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CONSERVATION GENETICS OF NORTH AMERICAN WOLVERINE (*GULO GULO*) POPULATIONS: MANAGEMENT IMPLICATIONS

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CONSERVATION GENETICS OF NORTH AMERICAN WOLVERINE (*GULO GULO)* POPULATIONS: MANAGEMENT IMPLICATIONS

Abstract

Habitat loss, fragmentation, overharvest, and other anthropogenic factors have resulted in declines of North American populations of wolverines (*Gulo gulo*). Currently, wolverines east of Hudson Bay are endangered and possibly extinct, whereas the status of wolverines throughout the remaining Holarctic is vulnerable. Because they are highly vagile, wolverines in Canada have been considered to be a single, panmictic population. In this study, we assessed microsatellite and mitochondrial DNA (mtDNA) variation of 270 wolverines from nine collecting localities throughout Canada. Microsatellite analyses revealed low levels of population substructure as indicated by F_{ST} (0.0331) and genotype assignments. However, analysis of mtDNA detected 11 haplotypes throughout Canada and analysis of molecular variance revealed that 78.92% of the total genetic variability was attributable to variation among individuals within populations and 21.08% of the variation was due to variation among populations. Nested clade analysis identified restricted gene flow with isolation by distance coupled with infrequent long-distance dispersal as processes responsible for distribution of wolverine mtDNA haplotypes. In contrast to the recent study of the genetic structure of Canadian wolverine populations, results of this study document significant genetic structuring at both nuclear and mitochondrial loci. Moreover, these independent loci best fit a pattern of isolation by distance.

Key words: carnivore, *Gulo gulo*, intraspecific phylogeography, microsatellite, population structure, wolverine

Introduction

Wolverines (*Gulo gulo*) are solitary animals that occur at low population densities throughout tundra, taiga, and boreal forests of North America and Eurasia (Wilson 1982; Nowak 1991). Prior to human settlement in North America, wolverines were distributed throughout Canada and Alaska with populations reaching as far south as Arizona and New Mexico (Hash 1987). However, due to habitat loss, fragmentation, overharvest, and other anthropogenic factors associated with the arrival of human settlers, wolverines experienced severe population declines throughout much of their distribution (Wilson 1982). In North America, wolverines currently are distributed throughout western Canada and Alaska with individuals extending southward into remote areas of Washington, Oregon, California, Idaho, Montana, Wyoming, and Colorado (Banci 1994). Although wolverines historically occurred throughout Canada, today, east of Hudson Bay wolverines are extremely rare, with only incidental sightings (COSEWIC 2001).

Although genetic issues have become important in the management and conservation of natural populations, only two published studies have examined the genetic structure of wolverine populations. Wilson *et al.* (2000) examined allozyme and mtDNA sequence variation for 43 wolverines from the Northwest Territories, Canada. Allozymes revealed a low degree of genetic differentiation (F_{ST} = 0.0760) whereas mtDNA analysis revealed a high degree of genetic

differentiation (ϕ_{ST} = 0.5360) among localities. From those data, Wilson *et al.* (2000) concluded that gene flow was male biased and wolverine populations in northern Canada were structured genetically as a result of female philopatry. They further concluded that each collecting locality represented an independent management unit that needed to be preserved to maintain the current level of genetic diversity.

Kyle & Strobeck (2001) examined microsatellite variation among 461 wolverines from Idaho, Montana, Wyoming, Alaska, and parts of western and central Canada. To investigate population genetic structure, they used a genotype assignment test, pairwise comparison of F_{ST}, and distance-based measurements. Based on those analyses, they concluded that populations of wolverines in northern Canada exhibited low levels of genetic structuring and due to a lack of dispersal barriers, represented a single, randomly breeding population.

Wilson *et al.* (2000) and Kyle & Strobeck (2001) arrived at discordant conclusions regarding the metapopulation dynamics and resulting management strategy for wolverines in northern Canada. This may, in part, be due to the serious limitations of each of these studies. At the time of publication, the study by Wilson *et al.* (2000) represented the largest sampling of North American wolverines, however, it was limited to 43 individuals from five localities. The study by Kyle & Strobeck (2001) was limited by examining only biparentally inherited markers for a species that exhibits male-biased dispersal (Wilson *et al.* 2000). Slatkin (1985) demonstrated the importance of using at least two

independent loci when estimating levels of gene flow and, more importantly, use of a nuclear and mitochondrial marker when determining dispersal.

The need to re-evaluate the metapopulation dynamics of wolverines in Canada becomes more critical in light of two other factors. One is the lack of a conservation/management plan for Canadian wolverines. The other is the fact that the present number of wolverines in Canada is unknown and the current practice of unlimited harvesting by trappers may significantly impact the species. Because the investigation of genetic structure can provide insight into levels of gene flow and connectivity among populations, the objective of this study was to provide a stronger assessment of the genetic structure of wolverine populations by increasing the geographical range of sampling and using two independent loci (hypervariable microsatellites and mtDNA control region sequences).

Materials and Methods

Sample collection

Tissue samples for 270 trapped wolverines were obtained from nine collecting localities in the Northwest Territories, Nunavut, and Manitoba, Canada by personnel from the Department of Sustainable Development and the Manitoba Trappers Association (Fig. 1). Tissues samples from the Northwest Territories and Nunavut were obtained from wolverine carcasses and stored at -20°C or -70°C whereas desiccated skin samples were obtained from Manitoba wolverines. Because wolverines were assigned to collecting localities according to the area in which they were tagged, it is possible for the harvest area to be different from the assigned collecting locality.

