Genetic variability in natural populations of the gray wolf, *Canis lupus*

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The genetic variability of gray wolves (*Canis lupus*) from northwestern Canada was assessed through starch-gel electrophoresis. Of 27 protein systems examined, 25, representing 37 presumptive loci, were consistently scorable; 7 proteins (5 were consistently scorable) exhibited polymorphism. The level of heterozygosity (3.0%) was medial relative to values reported for natural populations of Carnivora and high relative to values reported for natural populations of canids. An overall pattern of few deviations from Hardy–Weinberg expectations and some spatial heterogeneity was observed. Wolves associated with different caribou herds exhibited a low level of differentiation (F_{ST} = 0.029). The pattern of variability supports the view of a large panmictic population resulting from extensive movements of individuals and packs and from natural and human impacts on pack structure and formation.

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L'électrophorèse sur gel d'amidon a été utilisée pour évaluer la variabilité génétique des Loups (*Canis lupus*) du Nord-Ouest canadien. Des 27 systèmes de protéines examinés, 25, représentant 37 locus possibles, étaient toujours mesurables; 7 protéines (5 toujours mesurables) étaient polymorphes. L'hétérozygotie (3,0%) était moyenne comparativement aux valeurs signalées dans les populations naturelles de carnirvores et élevée comparativement aux valeurs signalées chez les populations naturelles de canidés. Dans l'ensemble, il y avait peu d'écart de l'équilibre Hardy–Weinberg et un peu d'hétérogénéité spatiale a été observée. Les loups associés aux différents troupeaux de caribous montraient peu de différenciation (F_{ST} = 0,029). Cette variabilité semble indicatrice d'une grande population panmictique résultant des déplacements importants de certains individus et de certaines hordes et aussi de l'impact des phénomènes naturels et de l'activité humaine sur la structure et la formation des hordes.

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Introduction

Woolpy and Eckstrand (1979) propose that the social structure of wolves (*Canis*) produces a population structure with the potential for rapid evolution. Wolves generally live in packs (Paradiso and Nowak 1982), which divides populations into small units. Independent evolution in small units of a population depends on the amount of gene flow among units, differences in selection pressures among units and random genetic drift within units as well as on the effective population size of each unit (Wright 1978). If gene flow among units was absent or very limited and if the environment was perceived as homogeneous for all units, genetic variation would decrease toward fixation within units because of genetic drift; genetic variation within the total population would increase as a result of fixation of one allele in one unit and an alternate allele in another unit. Woolpy and Eckstrand (1979) propose this scenario for wolves. On the basis of computer simulations using different effective population sizes and different levels of emigration and immigration for wolf packs, they estimated a fixation time of approximately 20 years for an "average locus in the average pack." They suggest that the wolf is highly inbred, with loss of genetic variation within packs and genetic distinction between adjacent packs. Thus, the gray wolf (*Canis lupus*) would be genetically variable as a species but the level of heterozygosity for the species would be very low.

Little information on the genetic composition of wolf populations is available, and even less is known about natural (= noncaptive) populations (Braend and Roed 1987; Clark et al. 1975; Ferrell et al. 1980; Fisher et al. 1976; Mardini 1984; Simonsen 1976). Genetic analysis of canids has primarily focused on taxonomic relationships within the Canidae or the Carnivora (e.g., Braend and Roed 1987; Clark et al. 1975; Ferrell et al. 1980; Fisher et al. 1976; Nobrega et al. 1970; Seal 1969, 1975; Serov et al. 1976; Simonsen 1976, 1982; Wayne and O'Brien 1987). A few studies offer estimates of genetic variability in natural populations of canids (Ferrell et al. 1980; Hamilton and Kennedy 1986; Simonsen 1982) and generally support Seal's (1975) assessment of limited genetic variability within canid species. Fisher et al. (1976) examined intraspecific as well as interspecific genetic variation for three species of canids, including *C. lupus*. Their study involved a large number of loci but small numbers of individuals, primarily from zoos. Braend and Roed (1987) examined two loci in a large sample of gray wolves from Alaska but focused on relationships between dogs and wolves. These two studies indicate genetic variability within *C. lupus*; however, information on the genetic structure of natural populations is still lacking. The present study assesses genetic variability in natural populations of the gray wolf.

