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MITOCHONDRIAL PHYLOGEOGRAPHY AND CONSERVATION GENETICS OF WOLVERINE (*GULO GULO*) OF NORTHWESTERN NORTH AMERICA

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Anthropogenic impacts such as habitat conversion and fragmentation, in combination with predator control and fur trapping, are responsible for substantial reductions in the ranges of many carnivores worldwide. The wolverine (*Gulo gulo*) is classified as vulnerable throughout the Holarctic Region by the International Union for Conservation of Nature and Natural Resources, is designated as endangered in eastern Canada, and has been petitioned twice for listing with the United States Fish and Wildlife Service. We examined genetic structure across populations in northwestern North America by using mtDNA sequences of the left domain of control region and the complete cytochrome-*b* gene (*Cytb*). Nucleotide diversity (π) and sequence divergence among haplotypes were low for both markers, whereas haplotype diversity (*h*) was generally high. Genetic divergence (F_{st}) values were significant, and high for control region (0.21), and moderate to high for *Cytb* (0.16). Globally, Eurasian and Scandinavian wolverines were distinguishable from North American. Within North America, the Kenai Peninsula, southeastern Alaska, and Nunavut populations were distinctive. Comparisons with studies based on nuclear markers reveal greater geographic structure in these maternally inherited mitochondrial markers, a finding consistent with male-biased dispersal in wolverines. Conservation plans for these medium-sized carnivores should emphasize maintenance of genetic diversity and recognize that successful dispersal of females between populations may be limited.

Key words: control region, cytochrome *b*, *Gulo gulo*, mitochondrial DNA, phylogeography, wolverine

Habitat loss and human-caused mortality are the most important factors affecting the conservation of carnivores worldwide (Gittleman et al. 2001; Hornocker and Hash 1981). In addition, climate change in the form of global warming is impacting environments, especially those inhabited by northern-latitude carnivores. Naturally low densities for many carnivores, even in areas not impacted by anthropogenic activities, increase the risk that local extirpations will isolate populations. Hence, there is a need to document geographic variation and assess connectivity among populations for effective management of these species and their biomes. Carnivores such as the wolverine (*Gulo gulo*) have been suggested as potential focal species for large-scale conservation monitoring (Carroll et al. 2001).

Historically, the wolverine ranged throughout boreal, mountain, and tundra regions of Eurasia and North America. In Eurasia, current range includes portions of Estonia, Finland, Mongolia, Norway, Russia, and Sweden (International Union for the Conservation of Nature and Natural Resources 2002). In North America, the range once included the vast majority of Alaska and Canada, the northern tier of the conterminous United States, and mountains as far south as the Sierra Nevadas in California, and the Rocky Mountains of northern New Mexico (Hall 1981). As a result of habitat loss and human-caused mortality, the current range in North America has been reduced to Alaska, northern and western Canada, and limited areas of Idaho, Montana, Washington, and Wyoming (Banci 1994). The range of the wolverine has also contracted in Europe and Asia (International Union for Conservation of Nature and Natural Resources 2002).

The International Union for Conservation of Nature and Natural Resources (www.redlist.org) classifies the wolverine as vulnerable throughout its Holarctic range. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) classifies the wolverine east of Hudson Bay as endangered (COSEWIC 2003). The wolverine has been petitioned twice for listing under the federal endangered species act in the conterminous United States. The most recent petition was denied citing lack of information on distribution, habitat requirements, and threats (United States Fish and Wildlife Service 2003). Alaska and Montana remain the only states where wolverines are legally

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harvested, but little information exists on density in Montana, and the wolverine may be declining in parts of its range in Alaska (www.wolverinefoundation.org).

The wolverine's affinity for remote wilderness and rugged terrain, low densities, large home range sizes, and sensitivity to human disturbance all contribute to the challenge of managing and conserving this solitary and secretive species (Ruggiero et al. 1994). A general characteristic of areas occupied by wolverines is remoteness from human developments (Banci 1994). Wolverines have low reproductive potential and are more similar ecologically to larger carnivores (Weaver et al. 1996) than to species of similar size. Life history characteristics of the wolverine result in low population resiliency (Banci and Proulx 1999; Weaver et al. 1996). Individual home ranges are relatively large and vary from less than 100 km^2 to greater than 1,500 km^2 in Alaska, the Yukon, Montana, and Idaho (Banci 1987; Copeland 1996; Gardner 1985; Magoun 1985). Males have larger home ranges than females (Copeland 1996; Hornocker and Hash 1981).

Despite the wolverine's capacity for long-range dispersal, studies investigating the phylogeography and conservation genetics of wolverines have found varying levels of geographic partitioning. Occasionally different perspectives have been developed based on mitochondrial and nuclear genomes (Walker et al. 2001; Wilson et al. 2000). The majority of genetic studies on the wolverine have been based on markers from the nuclear genome (Cegelski et al. 2003; Kyle and Strobeck 2001, 2002; Walker et al. 2001; Wilson et al. 2000), and these covered a greater geographic scope than previous mitochondrial-based studies. Nuclear studies revealed moderate to high levels of population differentiation (Kyle and Strobeck 2001, 2002; Wilson et al. 2000). These studies found that northern North American wolverine populations experienced higher levels of gene flow and less genetic structure than more southerly populations. These southern populations had higher levels of genetic structuring, likely associated with more limited gene flow (Kyle and Strobeck 2001, 2002). Published mtDNA studies are limited in geographic scope; one focused on Scandinavia (Walker et al. 2001), and the other on 5 populations in northern Canada (Wilson et al. 2000).

