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Microsatellite analysis of population structure in Canadian polar bears

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Abstract

Attempts to study the genetic population structure of large mammals are often hampered by the low levels of genetic variation observed in these species. Polar bears have particularly low levels of genetic variation with the result that their genetic population structure has been intractable. We describe the use of eight hypervariable microsatellite loci to study the genetic relationships between four Canadian polar bear populations: the northern Beaufort Sea, southern Beaufort Sea, western Hudson Bay, and Davis Strait – Labrador Sea. These markers detected considerable genetic variation, with average heterozygosity near 60% within each population. Interpopulation differences in allele frequency distribution were significant between all pairs of populations, including two adjacent populations in the Beaufort Sea. Measures of genetic distance reflect the geographic distribution of populations, but also suggest patterns of gene flow which are not obvious from geography and may reflect movement patterns of these animals. Distribution of variation is sufficiently different between the Beaufort Sea populations and the two more eastern ones that the region of origin for a given sample can be predicted based on its expected genotype frequency using an assignment test. These data indicate that gene flow between local populations is restricted despite the long-distance seasonal movements undertaken by polar bears.

Keywords: *Ursus maritimus*, DNA fingerprinting, microsatellite, population structure, population genetics

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Introduction

Polar bears (*Ursus maritimus*) are large mammals distributed at low densities throughout the circumpolar Arctic. In order to properly protect and manage this species, it is important to understand the structure of its populations, particularly in light of the international nature of the population distribution. Although polar bears were once thought to be nomadic – with individual ranges that were circumpolar – mark–recapture programs, later supplemented with radio and satellite telemetry, have demonstrated that they are philopatric. Data on the movements of many individual bears have been collected over the past 25 years and indicate centres of geographic distribution with limited overlap (Taylor & Lee, in press). In addition, polar bears show seasonal fidelity to particular areas. This pattern can be influenced by the distribution of seals – their primary prey – which, in turn, is influenced by ice conditions.

In Canada, 12 polar bear populations – with predictable boundaries and a separation of breeding populations – have been identified (Taylor & Lee, in press). While these population boundaries have facilitated the implementation of management plans, the genetic basis of this recognition of separate populations has not been established. Studies based on multiple relocations shed light on the movements of individuals, but do not reveal the degree of interbreeding between animals from different populations. The long-distance movements made by some polar bears might lead to the prediction that gene flow between populations is sufficient to homogenize them genetically, despite the clear fidelity of animals to particular breeding areas. To test this prediction, it is necessary to undertake

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studies of genetic markers that might identify population structure.

A general feature of such genetic studies is that no information can be gained on population structure if the markers employed are not polymorphic. This fact is pointedly illustrated by previous studies of genetic variation in polar bears. Allendorf *et al.* (1979) found no variation in a limited survey of protein variation. Similarly, Larsen *et al.* (1983) used high-resolution techniques to survey 75 proteins in a large number of polar bears, from several countries, and found only two variable loci. Variation in mitochondrial DNA sequence has also been studied and the results have been similar (Cronin *et al.* 1991; Shields & Kocher 1991). One group surveyed 137 individuals from two of the populations included in the current study – the northern Beaufort Sea and western Hudson Bay – and found only two haplotypes, one of which occurred in only a single individual (Y. Plante *et al.*, personal communication). Clearly the low level of genetic variation detected using these methods precludes their use in addressing questions of population differentiation.

A possible solution to the problem of low genetic variability in polar bears is the use of repetitive DNA markers characterized by extremely high variability. The potential utility of such 'DNA fingerprinting' techniques for studying population structure in wildlife species was demonstrated in a study of island populations of foxes whose colonization history was known (Gilbert *et al.* 1990). Much of the 'DNA fingerprinting' done on wildlife populations to date has been based on the multilocus minisatellite method originally described by Jeffreys *et al.* (1985). One drawback of this method is that most of the mathematical treatments for studying population structure are based on single-locus models, and cannot be used for these data.