Laboratory methods

Whole genomic DNA was extracted using the method of Longmire *et al.* (1997). Nine hypervariable microsatellite loci were amplified via the polymerase chain reaction (PCR) with previously developed primers from wolverine (Davis & Strobeck 1998; Duffy *et al.* 1998) and American mink (*Mustela vison*; O'Connell *et al.* 1996). PCR amplification for microsatellites were conducted in 15μl volumes containing 50 ng of genomic DNA, 10 pmols of each primer, 3.8μl ddH_20, and 9μl ABI Prism True Allele™ Premix (Perkin-Elmer Applied Biosystems, Foster City, California). The thermal profile consisted of a denaturation and enzyme activation cycle at 95°C for 12 min; 10 cycles of 94°C for 15 s, 55°C for 60 s, and 72°C for 30 s; followed by 25 cycles of 89°C for 15 s, 55°C for 60 s, and 72°C for 30 s. A final 72°C incubation for 30 min was used to ensure that all reactions went to completion. For samples that did not amplify after repeated steps of the aforementioned thermal profile, one or more of the following avenues were taken: the annealing temperature in the 10-step cycle was lowered, the original sample was redialyzed in 1XTE (Tris, EDTA) for two days to remove inhibitors, or new DNA was extracted from that particular individual. Microsatellite variation was visualized using a Perkin-Elmer Applied Biosystems 377 Automated DNA Sequencer. GENESCAN ANALYSIS 2.02 and GENOTYPER 2.0 (Applied Biosystems, Inc., Foster City, California) software were used to determine individual genotypes.

Approximately 200 base pairs (bp) of the mtDNA control region were amplified by PCR using flanking primers (OSU 7863L, 5'-

CTAAGACTCAAGGAAGAAGCAACAGC-3′ and OSU 7864H, 5′-AGCTCGTGATCTAAGTGAGA-3′). Amplifications were conducted in 50-µl volumes containing 200-500 ng of DNA, 1 mM each primer, 1 mM Mg free buffer, 1 mM $MgCl_2$, 1 mM dNTPs, and 1 unit *Taq* DNA polymerase. Cycling conditions consisted of a denaturation cycle at 94°C for 3 min followed by 35 cycles of 94°C for 40 s, 52°C for 60 s, and 72°C for 90 s. To ensure that all reactions have gone to completion, a final extension of 72°C for 30 min was used.

Double-stranded amplicons were electrophoresed through a 0.8% agarose gel stained with ethidium bromide and exposed to ultraviolet light for visualization. Successful amplicons were purified using the Wizard PCR Prep DNA Purification System (Promega Corporation, Madison, Wisconsin). Both strands of the amplified products were sequenced using the aforementioned flanking primers and cycle sequencing according to the manufacturer's instructions (Big-Dye™ chain terminators, Applied Biosystems, Inc., Foster City, California). Cycling conditions were as follows: 25 cycles at 96°C for 10 s, 50°C for 5 s, and 60°C for 4 min. Sequence products were electrophoresed on a 377 automated DNA sequencer (Applied Biosystems, Inc., Foster City, California).

Data analysis

To test for significant departures from Hardy-Weinberg equilibrium, all nine microsatellite loci were assessed by the computer program Arlequin version 2.000 (Schneider *et al.* 2000), which used a modified version of the Markov-chain random walk algorithm described by Guo & Thompson (1992). Genetic variation in terms of observed heterozygosity (H_O), unbiased expected heterozygosity (H_E), mean

number of alleles per locus, allele frequencies, and degree of genetic structure (*F*-statistics; Wright 1965) were estimated by Arlequin version 2.000 (Schneider *et al.* 2000). Finally, an assignment test was used to identify genotypes to populations from which they were sampled (Paetkau *et al.* 1995).

For all mtDNA sequences, the computer program AssemblyLIGN™ 1.0.9 (Oxford Molecular Group PLC 1998) was used to assemble overlapping fragments within individuals and CLUSTAL X (Thompson *et al.* 1997) was used to obtain a multiple sequence alignment of all individuals sequenced plus the 43 individuals originally examined by Wilson *et al.* (2000; GenBank accession numbers AF 210090-AF 210132). The multiple sequence alignment was subsequently imported into the computer program MacClade (Madison & Madison 2000) to identify variable nucleotides and resulting haplotypes. The REDUNDANT TAXA option of MacClade was used to compile redundant sequences for further analyses. Genetic divergence among haplotypes was estimated using the distance method of Tamura & Nei (1993) with the computer program PAUP version 4.0 (Swofford 2001). Haplotype diversity (h), nucleotide diversity (π), haplotype frequencies, and degree of genetic structure (ϕ-statistics; Wright 1965) were calculated using Arlequin 2.000 (Schneider *et al.* 2000). The computer program TCS Alpha version 1.13 (Clement *et al.* 2000) was used to generate an unrooted haplotype network with resulting ambiguities in the network resolved following the recommendations of Crandall & Templeton (1993) and Templeton & Sing (1993). The haplotype network was converted into a series of nested clades: haplotypes were grouped into 1-step clades, 1-step clades into 2-

step clades, 2-step clades into 3-step clades until all subclades were grouped into a single clade (Templeton *et al.* 1987). This information, along with geographic distances, was incorporated into the computer program GeoDis version 2.0 (Posada *et al.* 2000). GeoDis calculates clade distance (D_c), which measures the geographic distribution of a particular clade and nested clade distance (D_n), which measures how a clade is distributed geographically in relation to its closest evolutionary sister clade (Templeton *et al.* 1995). The distance distribution of the nested clade vs. geographical position were recalculated using 10,000 permutations under the null hypothesis of no geographic association between haplotypes. The resulting distance values of the nested design were used with a revised inference key (http://bioag.byu.edu/zoology/crandall_lab/programs.htm) to infer contemporary and historical factors responsible for clades showing significant associations of haplotype distributions and geography.

To evaluate whether these data fit a pattern of isolation by distance, pairwise F_{ST} and pairwise ϕ_{ST} values were incorporated into a two-way Mantel test (Smouse *et al.* 1986) with geographic distance using Arlequin 2.000 (Schneider *et al.* 2000) to determine the correlation between genetic distance and geography.

Results

Based on genotyping 270 wolverines for nine microsatellite loci, the mean number of alleles per locus ranged from 1.3 to 6.0 (Table 1). Among collecting localities, observed heterozygosity (H_o) ranged from 0.4127 to 0.7407 whereas

unbiased expected heterozygosity (H_E) ranged from 0.5177 to 0.7407. After correcting for multiple comparisons (Bonferroni adjustment; Rice 1989), seven loci deviated from Hardy-Weinberg expectations, all of which were due to heterozygote deficiencies. Because no locus deviated from Hardy-Weinberg expectations in all populations and because individuals were grouped according to check-station information, it is most likely that these deviations from Hardy-Weinberg equilibrium are the result of artificial lumping (i.e., Wahlund effect).

