

CONNECTIVITY OF PERIPHERAL AND CORE POPULATIONS OF NORTH AMERICAN WOLVERINES

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Wolverines are highly vagile carnivores, with long-distance dispersal documented for males and females. Consequently, the species was thought to represent 1 large, panmictic unit in North America. In this study, we examined the connectivity of populations on the edge of their historical distribution to the larger, continuous, northern distribution of wolverines. Twenty-two regions were sampled, and 671 individuals were genotyped at 12 microsatellite loci. Our results confirmed that high levels of gene flow do occur among all the northern wolverine populations sampled. We also observed progressively increasing genetic structure at the periphery of their southern and eastern distributions, suggesting that these populations may have been partially fragmented from what was once a panmictic unit. Peripheral populations may be more susceptible to extirpation and, therefore, may be the most appropriate targets for concerted conservation efforts to prevent the elimination of wolverines from yet more of their historical range.

Key words: genetic structure, *Gulo gulo*, mustelid, population fragmentation, wolverine

Wolverines are an enigmatic and rarely observed mustelid, inhabiting the tundra, taiga, and forest zones of portions of North America and Eurasia (Wilson 1982). In North America, the abundance and distribution of the species have declined since the advent of European settlement, most notably in eastern Canada, Vancouver Island, southern Rocky Mountains, and California (Wilson 1982; V. A. Banci, in litt.). Historical persecution (trapping and poisoning) and displacement from native habitat may be responsible for these declines. As a result, wolverines have been granted special conservation status across much of their current range. In Canada, the eastern population is listed as endangered (although potentially extirpated), whereas the western population is granted special concern status (COSEWIC 2001). In the contiguous United States, petitions have been put forth to

list the wolverine as endangered; to date these petitions have been unsuccessful due to the lack of adequate information supporting this designation (<http://www.wolverinefoundation.org>).

Wolverines are highly vagile creatures, with males and females able to disperse vast distances in a relatively short period of time (Copeland 1996; Gardner 1985; Magoun 1985; Vangen et al. 2001). This characteristic has prompted the theory that wolverines may exist as a single panmictic unit in North America. In northern North America, this is true (Kyle and Strobeck 2001) because high levels of gene flow were observed among populations from western Alaska to central Nunavut. In contrast, relatively high levels of genetic structure were found between southern and northern populations (Kyle and Strobeck 2001). It was proposed that increased anthropogenic pressures (e.g., fur harvest, habitat destruction,

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heavily traveled transportation corridors) on the southern populations could be reducing the level of gene flow between populations of this species.

A study of Scandinavian wolverines from northern and southern Norway and Sweden by Walker et al. (2001) reported findings similar to those found for southern North American populations (Kyle and Strobeck 2001). Using microsatellites, Walker et al. (2001) found significant levels of genetic structuring between wolverine populations ($F_{ST} = 0.045$) and low estimates of genetic variation ($H_E = 39\%$). They attributed their results to long-term anthropogenic influences, such as predator-removal programs and hunting, that reduced the number and range of wolverines in Scandinavia before 1970 (Landa and Skogland 1995). However, subsequent protective legislation has resulted in increased wolverine densities in these regions (Landa 1997) and in the recent recolonization of southern Norway.

This study expands upon previous work by investigating the genetic structure of additional northern wolverine populations, populations on the edges of their current North American distribution, and 1 population in eastern Russia. Our goal was to determine if populations on the periphery of the current distribution of wolverines, where their historic ranges and numbers have been reduced in the last century, are genetically isolated from the larger continuous core of populations. In such regions, the influences of genetic drift could lead to genetically distinct populations, especially for this mid-sized carnivore existing at a low population density (V. A. Banci, in litt.). If these peripheral populations are found to be small fragments of a larger, continuous core of northern wolverine populations, they may be more susceptible to stochastic events leading to local extirpation (Hanski 1999). As such, these regions would be appropriate for concerted conservation efforts to reestablish connectivity between frag-



FIG. 1.—Map depicting 22 sampled localities of wolverines. Squares represent sampled localities from Kyle and Strobeck (2001), circles represent localities sampled in this study.

mented populations and the larger continuous distribution of animals.