The study of microsatellites – short tandem repeats of 1–5 bases (Beckmann & Weber 1992) – provides an excellent alternative for studying wildlife species (for reviews see Bruford & Wayne 1993; Queller *et al.* 1993), although interpopulation comparisons using this method have been restricted primarily to human populations to date (e.g. Bowcock *et al.* 1994; Edwards *et al.* 1992; but see Paetkau & Strobeck 1994; Roy *et al.* 1994). Single-locus analysis, yielding discrete genotypes, is easy to develop with this method, and, since it is PCR-based, data collection is rapid, and small or degraded DNA samples can be used.

We describe the use of eight microsatellite markers to delineate the genetic relationship between four Canadian polar bear populations. The populations included in this study show varying degrees of geographical separation (Fig. 1). The northern Beaufort Sea (NB) and southern Beaufort Sea (SB) populations are adjacent to each other and may have up to 10% overlap in the region of their shared boundary (Stirling *et al.* 1988). By contrast, the western Hudson Bay (WH) and Davis Straight – Labrador Sea (DS) populations are widely separated from each other and no movements of polar bears have been recorded between the two (Stirling *et al.* 1977; Stirling *et al.* 1980; Stirling & Kiliaan 1980). Similarly, no movements between the Beaufort Sea and either WH or DS have been recorded. These populations span the widest geographical separation of Canadian polar bears, from Labrador to the Alaskan border.

Materials and methods

Laboratory methods

DNA was isolated from blood or tissue samples collected between 1986 and 1993. Whole blood preserved with EDTA, blood clots left after serum collection, and skin disks removed during ear-tagging were used. DNA was extracted on an Applied Biosystems Inc. (ABI) Genepure 341 Nucleic Acids Purification System using standard protocols. Only samples from adult animals with no known relationship to other sampled animals were used. Sample sizes were 22, 30, 30 and 26 for SB, NB, WH, and DS, respectively. Eighteen additional samples, originally included in the NB and SB populations, were analysed and subsequently excluded because they were obtained from individuals handled within 50 km of the proposed common boundary of these populations making it difficult to assign them to a population with confidence. These eighteen samples were included as a separate population (MB) for some calculations.

Eight pairs of primers (Table 1) were used to amplify $(GT)_n$ microsatellite loci using PCR. Four of these primer pairs were described previously (Paetkau & Strobeck 1994) and the remaining four were isolated from the same black bear genomic library, and using the same methods, as described in that report. PCR products were resolved on a denaturing polyacrylamide gel as previously described (Hughes 1993; Paetkau & Strobeck 1994; Weber & May 1989) except that one primer from each pair was synthesized with a fluorescent dye group – either FAM or HEX (ABI) – on the 5′ end. Primers were synthesized on an ABI 391 DNA Synthesizer. These dyes allowed detection and sizing of fragments on an ABI 373A DNA Sequencer maintained by Parks Canada at the University of Alberta. The availability of two dyes allows the analysis of loci whose PCR products overlap in size in the same lane. A detailed description of detection and analysis using this system is given elsewhere (Ziegle *et al.* 1992).

PCR products from four loci were multiplexed in each gel lane. Multiplexing by coamplification was used for seven of the eight pairs of primers by including either four or six primers in each PCR cocktail. The best coamplification was achieved with loci 10B, 10C, and 1D; loci 1A