Assignment test and pairwise F_{ST}

The genotypic assignment test correctly assigned 156 of 270 (57.8%) individuals to the area from which they were sampled (Table 2). With the exception of the sole individual from Arviat, considerable variability was detected in the percentage of correctly assigned individuals. The highest probability of assigning an individual to its collecting locality occurred for Aklavik, Rendezvous Lake, Kugluktuk, and Manitoba; the four most geographically separated collecting localities (Table 2; Fig. 1). For the five remaining collecting localities in central Canada, correct assignments ranged from 0.00 (for the area between Kugluktuk and Bathurst Inlet, Nunavut) to 0.52 (Bay Chimo, Nunavut). The inability of the assignment test to correctly assign a large proportion of individuals to the area of capture was supported by the low level of genetic differentiation among collecting localities (F_{ST} = 0.0331) and only 13 of 36 statistically significant pairwise F_{ST} comparisons (Table 3). The general pattern revealed by 13 statistically significant pairwise F_{ST} comparisons was that the two western-most collecting localities were significantly different from the three eastern-most localities and

that Bathurst Inlet and Bay Chimo were significantly different from Kugluktuk and Manitoba. Moreover, Kugluktuk and Manitoba were significantly different from each other (Table 3). Results from pairwise F_{ST} comparisons were entered into a two-way Mantel test with corresponding geographic distances to analyze for isolation by distance. Results of the Mantel test suggest that F_{ST} values are significantly correlated to geographic distance (F_{ST} vs. geographic distance $r = 0.42$ $P = 0.037$).

Mitochondrial variation

An approximately 200-bp fragment of the mtDNA control region was sequenced for all 270 wolverines. Alignment of these sequences revealed nine variable nucleotide positions (6 transitions, 1 transversion, and 2 insertion/deletion events), resulting in 11 haplotypes (Table 4). Due to larger sample size and increased geographic scope, we detected 2 haplotypes (J and K) not identified by Wilson *et al.* (2000). These two haplotypes were detected only in samples from Manitoba. A representative sequence of haplotypes J and K have been deposited in GenBank (accession numbers AY 185167-AY 185168). Percent sequence divergence among haplotypes ranged from 0.00% (2 haplotypes differing by a single insertion/deletion event) to 2.07%, with a mean of 1.10%.

The number of haplotypes per locality ranged from 1 to 5 with a mean of 3.3. Within population haplotype diversity (h) was generally high (range of 0.5265 to 1.000, with a mean of 0.7129; Table 5) whereas within population nucleotide diversity (π) was low (range of 0.0000 to 0.0154, with a mean of 0.0054; Table 5). Haplotypes A and C were widespread, occurring throughout

the sampled geographic area whereas haplotypes B, D, and E were restricted to the two most western localities; haplotypes G and H were found only in the five most central localities, and haplotypes J and K were restricted to the two most eastern collecting localities (Table 5). Hierarchical analysis of mtDNA variation revealed that 78.92% of the genetic variation was attributable to differences among individuals within populations whereas 21.08% of the variation was partitioned among collecting localities. Considerable genetic differentiation was detected among collecting localities based on mtDNA sequence data (ϕ_{ST} = 0.2890). When analyzed in a pairwise fashion, 15 of 36 statistically significant pairwise ϕ_{ST} comparisons also were revealed (P = 0.001; Table 3). The emerging pattern from the 15 statistically significant pairwise ϕ_{ST} comparisons was that the western-most localities were significantly different from Kugluktuk, Bay Chimo, and Manitoba and that Bay Chimo was significantly different from Kugluktuk and Manitoba. Arviat also was significantly different from the central collecting localities while Kugluktuk and Manitoba were significantly different from each other (Table 3). Results from pairwise ϕ_{ST} comparisons were entered into a two-way Mantel test with corresponding geographic distances to analyze for isolation by distance. Results of the Mantel test suggest that ϕ_{ST} values are correlated to geographic distance (ϕ_{ST} vs. geographic distance r = 0.60 P = 0.005).

Using the computer package TCS (Clement *et al.* 2000), which incorporates the formulae given in Templeton *et al.* (1992), mtDNA haplotypes separated by up to two mutational steps have a probability of ≥ 0.95 of being connected in a parsimonious fashion. Using the rules of Templeton & Sing

(1993), a nested design was generated (Fig. 2). Within this network, two loops indicate ambiguous haplotype connections. The first loop contained haplotypes C, F, G, and H, whereas the second loop consisted of haplotypes A, B, E, and F. Despite these ambiguities, the logic of Crandall & Templeton (1993) allowed these loops to be resolved. Although the nested contingency analyses did not incorporate information of geographic distance between localities, it revealed significant associations among haplotypes comprising clades 1-2, 1-3, 2-1, 2-2, and the entire cladogram and their geographic locations (Table 6). No other contingency tests were significant at the 5% level.

The null hypothesis of no association between geographic distribution of haplotypes and mtDNA genealogy was rejected for five clades (Table 7; Fig. 3). Use of the inference key led to the conclusion that the null hypothesis was rejected in favor of restricted gene flow with isolation by distance for clades 1-2, 2-1, and 2-2. The null hypothesis was rejected for clade 1-3, but our sampling design was inadequate to discriminate between fragmentation, range expansion, and isolation by distance. The null hypothesis also was rejected for the entire cladogram, but our sampling design was inadequate to discriminate between fragmentation, range expansion, or long-distance colonization.

Discussion

Levels of intrapopulation genetic variation

Three collecting localities (Kugluktuk and Bay Chimo, Nunavut and Manitoba) were sampled in both this study and the study of Kyle & Strobeck (2001), which allowed direct comparisons of mean number of alleles per locus and

heterozygosity based on several microsatellite loci. Kyle & Strobeck (2001) detected mean number of alleles per locus of 4.83, 5.00, and 4.50 for these collecting localities, respectively, which is in good agreement with the mean number of alleles that we detected for these same localities (Table 1). These two studies also were in agreement regarding levels of expected heterozygosity. Kyle & Strobeck (2001) detected expected heterozygosity values of 0.6361, 0.6468, and 0.6699 for Bay Chimo, Kugluktuk, and Manitoba, respectively, whereas our independent analysis for these same sampling areas revealed expected heterozygosity levels of 0.6365, 0.6370, and 0.6921. Because these descriptive statistics are based on independent analyses involving different individuals and several different loci, they indicate considerable agreement in documenting levels of genetic variation within these three populations of wolverines. Additionally, because calculations of expected heterozygosity are fairly robust to small sample sizes, the high levels of expected heterozygosity detected for each of our collecting localities (with the exclusion of Arviat in which we had only a single individual) probably are accurate depictions of current levels of genetic variation within our sampling of wolverines.