Materials and methods

Tissue samples were obtained from heads or whole carcasses of gray wolves (n = 188) brought by hunters and trappers to offices of the Department of Renewable Resources, Government of the Northwest Territories, from November 1986 through March 1987 and from November 1987 through March 1988. Wolves from western Northwest Territories and from northern Yukon Territory of Canada (Fig. 1) were represented in the samples (additional information is given in Clarkson and Liepins 1989*a*, 1989*b*). Skeletal muscle (n = 187), liver (n = 57), and kidney (n = 61) were separated into protein fractions by starch-gel electrophoresis through three buffer systems: JRP (Ayala et al. 1972); continuous tris-citrate, pH 8.0 (Selander et al. 1971); and lithium

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TABLE 1. Allele frequencies for five polymorphic loci and average individual heterozygosity for various groupings of samples (= sampling unit) of *Canis lupus* from northwestern Canada

Sampling unit	*n*	Allele	Locus[a]					Heterozygosity	
			Aat-1	*Mpi*	*Gpi*	*Pgm-1*	*Me-1*	A	B
1987	105	1			0.05		0.03	0.215	0.029
		2	0.52	0.89	0.86	0.98	0.97		
		3	0.48	0.11	0.09	0.02			
			(0.495)	(0.219)	(0.257)	(0.038)	(0.067)		
1988	83	1			0.06		0.02	0.231	0.031
		2	0.52	0.86	0.72	1.00	0.98		
		3	0.48	0.14	0.22				
			(0.470)	(0.193)	(0.446)		(0.048)		
Combined years	188	1			0.05		0.03	0.222	0.030
		2	0.52	0.88	0.80	0.99	0.97		
		3	0.48	0.12	0.15	0.01			
			(0.493)	(0.231)	(0.340)	(0.021)	(0.059)		
Males	55	1			0.08		0.07	0.245	0.033
		2	0.52	0.85	0.85	0.99	0.93		
		3	0.48	0.15	0.07	0.01			
			(0.527)	(0.273)	(0.236)	(0.018)	(0.170)		
Tuktoyaktuk	93	1			0.05		0.05	0.256	0.035
		2	0.48	0.88	0.77	0.98	0.95		
		3	0.52	0.12	0.18	0.02			
			(0.527)	(0.247)	(0.376)	(0.032)	(0.097)		
Paulatuk	25	1						0.176	0.024
		2	0.62	0.96	0.88	0.98	1.00		
		3	0.38	0.04	0.12	0.02			
			(0.520)	(0.080)	(0.240)	(0.040)			
Rendezvous Lake – Tadenet Lake	14	1			0.07			0.214	0.029
		2	0.68	1.00	0.71	1.00	1.00		
		3	0.32		0.22				
			(0.500)		(0.571)				
Inuvik	10	1						0.200	0.027
		2	0.75	0.80	0.85	1.00	1.00		
		3	0.25	0.20	0.15				
			(0.300)	(0.400)	(0.300)				
Aklavik	18	1			0.17		0.06	0.189	0.026
		2	0.31	0.81	0.80	1.00	0.94		
		3	0.69	0.19	0.03				
			(0.389)	(0.278)	(0.167)		(0.111)		
Fort McPherson	4	1			0.12			0.200	0.027
		2	0.63	1.00	0.88	1.00	1.00		
		3	0.37						
			(0.750)		(0.250)				
Fort Good Hope – Norman Wells	8	1			0.06			0.200	0.027
		2	0.56	0.62	0.81	1.00	1.00		
		3	0.44	0.38	0.13				
			(0.625)	(0.000)	(0.375)				
Fort Franklin	4	1						0.200	0.027
		2	0.62	0.75	0.88	1.00	1.00		
		3	0.38	0.25	0.12				
			(0.250)	(0.500)	(0.250)				
Fort Norman	3	1						0.200	0.027
		2	0.50	1.00	0.67	1.00	1.00		
		3	0.50		0.33				
			(0.333)		(0.667)				
Region 1	142	1			0.04		0.03	0.234	0.032
		2	0.54	0.90	0.79	0.99	0.97		
		3	0.46	0.10	0.17	0.01			
			(0.507)	(0.204)	(0.366)	(0.028)	(0.063)		