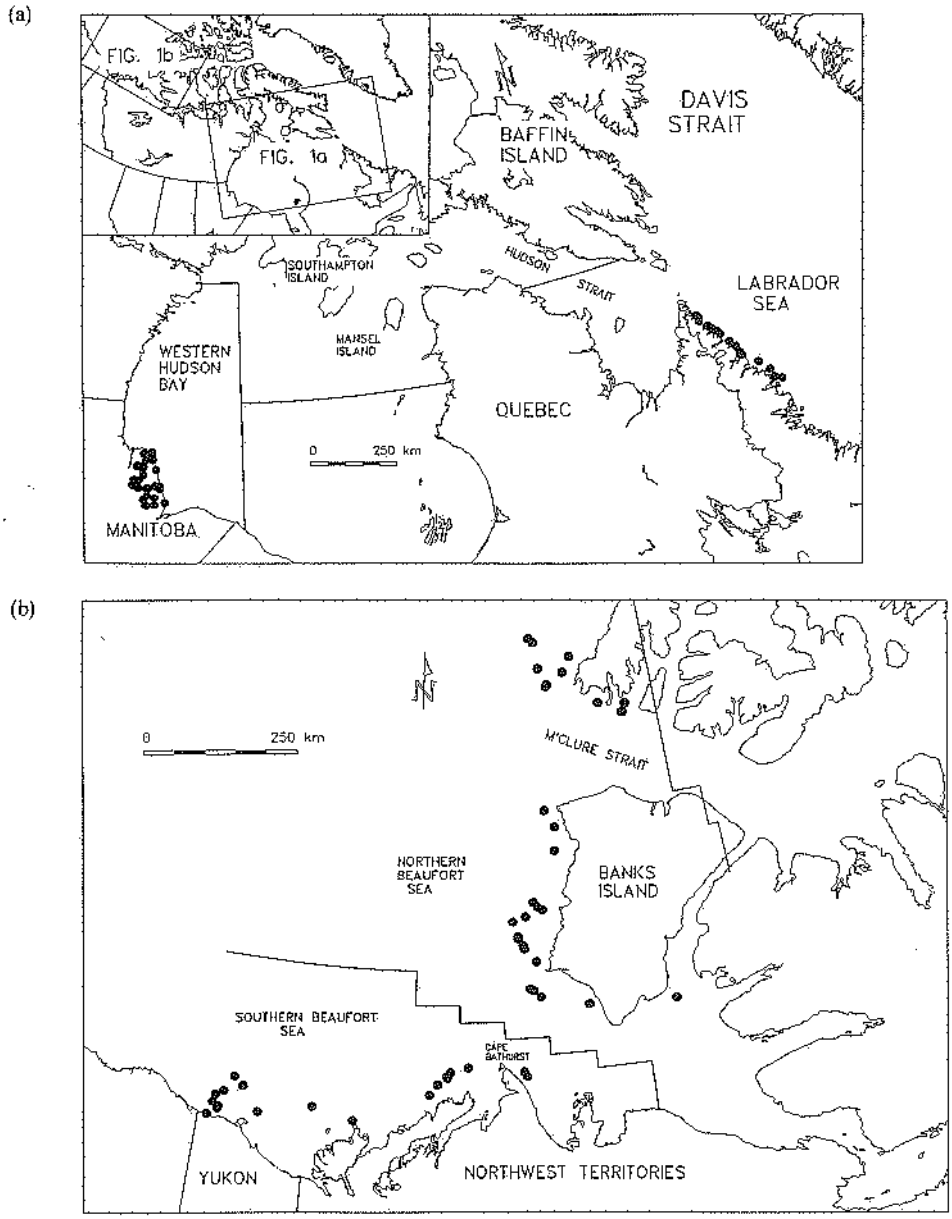

Fig. 1 (a) Map of the south-eastern Canadian Arctic showing sampling locations for the WH and DS populations. (b) Map of the Beaufort Sea region showing sampling locations for the SB and NB populations.