North American wolverines exhibit greater levels of genetic variability than their Scandinavian counterparts. Walker *et al.* (2001) examined microsatellite and mtDNA sequence variation of 169 wolverines from Scandinavia and revealed mean expected heterozygosity values of 0.3930, 0.3450, 0.3710, and 0.3480 from northern Norway, southern Norway, Sweden, and a historical population (extinct), respectively. Also, mean number of alleles per locus was 3.0.

Sequence analysis of a 338-bp fragment of the mtDNA control region revealed only a single haplotype among all individuals whereas the number of haplotypes occurring per locality in our study ranged from 1 to 5 with a mean of 3.3. This single Scandinavian haplotype was not detected among the 270 individuals we examined, indicating a long separation between Eurasian and North American wolverines. Additionally, the number of nucleotide differences between the Scandinavian haplotype and haplotypes detected in our study ranged from 3 to 8, with a mean of 5. Walker *et al.* (2001) concluded that low levels of genetic variation observed in extant and extinct populations of Scandinavian wolverines are likely the result of an extirpation-induced bottleneck and post-glacial founder events.

Levels of genetic structure

Two previous studies examined levels of genetic structuring among populations of wolverines from Canada. Wilson *et al.* (2000) examined five polymorphic allozyme loci whereas Kyle & Strobeck (2001) examined 12 hypervariable microsatellite loci. Both studies concluded that wolverines in northern Canada exhibited little geographic structuring. Although Kyle & Strobeck (2001) examined a large number of wolverines (461), they were unable to examine wolverines from the Northwest Territories and concluded that without these samples, it is unclear as to whether the lack of genetic differentiation observed in northern regions is an accurate representation. Although sample sizes in our study were small, we were able to include samples from two distinct areas of the Northwest Territories (Fig. 1). Based on pairwise F_{ST} comparison of

microsatellite variation and, to a lesser degree, the genotypic assignment tests, these two areas appear to exhibit significant genetic differentiation from the eastern localities of Kugluktuk and Manitoba (Tables 2 and 3). Moreover, these statistics indicate significant genetic differentiation within and among many of the sampling localities in Nunavut and Manitoba. Similarly, results of the Mantel test indicate that F_{ST} values are correlated with geographic distance, supporting this level of genetic differentiation. The most likely explanation for low levels of genetic structuring based on biparentally inherited genetic loci is the result of long-distance dispersal of subadult males to establish their home ranges and a lack of topographical features inhibiting dispersal (Magoun 1985).

In contrast to results based on nuclear microsatellite variation, but in agreement with the conclusions of Wilson *et al.* (2000), significant genetic structuring among collecting localities was detected based on a mitochondrial locus (ϕ_{ST} = 0.2890). Furthermore, 15 of 36 statistically significant pairwise ϕ_{ST} comparisons (P = 0.001; Table 3) indicate considerable genetic structuring among localities. Our western-most localities are significantly different from Kugluktuk, Bay Chimo, and Manitoba. Moreover, Bay Chimo is significantly different from Kugluktuk and Manitoba (Table 3). Also, significant structuring was detected between Arviat and central collecting localities, and between Kugluktuk and Manitoba (Table 3). Results of the Mantel test (ϕ_{ST} *vs. geographic distance),* which tests for isolation by distance, re-affirms the level of genetic structure among collecting localities. The contrasting patterns of nuclear and mitochondrial variation suggest that gene flow in wolverines is male biased.

Moreover, the observed high levels of haplotype diversity coupled with low nucleotide diversity suggests that wolverines in northern Canada may have experienced a rapid expansion from an ancestral population with a small effective population size (Avise 2000).

Nested-clade analysis has been shown to have more statistical power for detecting population subdivision than traditional *F*-statistics and can distinguish between contemporary and historic processes responsible for the observed patterns of genetic variation (Templeton 1998). Eight clades were detected in the mtDNA haplotype network for wolverines (Fig. 2). The null hypothesis of no association between haplotype distribution and geography could not be rejected for three of these clades (1-1, 1-4, and 1-5); failure to reject the null hypothesis results from sufficient gene flow between localities, small sample sizes, inadequate geographic sampling, or insufficient genetic variation in sampled populations (Templeton *et al.* 1995). Considering haplotypes comprising these clades, the most plausible explanation for the failure to reject the null hypothesis is inadequate sampling in terms of numbers of individuals and geography. Clade 1-1 comprises haplotypes A and B. Haplotype A was detected in 16 individuals representing all collecting localities except for Rendezvous Lake, Northwest Territories (n = 3), Kugluktuk, Nunavut (n = 181), Bathurst Inlet, Nunavut (n = 7), and Arviat, Nunavut (n = 1). Because of the large sample size for Kugluktuk, if haplotype A occurs in this area, it must be present at a very low frequency. In contrast, haplotype B was detected only in three individuals from our western-most collecting locality (Table 5). Therefore, the most likely explanation for

failure to reject the null hypothesis for this clade is inadequate geographic sampling.

The presence of three haplotypes (D,E, and F) comprising clade 1-2 occur only in the western-most collecting localities (Aklavik, Northwest Territories; Rendezvous Lake, Northwest Territories; and Kugluktuk, Nunavut) contributes to the high degree of genetic differentiation detected. However, the failure to detect a significant association between geography and these closely related haplotypes is perhaps due to insufficient sampling of individuals at most collecting localities and inadequate geographic sampling. Finally, clade 1-5 comprises a hypothetical intermediate haplotype and haplotype K, which was present only in Manitoba (Fig. 2). The presence of haplotype K in eight individuals from Manitoba further supports the genetic uniqueness of this collecting locality.

