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ABSTRACT Wolverines were greatly reduced in number and possibly extirpated from the contiguous United States (U.S.) by the early 1900s. Wolverines currently occupy much of their historical range in Washington, Idaho, Montana, and Wyoming, but are absent from Utah and only single individuals are known to occur in California and Colorado. In response, the translocation of wolverines to California and Colorado is being considered. If wolverines are to be reintroduced, managers must identify appropriate source populations based on the genetic affinities of historical and modern wolverine populations. We amplified the mitochondrial control region of 13 museum specimens dating from the late 1800s to early 1900s and 209 wolverines from modern populations in the contiguous U.S. and Canada and combined results with previously published haplotypes. Collectively, these data indicated that historical wolverine populations in the contiguous U.S. were extirpated by the early 20th century, and that modern populations in the contiguous U.S. are likely the descendants of recent immigrants from the north. The Cali1 haplotype previously identified in California museum specimens was also common in historical samples from the southern Rocky Mountains, and likely evolved in isolation in the southern ice-free refugium that encompassed most of the contiguous U.S. during the last glaciation. However, when southern populations were extirpated, these matrilines were eliminated. Several of the other haplotypes found in historical specimens from the contiguous U.S. also occur in modern North American populations, and belong to a group of haplotypes that are associated with the rapid expansion of northern wolverine populations after the last glacial retreat. Modern wolverines in the contiguous U.S. are primarily haplotype A, which is the most common and widespread haplotype in Canada and Alaska. For the translocation of wolverines to California, Colorado, and other areas in the western U.S., potential source populations in the Canadian Rocky Mountains may provide the best mix of genetic diversity and appropriate learned behavior.

KEY WORDS extirpated, *Gulo*, haplotype, historical, introduction, mitochondrial, wolverine.

Wolverine (*Gulo gulo*) populations that occupied portions of the contiguous United States (U.S.) historically were greatly reduced by the early 1900s and may have been extirpated (Newby and Wright 1955, Nowak 1973, Aubry et al. 2007).

Received: 3 January 2013; Accepted: 13 October 2013
Published: 3 February 2014

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Currently, wolverines occupy much of their historical range in Washington, Idaho, Montana, and Wyoming, but are absent from Utah (Aubry et al. 2007) and only single individuals are known to exist in California (McKelvey et al. 2008, Moriarty et al. 2009) and Colorado (Inman et al. 2009). Spatial patterns in historical records from Montana led Newby and Wright (1955) to conclude that wolverines had been extirpated from the state by the early 1900s, but began to recolonize the area from the north in the

early 1930s; by the early 1960s, wolverines had apparently recolonized most of western Montana (Newby and McDougal 1964). A later assessment of historical and current wolverine records by Nowak (1973) indicated that by the 1970s many areas in the contiguous U.S. from which wolverines had been extirpated were being recolonized. Additionally, during the last several decades, wolverines have recolonized the Cascade Range in northern Washington and southernmost British Columbia, and are continuing to expand their range southward (McKelvey et al. 2011*b*, Aubry et al. 2012). However, despite the recent long-distance movement of a lone male wolverine into Colorado from Wyoming in 2009 (Inman et al. 2009), and the discovery of a wolverine in California in 2008 that had originated in Idaho (McKelvey et al. 2008, Moriarty et al. 2009), there is no evidence of extant wolverine populations in areas south of the Greater Yellowstone Area in Wyoming, the Sawtooth Range in Idaho, or the northern Cascade Range in Washington (Aubry et al. 2007).

It may appear contradictory that wolverine populations are expanding their distribution southward and reclaiming portions of their former range at a time when global warming is reducing the areal extent and connectivity of wolverine habitat in the western contiguous U.S. (McKelvey et al. 2011*a*). However, recolonization of the western U.S. by wolverines is occurring at much larger spatial scales and more rapidly than habitat losses from global warming; predictive modeling indicates that many areas in the western mountains, including sizable areas in Colorado, will provide relatively large expanses of wolverine habitat into the next century, even if current trends in global warming continue (see Fig. 13b in McKelvey et al. 2011*a*).

Although wolverines may eventually recolonize the southern portions of their historical range naturally, the state of Colorado is considering translocating wolverines to accelerate this process (Colorado Division of Wildlife 2013), and less-formal discussions have also been occurring in California (Institute for Wildlife Studies 2013). Because of the potential for reintroduction of wolverines to southern portions of the contiguous U.S. in the near future, managers must identify the most appropriate source populations to use for such efforts. Such decisions will depend on the genetic objectives of reintroduction efforts, which can vary depending on local circumstances. For example, one goal may be to restore populations that are genetically similar to those that were extirpated to improve the likelihood that the introduced population will contain local adaptations (cf. Templeton et al. 1986), whereas another may be to provide a genetically diverse founding population to avoid inbreeding depression and associated increases in extinction risks (Frankham 1998).

The historical wolverine population in California was genetically distinct from modern populations in North America, indicating an extended period of isolation (Schwartz et al. 2007). Thus, this population may have evolved local adaptations that improved its fitness. Elliot (1903) originally considered wolverines in California to represent a distinct species (*Gulo luteus*), but this taxon was later reduced to subspecific status by Grinnell (1913). No studies have determined whether the unique haplotypes found in California wolverines by Schwartz et al. (2007) were limited to California, nor if unique haplotypes existed in other isolated populations in the western U.S. (Aubry et al. 2007).