MATERIALS AND METHODS

This study combines the data of Kyle and Strobeck (2001) from Alaska, Nunavut, Williston Lake (British Columbia), Revelstoke (British Columbia), Manitoba, and Idaho, with samples from 10 additional geographic regions. Hair, pelt, and tissue samples were obtained from eastern Russia, the Whitehorse region in the Yukon, the Fort Rae and Rennie Lake regions of the Northwest Territories, the Smithers and Prince George regions of British Columbia, the Grande Cache region of Alberta, northwestern Saskatchewan, northwestern Ontario, and the Yellowstone region of Wyoming (Fig. 1).

DNA was extracted using a DNAeasy® Tissue Extraction Kit (QIAGEN Inc., Mississauga, Ontario). Twelve polymorphic microsatellites were amplified using primers developed in badgers (BA-1, BA-4—Davis and Strobeck 1998), martens (MA-3—Davis and Strobeck 1998), wolverines (GG-3, GG-4, GG-7, GG-14—Davis and Strobeck 1998; and Ggu 101, Ggu 216, Ggu 234—Duffy et al. 1998), mink (Mvis-75—Flemming et al. 1999), and Eurasian otters (L-604—Dallas and Piernney 1998). Amplification conditions are given in Davis and Strobeck (1998). DNA fragments were visualized using an ABI Prism® 377 DNA sequencer (PE Applied Bio-

systems Inc., Foster City, California). DNA fragments were analyzed using the programs GeneScan[™] Analysis 2.02 and Genotyper[®] 2.0 (PE Applied Biosystems Inc.).

A *G*-test for heterogeneity of allele distributions, averaged across all loci (Sokal and Rohlf 1995), was performed for each pair of the sampled areas. Departures from Hardy–Weinberg equilibrium were tested for each of the 12 loci using Genepop 3.1d (Raymond and Rousset 1995) that uses a Markov chain method following the algorithm of Guo and Thompson (1992). Genepop also was used to evaluate genotypic disequilibria among loci.

Relative genetic variation in each population was assessed using mean number of alleles and unbiased expected heterozygosity, H_E (Nei and Roychoudhury 1974). Pairwise genetic distances were estimated using Nei's standard genetic distance, D_S (Nei 1972), calculated from genotype frequencies, and the genotype likelihood-ratio distance, D_{LR} (Paetkau et al. 1997), calculated from genotype probabilities. Both pairwise distances were calculated using programs designed by John Brzustowski (<http://www.biology.ualberta.ca/jbrzustowski/Doh/php>).

Pairwise F_{ST} estimates were obtained from the software package Genepop 3.1d (Raymond and Rousset 1995, as per Weir and Cockerham 1984).

An unrooted neighbor-joining tree of D_S values was created using PHYLIP 3.573 (J. Felsenstein, in litt.). The programs Seqboot (1,000 bootstraps) and Consense, also within the software package PHYLIP, were used to obtain statistical support for the neighbor-joining tree. The association between geographic and genetic distance values was tested with a 2-way Mantel test (Mantel 1967—<http://www.fas.umontreal.ca/BIOL/legendre/>), and regressions of the data were performed to obtain comparisons of genetic structure per unit geographic distance.

The assignment test (Paetkau et al. 1995—<http://www.biology.ualberta.ca/jbrzustowski/Doh/php>) was conducted on all populations. This program determines the probability of a genotype occurring in the region from which it was sampled and the probability of it occurring in each of the other regions included in the test. Individuals are then assigned to the population where their genotype has the highest probability of occurrence (see Waser and Strobeck 1998). Randomizations (10,000) of the data were per-

formed within each gene pool assuming Hardy–Weinberg equilibrium. This test identifies cross-assignments that are unlikely to have occurred due to chance alone, thus identifying individuals that may be migrants.