Regarding clades for which the null hypothesis was rejected (Table 7), the most likely explanation for the distribution of haplotypes in clades 1-2, 2-1, and 2-2 is restricted gene flow with isolation by distance. Clade 1-2 consists of the closely related haplotypes D, E, and F (Fig. 2). Haplotypes D and E are restricted to Aklavik and Rendezvous Lake, Northwest Territories, respectively, whereas haplotype F is present at Aklavik, Northwest Territories and Kugluktuk, Nunavut. It is interesting to note that greater geographic distance separates Rendezvous Lake and Kugluktuk than Kugluktuk and the other four central collecting localities, however, haplotype F was not detected in the other localities. Similarly, clade 2-1 contains two 1-step clades (1-1 and 1-2) and with the

exception of the geographically widespread haplotype A, the remaining haplotypes are indicative of low levels of gene flow between the collecting localities in western parts of the Northwest Territories and localities in western Nunavut. Clade 2-2 consists of three 1-step clades (1-3, 1-4, and 1-5). Haplotype C is present in all localities from Kugluktuk to Manitoba (except for the area between Kugluktuk and Bathurst Inlet (n = 3), haplotypes J and K are restricted to Manitoba whereas haplotype I is present in Rendezvous Lake, Kugluktuk, and Bay Chimo. When the haplotype network is interpreted in light of geographic distribution of the three 1-step clades, the most probable explanation is restricted gene flow with isolation by distance.

Clade 1-3 consists of haplotypes G, H, and J. Haplotypes G and H are found only in wolverines from the five most central collecting localities in western Nunavut whereas the closely related haplotype J is restricted to Manitoba. The explanation for rejection of the null hypothesis for clade 1-3 is fragmentation, range expansion, or isolation by distance. Although it is not possible to discriminate among these hypotheses based on our data, the most plausible explanation is isolation by distance.

Finally, the null hypothesis was rejected for the entire cladogram with the possible explanation being either fragmentation, range expansion, or long-distance colonization. Rejection of the null hypothesis for this clade is primarily due to haplotypes B, E, F, and D occurring in the western-most collecting localities, haplotypes C, G, and H being restricted to the central and eastern localities, and haplotypes J and K being restricted to the southeastern-

most collecting locality in Manitoba. It is unlikely that fragmentation is a suitable explanation for the distribution of haplotypes because there appear to be no barriers to dispersal in these areas (Hornocker & Hash 1981; Banci 1994). The most probable explanation for the distribution of haplotypes making up the entire clade is long-distance colonization, which is well supported by several life-history characteristics (i.e. long distance dispersal capability, subadult males disperse far from natal areas to establish home ranges, and topographic features such as mountains, rivers, and lakes do not serve as barriers to gene flow) of wolverines.

Although previous studies (Wilson *et al.* 2000; Kyle & Strobeck 2001) and results of our analyses suggest that gene flow is male biased, female wolverines are capable of dispersing long distances (Gardner 1985; Gardner *et al.* 1986; Copeland 1996). Magoun (1985) reported a 300-km excursion by a female yearling over a five-month period. Similarly, investigation of dispersal among 24 Scandinavian wolverines revealed that 100% of males and 69% of females dispersed (Vangen *et al.* 2001). Dispersal distance of males averaged 51 km whereas females averaged 60 km (likely underestimates due to loss of radio contact). Moreover, Vangen *et al.* (2001) concluded that resource competition influenced female dispersal patterns, whereas competition for mates influenced male dispersal.

Conclusions and management recommendations

The unregulated harvesting of any organism can have serious implications for the survival and well being of the species. Thus, for most harvested wildlife, detailed management plans are developed to maintain sustainable populations in

conjunction with harvesting. However, a management plan for wolverines in Canada does not currently exist. Even though estimates of population size, connectivity, and autonomy are uncertain, wolverines continue to be harvested throughout much of their North American distribution (Banci & Harestad 1990; Banci 1994). Because of their circumpolar distribution and ability to disperse long distances in a relatively short time (Gardner 1985; Magoun 1985, Gardner *et al.* 1986, Copeland 1996, Vangen *et al.* 2001), it has been assumed that wolverines in Canada represent a single, panmictically breeding population (Banci 1994). Development of a management plan to allow continued harvesting of wolverines has been complicated by these factors coupled with the solitary and secretive nature of the taxon in which it inhabits very remote regions of North America.

Two recent studies have contributed information on the partitioning of genetic variation of Canadian wolverines but made contradictory conclusions regarding the potential management implications of their data. Wilson *et al.* (2000) concluded that wolverines in Canada exhibited male-biased gene flow with female philopatry and as such, to maintain genetic diversity within the species, each of the collecting localities examined should be regarded as separate management units. In contrast, Kyle & Strobeck (2001) concluded that low levels of genetic structure in northern Canada were a result of high levels of gene flow and few barriers to dispersal. However, the pattern of genetic structuring revealed by mitochondrial data (Wilson *et al.* 2000), which Kyle & Strobeck (2001) failed to address, provides additional information regarding

population dynamics and failure to include this information can lead to the development of misguided management plans.

As discussed by Avise (1995, 2000), a significant connection between population demography and matrilineal structuring can occur when female dispersal is extremely low and male dispersal is high, as shown by our study and that of Wilson *et al.* (2000). In such a case, populations could be independent demographically even in the absence of significant genetic structure based on nuclear loci (Avise 2000). Moreover, estimates of genetic structuring based solely on nuclear loci could provide a misleading base for management decisions (Avise 2000). Therefore, given the low level of genetic structuring portrayed by nuclear loci (Wilson *et al.* 2000; Kyle & Strobeck 2001; This study) in conjunction with results from the analysis of mitochondrial DNA sequence variation (Wilson *et al.* 2000; This study), the most conservative recommendation for the development of a management plan for wolverines in northern Canada is to treat our western (Aklavik, Rendezvous Lake, Northwest Territories), central (Kugluktuk, Bathurst Inlet, Bay Chimo, Cambridge Bay, and the area between Kugluktuk and Bathurst Inlet, Nunavut), and eastern (Arviat, Nunavut and Manitoba) collecting localities as separate management units. Support for this recommendation is obtained from eight pairwise comparisons that reveal values statistically different from zero (Table 3). Six of these eight comparisons involve our sampling localities with the largest sample sizes (Aklavik, n = 12; Kugluktuk, n = 181; Bay Chimo, n = 29; Manitoba, n = 28). The fact that these sampling areas contain significant structuring at both autosomal

and mtDNA loci suggests demographic autonomy of these localities (Avise 2000).