The objectives of this study were to 1) investigate the hypothesis that wolverines were extirpated from their historical range in the contiguous U.S. by the early 1900s; and 2) evaluate potential source populations for future translocations to reestablish wolverine populations in California, Colorado, and other portions of the western U.S.

METHODS

To locate historical wolverine specimens from the contiguous U.S., we contacted curators from 114 museums in the United States and Canada, and searched online museum databases for wolverines collected prior to 1930. To minimize damage to museum specimens, we collected nasal turbinate bone samples from each skull (Wisely et al. 2004). To develop a more complete understanding of the genetic characteristics of modern wolverine populations, we also obtained tissue or hair samples from individual wolverines in North America from various sources. We added the haplotypes we derived to previously published data from both historical and modern populations (Wilson et al. 2000, Tomasik and Cook 2005, Cegelski et al. 2006, Schwartz et al. 2007, Zigouris et al. 2012).

To analyze ancient DNA, we followed the methods and protocols used by Schwartz et al. (2007). Previous extractions from turbinate bones of historical wolverine specimens provided low (0.6–1.0 ng/μl) DNA concentrations and erratic amplification of nuclear DNA (2 successes out of 9 attempts; Schwartz et al. 2007). Consequently, for this study we analyzed only mitochondrial DNA (mtDNA) from the control region. We chose the control region because all published studies of wolverine mtDNA amplified this region, allowing cross-study comparisons. We extracted DNA in an isolated, satellite laboratory equipped and used solely for the processing of ancient and historical DNA, and followed recommended ancient DNA protocols to avoid contamination (Hofreiter et al. 2001, Gilbert et al. 2005). We initially sequenced 344 bp of the left domain of the mtDNA control region from a modern wolverine tissue sample using universal primers, protocols from Shields and Kocher (1991), and the polymerase chain reaction (PCR). Using this sequence, we then designed a set of 3 short, overlapping segments to amplify DNA obtained from museum specimens. These segments ranged in size from 152 bp to 165 bp (see Table 3 in Schwartz et al. 2007 for details). For extractions from museum specimens, controls included an ambient (empty tube) from the sampling museum and a negative control. Additionally, we re-amplified and re-sequenced all historical samples that produced a haplotype to verify previous results.

We amplified modern tissues using primers *Gulo 0F* and *H16498* (Schwartz et al. 2007). Reaction volumes of 50 μl contained 50–100 ng DNA, 1× reaction buffer (Applied

Biosystems, Foster City, CA), 2.5 mM MgCl2, 200 μM each dNTP, 1 μM each primer, and 1 U Taq polymerase (Applied Biosystems). The PCR program for all primer sets was 94° C/5 min, (94° C/1 min, 55° C/1 min, 72° C/1 min 30 s) × 34 cycles, and 72° C/5 min. We determined the quality and quantity of template DNA using 1.6% agarose gel electrophoresis, and purified PCR products using ExoSap-IT (Affymetrix-USB Corporation, Cleveland, OH) according to manufacturer's instructions. We obtained DNA sequence data using the Big Dye kit and the 3700 DNA Analyzer (ABI; High Throughput Genomics Unit, Seattle, WA). We generated DNA sequence data using the given primers, viewed and aligned sequences using Sequencher (Gene Codes Corp., Ann Arbor, MI), and determined resulting haplotypes using DAMBE (University of Ottawa).

Following Schwartz et al. (2007) and Zigouris et al. (2012), we examined relationships among haplotypes by constructing a minimum spanning network (Posada and Crandall 2001). We input network connections generated from Arlequin version 3.5.1.2 (Excoffier and Lischer 2010) into HapStar version 0.7 (Teacher and Griffiths 2011). To properly place haplotypes into their worldwide context, we included all North American haplotypes, as well as all published haplotypes from Eurasia, including Scandinavia (Walker et al. 2001), unknown locations in Asia (Tomasik and Cook 2005), and Mongolia (Schwartz et al. 2007).

RESULTS

Historical Samples

Schwartz et al. (2007) successfully amplified DNA from 7 wolverine specimens collected in California between 1891 and 1922. To these, we added 13 specimens collected between 1870 and ca. 1900 (4 from Colorado, 4 from Idaho, and 1 each from Washington, Montana, Wyoming, Utah, and Minnesota; Table 1). The most common haplotype among historical wolverine specimens from the contiguous U.S. was Cali1 (11/20, 55%; Schwartz et al. 2007). Haplotype O was the next most common (4/20, 20%; Cegelski et al. 2006), 2 (10%) were haplotype A (Wilson et al. 2000), 1 (5%) was haplotype Cali2 (Schwartz et al. 2007), 1 was haplotype F (Wilson et al. 2000), and 1 was haplotype I (Wilson et al. 2000). Haplotypes Cali1 and O were widely distributed historically; we found Cali1 in

Table 1. Historical museum specimens from the contiguous U.S. genotyped during this study, including California specimens genotyped by Schwartz et al. (2007).