We studied the complete cytochrome-*b* gene (*Cytb*) and the left domain of the control region to provide a female-mediated perspective on geographic structure in North American wolverine. There are limitations when considering mtDNA evidence alone (Ballard and Whitlock 2004). Initial analysis of a spatially extensive *Cytb* data set uncovered relatively low variation and divergence. The control-region data set then was developed for a larger number of individuals and additional populations.

The study area encompassed a considerable portion of the wolverine's range in North America and also included limited samples from Eurasia. North American populations were primarily from the northwestern region of the continent, which is a naturally heterogeneous landscape comprised of a diversity of habitats such as taiga, tundra, temperate rain forests, and large glaciated expanses. This high-latitude area and associated biota were intensely impacted during the Pleistocene glacial cycles, including the most recent glacial maximum 15,000–18,000 years ago (Hewitt 1996; Pielou 1991) when portions of the Cordilleran and Laurentide ice sheets coalesced east of the coastal mountains. During full glacial advances a Beringian glacial refugium connected Asia and North America, with the rising of the Bering Strait separating the continents 10,000–12,000 years ago (Hoffmann 1981, 1984; Hopkins 1967, 1982; Hultén 1937; Macpherson 1965; Pielou 1991). These climatic events likely influenced genetic diversity in modern wolverines.

Populations of particular interest include those on the Kenai Peninsula and from southeastern Alaska. The Kenai Peninsula is isolated as a result of a relatively narrow connection to south-central Alaska, and this population was described as a distinct subspecies (Matschie 1918). Southeastern Alaska has been recognized as a unique biogeographical province by some authors (Klein 1965; Swarth 1936) and is isolated from the remainder of North America (MacDonald and Cook 1996). These peripheral populations may contain genetic signatures of physiographic isolation, but neither has been included in previous molecular studies.

Although mammals are generally regarded as well understood taxonomically, much of this framework has not been tested with molecular approaches and should be reviewed (Engstrom et al. 1994; Nagorsen et al. 2000), particularly for cases such as the wolverine, where taxonomy has been dynamic for both specific and subspecific designations. Wolverines from Eurasia and North America were considered separate species (*G. gulo* and *G. luscus*) by some authors (Cowan 1930; Hall 1981; Miller 1912; but see Bryant 1987). Others have recognized Eurasian and North American populations as distinct subspecies (Kurtén and Rausch 1959). Within North America, Hall (1981) listed 4 subspecies, *Gulo luscus katschemakensis* on the Kenai Peninsula of Alaska, *G. l. vancouverensis* on Vancouver Island, British Columbia, Canada, *G. l. luteus* from western North America, and *G. l. luscus* from the Rocky Mountains eastward across higher latitudes. The Vancouver Island wolverine may have been extirpated (COSEWIC 2003). Currently, the 2 most common taxonomic views either split the wolverine into 2 subspecies with *G. gulo gulo* in Eurasia and *G. gulo luscus* in North America, or recognize *G. gulo* as a single Holarctic taxon.

Specifically, this investigation compares mitochondrial and nuclear perspectives on genetic structure across several high-latitude populations of wolverine, explores the effects of Pleistocene climatic changes on historical biogeography, tests if suspected isolated or peripheral populations are distinctive, and investigates whether phylogeographic patterns in this large mustelid are consistent with taxonomic hypotheses.

Materials and Methods

Samples.—Samples were primarily frozen or ethanol-preserved tissues, and 6 samples were from museum study skins. Voucher specimens are deposited at the University of Alaska Museum or the Museum of Southwestern Biology and were salvage specimens obtained largely from hunters, trappers, and natural resource agencies (Appendix I). Samples of this relatively uncommon carnivore are in short supply across much of its range. Many of the samples that do exist have poor location information. The limited availability and accessi-

bility of good-quality samples prohibited our use of equal or larger sample sizes, or inclusion of samples from a greater portion of the wolverine's range. The sampling scheme was designed to cover the greatest geographic area possible given sample availability, and included 2 geographically isolated populations. Sample accessibility was particularly limited for the southern reaches of the wolverine's range.

Markers.—The mitochondrial genome is phylogenetically informative as a result of maternal inheritance, lack of recombination, and relatively high variability (Hartl and Clark 1997). The hypervariable left domain of the mtDNA control region is commonly used for intraspecific studies given its relatively high mutation rate, and is particularly useful for detecting genetic variation within and among populations of mammals (Avise 1994; Taberlet 1996; Waits et al. 1998). This region is thought to evolve more rapidly than the protein-coding *Cytb* (Avise 2000). Control-region sequences were used in previous investigations that included mitochondrial markers (Walker 2001; Wilson et al. 2000). *Cytb* has been used extensively in phylogeographic studies of other mammals (Irwin et al. 1991; Ledje and Arnason 1996; Lucid and Cook 2004). Populations were represented by 6–47 individuals for control region (Table 1; excluding populations from the Seward Peninsula, Scandinavia, and Eurasia) and 5–7 individuals for *Cytb* (Tomasik 2003).