RESULTS

Tests of disequilibrium.—After accounting for samplewise error (Dunn–Sidak method—Sokal and Rohlf 1995), 1 departure from Hardy–Weinberg equilibrium was found at locus L-604 in the Yukon population. Heterozygote deficiencies were responsible for this result, suggesting the presence of null alleles in this population. Because L-604 conformed to Hardy–Weinberg equilibrium in all other populations, it was retained for further analyses.

Genotypic disequilibrium was observed for 2 pairs of loci in the Alberta population: GG3 with GG4, and BA1 with L604. Because genotypic disequilibria were not found for these loci in any other population, it is unlikely that they are physically linked and were therefore retained for further analyses. This result may reflect the presence of a number of related individuals in the Alberta population.

Heterogeneity of sampled regions.—Due to the broad sampling scheme, large number of regions sampled, low pairwise genetic distances and F_{ST} values, and for ease of comparison, all adjacent regions that did not differ significantly in their genotypic frequencies ($\alpha = 0.005$) were pooled (cf. Kyle and Strobeck 2001, where $\alpha = 0.05$). Hence, the Williston Lake, Prince George, and Smithers regions were combined into 1 population and referred to as central British Columbia; the Rennie Lake and Fort Rae regions of the Northwest Territories were combined into 1 population; all Alaskan regions were pooled, and the Kugluktuk and Bay Chimo regions of Nunavut were pooled. Additional details on the genetic variation within and among the Alaskan and Nunavut populations can be found in Kyle and Strobeck (2001).

Genetic variation.—The mean number of

TABLE 1.—Genetic variation of wolverines as revealed by microsatellite data (n = sample size, A = mean number of alleles, and H_E = average expected heterozygosity).

Population	n	A	% H_E
Russia	64	5.7	63
Alaska	228	5.2	65
Yukon	23	4.7	65
Northwest Territories	40	4.7	65
Nunavut	107	4.9	64
Central British Columbia	68	5.0	61
Revelstoke	47	5.2	61
Alberta	17	5.0	61
Saskatchewan	15	4.3	64
Idaho	14	2.8	42
Wyoming	8	3.6	56
Manitoba	28	4.5	67
Ontario	12	3.8	63
Total	671		
Average		4.6	61

alleles ranged from 2.8 (Idaho) to 5.7 (Russia). The average level of heterozygosity (H_E) among all sampled regions was 61% (Table 1). At 42%, Idaho was the only population with a significantly lower level of genetic variation (pairwise comparisons; Wilcoxon's signed-ranks test, $\alpha = 0.05$ —Sokal and Rohlf 1995).

Pairwise F_{st} and genetic distance measures.—Pairwise F_{ST} values ranged essen-

tially from 0 to 0.235 (Table 2). Among the northern regions (Alaska, Yukon, Northwest Territories, Nunavut, central British Columbia, and northern Saskatchewan), pairwise F_{ST} values ranged essentially from 0 to 0.029. F_{ST} values were relatively low (0.012) among eastern (Manitoba and Ontario) populations and were moderate between eastern and northern populations (0.032–0.057). Among the southern regions (Revelstoke, Idaho, and Wyoming) the pairwise values were relatively high (0.047–0.147). These values were even higher when comparing southern regions with northern regions (0.034–0.200), with the exception of comparisons between southern and Alaskan populations where the F_{ST} values were relatively low (0.004–0.015). The lowest values observed between Russian and North American populations were to Alaska (0.038). All other comparisons between Russia and North America yielded relatively high values (0.116–0.235).

The genetic distances, D_{LR} (data not shown) and D_S (Table 2), were found to correlate with one another by a 2-way Mantel test ($r = 0.72$, $P = 0.0004$). D_S values ranged from about 0.021 to 0.490. The D_S values paralleled and were correlated with the findings from the F_{ST} estimates ($r = 0.77$, $P = 0.0005$). The main exceptions

TABLE 2.—Pairwise genetic distances for wolverine populations using microsatellite data: Nei's standard genetic distance, D_S (below diagonal) and F_{ST} (above diagonal); see Fig. 2 for abbreviations.