Museum	Catalog number	Date of collection	State	County	Location	Sex	Specimen type	Collector	Haplotype
USNM	32571	1891	California	Mono	Pine City	M	Skull	J. H. Lowry	?
USNM	32487	1892	California	Fresno	Chiquito Lake	F	Skin, Skull	J. H. Lowry	Cali1
USNM	51317	1893	California	Fresno	Chiquito Lake	F	Skin, Skull	J. H. Lowry	Cali1
MVZ	16373	1911	California	Tulare	Monache Meadows	F	Skin, Skull	J. W. Drouillard	Cali1
MVZ	22121	1915	California	Mariposa	Head of Lyell Canyon	F	Skin, Skull, Partial Skeleton	C. L. Camp	Cali1
MVZ	22120	1915	California	Mariposa	Head of Lyell Canyon	F	Skin, Skull, Partial Skeleton	C. L. Camp	Cali2
MVZ	30049	1919	California	Tulare	Head of Twin Lake	?	Skin, Skull	E. W. McDonald	?
MVZ	32807	1921	California	Mono	Virginia Lake	F	Skin, Skull	A. J. Gardinsky	Cali1
MVZ	33475	1922	California	Mono	Saddlebag Lake	F	Skin, Skull, Partial Skeleton	A. J. Gardinsky	Cali1
YPM	MAM 6566	1870	Colorado	Denver	Denver	?	Skeleton	Yale College Scientific Expedition	O
DMNS	Mammals 85	1876	Colorado	Summit	Pass Creek	F	Skin, Skull	E. Carter	Cali1
DMNS	Mammals 2723	circa 1900	Colorado	Clear Creek	Idaho Springs	M	Skin, Skull	E. Carter	O
YPM	MAM 6567	?[a]	Colorado	Denver	Denver	?	Skull	?	Cali1
USNM	188246	1875	Idaho	?	Eastern	?	Skull	?	Cali1
USNM	A 30912	1890	Idaho	?	Salmon River Mountains	F	Skull	Bailey, Dutcher	F
USNM	26463	1891	Idaho	?	Sawtooth Mountains	F	Skin, Skull	F. C. Parks	Cali1
USNM	81799	1896[b]	Idaho	?	Sawtooth	F	Skull, Skeleton	F. C. Parks	A
USNM	110281	1899	Minnesota	Itasca	T61N, R25W, Sec. 7	M	Skull	H. V. Ogden	I
USNM	67370	1894	Montana	?	Bear Tooth Mountains	F	Skin, Skull	B. H. Dutcher	O
USNM	A 21493	Late 1800s	North Dakota	?	Fort Union	?	Skull, Skelton	H. A. Ward	?
USNM	236529	1921	Utah	?	Upton	M	Skin, Skull	G. E. Rickins	Cali1
USNM	64358	1894	Washington	Chelan	Chelan	?	Skull	C. D. Woodin	?
USNM	64359	1894	Washington	Chelan	Chelan	?	Skull	C. D. Woodin	A
USNM	62614	1895[c]	Wyoming	?	Yellowstone National Park	F	Skin, Skull	?	O

DMNS, Denver Museum of Nature and Science, Denver, Colorado; MVZ, Museum of Vertebrate Biology, Berkeley, California; USNM, National Museum of Natural History, Washington, D.C.; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut. Haplotypes A, F, and I were identified by Wilson et al. (2000), O by Cegelski et al. (2006), and Cali1 and Cali2 by Schwartz et al. (2007); haplotype ? means DNA from that sample did not amplify.

[a] Probably collected in 1870.

[b] Received at the museum in 1896, date of collection unknown.

[c] Received at the museum in 1895, date of collection unknown.

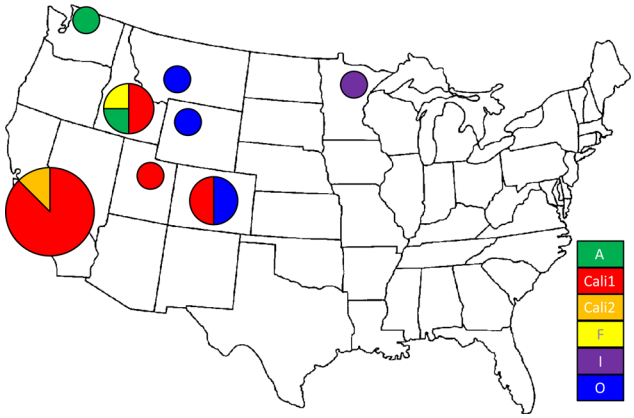

Figure 1. Proportions of haplotypes associated with historical museum specimens from the contiguous U.S. by state. A, F, and I refer to haplotypes identified by Wilson et al. (2000), O by Cegelski et al. (2006), and Cali1 and Cali2 by Schwartz et al. (2007). Pie chart sizes approximate the total number of samples from each state.

California, Colorado, Utah, and Idaho and O in Colorado, Wyoming, and Montana (Fig. 1). We found haplotype A in Washington and Idaho, and haplotypes Cali2, F, and I in California, Idaho, and Minnesota, respectively (Fig. 1).

Modern Samples

We obtained 209 DNA samples from Alaska, Idaho, Montana, Oregon, Washington, and Wyoming in the U.S., and from Alberta, British Columbia, and Ontario in Canada (Appendix). Modern wolverine samples were dominated by haplotype A (150/209, 72%; Fig. 2, Appendix), and exhibited patterns in the geographical distribution of haplotypes that were similar to those reported by Schwartz et al. (2007). Wolverines from the Cascade Range in northern Washington and southernmost British Columbia were a notable exception; all 18 of the samples we analyzed were haplotype C, and this was the only population sampled in the contiguous U.S. that contained this haplotype (Fig. 2, Appendix).

Combined with previously published haplotypes, 741 wolverines from modern populations in North America have now been haplotyped (Appendix). Samples from the contiguous U.S. are plentiful (319; Fig. 2) with A being the dominant haplotype throughout that region (266/319, 83%; Fig. 2, Appendix).