Table 1 Primer sequences listed 5′→3′. 'F' and 'H' denote the dye labels FAM and HEX (ABI), respectively

Locus	$(GT)_n$ strand primer	$(CA)_n$ strand primer	Allele cloned†	Number of repeats‡
G1A	FGACCCTGCATACTCTCCTCTGATG*	GCACTGTCCTTGCGTAGAAGTGAC	192	19.5
G1D	GATCTGTGGGTTTATAGGTTACA*	FCTACTCTTCCTACTCTTTAAGAG	176	17.5
G10B	FGCCTTTTAATGTTCTGTTGAATTTG	GACAAATCACAGAAACCTCCATCC	158	21
G10C	AAAGCAGAAGGCCTTGATTTCCTG	FGGGGACATAAACACCGAGACAGC	113	21.5
G10L	FGTACTGATTTAATTCACATTTCCC	GAAGATACAGAAACCTACCCATGC	165	34
G10M	TTCCCCTCATCGTAGGTTGTA	HGATCATGTGTTTCCAAATAAT	210	21
G10P	AGGAGGAAGAAAGATGGAAAAC	HTCATGTGGGGAAATACTCTGAA	159	21
G10X	CCCTGGTAACCACAAATCTCT	HTCAGTTATCTGTGAAATCAAAA	147	20.5

*The actual primers used in two cases were longer than listed, having been modified at the 5′ end to create restriction sites.
†To determine which allele was cloned, phage stocks were amplified and analysed under the same conditions used for genomic samples.
‡The number of uninterrupted tandem repeats observed in the sequence of cloned alleles

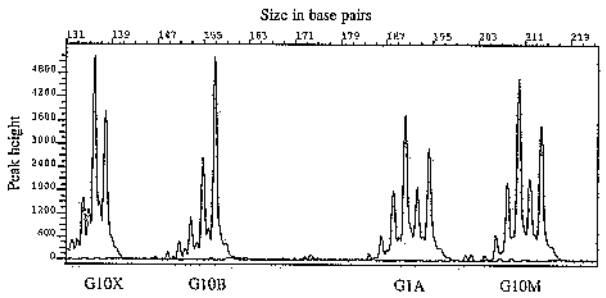

Fig. 2 Electropherogram from one lane of a polyacrylamide gel showing resolution of PCR products for four microsatellite loci. Sizes of sample peaks are determined relative to internal standards (Ziegle *et al.* 1992). Peak sizes may not correspond exactly to the actual length of PCR products due to the difference in base composition between the standard and the samples. This individual is heterozygous at locus G10X with two alleles sized at ~ 135 bases and 137 bases, respectively. Genotypes for loci G10B, G1A, and G10M are 156/156, 190/194, and 210/214, respectively. Smaller peaks two and four bases shorter than main peaks are an artefact of the amplification of dinulceotide repeats (Smeets *et al.* 1989). These 'shadow bands' do not interfere with the assignment of genotypes.

and 10L; and loci 10X and 10M. PCR cocktails were 0.16 μM for each primer, 1.9 mM $MgCl_2$, 50 mM KCl, 10 mM Tris-HCl (pH 9.0), 0.1% Triton X-100, 120 mM for each dNTP (160 mM when multiplexing by coamplification), and contained 0.5 U of *Taq* DNA polymerase, and 100 ng of genomic DNA. Cycling was carried out without an oil overlay in a Perkin Elmer Cetus 9600 thermal cycler. Samples were heated to 94 °C for 2 min followed by two cycles of 30 s at 94 °C, 20 s at 58 °C, and 1 s at 72 °C, and then 33 cycles which were identical except that the melting time was reduced to 15 s. Cycling was followed by 30 s at 72 °C.

After PCR, samples labelled with FAM were diluted 1 in 6 into samples labelled with HEX; the latter giving a weaker signal. This mixing allows multiplexing of more samples than can be coamplified together. 1.75 μL of each sample mixture was loaded on the gel in a formamide loading buffer along with an internal standard labelled with a third dye (GS2500 ROX, ABI). Data collection and analysis, as well as automatic sizing of bands, was done using Genescan 672 software supplied with the sequencer (Fig. 2).