	Population												
	RU	AK	YK	NT	NU	BC	RV	AB	SK	ID	WY	MB	ON
RU	—	0.038	0.116	0.127	0.128	0.138	0.170	0.126	0.124	0.235	0.165	0.145	0.156
AK	0.287	—	0.003	0.004	0.007	0.007	0.015	0.005	0.001	0.016	0.004	0.008	0.003
YK	0.298	0.068	—	0.018	0.028	0.028	0.055	0.026	0.019	0.159	0.063	0.032	0.034
NT	0.323	0.053	0.068	—	0.002	0.020	0.035	0.16	0.000	0.176	0.047	0.037	0.045
NU	0.317	0.041	0.084	0.021	—	0.029	0.054	0.036	0.000	0.169	0.060	0.046	0.057
BC	0.323	0.44	0.076	0.053	0.065	—	0.034	0.034	0.026	0.127	0.049	0.057	0.055
RV	0.433	0.125	0.131	0.081	0.116	0.071	—	0.051	0.055	0.141	0.047	0.078	0.076
AB	0.313	0.124	0.097	0.065	0.101	0.087	0.117	—	0.026	0.201	0.057	0.041	0.043
SK	0.327	0.059	0.086	0.034	0.034	0.081	0.135	0.103	—	0.200	0.076	0.031	0.045
ID	0.490	0.290	0.257	0.303	0.297	0.188	0.208	0.311	0.322	—	0.147	0.185	0.234
WY	0.433	0.181	0.181	0.138	0.165	0.139	0.126	0.168	0.218	0.210	—	0.094	0.102
MB	0.405	0.119	0.109	0.101	0.116	0.127	0.181	0.129	0.273	0.330	0.273	—	0.012
ON	0.437	0.132	0.126	0.138	0.158	0.144	0.185	0.146	0.149	0.395	0.264	0.084	—

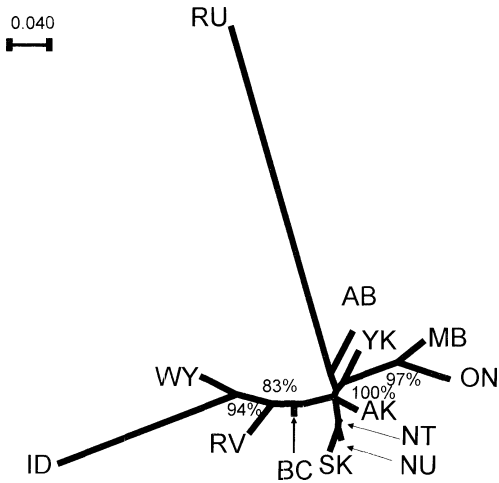


FIG. 2.—Unrooted neighbor-joining tree of Nei's standard genetic distance, D_S . The length of tree branches is relative to genetic distances. Only branch support (from 10,000 bootstraps) of greater than 60% is shown. Localities include Russia (RU); Idaho (ID); Wyoming (WY); Revelstoke (RV); central British Columbia (BC); Alberta (AB); Saskatchewan (SK); Manitoba (MB); Ontario (ON); Kugluktuk and Bay Chimo, Nunavut (NU); Fort Rae and Rennie Lake, Northwest Territories (NT); Whitehorse, Yukon (YK); Arctic, Anchorage, Nome, Nabesna, Natak, and Russian Mission, Alaska (AK).

were the pairwise D_S values between Russia and North America; unlike the F_{ST} values, D_S values were relatively consistent, ranging from 0.287 to 0.490. An unrooted neighbor-joining tree, based on pairwise D_S values (Fig. 2), summarizes relationships between populations. In this tree the Idaho and Russian populations appear nearly equally distinct from the northern North American populations.