Sequences.—Genomic DNA was isolated from tissue samples by using either a Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, California) or a modified NaCl extraction protocol (Fleming and Cook 2002) with the 2nd desalting wash omitted. Sequencing generally followed protocols outlined in Fleming and Cook (2002), except products were analyzed on an Applied Biosystems 3100 Genetic Analyzer (Applied Biosystems, Inc., Foster City, California). Sequences were aligned by eye by using Sequence Navigator (Applied Biosystems) and compared to reference sequences.

The left domain of control region was sequenced by using the primers L15926 and H16498 (Shields and Kocher 1991; Taberlet 1996). These primers produced reliable sequences of 365–367 base pairs (bp) for both DNA strands including 28 bp of the gene coding for t-RNA^{thr}, 66 bp of the gene coding for t-RNA^{pro}, and 270–272 bp of the left domain of the control region (these 3 segments are hereafter referred to collectively as ''control region''). Total sample size was increased to 159 individuals by using reference sequences obtained from GenBank, including 8 individuals from Scandinavia (GenBank AF245496—Walker et al. 2001), and 43 individuals from Northwest Territories and Nunavut, Canada (GenBank AF210090–AF210132—Wilson et al. 2000). See Wilson et al. (2000) for more detailed location information. Many reference haplotypes were identical to wolverine samples we sequenced. *Cytb* was sequenced by using the primers MVZ04, 05, 16, 14, and 23 (Smith and Patton 1993) and Marten 37 (Demboski et al. 1999). These primers produced reliable sequences of 1,140 bp for both DNA strands of all samples ($n = 27$). Reference sequences obtained from GenBank represented Scandinavia (GenBank X94921—Ledje and Arnason 1996) and Sakhalin Island (GenBank AB051245—Hosada et al. 2000) and increased the total *Cytb* data set to 29. These reference haplotypes were identical to haplotypes that we sequenced.

Analyses.—The software package Arlequin 2.000 (Schneider et al. 2000) was applied to calculate measures of genetic diversity and subdivision including nucleotide diversity (π), haplotype diversity (h), corrected average pairwise differences, genetic divergence (F_{st}), number of female migrants per generation (N_m), and an analysis of molecular variance (AMOVA). The single individual from the Seward Peninsula and the monotypic Scandinavian population were excluded from those calculations.

Table 1.—Nucleotide diversity (π), haplotype diversity (h), number of samples (n), and number of haplotypes for each population (control region).

	n	No. haplotypes	π (%) Mean	π (%) SE	h Mean	h SE
Eurasia	5	3				
Kenai Peninsula	22	4	0.003956	0.002789	0.7143	0.0480
Northern Alaska	10	4	0.003535	0.002724	0.7111	0.1175
Northwestern Alaska	22	4	0.005102	0.003383	0.7229	0.0416
Northwest Territories	15	6	0.003495	0.002602	0.7619	0.0961
Nunavut	47	8	0.002730	0.002078	0.8205	0.0266
Scandinavia	8	1				
Seward Peninsula	1	1				
Southeastern Alaska	12	3	0.004691	0.003305	0.5909	0.1079
Southern Alaska	17	4	0.002985	0.002304	0.6544	0.0891
Total	159	17				

Nucleotide diversity (π) is the probability that a sample of a particular nucleotide site drawn from 2 individuals will differ (Hartl and Clark 1997), and is a weighted sequence divergence between individuals in a population, regardless of the number of different haplotypes (Avise 2000). Haplotype diversity (h) is the probability that 2 haplotypes drawn from a population will differ (Hartl and Clark 1997), and condenses information on the numbers and frequencies of different alleles at a locus, regardless of their evolutionary relationships (Avise 2000). These 2 measures of diversity were compared to draw inferences on demographic history (Avise 2000).

Corrected average pairwise differences are the average percentage of nucleotide sites for which 2 populations are different, and F_{st} values are a measure of population differentiation. AMOVA was used to examine partitioning of genetic variation among and within populations (Excoffier et al. 1992). North American populations were tested for genetic subdivision by calculating pairwise F_{st} and N_m values for control-region sequences.

The number of female migrants per generation (N_m) has an inverse relationship with F_{st}, and estimates the effective number of female migrants between populations per generation. N_m values < 1 indicate that the homogenizing influences of gene flow have not overridden the diversifying effects of genetic drift (Avise 2000; Birky et al. 1983). The mathematical model used to calculate N_m values makes assumptions that may be violated by real populations. Hence, quantitative information regarding dispersal obtained from gene frequency data may have limited applications (Whitlock and McCauley 1999). F_{st} represents the primary indicator of population structure in the current study.

Isolation by distance analysis for control region used Mantel tests (Mantel 1967; Sokal and Rohlf 1995) conducted with MANTEL V2.0 (Liedloff 1999) to estimate the association (1,000 iterations) between the average geographic distance matrix for the 7 North American populations, and their population pairwise F_{st} values and corrected average pairwise differences matrices.

Evolutionary relationships were analyzed with unrooted neighbor-joining trees generated with PAUP* (V4.0b8—Swofford 2000) based on the Jukes–Cantor distances (Jukes and Cantor 1969) because sequence divergence was low (Nei and Kumar 2000). Support for relationships was estimated with 1,000 bootstrap replicates. Minimum spanning networks were constructed to assess relatedness of haplotypes. Population frequencies were included in the minimum spanning networks and illustrated where unique and rare haplotypes occurred.