Phylogenetic Relationships Among Haplotypes

The network we generated is very similar to that produced by Schwartz et al. (2007), but contains additional haplotypes

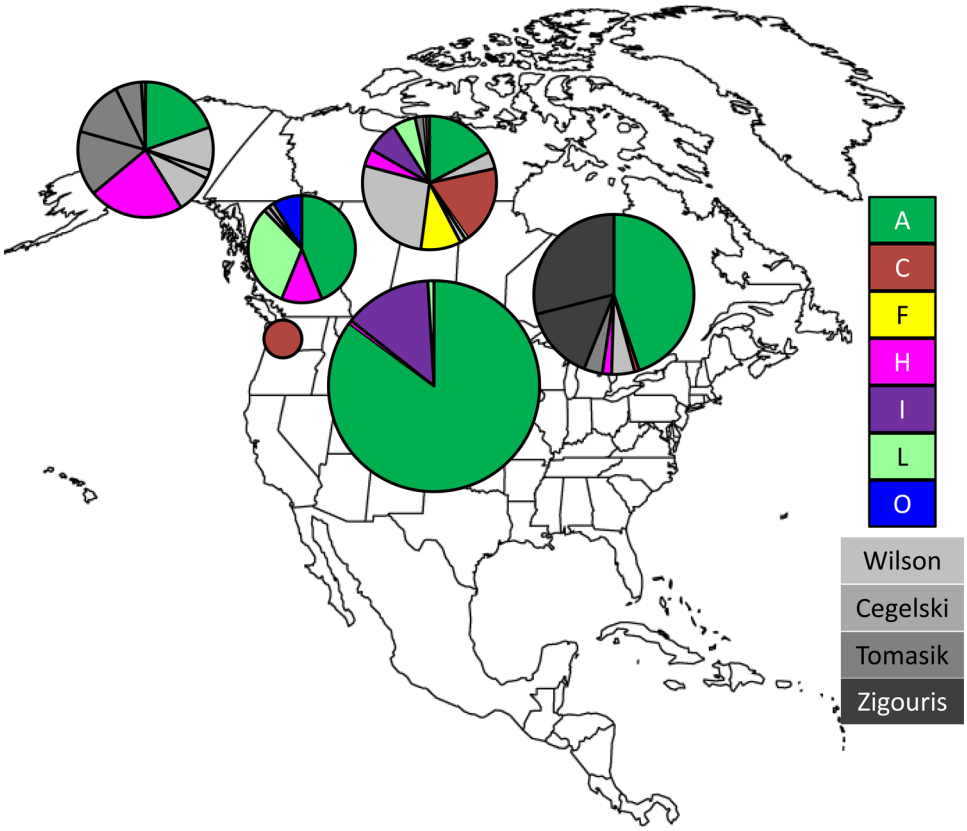

Figure 2. A simplified presentation of wolverine population structure among modern wolverine populations in North America. Colored wedges are haplotypes that either occur in modern populations or occurred in historical populations within the contiguous U.S. A, C, F, H, and I refer to haplotypes identified by Wilson et al. (2000), and L and O by Cegelski et al. (2006). Grayed wedges, representing haplotypes only found in Alaska or Canada, are grouped by the paper where they were first published. Wilson refers to Wilson et al. (2000), Cegelski to Cegelski et al. (2006), Tomasik to Tomasik and Cook (2005), and Zigouris to Zigouris et al. (2012). Pie chart sizes approximate the total number of samples from each area.

24 and 25 reported by Zigouris et al. (2012; hereafter, Z_24 and Z_25). Thus, our minimum spanning network includes all published haplotypes. Similar to the findings of Schwartz et al. (2007), our minimum spanning network places Cali1 and Cali2 onto a branch that contains mostly Asian haplotypes (Fig. 3). Haplotype Z_25, which is common in Ontario and Manitoba, Canada (Zigouris et al. 2012), is on this same branch but is removed from Cali1 by an additional 2 substitutions (Fig. 3). As in the network presented by Schwartz et al. (2007), haplotype H—the only haplotype found in both North America and Asia—appears to be the haplotype that links these continents. In North America, we observed a star phylogeny (Gillespie 1984) with haplotype A, the most common and widely distributed haplotype in North America (Fig. 2, Appendix), and with haplotype F, which has been found in modern samples from Alaska and northern Canada, and in 1 historical sample from the western contiguous U.S. Both haplotypes A and F are connected to 7 haplotypes by a single substitution (Fig. 3). A chain of substitutions consisting of North American haplotypes and culminating in haplotype Z_24, which is also common in eastern Canada (Zigouris et al. 2012), represents a unique branch of this phylogeny (Fig. 3).

DISCUSSION

Genetic Characteristics of Historical and Modern Wolverine Populations

Three hypotheses could explain the haplotype shifts we documented between historical and modern wolverine populations in the contiguous U.S. The first is that historical haplotypes Cali1, Cali2, F, and O are still present in the contiguous U.S. but have not yet been found because of insufficient sampling. The second is that wolverines were nearly extirpated from the contiguous U.S., but some individuals with haplotypes A, C, H, I, and L persisted and subsequently founded modern populations in the contiguous U.S. The third is that wolverines were extirpated from the contiguous U.S., and modern populations resulted from recent colonizations by northern wolverine populations.