Pairwise geographic and genetic distance (D_S) were plotted against each other (Fig. 3). Using a 2-way Mantel test, geographic and genetic distance, D_S , were correlated with each other ($r = 0.52$, $P = 0.00001$). Fig. 4 illustrates the genetic structure of several carnivores relative to that of wolverines, in relation to geographic distance. The steepest slopes were found in brown

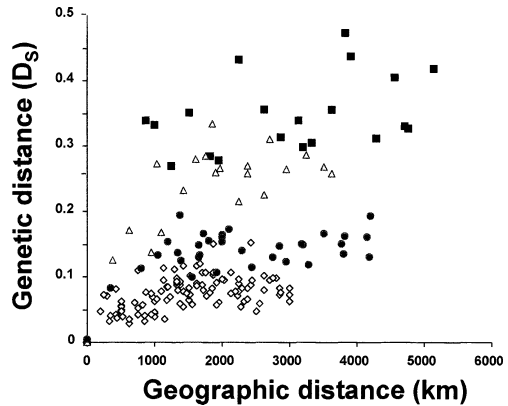


FIG. 3.—Plot of geographic distance relative to Nei's standard genetic distance, D_S , for all sampled wolverine localities. Closed squares represent pairwise values to Russia, open triangles are pairwise values to Idaho, open diamonds are northern population pairwise values, and closed circles are pairwise comparisons to eastern populations (Ontario and Manitoba).

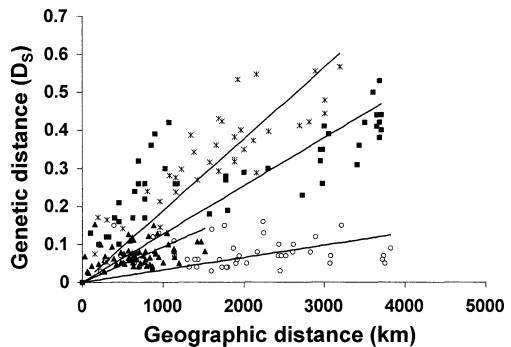


FIG. 4.—Plot of geographic distance relative to Nei's standard genetic distance, D_S , for wolverines (open circles), martens (closed triangles—Kyle et al. 2000), fishers (closed squares—Kyle et al. 2001), and brown bears (asterisks—Paetkau et al. 1998), with trendlines for each species. Peripheral populations and reintroduced populations with disproportionate genetic distances per unit geographic distance are excluded (brown bears, Wyoming and Kodiak Island bears excluded; fishers, reintroduced populations excluded; martens, all populations included; wolverines, Russia, Idaho, Wyoming, and Revelstoke populations excluded).

TABLE 3.—Genotype assignment test for wolverine populations. Left column represents sampling locality and row headings represent populations wolverines were assigned to. For example, 96.9% of the samples obtained from Russia were assigned to Russia, whereas 1.56% of the Russian animals were assigned to the Yukon and 1.56% to Alberta. Note that rounding of percentages may result in values not summing to 100%. Asterisk represents cross-assignments that were found to be significant ($\alpha = 0.05$) by randomizations of individual gene pools assuming Hardy–Weinberg equilibrium. See Fig. 2 for abbreviations.

	% of individuals assigned to each region												
	RU	AK	YK	NT	NU	BC	RV	AB	SK	ID	WY	MB	ON
RU	96.9		1.56					1.56					
AK	0.4	56.1	6.1	3.1	10.1	9.6	1.8	1.3	7.5		1.3	1.3	1.3
YK		4.3	43.5	13.0		17.4*		4.3				13.0*	4.3
NT		10.0	2.5	20.0	20.0	2.5	5.0	10.0	20.0*			10.0	
NU		6.5	2.8	15.9	49.5	3.7	0.9	3.7	10.3			4.7	1.9
BC	1.5	8.8	5.9	8.8	4.4	42.6	10.3	4.4	2.9	2.9*	2.9	2.9	1.5
RV		2.1	6.4*	6.4		12.8	61.7		4.3	2.1	2.1		2.1
AB		5.9	5.9	23.5				41.2	11.8		5.9	5.9	
SK		13.3	7.7	13.3	26.7				26.7			13.3	
ID					7.1*					92.9			
WY				12.5	12.5				25.0*		50.0		
MB		14.3*	3.6	7.1	3.6			3.6				75.0	17.9*
ON			25.0*									16.7	58.3

bears (0.137/1,000 km, *SE* 0.013—Paetkau et al. 1998) and fishers (0.092/1,000 km, *SE* 0.008—Kyle et al. 2001), whereas the lowest values were obtained for wolverines (0.0183/1,000 km, *SE* 0.005) and northern martens (0.057/1,000 km, *SE* 0.009—Kyle et al. 2000).