TABLE 1 (*concluded*)

Sampling unit	n	Allele	Locus[a] *Aat-1*	*Mpi*	*Gpi*	*Pgm-1*	*Me-1*	Heterozygosity A	B
Region 2	15	1			0.03			0.200	0.027
		2	0.57	0.73	0.80	1.00	1.00		
		3	0.43	0.27	0.17				
			(0.467)	(0.133)	(0.400)				
Region 3	22	1			0.16		0.04	0.191	0.026
		2	0.36	0.84	0.82	1.00	0.96		
		3	0.64	0.16	0.02				
			(0.455)	(0.227)	(0.182)		(0.091)		

NOTE: For explanation of locus abbreviations see text. Alleles are numbered sequentially on the basis of the rate of migration of the corresponding electromorph (1 = fastest migration). The common allele is designated 2. Heterozygosity was calculated by direct count, excluding (A) and including monomorphic loci (B).

[a]Numbers in parentheses are the heterozygosity values for polymorphic loci of each sampling unit.

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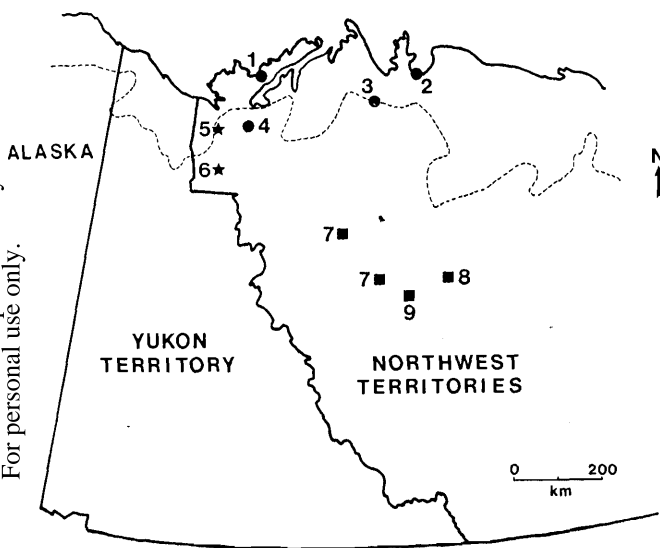

FIG. 1. Collection stations for *Canis lupus* from northwestern Canada. Locations are as follows: 1, Tuktoyaktuk; 2, Paulatuk; 3, Rendezvous Lake and Tadenet Lake; 4, Inuvik; 5, Aklavik; 6, Fort McPherson; 7, Fort Good Hope and Norman Wells; 8, Fort Franklin; 9, Fort Norman. Collection stations marked by a solid circle represent region 1, those marked by a square represent region 2, and those marked by a star represent region 3 (for explanation of regions see the text). The broken line denotes the northern limit of wooded country.