In our view, the hypothesis that historical haplotypes have been overlooked because of insufficient sampling is highly unlikely. In large areas of the contiguous U.S. where these historical haplotypes were found (California, Colorado, and Utah), wolverines were extirpated early in the 20th century (Aubry et al. 2007). In the remaining areas (Idaho, Montana, Oregon, Washington, and Wyoming), recent sampling has been intensive, resulting in haplotypes from 319 wolverines. In Idaho, samples were obtained during a radiotelemetry study in the Sawtooth Mountains of central Idaho (Copeland et al. 2007), a similar study in the Teton Range (Inman et al. 2012), and opportunistically from both central and northern Idaho. In western Montana, samples were obtained from the state Department of Fish, Wildlife, and Parks, where trappers are required to submit the skulls of all trapped wolverines (Schwartz et al. 2009), and from 4 scientific studies (Squires et al. 2007, Schwartz et al. 2009, Copeland et al. 2010, Inman et al. 2012). In Oregon, recent surveys detected 3 wolverines in the Wallowa Mountains, one of which was genotyped (Magoun et al. 2013; Appendix). In Washington and Wyoming, samples were obtained both opportunistically and from ongoing radiotelemetry studies in the Cascade Range (Aubry et al. 2012; Appendix) and Greater Yellowstone Area (Inman et al. 2012; Appendix). Thus, within their current range in the contiguous U.S., wolverines have been well sampled everywhere they are known to exist. Additionally, organized sampling has been

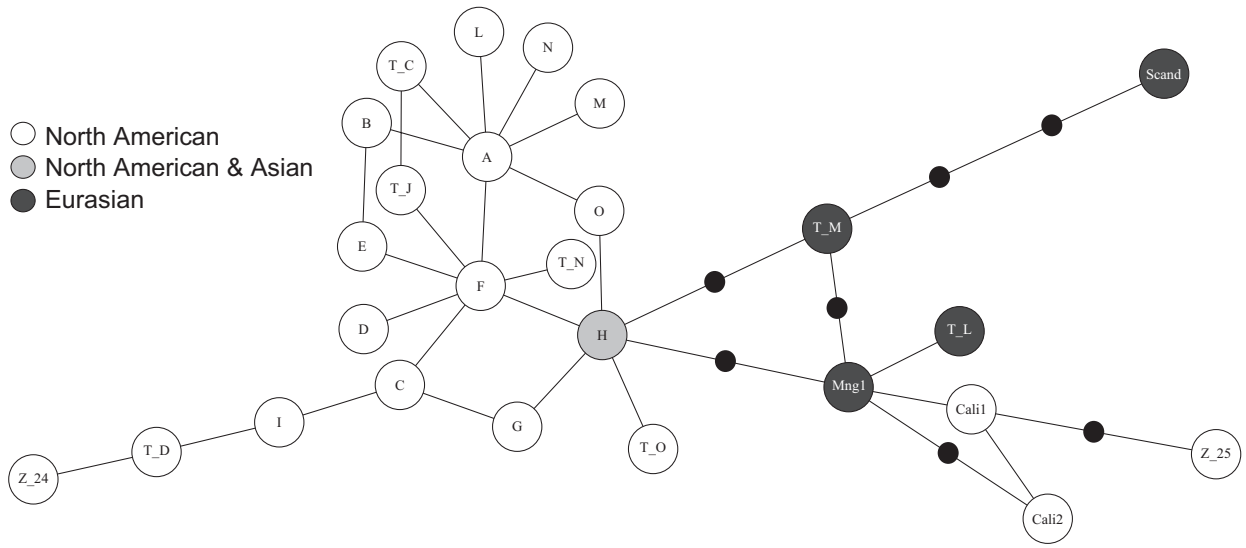

Figure 3. Minimum spanning network for all published wolverine haplotypes. Each node indicates a single base-pair substitution. Haplotypes A–I were identified by Wilson et al. (2000), L–O by Cegelski et al. (2006), T_C–T_O by Tomasik and Cook (2005), and Z_24–Z-25 by Zigouris et al. (2012). Scand was identified by Walker et al. (2001) and Cali1, Cali2, and Mng1 by Schwartz et al. (2007). Scand was found in Scandinavia, Mng1 in Mongolia, and T_L and T_M in unspecified Asian locations. Haplotype H is the only haplotype known to occur in both North America and Asia; all other haplotypes were found exclusively in North America.

attempted in other areas where they have been reported (e.g., Hiller and McFadden-Hiller 2013). Thus, there is little chance that entire matrilines have gone unsampled in the contiguous U.S. In North America, 741 individuals have been genotyped based on samples that encompass the current geographic range of wolverines (Fig. 2, Appendix). The absence of haplotypes Cali1 and Cali2 from this large collection of modern samples makes their continued existence anywhere in North America extremely unlikely. Zigouris et al. (2012) report 2 haplotypes (Z_24 and Z_25; Appendix) that were previously unpublished; however, these types are consistent with types J and K reported by Chappell et al. (2004, Zigouris et al. 2012: Table 6), which were based on a shorter sequence of mitochondrial DNA. If we assume that Z_24 and Z_25 were previously reported by Chappell et al. (2004), then no new haplotypes from extant populations have been reported since Cegelski et al. (2006), even though 444 individuals have subsequently been examined.

Wolverine populations in the contiguous U.S. were greatly reduced and locally extirpated during the early 20th century (Aubry et al. 2007). For current populations to be derived from resulting relictual populations rather than immigrants, this bottleneck event would need to have eliminated most of the matrilines present in our historical sample (haplotype A in the Cascades and haplotypes Cali1, F, and O from the northern Rocky Mountains) while allowing the persistence of matrilines that we did not detect (haplotypes C in the Cascades and H, I, and L in the northern Rocky Mountains). Moreover, because population bottlenecks preferentially remove rare haplotypes (Nei et al. 1975), our historical sample would need to contain mostly rare haplotypes while lacking common ones, which seems highly unlikely. Additionally, the spatial recolonization patterns described by Newby and Wright (1955) in Montana are not consistent with expansion from relictual sources.