As indicated by Kyle & Strobeck (2001), a limitation of their study, as well as our study, is the inability to fully describe the likely complicated local social structure of wolverines. Kyle & Strobeck (2001) point out that due to their broad geographic sampling of wolverines, it is unlikely that local wolverine groups, in which juvenile females establish home ranges adjacent to their mothers would be revealed. Although we also sampled over a broad geographic area, we were able to document female site fidelity, however, due to their large home ranges and remoteness of their habitat, it is unlikely that our grouping of wolverines accurately reflects autonomous demographic units. Therefore, additional ecological, behavioral, and genetic studies need to be conducted to better understand metapopulation dynamics of wolverines in North America. Future genetic studies should attempt to include additional individuals from the localities sampled in this study, intermediate areas between ours, and between localities sampled by Kyle & Strobeck (2001). Finally, all samples examined by Kyle & Strobeck (2001) should be sequenced for the 200-bp mtDNA fragment that we examined, and these data should be combined with our results to provide a more accurate portrayal of the partitioning of genetic variation within and among populations. These additional data would add considerable information to the management plan for wolverines in northern Canada.

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Table 1. Descriptive statistics of microsatellite genetic variation from collecting localities including number of individuals (*n*), mean number of alleles per locus (A), observed heterozygosity (H_O), and unbiased estimate of expected heterozygosity (H_E).

	n	A	H_O	H_E
Aklavik, NWT	12	3.88	0.5556	0.5894
Rendezvous Lake, NWT	3	2.78	0.7407	0.6518
Kugluktuk, NU	181	6.00	0.5672	0.6370
Kug-BI, NU*	3	2.89	0.6296	0.7407
Bathurst Inlet, NU	7	3.44	0.5357	0.6538
Bay Chimo, NU	29	4.78	0.5939	0.6365
Cambridge Bay,NU	6	4.00	0.5926	0.6768
Arviat, NU	1	1.33	--	--
Manitoba	28	4.67	0.5238	0.6921

* Samples collected from the area between Kugluktuk and Bathurst Inlet, Nunavut.

Table 2. Population assignments from genotype assignment test following the method of Paetkau *et al.* (1995). The number of correctly assigned individuals for each collecting locality appear along the diagonal. R. Lake = Rendezvous Lake, Northwest Territories; Kug = Kugluktuk, Nunavut; Kug-BI = area between Kugluktuk and Bathurst Inlet, Nunavut; BI = Bathurst Inlet, Nunavut; Bay = Bay Chimo, Nunavut; CB = Cambridge Bay, Nunavut; Man = Manitoba.

	n	Aklavik	R. Lake	Kug	Kug-BI	BI	Bay	CB	Arviat	Man
Aklavik	12	8	1	1	0	2	0	0	0	0
R. Lake	3	0	2	0	0	1	0	0	0	0
Kug	181	12	5	109	5	8	34	3	2	3
Kug-BI	3	0	2	1	0	0	0	0	0	0
BI	7	1	0	3	0	2	1	0	0	0
Bay	29	1	1	7	1	0	15	4	0	0
CB	6	1	0	0	0	0	4	1	0	0
Arviat	1	0	0	0	0	0	0	0	1	0
Man	28	1	0	4	0	0	5	0	0	18

Table 3. Pairwise comparisons of genetic differentiation among the nine collecting localities throughout Canada. Values above the diagonal are ϕ_{ST} whereas numbers below the diagonal are F_{ST}. Values denoted by an asterisk (*) are significantly different from 0 (α = 0.05) based on the Bonferroni adjustment for multiple comparisons. R. Lake = Rendezvous Lake, Northwest Territories; Kug = Kugluktuk, Nunavut; Kug-BI = area between Kugluktuk and Bathurst Inlet, Nunavut; BI = Bathurst Inlet, Nunavut; Bay = Bay Chimo, Nunavut; CB = Cambridge Bay, Nunavut; Man = Manitoba.

	Aklavik	R. Lake	Kug	Kug-BI	BI	Bay	CB	Arviat	Man
Aklavik	---	0.3548*	0.2970*	0.1979	0.3507*	0.4177*	0.1856	0.3636	0.2543*
R. Lake	0.0370	---	0.2284*	0.3333*	0.3333	0.4131	0.2093	0.3333*	0.3309
Kug	0.0430*	0.0624	---	0.0373	0.0519	0.0770*	0.0159	0.0869*	0.2961*
Kug-BI	0.0635	0.0541	0.0275	---	0.0000	0.0000	0.0000	0.3333*	0.2814
BI	0.0243	0.0623	0.0389*	0.0987	---	0.0000	0.0000	0.2222*	0.3279*
Bay	0.0644*	0.0653	0.0125*	0.0591	0.0609*	---	0.0566	0.3858	0.3938*
CB	0.0000	0.0102	0.0330*	0.0184	0.0279	0.0226	---	0.0000	0.2215
Arviat	0.1494	0.2648*	0.0583	0.1005	0.1682	0.0407	0.0783	---	0.3061
Man	0.0902*	0.1057*	0.0403*	0.0281	0.1106*	0.0425*	0.0374*	0.0470	---

Table 4. Polymorphic nucleotide sites within the 200 bp fragment of mtDNA control region sequences and resulting haplotypes (A - K) for 270 wolverines sampled from nine collecting localities in the Northwest Territories, Nunavut, and Manitoba, Canada. Numbers at the top indicate the position among 200 aligned sites. Small, solid circles represent nucleotide characters identical to that found in haplotype A at that position. Insertion-deletion events are denoted by dashes.