Demographic history of North American populations was inferred by using FLUCTUATE V1.3 (Kuhner et al. 1998) for control-region

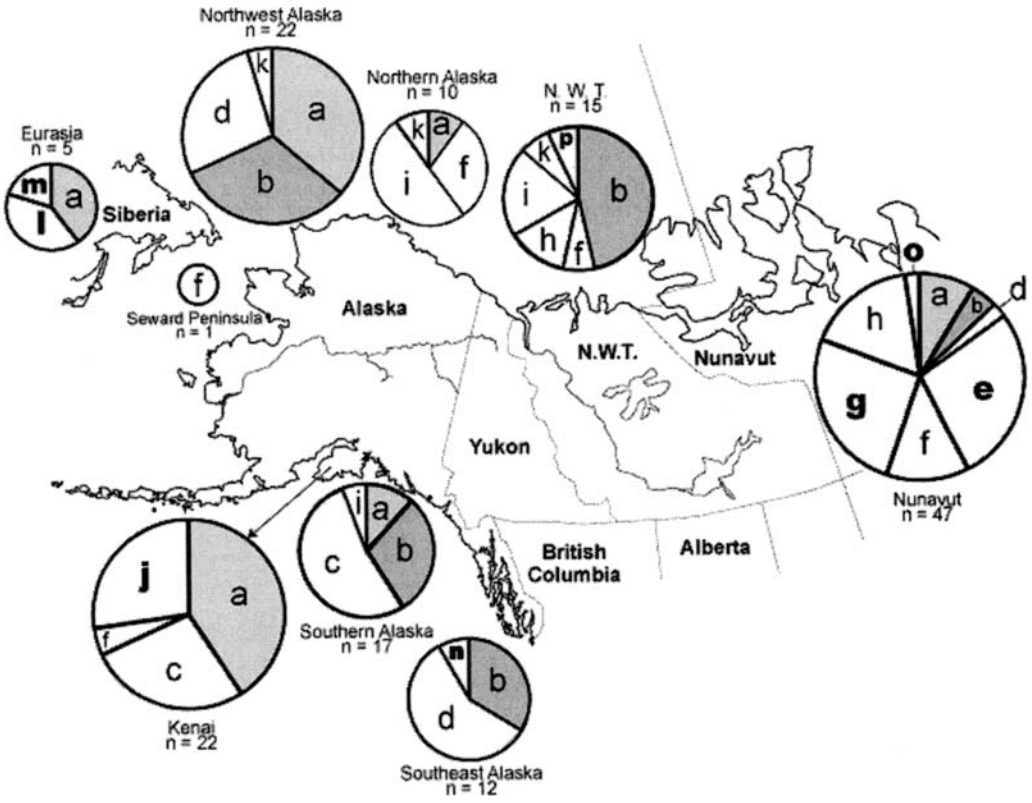

FIG. 1.—Geographic distribution of control-region haplotypes of *Gulo gulo* among sampling locales. Pie diagrams indicate frequencies of haplotypes. Shading indicates most common and widespread haplotypes (haplotypes a and b). Bold indicates haplotypes unique to a single population. The control region haplotype labels in this work correspond to those in Wilson et al. (2000) as follows: a = H, b = A, e = G, f = F, g = C, h = I, i = B, k = E, and p = D.

sequences. This program tests the significance of population expansion or decline using likelihood estimation by the Metropolis–Hasting sampling algorithm (see Kuhner et al. 1998; violating the assumption of no migration). The method estimates the goodness of fit of a model of exponential growth or decline, and generates maximum-likelihood estimates of the growth parameter (g) and its standard deviation. Positive values of g indicate demographic growth, negative values indicate decline. Conservative confidence limits of 99% were used to test significance of difference from 0.

Fu's F_s test of neutrality (Fu 1997) was performed on the control-region sequences by using 1,000 replicates in ARLEQUIN (Schneider et al. 2000). F_s values tend to be negative when there is an excess of recent mutations (therefore an excess of rare alleles). Large negative values of F_s are evidence against the neutrality of mutations and may reflect population demographic expansion (Fu 1997; Schneider et al. 2000). To be significant, probability values should be below 0.02, rather than 0.05 (Fu 1997; Schneider et al. 2000).

RESULTS

Control region.—Control-region sequences were composed of 28% adenine, 30% thymine, 28% cytosine, and 14% guanine. Seventeen haplotypes resulted from 17 polymorphic sites (11 transitions, 2 transversions, and 4 insertion–deletions). Nine of the 17 haplotypes were unique to 1 sampling locale (Fig. 1).

Haplotype diversity values ranged from 0.59 to 0.82, and nucleotide diversity values ranged from 0.0027 to 0.0051 (Table 1). The high number of haplotypes relative to sample size for some populations ($n = 5$ with 3 haplotypes in Eurasia, $n = 15$ with 6 haplotypes in the Northwest Territories, and $n = 10$ in northern Alaska with 4 haplotypes) implies that all haplotype diversity was not captured. Overall F_{st} value was 0.20579 (1,023 permutations; total $d.f. = 149$, $P = 0.000 \pm 0.00$). AMOVA revealed 21% of variation partitioned among populations and 79% within populations.

Corrected average pairwise difference values ranged from 0.079 to 0.349 (Tomasik 2003), with 7 values above 0.25 and the 4 highest values associated with southeastern Alaska. Population pairwise F_{st} values ranged from 0.100 to 0.352 (Table 2), with 9 values above 0.25, and the 4 highest F_{st} values associated with southeastern Alaska. N_m values ranged from 0.921 to 4.227 (Table 2).