We believe, therefore, that the hypothesis that wolverines were extirpated from the contiguous U.S. and modern populations resulted from recolonization from the north provides the most compelling and parsimonious explanation for observed haplotype shifts. Most historical wolverine samples from the western U.S. were haplotypes Cali1, Cali2, F, or O (17/19, 89%; Fig. 1), none of which occur in modern populations from that region (Fig. 2, Appendix). Moreover, neither haplotype Cali1 nor Cali2 has been found among extant wolverines anywhere in North America. As noted above, it is highly unlikely that these haplotypes are present but undetected. Historically, both Cali1 and O were widespread geographically in the western U.S. (Fig. 1). Among modern populations, haplotype O (Cegelski et al. 2006) has been found only near Revelstoke, British Columbia, which is approximately 230 km north of the U.S. border. In this localized area, it was found both by Cegelski et al. (2006) and in more recent surveys (Appendix).

The only haplotype found among historical samples from the western U.S. that also occurs among modern populations in that region is haplotype A (Figs. 1 and 2). However, A is the most common haplotype in Alaska and Canada, including southern British Columbia and Alberta (Appendix), the most likely source areas for immigration into the western contiguous U.S. Although the historical specimen from Washington is haplotype A, all 18 modern wolverine specimens from the Cascade Range in northern Washington and southernmost British Columbia are haplotype C. Outside that region, C has been found only in Alberta, Saskatchewan, and Nunavut. This provides strong evidence that the recent recovery of wolverines in the Cascades resulted from colonization by northern populations, not the expansion of relictual populations. The implications of finding haplotype I in Minnesota, which was the only historical sample available from the eastern U.S., are unknown because I is a common haplotype in modern populations throughout North America, including the western U.S. (Figs. 1 and 2, Appendix). However, in a recent study of wolverine genetics in central Canada, Zigouris et al. (2012) did not detect haplotype I in Ontario, the closest (approx. 500 km) extant population to Minnesota.

Modern wolverine populations have many control region haplotypes (at least 20; Appendix), and exhibit a high level of matrilineal spatial structure. For example, haplotype L (Cegelski et al. 2006) appears to be a relatively common haplotype in British Columbia and Alberta (27/79, 34%), but is nearly absent in Montana and Idaho (Appendix). Based on the distribution of suitable habitat conditions for wolverines (Copeland et al. 2010), northern populations in Alaska and Canada have the potential for gene flow, yet exhibit a high level of genetic structure and contain uncommon and apparently local haplotypes (Tomasik and Cook 2005). Thus, the presence of unique haplotypes among historical populations in the contiguous U.S. is not unexpected.

The vast majority of North American haplotypes are associated with star phylogenies around common haplotypes and therefore likely represent recent radiation. However, the association between haplotypes Cali1, Cali2, and Z_25 and exclusively Asian haplotypes is unlikely to be the product of recent radiation. The calculated temporal depth of the genetic split between Cali1, Cali2, and the other North American haplotypes depends strongly on assumed mutation rates and could plausibly vary between approximately 2,000–100,000 years (Table 5 in Schwartz et al. 2007). However, Cali1, Cali2, and Z_25 are as divergent from the other North American haplotypes as are purely Eurasian types (Fig. 3), and these have been separated at least since the submergence of the Beringian land bridge at the end of the Pleistocene. This would suggest a temporal depth of between approximately 10,000–100,000 years.

Evolutionary History of the Wolverine in Western North America

Tomasik and Cook (2005) argued that during the Holocene wolverines that had been isolated in Beringia by continental glaciers rapidly spread southeastward into present-day Alaska and Canada; additional haplotypes found by Cegelski et al. (2006) supported this hypothesis. Thus, the diversity of haplotypes found among modern wolverine populations in North America likely represents a relatively recent radiation

that led to many closely related haplotypes (Tomasik and Cook 2005, Cegelski et al. 2006, Schwartz et al. 2007). As noted above, Cali1 Cali2, and Z_25 were not associated with this recent radiation. Here, we examine the case for haplotypes Cali1 and Cali2 being associated with glacial vicariance.

In the late Pleistocene, wolverine specimens dating to the last glacial period (ca. 100,000 to 10,000 years ago [yBP]) have been found in both Alaska and Yukon, and in the western contiguous U.S. (Bryant 1987, Neomap 2013). At the height of the last glaciation (ca. 18,000 yBP), when continental ice completely separated Beringia from the contiguous U.S. (see Fig. 1B in Davison et al. 2011), wolverine populations in North America were isolated in 2 disjunct ice-free refugia: one in Beringia in the north and another, or perhaps several (Shafer et al. 2010, Zigouris et al. 2012), in the contiguous U.S. south of the continental ice sheets (Kurtén and Anderson 1980, Neomap 2013).

Tundra conditions were prevalent in the southern Rocky Mountains ca. 12,000–10,000 yBP, and were replaced by spruce-fir (*Picea-Abies*) forests in the early Holocene (Anderson et al. 2008). Thus, environmental conditions in the southern Rocky Mountains during the late Pleistocene and early Holocene were consistent with contemporary wolverine habitat (Copeland et al. 2010). The hypothesis that wolverines used the southern Rocky Mountains as a refuge during this period is supported by the fossil record. Wolverine specimens dating from the late Pleistocene to early Holocene have been recovered from sites in Colorado, Idaho, Wyoming (Kurtén and Anderson 1980, Anderson 1998), Nebraska, Utah (Neomap 2013), and eastern Nevada (Mead and Mead 1989, Neomap 2013).