hydroxide (Ridgway et al. 1970). Proteins (following Harris and Hopkinson 1976, except where noted) examined, with designations of loci in parentheses, were as follows: acid phosphatase (*Ap*), aconitate aminotransferase (*Acon*), adenosine deaminase (*Ada*), adenylate kinase (*Ak*), alcohol dehydrogenase (*Adh*), aspartate aminotransferase (*Aat-1* and *Aat-2*), creatine kinase (*Ck*), NADH diaphorase (*Dia*), esterase (*Es*, α-naphthol proprionate as substrate), fumarate hydratase (*Fh*), general proteins (*Gp-1*, *Gp-2*, *Gp-3*, and *Gp-4*; Selander et al. 1971), glucose phosphate isomerase (*Gpi*), β-glucuronidase (*Gus*), α-glycerophosphate dehydrogenase (*Gpd*; Selander et al. 1971). isocitrate dehydrogenase (*Icd-1* and *Icd-2*), lactate dehydrogenase (*Ldh-1* and *Ldh-2*), leucine aminopeptidase (*Lap*; Selander et al. 1971), malate dehydrogenase (*Mdh-1* and *Mdh-2*), malic enzyme (*Me-1* and *Me-2*), mannose phosphate isomerase (*Mpi*), menadione reductase (*Mnr*; Conkle et al. 1982), nucleoside phosphorylase (*Np*), phosphogluconate dehydrogenase (*Pgd*), phosphoglucomutase (*Pgm-1*, *Pgm-2*, and *Pgm-3*), peptidase (*Pep-1*, *Pep-2*, and *Pep-3*, leucyl-alanine, leucyl-glycyl-glycine, and phenylalanyl-proline as substrates), superoxide dismutase (*Sod*), and sorbital dehydrogenase (*Sordh*). For protein systems governed by multiple loci, loci were numbered sequentially, from the most anodally to the most cathodally migrating protein product.

Allele frequencies, heterozygosity (direct-count estimate) for polymorphic loci, Hardy-Weinberg equilibrium, χ^2 contingency analysis, Wright's *F*-statistics (Wright 1965, 1978; Nei 1977), hierarchical analysis (Wright 1978), and Rogers' genetic similarity coefficients (Rogers 1972) were determined with the program BIOSYS-1 (Swofford and Selander 1981). Polymorphic loci (frequency of the common allele less than 0.99) that were consistently scorable were used in data analyses. Individuals were grouped by year of collection for temporal analysis and by sex (with unknowns excluded) for sexual analysis. Individuals were also grouped by sex and year (four groups) for analysis. Because of small sample sizes, individuals were not partitioned by locality for sexual or temporal analyses; however, sample sizes for one area were sufficient for partitioning individuals within that sample by sex and year for analysis. Spatial differences were assessed by treating communities as different population subunits (nine) of the total and by grouping samples into three regions (Fig. 1). Although subunits may not have represented exclusive populations, regions probably represented three large populations. Region 1 represented wolves taken on the delta or barren ground and associated with the Bluenose caribou herd (*Rangifer tarandus groenlandicus*); region 2 represented wolves in wooded country which are associated with the Woodland caribou (*R. t. caribou*) and the Bluenose caribou herd; region 3 represented wolves in the area of the Richardson Mountains, which are associated with the Porcupine caribou herd (*R. t. granti*; Bergerud 1978; Miller 1982). Samples without a community designation were excluded from spatial analyses.

Results

Of 27 protein systems examined, 25, representing 37 presumptive loci, were consistently scorable (excludes *Adh* and *Dia*). Multiple esterases were observed from liver samples; however, only one locus was consistently expressed in muscle samples. Only one esterase exhibited polymorphism; this esterase was expressed only in liver samples and was not consistently scorable, owing to denaturation. *Adh* and *Dia* were also only detected in liver but were not consistently scorable for most samples, owing to denaturation. Polymorphism was present for *Dia*. Polymorphism appeared to be present for *Adh*; however, some interpretations of electromorphs were questionable. Five polymorphic loci (*Aat-1, Mpi, Gpi, Pgm-1, Me-1*) were used in subsequent analyses. The *Gpi* locus expressed three alleles, while the other four loci expressed two alleles each. The percentage of polymorphic loci was 17.9 on the basis of seven polymorphic loci (includes *Dia* and the polymorphic *Es*) and 13.5 on the basis of five polymorphic loci.