Isolation by distance was not supported by Mantel tests ($P = 0.05$; critical value $= -1.645$) using the average geographic distance versus the population pairwise F_{st} values ($g = -0.382$; $Z = 9768.84$; $r = -0.098$), or corrected average pairwise differences ($g = 0.003$; $Z = 9364.41$; $r = -0.001$). Isolation by distance remained unsupported when southeastern Alaska and the Kenai Peninsula were removed from analysis (population pairwise F_{st} values; $g = -0.565$; $Z = 3983.02$; $r = -0.223$, corrected average pairwise differences; $g = -0.895$; $Z = 2659.77$; $r = -0.500$).

Estimates of exponential growth rates significantly exceeded 0 in 2 populations ($g = 644$ and 99% confidence interval [CI]

TABLE 2.—Population pairwise comparisons of number of female migrants per generation (N_m; upper) and genetic divergence (F_{st}; lower) for populations of *Gulo gulo* based on control-region sequences. Asterisks indicate F_{st} values insignificant at the 0.05 level.[a]

Population	Eurasia	Kenai Peninsula	Southeastern Alaska	Southern Alaska	Northern Alaska	Northwestern Alaska	Northwest Territories	Nunavut
Eurasia		4.22720	**1.01819**	**1.44494**	1.76471	3.70354	1.73719	2.66190
Kenai Peninsula	0.10577*		**0.97375**	2.80458	**1.53295**	2.70920	**1.41355**	2.06443
Southeastern Alaska	**0.32934**	**0.33927**		**1.12847**	**0.92132**	4.49646	2.06137	**1.64183**
Southern Alaska	**0.25708**	0.15131	**0.30704**		**1.21688**	1.98669	2.45912	**1.64183**
Northern Alaska	0.22078	**0.24595**	**0.35179**	**0.29123**		**1.48801**	2.72921	2.19319
Northwestern Alaska	0.11895*	0.15580	0.10007*	0.20107	**0.25151**		3.46774	2.23436
Northwest Territories	0.22349	**0.26129**	0.19521	0.16897	0.15484	0.12602		2.58008
Nunavut	0.15813	0.19498	**0.25122**	0.23345	0.18565	0.18286	0.16233	

[a] Highest 10 F_{st} values and lowest 10 N_m values are indicated in bold.

325–963 for the Northwest Territories, and $g = 1{,}009$ and 99% CI 528–1,490 for Nunavut). No significant F_s values were detected (Tomasik 2003), indicating a neutral model of evolution (Fu 1997; Schneider et al. 2000).

Cytochrome b.—Twenty-nine complete sequences had base compositions typical of genuine mammalian mitochondria (28% adenine, 27% thymine, 30% cytosine, and 15% guanine), indicating that a nuclear pseudogene was not amplified. Sequences also exhibited expected codon biases reported for other mammalian taxa (Irwin et al. 1991). Five of the 7 amino acid changes were at sites described as highly variable in mammals (Irwin et al. 1991). One of the remaining amino acid changes occurred in a haplotype (c) unique to the southeastern Alaska population, and the other in a haplotype (f) unique to the Nunavut population. Ten haplotypes resulted from nucleotide substitutions at 15 (1.3%) of 1,140 sites. All 15 nucleotide substitutions were transitions, with substitutions at 6 first, 1 second, and 8 third positions. Eight of the 10 haplotypes were unique to 1 sampling locale (Tomasik 2003). As a result of the relatively small sample sizes used for *Cytb,* inferences based on the distribution of unique alleles are limited.

For *Cytb,* haplotype diversity values ranged from 0.29 to 0.80, and nucleotide diversity values ranged from 0.00025 to 0.00123 (Tomasik 2003). The overall F_{st} value was 0.15802 (1,023 permutations; total $d.f. = 28$, $P = 0.01075 \pm 0.0030$), indicating great genetic differentiation (Hartl and Clark 1997; Wright 1978). AMOVA revealed that approximately 16% of genetic variation was partitioned among populations and 84% within populations. Frequencies of common and unique haplotypes varied across populations for both markers (Tomasik 2003).

Trees and networks.—A minimum spanning network for control-region sequences (Fig. 2) indicated that North American haplotypes were minimally diverged. A single haplotype (a) was shared between Eurasia and North America. One to 5 mutational steps separated Eurasian haplotypes, whereas all North American haplotypes were separated by a single mutational step from other North American haplotypes. Unique haplotypes were found primarily in the Eurasian, Nunavut, southeastern Alaska, and Kenai Peninsula populations. A minimum spanning network for *Cytb* sequences revealed similar geographic patterns (Tomasik 2003).

A neighbor-joining tree of control-region haplotypes (Fig. 3) indicated strong bootstrap support for a monophyletic clade of Eurasian haplotypes. Both *Cytb* and control-region neighbor-joining trees reflected a star phylogeny for North American haplotypes.