Deserts were much more limited in the American Southwest during the last glaciation than they are today (Thompson and Anderson 2000). Cool moist conditions in the Great Basin were reinforced by lake-effect weather associated with large pluvial lakes (Hostetler et al. 1994) and boreal mammals, such as the pika (*Ochotona princeps*) and yellow-bellied marmot (*Marmota flaviventris*), were present at low-elevation sites that are currently desert (Grayson 1987, 2006; Schmitt and Lupo 2012). Presumably, the climatic and ecological conditions present in the Great Basin during the late Pleistocene were more favorable for wolverines moving between the Sierra Nevada and Rocky Mountains than they are currently. Climatic conditions in the American Southwest changed rather abruptly in the early Holocene (ca. 10,000 to 8,000 yBP), however, and became particularly warm and dry in the Great Basin (Grayson 2000).

During the Holocene, desert vegetation replaced the woodlands that characterized the Great Basin during the last glacial maximum (Thompson and Anderson 2000, Anderson et al. 2008), whereas the Sierra Nevada became progressively wetter; tree species such as true firs (*Abies* spp.) and mountain hemlock (*Tsuga mertensiana*) became increasingly common in high-elevation pollen deposits after ca. 6,000 yBP (Anderson 1990) and particularly within the last 3,000 years (Davis et al. 1985), a period also characterized by the growth of mountain glaciers (Bowerman and Clark 2011). Thus, during the Holocene, habitat conditions for the wolverine probably improved in the Sierra Nevada as this area became wetter and snowier. Concurrently, the spread of hot, dry desert conditions throughout the Great Basin would have increased the isolation of wolverine populations in the Sierra Nevada from those in the Rocky Mountains.

Genetic evidence supports the isolation of wolverine populations in the Sierra Nevada from those in the Rocky Mountains and Cascade Range during the Holocene. This is indicated both by the presence of Cali2, which is derived from Cali1 (Fig. 3; Schwartz et al. 2007), and which we did not find elsewhere, as well as the lack of Beringian haplotypes (e.g., A, F, and O) in California. Lastly, nuclear markers (microsatellites) from wolverines in California were divergent from those associated with other North American populations (Schwartz et al. 2007), suggesting that the isolation of California wolverine populations was not limited to matrilines but occurred in all segments of the population. Consequently, we believe that the unique haplotypes we found among historical wolverine populations in the western U.S. arose during 2 successive isolation events. The Cali1 haplotype evolved during the isolation of southern refugial populations in the contiguous U.S. during the last glaciation, whereas Cali2 evolved during the subsequent isolation of wolverine populations in the Sierra Nevada from those in the Rocky Mountains and Cascade Range as present-day climatic conditions developed during the Holocene. Zigouris et al. (2012) posit a similar scenario to explain the occurrence of haplotype Z_25 in Ontario.

Comparative Phylogeography

Available information on the genetic characteristics of historical wolverine populations in the contiguous U.S. is extremely limited but is unlikely to be augmented by the discovery of additional specimens. Because of this paucity of information, comparing phylogeographic patterns of the wolverine with those of other species may help elucidate their evolutionary history (Arbogast and Kenagy 2001). Patterns of glaciation, in particular the isolation of southern North America from Beringia during the last glacial maximum, strongly influenced the phylogeography of many species (reviewed by Shafer et al. 2010). Here, we focus on 2 well-studied North American terrestrial carnivores whose phylogeography has been linked to glacial vicariance: the montane red foxes (*Vulpes vulpes cascadensis*, *V. v. necator*, and *V. v. macroura*) and brown bears (*Ursus arctos*).

In the western mountains of the contiguous U.S., the red fox occupied historical ranges that were largely concordant with that of the wolverine (e.g., Cary 1911, Bailey 1936, Grinnell et al. 1937, Dalquest 1948). Both species occupied the western portion of the southern refugium during the last glaciation in isolation from populations in the northern refugium (Bryant 1987, Neomap 2013). North American red foxes separate into 2 strongly distinct genetic clades: the Holarctic clade found in Alaska, western Canada, and Eurasia, and the Nearctic clade, which occupies montane regions of the western U.S. and portions of southeastern

Canada (see Fig. 1 in Aubry et al. 2009). Red foxes in the Nearctic clade are descended from populations that were isolated in the southern refugium during the last glacial maximum, whereas northern red fox populations are descended from populations that colonized North America from Asia during the last glaciation (Aubry et al. 2009).

A similar pattern occurs in brown bears, whereby those in Alaska and Eurasia form a common northern clade (clade 3a in Davison et al. 2011) that colonized North America from Asia during the last glacial maximum (Davison et al. 2011). As with the montane red foxes and wolverines, brown bears in southern North America represent a distinct clade (clade 4 in Davison et al. 2011) that, interestingly, also occurs in Japan (see Figs. 1 and 3 in Davison et al. 2011). Thus, both montane red foxes and brown bears exhibit phylogeographic patterns that are similar to those of the wolverine, and in all 3 species these patterns can be directly linked to glacial vicariance during the Pleistocene.