Assignment test.—Of the Russian samples processed, 97% of the individuals were assigned to Russia (Table 3). For the 2 cross-assignments observed from Russia to North America, assignment probabilities suggest that the individuals were nearly as likely to occur in Russia as in North America (Fig. 5A).

In the northern regions, the vast majority of cross-assignments went to other northern regions. In eastern populations, most cross-assignments were exchanged between the 2 populations in Ontario and Manitoba, with the remainder being assigned to northern regions.

The southern populations, compared with northern regions, produced fewer cross-assignments, with the exception of Wyoming. In this population, 50% of the assignments

were assigned to northern populations (Figs. 5B and 5C).

DISCUSSION

Wolverine populations in northern North America experience high levels of gene flow. This is consistent with the impressive dispersal abilities of both male and female wolverines (Copeland 1996; Gardner 1985; Magoun 1985; Vangen et al. 2001) and with a previous study by Kyle and Strobeck (2001). But genetic structure in the southern and eastern extremes of the distribution of wolverines is relatively high, possibly reflecting the fragmented nature of these populations at the periphery of their historical range.

The Russian wolverine population was found to be distinct from all other North American populations (Tables 2 and 3), with the few cross-assignments observed from Russia to North America likely occurring due to chance (Fig. 5A). But rare transcontinental migration events may not be impossible for this species. Arctic foxes are known to cross the Bering Sea via St.

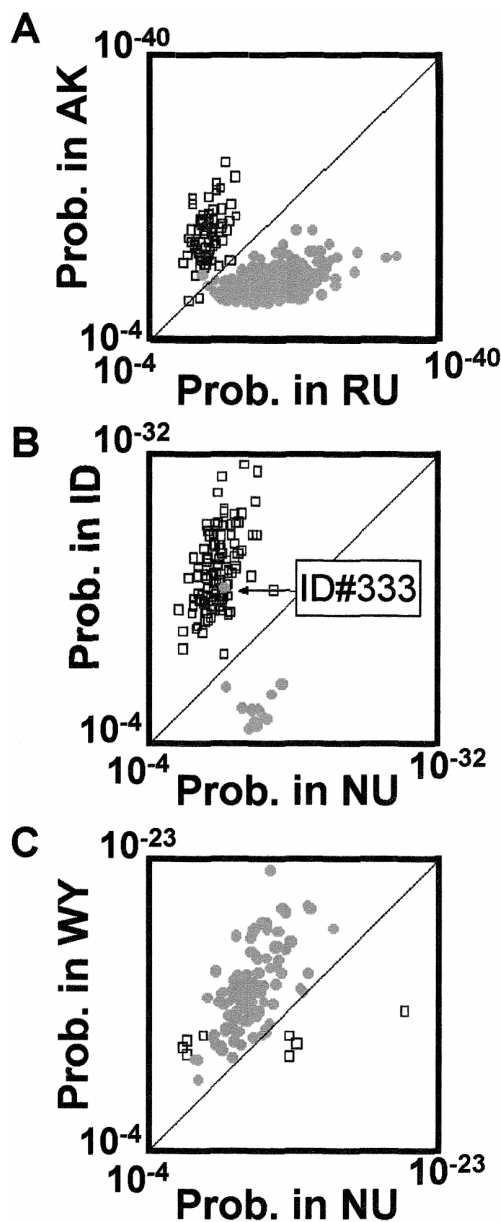


FIG. 5.—Pairwise plots of genotypic probabilities. Individuals found on the opposite side of the diagonal represent cross-assignments. A) Russia versus Alaska, B) Idaho versus Nunavut, C) Wyoming versus Nunavut.