DISCUSSION

Genetic structure.—Overall F_{st} values reflected significant differentiation between populations (Hartl and Clark 1997; Wright 1978) and contrast with nuclear perspectives of relatively homogenous populations of wolverines in the Northwest. Unique haplotypes were prevalent in Kenai, Nunavut, and southeastern Alaska populations. High to moderate gene flow has been documented with nuclear DNA studies of wolverine populations in northwestern North America (Kyle and Strobeck 2001, 2002; Wilson et al. 2000). Given the higher levels of population differentiation exhibited in this mitochondrial study, gene flow appears to be predominantly male mediated, a finding likely associated with increased female philopatry to natal territory, less long-distance dispersal, and lower reproductive success subsequent to long-distance dispersal by females. Lower population differentiation exhibited with nuclear microsatellites may also result from their faster rate of mutation and increased homoplasy. Lack of observed isolation by distance further suggests that geographic barriers may have played a role in differentiation of some populations (Britten et al. 1995; Hartl and Clark 1997; Wright 1943; but see Ballard and Whitlock 2004).

Gene flow among wolverine populations is primarily accomplished by long-range dispersal between low-density populations, which requires large areas of continuous habitat and extensive travel corridors. Human settlement and high-traffic roadways may function as more effective barriers to dispersal than natural features such as rivers and mountains (Banci 1987; Hornocker and Hash 1981). Although wolverines are highly vagile carnivores, we uncovered genetic variation that was spatially partitioned. Diversity among populations should be reduced when dispersal capability is high and barriers do not impede gene flow (Mills and Allendorf 1996; Wright 1969). Long distance dispersal has been observed for both male and female wolverines (Gardner 1985; Gardner et al. 1986; Magoun 1985). Juvenile wolverines can disperse great distances before

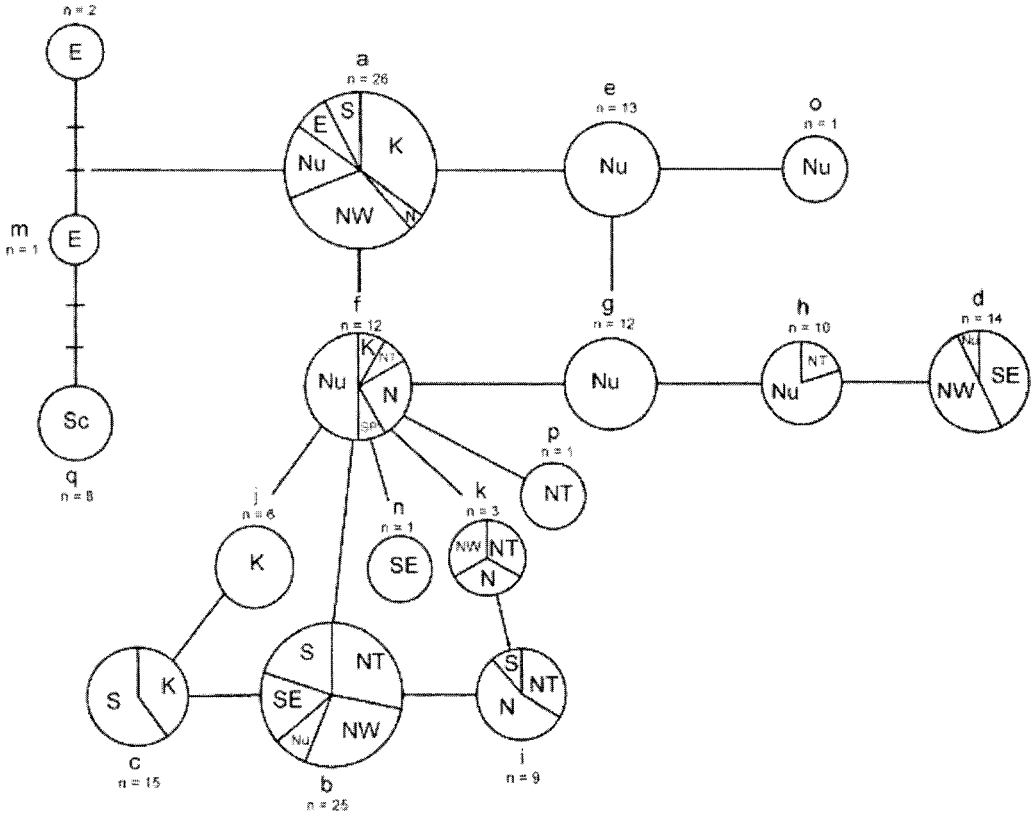

Fig. 2.—Minimum spanning network for 17 control-region haplotypes of *Gulo gulo*. Haplotype and population labels are provided. Bars indicate the minimum numbers of inferred mutational steps along a pathway. Pie diagrams indicate frequencies of populations within haplotypes. E = Eurasia, K = Kenai Peninsula, N = northern Alaska (AK), NT = Northwest Territories, Nu = Nunavut, NW = northwestern AK, S = southern AK, Sc = Scandinavia, SE = southeastern AK, SP = Seward Peninsula.

establishing their own territories. One male moved 378 km over 8 months from south-central Alaska to the Yukon (Gardner et al. 1986); however, dispersal and establishment of territories of juvenile wolverines apparently differs between sexes. Long-distance dispersal and successful reproduction is male biased (Flagstad et al. 2004), with juvenile females frequently establishing territories adjacent to or overlapping their natal territory (Banci 1987; Gardner 1985; Magoun 1985; Persson 2003; Vangen et al. 2001). Hence, maternally inherited markers should provide a distinctive signature of genetic structure.