TABLE 2. Wright's *F*-statistics for *Canis lupus* from northwestern Canada grouped into eight subunits and three regions

Grouping	Locus	F_{IS}	F_{IT}	F_{ST}	P
Subunits	*Aat-1*	−0.014	0.048	0.062*	0.023
	Mpi	0.150	0.268	0.138*	0.004
	Gpi	−0.143	−0.084	0.052	0.099
	Pgm-1	−0.019	−0.004	0.014	0.976
	Me-1	−0.055	−0.012	0.041	0.536
	Total	−0.023	0.053	0.074*	0.011
Regions	*Aat-1*	0.015	0.048	0.033	0.077
	Mpi	0.329	0.351	0.032*	0.024
	Gpi	0.031	0.054	0.024*	0.003
	Pgm-1	−0.014	−0.005	0.009	0.590
	Me-1	−0.041	−0.026	0.014	0.527
	Total	0.094	0.120	0.029*	0.002

NOTE: For explanation of locus abbreviations see the text. Probability values are from χ^2 contingency analysis.
* F_{ST} significantly ($P < 0.05$) different from zero.

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No significant differences (χ^2 contingency analysis; $P >$ 0.05) were detected between sexes or between years (allele frequencies and observed heterozygosity are given in Table 1). Rogers' coefficient of genetic similarity (S) was 0.966 between males and females and 0.960 between years. χ^2 contingency analysis of individuals grouped by sex and year yielded no significant differences among groups; this was also the result when only individuals from Tuktoyaktuk were examined. Therefore, data for different years and sexes were combined for further analyses.

The level of observed heterozygosity for the total sample of wolves was 3.0% over 37 loci (22.2% over 5 polymorphic loci). Major contributors to heterozygosity were *Aat-1, Mpi,* and *Gpi* (Table 1). *Me-1* and *Pgm-1* were only slightly polymorphic. For four polymorphic loci, one allele greatly predominated; however, frequencies of the two alleles for *Aat-1* were nearly equal (Table 1).

Spatial heterogeneity in allele frequencies and heterozygosity was present among the nine subunits (Table 1). Levels of observed heterozygosity varied from 2.4 to 3.5%, with a mean of 2.8% over 37 loci. All subunits except Tuktoyaktuk had similar levels of heterozygosity. Significant deviation from Hardy–Weinberg equilibrium was observed for *Gpi* in the Aklavik subunit (P = 0.048; heterozygote deficiency and a deficiency of homozygotes of the two less common alleles) and for *Mpi* in the Fort Good Hope – Norman Wells subunit (P = 0.002; heterozygote deficiency). F_{IS} and F_{IT} values (Table 2) indicate a slight excess of heterozygotes (negative values) for most loci. The overall degree of differentiation among subunits was 0.074 (significantly different from zero at $P \leq 0.05$), with the highest levels at *Mpi* and *Aat-1* (Table 2). Relationships among subunits, based on Roger's genetic similarity coefficients (ranging from 0.843 to 0.962), are presented in Fig. 2. The separation of Aklavik from the other subunits is primarily due to its frequency of the common allele (0.306) for *Aat-1*, which was the lowest among the subunits. The grouping of Inuvik with Fort Franklin and Fort Good Hope – Norman Wells separately from the five subunits in the larger cluster reflects lower frequencies of the common allele at *Mpi*. Regions also exhibited spatial differences in allele frequencies and levels of heterozygosity over 37 loci (Table 1). Regions 2 and 3 exhibited similar levels of heterozygosity, which were slightly lower than that for region 1. Region 2 deviated significantly (P = 0.006) from Hardy–Weinberg equilibrium at *Mpi* (heterozygote deficiency).

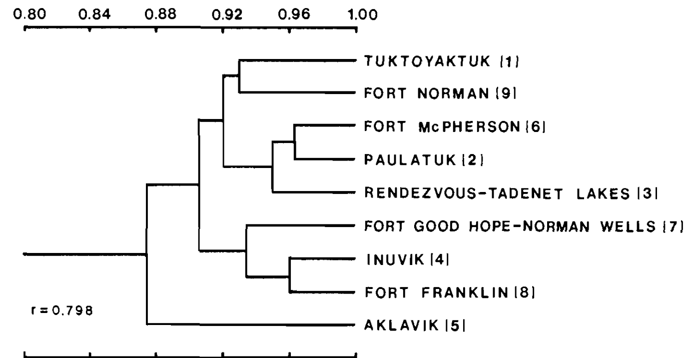

FIG. 2. Relationships among groupings of *Canis lupus* based on Rogers' coefficient of genetic similarity. Locality numbers (in parentheses) correspond to those in Fig. 1.