Haplotype	21	50	60	63	125	126	149	180	187
A	C	T	T	C	---	---	C	A	G
B	•	•	C	•	•	•	•	•	•
C	•	•	•	T	•	•	T	•	•
D	A	•	•	•	•	•	T	•	•
E	•	•	C	•	•	•	T	•	•
F	•	•	•	•	•	•	T	•	•
G	•	•	•	T	•	•	T	•	A
H	•	•	•	•	•	•	T	•	A
I	•	•	•	T	C	•	T	•	•
J	•	C	•	•	•	•	T	•	A
K	•	•	•	T	C	C	T	G	•

Table 5. Distribution of each of the 11 mtDNA haplotypes within the nine collecting localities throughout northern Canada and within locality haplotype (h) and nucleotide (π) diversity along with their respective standard error (SE). R. Lake = Rendezvous Lake, Northwest Territories; Kug = Kugluktuk, Nunavut; Kug-BI = area between Kugluktuk and Bathurst Inlet, Nunavut; BI = Bathurst Inlet, Nunavut; CB = Cambridge Bay, Nunavut; Bay = Bay Chimo, Nunavut; Man = Manitoba.

	mtDNA haplotypes														
Locality	A	C	G	H	I	F	D	B	E	J	K	h	*SE*	π	*SE*
Aklavik	7					1		3	1			0.6364	0.1277	0.0040	0.0035
R. Lake					2		1					0.6667	0.3143	0.0102	0.0096
Kug		39	74	1	24	43						0.6667	0.3143	0.0102	0.0096
Kug-BI	1		2									0.6667	0.1598	0.0039	0.0037
BI		1	4	2								0.8667	0.1291	0.0075	0.0060
Bay	1	4	19	2	2							1.0000	0.0000	0.0000	0.0000
CB	1	2	2	1								0.5265	0.1039	0.0040	0.0034
Arviat		1										0.7163	0.0162	0.0055	0.0040
Man	6	1								14	8	0.6700	0.0540	0.0155	0.0092

Table 6. Nested contingency analysis of geographic associations based upon 1,000 iterations. Clades are the same as in Fig. 2 and include only those clades with a probability value less than 0.05, indicating significant geographic structuring.

Clade	Observed Chi-square statistic	Probability
1-2	68.48	0.002*
1-3	140.74	0.000*
2-1	56.94	0.000*
2-2	203.45	0.000*
Entire cladogram	54.94	0.000*

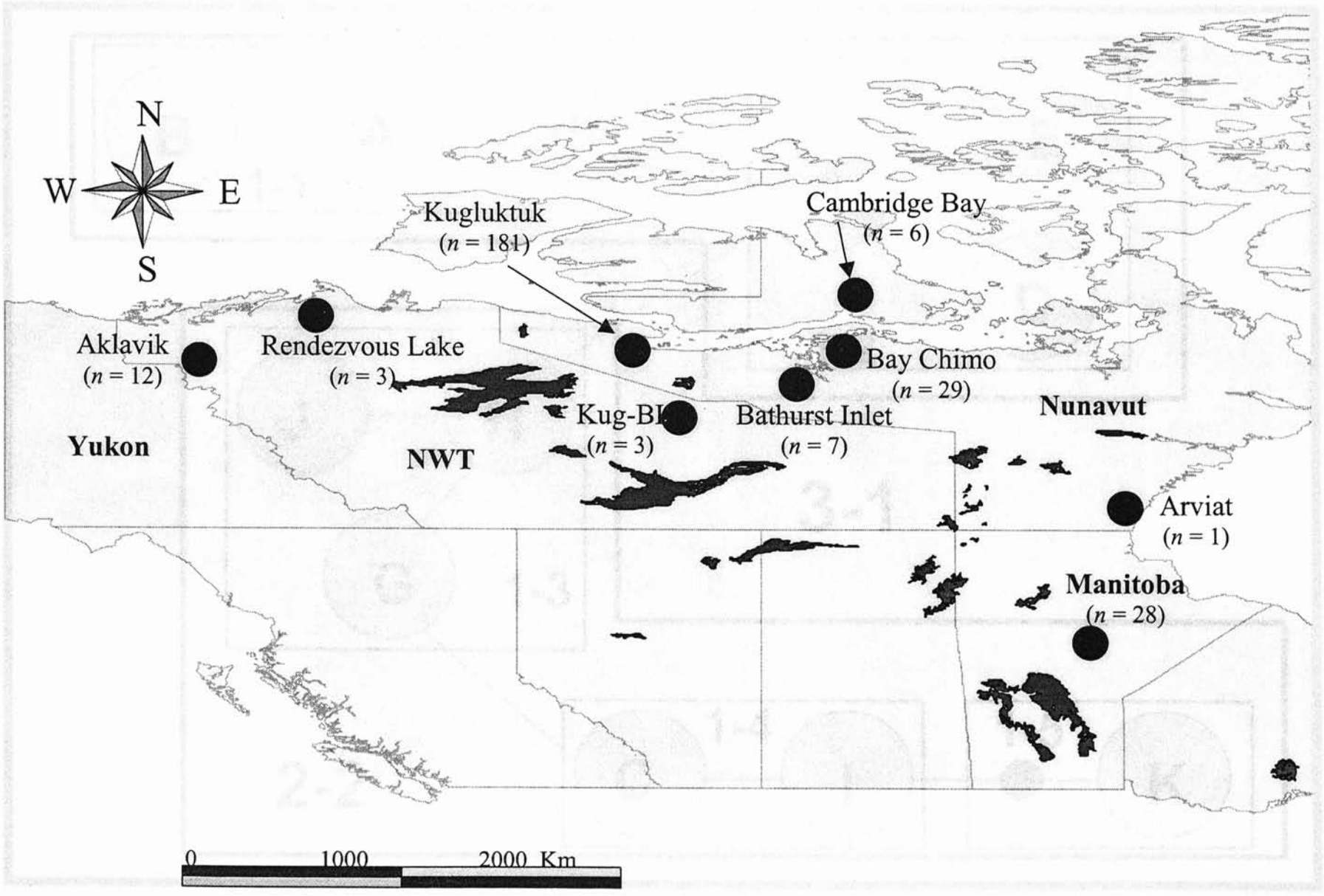
Table 7. Interpretation of the evolutionary processes responsible for the clades depicted in Fig. 3 for which the null hypothesis of no association between haplotype distribution and geography was rejected. Final inferences were determined by use of an inference key available at (http://bioag.byu.edu/zoology/crandall_lab/programs.htm).

Clade	Inference
1-2	Restricted gene flow with isolation by distance.
1-3	Sampling design inadequate to discriminate between fragmentation, range expansion, and isolation by distance.
2-1	Restricted gene flow with isolation by distance.
2-2	Restricted gene flow with isolation by distance.
Entire cladogram	Sampling design inadequate to discriminate between fragmentation, range expansion, and long distance colonization.