Lawrence Island on the pack ice (Fay and Stephenson 1987), so it may also be possible for wolverines to do the same. In general, however, Russia and Alaska have been considered isolated for >10,000 years, and observed genetic distance/ F_{ST} results may provide a baseline for evaluating isolation among North American populations.

Little genetic structure exists among northern regions (Tables 2 and 3), suggesting the occurrence of extensive gene flow. These findings are expected, given the life history characteristics of wolverines, including their ability to move long distances with relative ease, as documented by Copeland (1996), Gardner (1985), Gardner et al. (1986), and Magoun (1985), and the presence of relatively continuous habitat. It appears that these characteristics have had the effect of genetically homogenizing wolverine populations in habitats with relatively few anthropogenic influences.

An alternative to the aforementioned hypothesis is that the lack of structure in northern regions may reflect a relatively recent postglacial colonization of this area. But wolverines were thought to exist in several refugia during the Wisconsin glaciation, both in regions south of the ice sheets and in Beringia (fossil evidence—Bryant 1987). Genetic trends currently observed have most likely not been influenced by a rapid radiation of wolverines northward from a southern glacial refugium, but reflect recent and consistent migration events.

Our results conflict slightly with a previous study by Wilson et al. (2000) who investigated the genetic structure of wolverines from the Northwest Territories and found a moderate level of genetic structure with enzymes ($F_{ST} = 0.076$) and relatively strong structure with mtDNA ($\Phi_{ST} = 0.536$). The mtDNA results, however, likely reflect male-biased dispersal that is thought to occur in this species (V. A. Banci, in litt.).

A high level of gene flow was found to occur between most western Canadian populations and regions further north suggest-

ing that they are part of the nearly continuous northern distribution of wolverines. But as suggested by Kyle and Strobeck (2001), the Revelstoke population in British Columbia shows signs of genetic isolation from more northern populations. The apparent lack of gene flow to and from Revelstoke may reflect heightened anthropogenic pressures in this region. Studies by Alexander and Waters (2000) and Austin (1998) indicate that the Trans Canada Highway (running through Revelstoke) acts as an impediment to movement for wolverines (among other species). Furthermore, historical effects from predator control programs (L. Hancock, in litt.) and trapping from the early to mid-1900s, have reduced, and thus to some extent isolated, populations in this region. This and the effects of changes as a result of transportation development may, in part, be responsible for the current levels of genetic structure observed.

All results suggest that the 2 eastern populations, Manitoba and Ontario, are quite similar to each other, but relatively distinct from the other regions. Due to the their proximity to the prairies (vast expanse of unsuitable habitat) and Hudson's Bay, and the fact that these populations are on the periphery of the current distribution of wolverines, gene flow between these eastern populations and northern sources may be limited. This is reinforced partially by the genetic distances and number of cross-assignments to northern regions.

The Idaho population appears to be genetically distinct from all other regions. Interestingly, the Idaho and Russian populations are nearly equally genetically distant from northern regions (Fig. 2). But the genetic distances to the northern North American populations from Russia are the result of isolation since the last glaciation. In contrast, the genetic distances between Idaho and other North American populations may represent more recent (early to mid-1900s) population fragmentation or founder events. Historical persecution and displacement from native habitat were thought to have

led to the extirpation of wolverines from much of the lower 48 states by the 1920s, including Idaho (Davis 1939), Montana (Newby and McDougal 1963; Newby and Wright 1955), and Washington (Johnson 1977). Thus, current populations in Montana and Idaho are a result of a relatively recent expansion from the north or an expansion of small populations that may have been reduced to minimum levels during the early to mid-1900s. In either case, the likely small effective size of the Idaho population has led to rapid genetic drift and the current distinctiveness of this population.