This is reflected in the positive F_{IS} and F_{IT} values for *Mpi* (Table 2). The overall level of differentiation among regions was 0.029 (significantly different from zero); the greatest level was at *Aat-1* and *Mpi* (Table 2). χ^2 contingency tests indicate significant (P <0.05) differentiation among regions for *Mpi, Gpi,* and the total five loci (Table 2). For *Aat-1*, the P value was greater than 0.05 but less than 0.10. Rogers' coefficient of genetic similarity was highest between regions 1 and 2 (S = 0.952). The similarity between regions 3 and 1 (S = 0.920) was greater than that between regions 3 and 2 (S = 0.902). Region 3 differs from the other regions primarily in allele frequencies at *Aat-1* and *Gpi*.

Hierarchical analysis indicated only slightly more diffentiation among subunits within regions (F_{SR} = 0.026) than among subunits within the total sample (F_{ST} = 0.020). These levels were greater than that among regions within the total sample (F_{RT} = 0.000).

Discussion

Protein variation observed in the present study generally agrees with available information for the gray wolf. Mardini (1984) examined electrophoretic patterns of general proteins for 20 gray wolves from eastern Canada and found no variation. General proteins for gray wolves from northwestern Canada were also invariant. Braend and Roed (1987) noted transferrin and esterase (blood) polymorphism in 146 gray wolves from Alaska; this polymorphism, however, was detected with isoelectric focusing. Twenty-three protein systems of the present study were also examined by Fisher et al. (1976) for eight gray wolves from zoos and four from Minnesota. Of these systems, results for three differ between the two studies: *Aat*, *Gpi*, and *Me* were polymorphic in the present investigation but are reported as monomorphic in gray wolves by Fisher et al. (1976). Sampling error may account for the difference. Examination of one sample from Minnesota along with samples from the present study revealed heterozygous genotypes at *Aat-1*, *Gpi*, and *Mpi* for alleles present in Canadian wolves. Polymorphism for *Dia*, *Es*, *Mpi*, and *Pgm* in gray wolves was detected in both studies. Wayne and O'Brien (1987) also indicated *Mpi* and *Pgm* variation for one wolf from a zoo. Fisher et al. (1976) noted polymorphism at adenosine phosphoribosyltransferase which was not examined in the present study. The present study included *Fh*, *Gus*, *Lap*, and *Mnr*, which were not examined by Fisher et al. (1976); these proteins were invariant. The overall percentage of polymorphic loci determined for wolves in northwestern Canada (13.5 and 17.9%) is higher than the 11.3% reported by Fisher et al. (1976).

The overall level of heterozygosity (3.0%) for wolves from northwestern Canada is slightly higher than the 2.8% calculated from data given in Fisher et al. (1976). The value of 3.0% is an underestimate, since *Dia* and *Es* were not included in its calculation. If heterozygosity at *Dia* and *Es* is at least at the level reported by Fisher et al. (1976), the average value for Canadian wolves would be approximately 3.6%. Average heterozygosity values of 0.0 and 0.9% have been reported for natural populations of *Vulpes vulpes* (Simonsen 1982) and *Canis latrans* (Hamilton and Kennedy 1986), repectively. Values (excluding that of Mitton and Raphael 1990) for natural populations of other families of Carnivora range from 0.0 to 8.0%, with most less than 3.0% (Allendorf et al. 1979; Beck and Kennedy 1980; Dew and Kennedy 1980; Hamilton and Kennedy 1987; Manlove et al. 1980; Simonsen 1982; Wathen et al. 1985). Mitton and Raphael (1990) reported an unusually high level of heterozygosity (17.0%) for 10 *Martes americana* from a single locality and suggested that "sampling of related individuals may have inflated the estimate of heterozygosity." The degree of heterozygosity in natural populations of wolves is medial relative to that of natural populations of Carnivora and high relative to that of natural populations of canids.