Statistical methods

Expected heterozygosity and probability of identity were calculated using the formulae

$$h = 1 - (n\sum_i p_i^2 - 1)/(n-1)$$

(Nei & Roychoudhury 1974) and

$$I = \sum_i p_i^4 + \sum_i \sum_{j>i} (2p_i p_j)^2$$

respectively, where p_i and p_j are the frequencies of the ith and jth alleles in a given population. The observed numbers of heterozygotes and homozygotes – for each locus in each population – were tested against expected numbers using a χ^2 goodness-of-fit test (Hartl & Clark 1989). While this test does not explicitly test for Hardy–Weinberg equilibrium, it should detect the presence of null alleles (Callen *et al.* 1993), which have been found in other bear species at one of the loci used in this study (Paetkau & Strobeck, in press).

The homogeneity of allele distributions was tested using a G-test (Sokal & Rohlf 1981). Pairwise comparisons between all populations were made for each locus and values summed over all loci. Nei's standard genetic distance (Nei 1972) was also calculated between all population pairs.

In addition, a test was developed to determine how indicative an individual's genotype was of the population in which it was sampled. This 'assignment test' involved calculating the expected frequency of each individual's genotype in each of the four populations and subsequent assignment of each individual to the population where its expected genotype frequency was highest. The calculation was a simple product of expected genotype frequency at each of the eight loci, based on the observed distributions of alleles. This calculation assumes random mating and linkage equilibrium within each population.

The only modification made to calculations for the assignment test was that the allele distributions for each of the populations in which a given individual was not included (three out of four populations in each case) were modified by adding the individual's alleles to the distribution before undertaking calculations. This modification eliminates the bias resulting from the inclusion of each individual's genotype in the allele distribution for its own population. It also prevents getting expected genotype frequencies of zero as will occur any time an individual has a rare allele that is not present in a particular population's allele distribution. This modification should result in a conservative yet acceptable measure of interpopulation differences. A program was written in Filemaker Pro (Claris) to perform the calculations.

Results

Complete genotypes at eight microsatellite loci were determined for a total of 126 individuals. Multiplexing allowed 18 individuals to be completely typed on one gel. An added convenience was that the entire procedure from the isolation of microsatellites (Paetkau & Strobeck 1994) to the analysis of variation was done without radioactivity.

Considerable variation was observed at the eight microsatellite loci studied. Three measures of genetic diver-

sity were calculated (Table 2) based on observed allele distributions (Table 3). Between four and nine alleles were found at each locus in each population. Expected heterozygosity within populations, at individual loci, ranged from 25% to 84%, with mean expected heterozygosity near 60% in each population. Overall probability of identity – the probability that two individuals drawn at random from a given population have identical genotypes at all

Table 2 Measures of diversity: expected heterozygosity, probability of identity, and observed number of alleles, by locus and population. Overall values are 8-locus means for heterozygosity and number of alleles. The overall value for probability of identity is the product of individual values, and assumes linkage equilibrium between loci

	Heterozygosity				Probability of Identity				Number of Alleles			
Locus	SB	NB	WH	DS	SB	NB	WH	DS	SB	NB	WH	DS
G1A	0.757	0.787	0.459	0.413	0.105	0.083	0.338	0.390	6	6	5	5
G1D	0.626	0.642	0.612	0.619	0.195	0.179	0.200	0.197	5	6	4	4
G10B	0.785	0.754	0.440	0.653	0.092	0.102	0.354	0.162	6	6	4	6
G10C	0.251	0.398	0.703	0.495	0.584	0.396	0.134	0.299	4	6	6	6
G10L	0.324	0.338	0.485	0.355	0.484	0.483	0.306	0.464	4	4	5	4
G10M	0.815	0.771	0.795	0.752	0.071	0.092	0.078	0.108	7	7	7	7
G10P	0.713	0.700	0.790	0.769	0.120	0.123	0.086	0.088	7	9	5	7
G10X	0.859	0.754	0.723	0.823	0.047	0.103	0.118	0.062	7	7	7	8
Overall	0.642	0.643	0.626	0.610	2.1×10^{-7}	3.4×10^{-7}	7.7×10^{-7}	1.0×10^{-6}	5.75	6.38	5.38	5.88