The 1 cross-assignment from the Idaho population went to Nunavut (Table 3). Although we are not suggesting that an individual migrated from Nunavut to Idaho, the individual genotype was much more likely ($\alpha < 0.05$) to be from a more northern population than from Idaho (probability of 10^{-19} in Idaho compared with 10^{-12} – 10^{-14} for northern populations, individual probability data not shown; Fig. 5B). Given the potential for dispersal in this species, it is not unreasonable to suggest that there is some amount of gene flow between central Alberta or British Columbia and Idaho. Although less likely, it should be mentioned that reintroductions to the lower 48 states have taken place with wolverines originally obtained from northern Canada (e.g., John Denver and Stouffer Productions of Aspen, Colorado, released 2 Canadian wolverines into the Maroon Bells-Snowmass Wilderness area of Colorado in 1978—Murray 1987).

The results for Wyoming were mixed, with several individual genotypes resembling northern genotypes, whereas others appeared distinct from all other regions sampled. The cross-assignments from Wyoming to the northern regions were highly significant ($\alpha < 0.05$; Fig. 5C). The lack of samples from intermediate populations in Montana makes it unclear if there is some amount of gene flow between Wyoming and Canadian populations.

The genetic structure observed in wol-

verines is similar to that of other carnivores; American pine martens (*Martes americana*) sampled from the Canadian north show little population genetic structure between populations (Kyle et al. 2000). A similar result was also obtained in lynx (*Lynx canadensis*) sampled from across their North American distribution. In lynx, like wolverines, a high potential for dispersal is thought to be responsible for the lack of genetic structure across vast distances (Schwartz et al. 2002). Although more structure exists between brown bear (*Ursus arctos*) populations than between wolverine populations, Paetkau et al. (1998) found that populations in the southern reaches of the bear range were more genetically distinct and showed less genetic variation than did bears occupying less disturbed northern habitats. The parallels between the genetic structure of wolverines and brown bears at the southern periphery of their range may be correlated with low densities of humans and roads (Carroll et al. 2001).

CONCLUSIONS

Our results confirm that high levels of gene flow do occur among northern wolverine populations. We also observe progressively increasing genetic structure at the southern and eastern peripheries of their current distribution. Historical persecution and displacement from native habitat may have resulted in smaller populations, partially fragmented from what was once, likely, a panmictic unit. Small, isolated populations are more susceptible to extirpation (Hanski 1999) and, therefore, should be targets of concerted conservation efforts. To reverse these trends, consideration should be given to reestablishing gene flow between peripheral and core populations to ensure the persistence of this species in regions that are under increasing anthropogenic pressure.

ACKNOWLEDGMENTS

We thank R. A. Van Den Bussche, J. Copeland, J. Krebs, E. Lofroth, A. Magoun, and an

anonymous reviewer for their comments on the manuscript. We also thank the following people and institutions for providing samples for this study: J. Krebs and D. Lewis (Columbia Basin Fish and Wildlife Compensation Program), D. Reid and E. Lofroth (British Columbia Ministry of the Environment; Northern Wolverine Project), R. Mulders and A. Bourque (Department of Resources, Wildlife and Economic Development, NWT), J. Cook and G. Jarrell (University of Alaska Museum), J. Copeland (Rocky Mountain Research Station, Missoula, Montana), K. Pilgrim, N. Dawson (Ontario Ministry of Natural Resources), F. Mallory (Laurentian University), B. Verbiwski and D. Berezanski (Manitoba Wildlife Branch), F. Corbould (Peace/Williston Fish and Wildlife Compensation Program), Alberta Trapper's Association, R. McClymont and B. Trichel (Alberta Fish and Wildlife), D. Pederson, G. Mowat (Aurora Wildlife Research), J. Mattie (Alaska Raw Furs Co.), W. Sharpe and M. Sharpe (North American Fur Auctions). This research was funded by NSERC and Parks Canada grants to C. Strobeck.

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Submitted 11 December 2001. Accepted 25 April 2002.

Associate Editor was Robert D. Bradley.