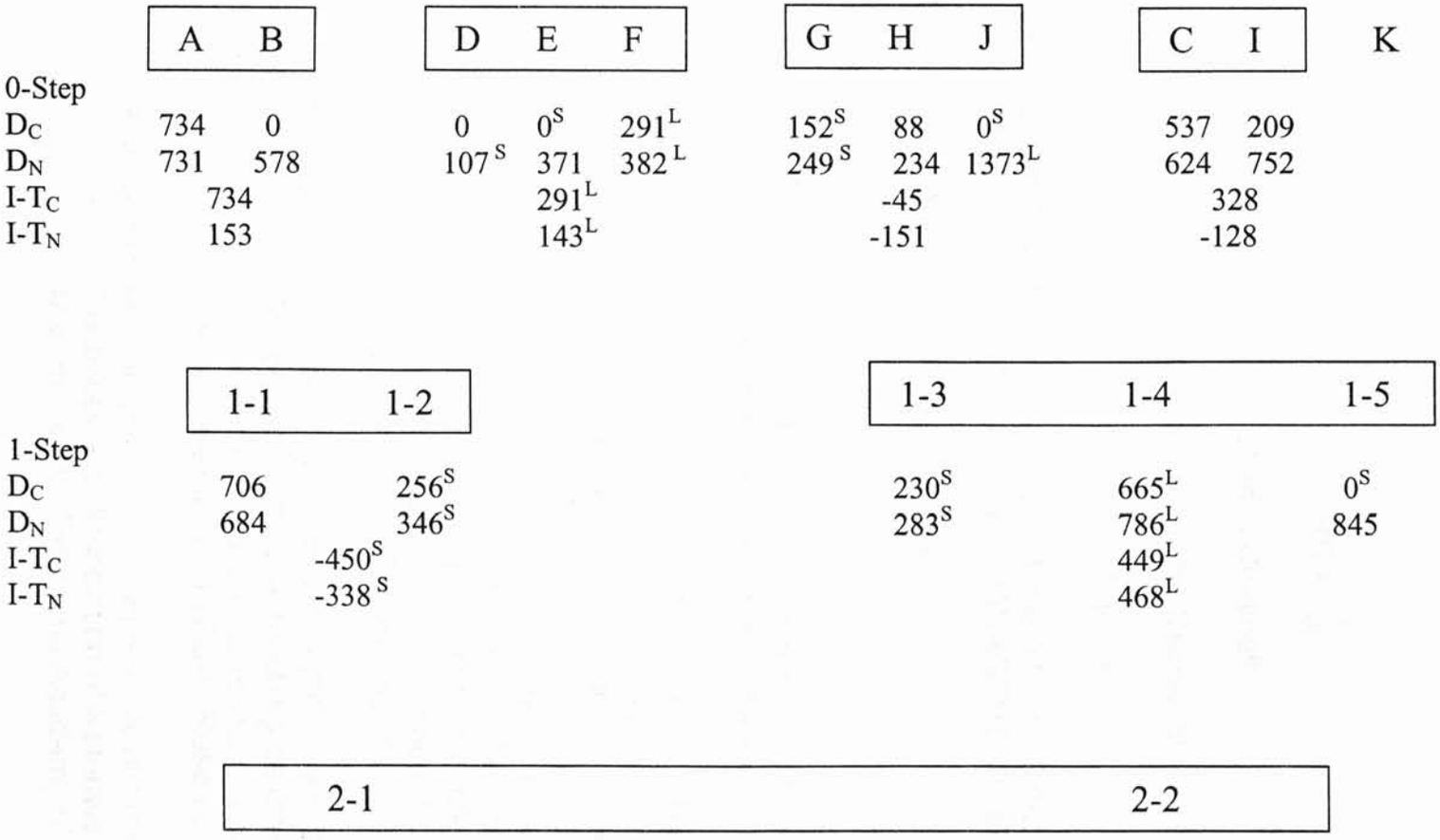
Fig. 1.--- Collecting localities (1-9) within the Northwest Territories, Nunavut, and Manitoba, Canada. Site 1: Aklavik; site 2: Rendezvous Lake; site 3: Kugluktuk; site 4: Kug-BI (area between Kugluktuk and Bathurst Inlet); site 5: Bathurst Inlet; site 6 Bay Chimo; site 7: Cambridge Bay; site 8: Arviat; site 9: Manitoba.

Fig. 2.--- Unrooted estimated 95% parsimony cladogram of 11 haplotypes detected in wolverines. Haplotypes are connected by a single line, which represents a single mutational event. Haplotypes are represented by letters A – K whereas solid circles represent intermediate haplotypes that are not present in the sample, but are necessary to link all observed haplotypes via a single mutational event.

Fig. 3.--- Results of nested clade analysis of geographical distance for wolverine mtDNA haplotypes. Haplotype designations are at the top of the figure and organized to depict the nested design shown in figure 2. D_C and D_N are the clade distance and nested-clade distance, respectively whereas, $(I\text{-}T)_C$ and $(I\text{-}T)_N$ are distances for the difference between interior and tip clades, respectively. A superscript "S" indicates that the measured distance was significantly small at the 5% level whereas, a superscript "L" indicates that the measured distance was significantly large at the 5% level.


N
W
E
S
Kugluktuk
(n = 181)
Cambridge Bay
(n = 6)
Aklavik
(n = 12)
Rendezvous Lake
(n = 3)
Bay Chimo
(n = 29)
Kug-Bl
(n = 3)
Bathurst Inlet
(n = 7)
Nunavut
Yukon
NWT
Arviat
(n = 1)
Manitoba
(n = 28)
0
1000
2000 Km

B
A
1-1
2-1
E
D
F
1-2
H
J
G
1-3
2-2
3-1
C
1-4
I
1-5
K


A B
D E F
G H J
C I
K
0-Step
D_C 734 0 0 0^S 291^L 152^S 88 0^S 537 209
D_N 731 578 107^S 371 382^L 249^S 234 1373^L 624 752
$I\text{-}T_C$ 734 291^L -45 328
$I\text{-}T_N$ 153 143^L -151 -128
1-1 1-2
1-3 1-4 1-5
1-Step
D_C 706 256^S 230^S 665^L 0^S
D_N 684 346^S 283^S 786^L 845
$I\text{-}T_C$ -450^S 449^L
$I\text{-}T_N$ -338^S 468^L
2-1
2-2
2-Step
D_C 634 340^S
D_N 1279^L 399^S

VITA 2

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