Historical biogeography.—Events such as Pleistocene glacial cycles and sea level fluctuations result in complex scenarios regarding timing, plurality, and specifics of vicariance and dispersal events. The fossil record indicates a long and approximately contemporaneous history of modern *Gulo* on both continents, although the North American fossils may be older (Kurtén and Anderson 1980). Fossils of *G. gulo* occurred in deposits of Irvingtonian age or later in North America (Kurtén and Anderson 1980). Remains of *G. gulo* of possible Sangamonian to Wisconsin age have been recovered in the Yukon and had minor differences in dental morphology (see Bryant 1987 for specifics). Based on fossil evidence, *G. gulo* was thought to exist in both Beringia and refugia south of the ice sheets during the Wisconsin glaciation (Bryant 1987). Modern populations potentially may be descended from these distinctive refugia, or other hypothesized refugia such as the High Arctic (Rand 1954), or along the North Pacific Coast (Rogers et al. 1991).

Given this history at high latitudes, we explored the magnitude of evolutionary divergence associated with the Bering Strait and whether contemporary populations reflect persistence in multiple glacial refugia. Reciprocal monophyly has not been reached between Eurasia and North America populations. Relatively low evolutionary divergence between Eurasian and North American haplotypes does not support the hypothesis that the Bering Strait divided 2 distinct species of wolverine. It is possible that occasional dispersal across the frozen Bering Strait in winter occurs. Matrilines within North America generally formed a monophyletic group nested within the broader matrilineal variation of Eurasia. Greater genetic variation and divergence in Eurasia is consistent with colonization of North America from Eurasia by modern wolverines, but more extensive geographic sampling in Eurasia is needed to test this hypothesis.

For North American wolverines, the star phylogeny, low sequence divergence, lack of distinct phylogroups, and generally high haplotype and low nucleotide diversity for both markers are all consistent with rapid population growth from an ancestral population with relatively small effective population size (N_e) (Avise 2000; Grant and Bowen 1998; Slatkin and Hudson 1991). Although the fossil record suggests that modern *Gulo* persisted south of the ice sheets in North America, there is

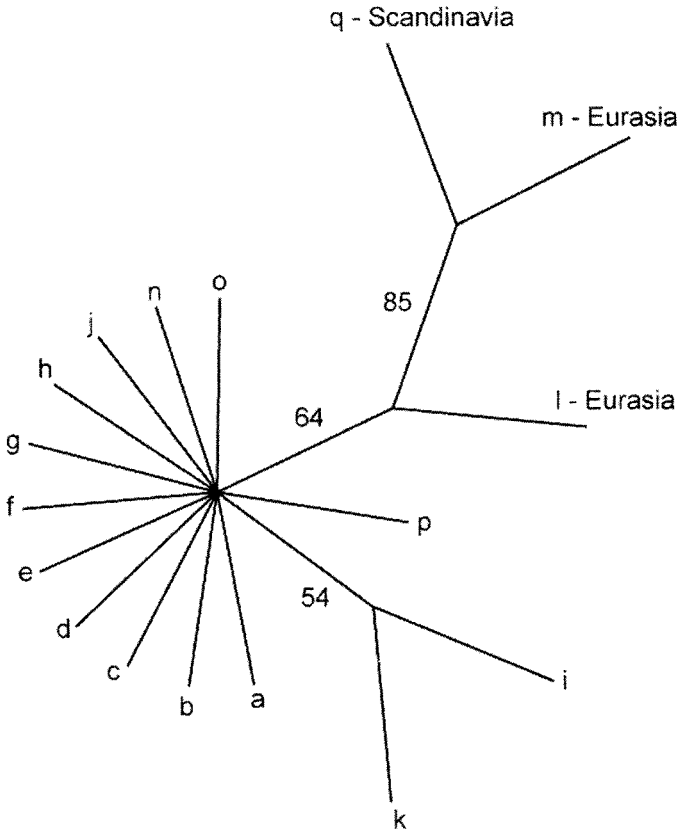

FIG. 3.—Neighbor-joining tree based on Jukes–Cantor distances calculated for control-region haplotypes of *Gulo gulo*. Haplotype labels and Eurasian populations are indicated (remaining haplotype label and population associations as in Fig. 2). Numbers represent bootstrap values > 50 based on 1,000 iterations.

no genetic signature of more than a single source for North American wolverines. Instead, the likely origin of extant North American wolverines is Beringia, with a rapid expansion south and east after deglaciation. Our inability to sample southern populations, most of which have been extirpated, precluded a rigorous assessment of this finding. A single control-region haplotype not found in this study or that of Wilson et al. (2000) was revealed with samples from the wolverine's southerly range in Idaho, Montana, and Wyoming (Cegelski 2001). A Beringian origin for a few other North American boreal mammals also has been suggested by molecular studies, including moose (*Alces alces*—Hundertmark et al. 2001) and tundra voles (*Microtus oeconomus*—Galbreath and Cook 2004). Rausch (1994) hypothesized a similar pattern for bison (*Bison*), wolves (*Canis lupus*), brown bears (*Ursus arctos*), and many coevolved parasites of transberingial host species. In contrast, marten (*Martes americana*—Small et al. 2003; Stone and Cook 2002) and black bear (*Ursus americanus*—Stone and Cook 2000; Wooding and Ward 1997) apparently diversified in southern refugia in North America during Pleistocene glacial cycles.

Isolated or peripheral populations.—Peripheral populations generally are isolated to varying degrees and may experience different selective pressures that enhance genetic divergence (Lesica and Allendorf 1995; Mayr 1970; Safriel et al. 1994).