Table 3 Observed allele frequency distributions by locus and population. MB refers to a sample of 18 individuals that were excluded from either SB or NB because of their proximity to the common boundary of these populations

		Population							Population				
Locus	Allele	SB	NB	MB	WH	DS	Locus	Allele	SB	NB	MB	WH	DS
G1A	190	0.409	0.350	0.500	0.083	0.173	G1D	180	0.068	0.017	0.056	0.133	0.135
	192	0.205	0.150	0.194	0.000	0.019		182	0.568	0.550	0.667	0.583	0.577
	194	0.114	0.233	0.139	0.717	0.750		184	0.136	0.200	0.111	0.133	0.154
	196	0.182	0.100	0.083	0.017	0.000		186	0.023	0.050	0.000	0.000	0.000
	198	0.023	0.050	0.056	0.167	0.038		188	0.205	0.150	0.167	0.150	0.135
	200	0.068	0.117	0.028	0.000	0.000		190	0.000	0.033	0.000	0.000	0.000
	202	0.000	0.000	0.000	0.017	0.019							
G10B	142	0.295	0.083	0.056	0.000	0.038	G10L	141	0.000	0.000	0.000	0.017	0.019
	150	0.045	0.017	0.111	0.067	0.096		143	0.000	0.000	0.000	0.033	0.019
	152	0.045	0.150	0.028	0.000	0.038		145	0.818	0.800	0.611	0.700	0.788
	154	0.295	0.417	0.500	0.150	0.115		147	0.091	0.167	0.278	0.133	0.173
	156	0.114	0.150	0.250	0.733	0.558		149	0.023	0.017	0.056	0.000	0.000
	158	0.205	0.183	0.056	0.050	0.154		151	0.068	0.017	0.056	0.117	0.000
G10C	101	0.000	0.000	0.000	0.017	0.000	G10M	200	0.114	0.033	0.028	0.083	0.058
	103	0.864	0.767	0.722	0.483	0.692		206	0.023	0.033	0.028	0.000	0.058
	105	0.091	0.133	0.111	0.000	0.038		208	0.205	0.383	0.306	0.133	0.096
	107	0.023	0.017	0.028	0.050	0.019		210	0.205	0.250	0.167	0.283	0.308
	109	0.023	0.050	0.083	0.150	0.173		212	0.023	0.117	0.083	0.067	0.058
	111	0.000	0.017	0.000	0.100	0.019		214	0.295	0.083	0.306	0.317	0.385
	113	0.000	0.000	0.000	0.200	0.058		216	0.136	0.100	0.083	0.033	0.038
	115	0.000	0.017	0.056	0.000	0.000		218	0.000	0.000	0.000	0.083	0.000
G10P	145	0.500	0.517	0.583	0.267	0.423	G10X	133	0.182	0.267	0.167	0.100	0.096
	147	0.045	0.017	0.000	0.200	0.077		135	0.159	0.050	0.083	0.183	0.135
	149	0.091	0.050	0.194	0.117	0.038		137	0.205	0.083	0.139	0.467	0.308
	151	0.091	0.033	0.000	0.133	0.154		139	0.000	0.000	0.000	0.000	0.038
	153	0.159	0.117	0.167	0.000	0.058		141	0.114	0.117	0.056	0.017	0.038
	155	0.091	0.117	0.000	0.283	0.154		143	0.182	0.400	0.417	0.150	0.231
	157	0.023	0.117	0.056	0.000	0.000		145	0.045	0.017	0.028	0.000	0.000
	159	0.000	0.017	0.000	0.000	0.096		147	0.114	0.067	0.111	0.067	0.038
	161	0.000	0.017	0.000	0.000	0.000		149	0.000	0.000	0.000	0.017	0.115

Table 4 Results of G-test (above diagonal) and Nei's (1972) genetic distance (below diagonal). Values for the G-test are χ^2 values (d.f.). All probabilities < 0.00001 except SB/NB ($P < 0.026$) and WH/DS ($P < 0.00005$)