Hamilton and Kennedy (1986) observed a general pattern of heterozygote deficiency and statistically significant differentiation among populations of *C. latrans*. Another carnivore, *Procyon lotor*, also exhibited this pattern (Hamilton and Kennedy 1987). Wolves from northwestern Canada exhibited minimal deviations from Hardy–Weinberg expectations. A slight excess of heterozygotes was indicated for most of the polymorphic loci. The observed heterozygote deficiency for *Mpi* and *Gpi* may simply be due to sampling error or to combining members of genetically different packs (Wahlund effect; Wahlund 1928; Chesser 1983). The level of differentiation among subunits of *C. lupus* ($F_{ST} = 0.074$) is comparable to that among populations of *C. latrans* in Tennessee ($F_{ST} = 0.080$; Hamilton and Kennedy 1986) and *P. lotor* in the southeastern ($F_{ST} = 0.112$ and 0.068) and northwestern ($F_{ST} = 0.072$) United States (Dew and Kennedy 1980; Hamilton and Kennedy 1987) but much less than that among *P. lotor* in the eastern ($F_{ST} = 0.208$) United States and across the United States ($F_{ST} = 0.374$; Hamilton and Kennedy 1987). Considerably less differentiation was present among wolves from different regions ($F_{ST} = 0.029$). Although statistically significant, the level of differentiation among wolves from different regions is low (<0.05; Hartl 1980). Thus, wolves associated with different caribou herds were generally similar. The differences that were present may reflect sampling error within each region, since hierarchical analysis indicates as much differentiation among all subunits as among subunits within each region. Wolves were genetically similar across most of the study area. A moderate level of differentiation (0.05–0.15; Hartl 1980) existed among wolves of different subunits. Differences were mainly between wolves from Aklavik and those from other parts of the study area.

The pattern of genetic variability in the wolves from northwestern Canada does not support the hypothesis that gray wolves are a highly inbred species because of their social structure (Chesser 1983; Foltz and Hoogland 1983; Patton and Feder 1981; Schwartz and Armitage 1980). Wolf populations are quite dynamic, with packs continually forming and dissolving as a result of natural and human (hunting and trapping) disruptions (Mech 1970; Paradiso and Nowak 1982; Clarkson and Liepins 1989*a*, 1989*b*). Observations showed extensive movement of wolves throughout the study area and considerable changes in pack structure (Clarkson and Liepins 1989*a*, 1989*b*). Many packs have split and moved to a new area; some males have associated with two or three different packs. Hunting and trapping have disrupted some packs and pack formation, causing some wolves to join other packs. Reproduction by more than one adult female per pack has also been observed in the study area by Clarkson and Liepins (1989*a*, 1989*b*). These observations of the natural ecology of wolves in the study area suggest a large panmictic population, a view suppoted by the genetic data.

The genetic structure of individual wolf packs could not be examined using the data set of the present study. However, the heterozygosity observed for subunits and regions does not suggest intense inbreeding. Adjacent packs of wolves could be genetically distinct from each other as a result of genetic differences between founding individuals (Wright 1978) rather than random genetic drift toward fixation of alternate alleles as a result of inbreeding, as proposed by Woolpy and Eckstrand (1979) for stable packs.

Although the present study deals with wolves subjected to considerable hunting and trapping pressure, a similar pattern of genetic variability may characterize populations that are not greatly impacted by hunting and trapping. Natural pack disruption and movements of wolves may allow enough genetic exchange in an area to prevent allelic fixation within a pack as a result of random genetic drift and to produce the levels of heterozygosity and genetic similarity observed in our study.

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