Southeastern Alaska is relatively isolated, and has been considered a distinct biogeographical province (Klein 1965; Swarth 1936), although the wolverine's ability to traverse rugged terrain may allow for genetic exchange with populations in British Columbia. The southeastern Alaska population is distinctive, as evidenced by high F_{st} values and pairwise distances, and low N_m values. Four of the 5 individuals sequenced for *Cytb* had haplotypes unique to this population (Tomasik 2003); however, limited sample size and lack of samples from adjacent British Columbia result in an incomplete view of genetic diversity. Additional research is needed to explore potential connectivity of wolverine populations across the coastal mountains, particularly given the high rate of habitat modification occurring in this region.

The Nunavut population also was distinctive, but variation is consistent with a recent and rapidly expanded population. The Nunavut population was 1 of 2 populations where estimates of the exponential growth rates significantly exceeded 0 (program FLUCTUATE V1.3—Kuhner et al. 1998). There were unique haplotypes for both markers, and rapid population growth can enhance the retention of new mutations (Avise et al. 1984).

In contrast, on the Kenai Peninsula, common and widespread haplotypes dominated, except for a single unique haplotype (control region; 6 of 22 individuals). The low haplotype and nucleotide diversity values (*Cytb*) on the Kenai (Tomasik 2003) may reflect lineage sorting, or a recent bottleneck, founder event, or selective sweep relative to other North American populations. The occurrence of common and widespread haplotypes on the Kenai Peninsula is not consistent with subspecies status for this population.

Conclusions.—The emerging mitochondrial view suggests low to modest levels of contemporary female-mediated gene flow between populations, but high levels of historic connectivity (Avise 2000). Matrilineal structure identified for wolverines is similar to that of gray wolves (*C. lupus*). Wolves show high population variability and several widely distributed and common mtDNA haplotypes distributed with frequencies differing between regions of North America, and greater mtDNA subdivision evident in Eurasian gray wolves (Wayne 1996; Wayne et al. 1992). The situation with wolverine contrasts with the high levels of genetic differentiation found in control-region sequences among North American brown bears (*U. arctos*—Waits et al. 1998).

Southeastern Alaska, Nunavut, and perhaps Kenai Peninsula populations harbor a disproportionate amount of the North American mitochondrial diversity. Wolverines may be more vulnerable to environmental stochastisity and anthropogenic disturbances because of limited long-distance dispersal by females, a consideration particularly relevant to those relatively isolated portions of the wolverine's range such as southeastern Alaska. Given our broad geographic coverage, additional finer-scale studies are needed for management and conservation purposes.

Human actions likely will be a controlling factor in the success and persistence of wolverine populations. The cumu-

lative effects of habitat alteration, timber harvest, increased road building, and traffic are not fully understood. Increased road access usually results in greater hunting and trapping pressure, which is a primary mortality factor for wolverines (Banci 1987; Hornocker and Hash 1981; Inman et al. 2002; Magoun 1985). This range contraction has occurred concurrently with human settlement and development. As a result of natural resource extraction, associated road building, and other human activities, wolverines on the Kenai Peninsula and southeastern Alaska may necessitate particular conservation emphasis.

Unique haplotypes are concentrated in areas of physiographic isolation such as the Kenai Peninsula and southeastern Alaska, as well as Nunavut. Appropriate management plans and conservation strategies should include provisions for conserving connectivity among populations, and conserving remaining genetic diversity of this species.

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APPENDIX I

Specimens examined. Population, marker sequenced, and individual Alaska Frozen Tissue Collection (AF) numbers or GenBank (*) numbers for individual *Gulo gulo*. Tissues with AF numbers are deposited at the University of Alaska, Fairbanks.

Population	Control region	Cytochrome *b*	Individual identification number
Eurasia		X	*AB051245, *X94921
Eurasia	X		*AF245496–245498, AF52360, AF52361
Eurasia	X	X	AF52357, AF52358, AF52388
Kenai Peninsula	X		AF55409, AF56832, AF56905, AF56910–56917, AF56919, AF56922–56924
Kenai Peninsula	X	X	AF56901, AF56902, AF56904, AF56906–56909
Northern Alaska	X		AF4033, AF4036, AF4042, AF4048, AF17989, AF24882, AF27134, AF27137, AF34266
Northern Alaska	X	X	AF354
Northwestern Alaska	X	X	AF45909, AF45948, AF45974
Northwestern Alaska	X		AF32004, AF45911, AF45914, AF45915, AF45917, AF45919, AF45921, AF45944, AF45950, AF45953, AF45955, AF45961, AF45966, AF45967, AF45970, AF45986–45988, AF47755
Northwestern Alaska	X		AF32004
Nunavut	X		*AF210105–210132, AF55314–55316, AF55322, AF55324, AF55393, AF55395, AF55397–55401, AF55403, AF55408
Nunavut	X	X	AF55320, AF55325, AF55394, AF55396, AF55402
Nunavut		X	AF55323
Northwest Territories	X		*AF210090–210104
Seward Peninsula	X		AF45482
Southeastern Alaska	X	X	AF15901, AF51817, AF51819, AF51874, AF51875
Southeastern Alaska	X		AF15902, AF16071, AF20010, AF51818, AF51820–51822
Southern Alaska	X		AF5208, AF11783, AF11784, AF11801, AF24800–24802, AF27577, AF30412, AF30422, AF39937, AF39938, AF39944, AF39946, AF39949, AF39951
Southern Alaska	X	X	AF1355