	MB	SB	NB	WH	DS
SB	0.072		65 (43)	237 (44)	154 (46)
NB	0.055	0.058		286 (50)	189 (49)
WH	0.312	0.306	0.308		91 (43)
DS	0.204	0.184	0.186	0.050	

Table 5 Results of assignment test. The expected frequency of each individual's genotype was calculated and animals were assigned to the population in which their genotype was most likely to occur. Values are the number of animals from each population assigned to each of the four populations in the study

Source population	Assigned population			
	SB	NB	WH	DS
SB(22)	14	7	1	0
NB(30)	11	17	1	1
WH(30)	0	0	20	10
DS(26)	3	1	8	14

eight loci – ranged from 1.0×10^{-6} to 2.1×10^{-7} within the four populations. The χ^2 goodness-of-fit test was used to check for an excess of homozygotes at each locus, in each population (32 tests). None of the values obtained were significant at the 5% level.

Three measures of interpopulation differentiation were used (Table 4). The G-test gave highly significant results between all population pairs ($P < 0.001$) except NB and SB which were still significantly different ($P < 0.026$). Nei's genetic distances ranged from approximately 0.05–0.07 between geographically close populations to near 0.31 for the most widely separated populations. The results of the assignment test (Table 5) were that 65 individuals (60%) were correctly assigned to their populations, 36 individuals (33%) were assigned to the closest neighbouring population, and seven (6.5%) were assigned to a more distant population.

Discussion

Analysis of variation within populations

Previous genetic studies of polar bear populations have focused on variation in allozymes and mitochondrial DNA – methods which have consistently found little or no variation. By contrast, the microsatellite markers used in this study detect high levels of genetic variation, with mean expected heterozygosity over 60% in each population. Two continental Canadian black bear (*Ursus americanus*) populations surveyed at the same eight loci had mean expected heterozygosities of approximately 80% while the value for a population from insular Newfoundland was 41% (Paetkau & Strobeck 1994; D. Paetkau, unpublished data). Polar bears are clearly within the range of variability seen in these populations, although the somewhat reduced variation in polar bears relative to continental black bears is consistent with allozyme data (Allendorf *et al.* 1979; Larsen *et al.* 1983; Manlove *et al.* 1980; Wathen *et al.* 1985) which suggest that polar bears are less genetically variable than black bears.

The calculated probabilities of identity within populations – which were never higher than one in a million – are also impressive; particularly given that the global population estimate for polar bears is ~ 25 000 (Calvert *et al.* in press). The fact that microsatellite genotypes are likely to be unique to individuals makes them potentially useful in a variety of applications including analysis of paternity or family relatedness, and forensics. The general observation of high genetic diversity within populations also suggests potential utility in studies of population structure.

Structure of the metapopulation

Three methods were used to study deviations from panmixia in the total sample. The G-test unequivocally demonstrates that polar bear populations across their Canadian distribution are not genetically homogeneous. Perhaps the most impressive result is that a significant difference, although less dramatic, was detected between the two neighbouring populations in the Beaufort Sea.

Nei's genetic distance was used to quantify genetic differences between populations. This measure of population structure was chosen over statistics such as F_{ST} because the latter provide a single measure which contains no information about how any pair of populations compare to one another. Consistent with the results of the G-test, the genetic distance between the Beaufort populations and the distance between the two eastern populations are smaller than the distances between any other pair of populations.

One shortfall of the two measures of interpopulation difference described above is that it is difficult to get a conceptual grasp of their meaning. For example, what does a genetic distance of 0.3 mean biologically? An alternative approach is to ask whether sufficient differences exist between populations to make an individual's genotype characteristic, or even diagnostic, of the population from which it came. Since this type of question might aid in explaining the significance of results, we developed a simple test in which each animal in the population is assigned to the population where the expected frequency of its geno-

type is highest. We could then ask how often animals are correctly assigned to the area in which they were sampled and use this as an indication of population differentiation (see methods).