MANAGEMENT IMPLICATIONS

Based on dental characteristics, early naturalists believed that wolverines in the Sierra Nevada in California represented a distinct subspecies, the southern wolverine (Grinnell et al. 1937). These were wolverines with Cali1 or Cali2 haplotypes that were restricted to the western montane regions of the contiguous U.S. Whether these wolverines warranted recognition as a distinct subspecies is unknown (see Newby and Wright 1955) but if, as we argue, these wolverines evolved in isolation due to glacial vicariance, southern wolverines may have evolved unique adaptations to the high-elevation montane ecosystems they occupied. Data indicate, however, that the wolverines described by Joseph Grinnell and others as being taxonomically distinct were extirpated by the early 1900s (Aubry et al. 2007) and their matrilines eliminated from North America.

Most modern wolverine populations in North America are closely related; those in the contiguous U.S., whether of local or Canadian origin, are closely related to populations to the north and are unlikely to contain specialized adaptations to southern climates. Thus, for any proposed reintroduction of wolverines in the western contiguous U.S., translocating genetically diverse individuals is likely to be more important than choosing a particular source population. The large contiguous populations in the north are more diverse than those in the south (Fig. 2, Appendix) and would provide an appropriate genetic stock for reintroductions. However, many of these populations occur in relatively flat terrain in tundra or taiga habitat conditions. In montane regions of southern North America, wolverines occupy more heterogeneous habitats and may have learned behaviors that contribute to survival and reproduction; these characteristics may be particularly important during the period immediately following release. The need to consider both genetic diversity and appropriate behavioral repertoires in future reintroductions suggests that the optimal source location for wolverine translocations to California or Colorado may be the Canadian Rocky Mountains, where genetic diversity is relatively high (Fig. 2, Appendix), and environmental conditions are similar to those in the western mountains of the contiguous U.S.

ACKNOWLEDGMENTS

We thank the following individuals for granting us access to historical wolverine specimens in their care: R. Fisher of the National Museum of Natural History, J. Stephenson of the Denver Museum of Nature and Science, and K. Zyskowski of the Yale Peabody Museum of Natural History. R. Callas, R. Garwood, A. Jones, D. Evans Mack, A. Magoun, D. Tyres, B. Waterbury, and B. Zielinski generously provided tissue samples from extant wolverine populations. We also thank the Resource Conservation staff at Mount Revelstoke and Glacier National Parks, British Columbia, Canada. Special thanks to C. Engkjer for laboratory assistance and D. Guscio for generation of the minimum spanning network. Lastly, we thank D. Bingham, D. Grayson, C. Raley, and 2 anonymous reviewers for helpful comments on previous versions of this manuscript.

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Associate Editor: Jeff Bowman.

Appendix 1. Haplotypes associated with recent (1989–2012) wolverine specimens in Alaska, Canada, and the contiguous U.S. Previously published samples are from Wilson et al. (2000), Tomasik and Cook (2005), Cegelski et al. (2006), and Schwartz et al. (2007). Data from Tomasik and Cook (2005) were extracted from their Figure 1. Haplotypes A–I were identified by Wilson et al. (2000), L–O by Cegelski et al. (2006), T_C–T_O by Tomasik and Cook (2005), and Z_24–Z-25 by Zigouris et al. (2012).

	Haplotype																		
Study area	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**L**	**M**	**N**	**O**	**T_C**	**T_D**	**T_J**	**T_N**	**T_O**	**Z_24[a]**	**Z_25[a]**
Wilson et al. (2000)																				
Site1 (West), NWT	7	3			1	1														
Site2 (West), NWT				1					2											
Site3 (East), NWT			8			4	4		4											
Site4 (East), NWT	1						2													
Site5 (East), NWT							2	1												
Tomasik and Cook (2005)[b]																				
Northwestern AK	7				1			8							6					
Northern AK		5			1	3		1												
Seward Peninsula, AK						1														
Kenai, AK						1		9						6		6				
Southern AK	5	1						2						9						
Southeastern AK	4														7		1			
Nunavut	1		4			2	5	3	2						1			1		
Cegelski et al. (2006)																				
Williston Lake, BC	11									6	1	1								
Revelstoke, BC	4							5		4			3							
Grande Cache, AB	5		2			2				8										
MT and WY	74							1	24	2										
Schwartz et al. (2007)																				
Alaska Range, AK	1	2				2		1												
West Central MT	3																			
South Central MT	25																			
Northwestern MT	10																			
Greater Yellowstone	20								2											
Sawtooth Mts., ID	13																			
Zigouris et al. (2012)																				
NWT	2		5				17	1							2				1	
Nunavut	2		8			4	11	2	1											
Saskatchewan	3		1				5	2							4				1	
Manitoba	6																		9	15
Ontario	35																		5	14
Previously unpublished																				
Washington			18																	
Banff/Kananaskis, BC	14							2		8										
Revelstoke/GNP, BC										1			2							
Ontario	4																		1	2
Alaska	11	2				2		1						5	8		1			
Oregon	1																			
Montana	60								5											
Idaho	35																			
Wyoming	25								1											

[a] Haplotypes Z_24 and Z_25, reported by Zigouris et al. (2012), are consistent with haplotypes reported by Chappell et al. (2004). However, Chappell et al. (2004) amplified a shorter region of approximately 200 base pairs (bp) compared to the 360-bp region amplified by Zigouris et al. (2012). Because of ambiguities associated with the shorter region in Chappell et al. (2004), results from that study are not reported here.

[b] Tomasik and Cook (2005) included samples from Wilson et al. (2000) in their populations for Nunavut and the Northwest Territories. The numbers presented here are for samples that were unique to Tomasik and Cook (2005).