The result of this test was that 65 of 108 animals were correctly assigned to their populations. Consistent with the results of the conventional tests described above, however, only seven animals were misassigned from a Beaufort Sea population to an eastern population, or vice versa. Thus, with only eight microsatellite markers, genotypes are characteristic of populations and highly characteristic of regions. This result indicates that it may be possible, with the addition of more loci and improvement of databases, to identify the region of origin for polar bear samples; a finding of considerable importance for wildlife forensics.

Comparison to field data

A considerable amount of mark–recapture and telemetry data exist for all four study populations (Stirling *et al.* 1975, 1977, 1980, 1988; Stirling & Kiliaan 1980). As mentioned, these data suggest strong seasonal fidelity of individual bears to particular areas. Long-distance movements of individuals are recorded periodically, although not undertaken by most animals. For example, three animals first caught in WH were relocated outside the normal boundaries of the population: one on Southampton Island and two along the north-east coast of Hudson Bay (Stirling *et al.* 1977). Isolated movements of bears between the Labrador coast and northern Hudson Bay have also been recorded (Stirling & Kiliaan 1980). In the Beaufort Sea, mark-recapture and telemetry data support the division of SB from NB (Stirling *et al.* 1988) although rare movements of radiocollared animals from Alaska to the ice off the west coast of Banks Island prove that the isolation is not complete (Amstrup 1986).

The genetic implications of these field data are not obvious. For example, while we know that animals from both WH and DS move on occasion to the Southampton Island area, if these movements do not occur during the breeding season, they have no genetic consequence. On the other hand, while movements between populations may be rare, only a few migrants are required to genetically homogenize populations that are at equilibrium for migration and genetic drift.

Although it appears that the WH and DS populations are separate during the breeding season – in late winter and early spring – this separation is less clear for the NB and SB populations. During the breeding season these Beaufort Sea populations are concentrated along the shore leads off either the mainland or the western Banks Island coasts. Some overlap occurs in the areas between Cape Bathurst and Banks Island (Fig. 1) or along the open lead in the ice that forms each year during the breeding season between Banks Island and the mainland coast.

The microsatellite data presented here demonstrate that the ability of polar bears to undertake long-distance movements has not resulted in the complete genetic mixing of populations. Clearly the philopatry observed in field studies works to prevent frequent matings between individuals from different populations. These data suggest that there is a genetic basis to the population boundaries defined from data on seasonal movements.

In addition to corroborating existing population boundaries, the microsatellite data may provide insight on movement between the eastern and western extremes of the Canadian polar bear distribution. Both the G-test and genetic distance suggest a closer relationship between DS and the Beaufort Sea populations than between WH and the Beaufort Sea. By contrast, SB and NB are equidistant to WH and equidistant to DS. Furthermore, when the 18 animals sampled close to the SB/NB boundary – and therefore excluded from either population – are treated as a separate population (MB) and used for genetic distance calculations (Table 4), the distances obtained to WH and DS are nearly identical to the values calculated for SB and NB, adding support to the significance of this pattern.

The greater separation of WH than DS from the two Beaufort Sea populations suggests that gene flow between WH and the Beaufort Sea occurs through the populations along the east coast of Baffin Island. Implications about the path of gene flow from the Beaufort Sea populations to points further east are less obvious. Studies of genetic material from the Parry Channel and the Central Canadian Arctic could provide an interesting direction for further research.

The results described here also have broader implications for genetic studies in species, such as many large mammals, characterized by low genetic variation. High variation at microsatellite markers has been described in species with little genetic diversity (Hughes & Queller 1993), and microsatellites have been suggested as a tool for monitoring loss of variation in isolated or remnant populations (Paetkau & Strobeck 1994). The work described here on polar bears indicates that microsatellite analysis can be highly informative for studying genetic structure in populations possessing insufficient diversity to be amenable to study with other techniques.

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