Genetic variation and relatedness in grizzly bears in the Prudhoe Bay region and adjacent areas in northern Alaska

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Abstract: The Prudhoe Bay region of northern Alaska has large oil fields and hunting on adjacent lands, and there are concerns about potential effects on grizzly bears (*Ursus arctos*) in this region. Because effects on grizzly bear populations may include loss of genetic variation, we assessed the genetic variation and family relationships among grizzly bears in this region as part of a long-term research and monitoring project. We determined genotypes at 14 microsatellite DNA loci for 78 bears from the Prudhoe Bay region from samples collected 1990–2002. The genetic data identified one or both potential parents of 33 offspring. Potential parent–offspring and siblings had pair-wise relatedness indices of approximately 0.5, as expected. The entire sample of related and unrelated bears in the Prudhoe Bay region had a mean pair-wise relatedness index of approximately zero. Approximately 5.3% of the bears had relatedness indices within the range of first-order relatives (parent–offspring or siblings). Genetic differentiation is low ($F_{st} = 0.0225$) among the bears in the Prudhoe Bay region and neighboring areas of the western Brooks Range and the Arctic National Wildlife Refuge. Bears in the Prudhoe Bay region have a high level of genetic variation relative to some other areas in North America. High genetic variation and low relatedness among individual bears in the Prudhoe Bay region are probably maintained by a stable population size with gene flow across the North Slope of Alaska. Our data indicate that reduction of genetic variation in the grizzly bears in the Prudhoe Bay region is not presently a management concern.

Key words: Alaska, genetic variation, grizzly bear, microsatellite DNA, pedigree, Prudhoe Bay oil fields, *Ursus arctos*

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Grizzly bears (*Ursus arctos*) have been the subject of considerable management and research interest because their numbers and range have been dramatically reduced in much of North America (Servheen et al. 1999). The grizzly bear population on Alaska's North Slope of the Brooks Range has been generally stable, but there are management concerns about grizzly bears in and around the oil fields in the Prudhoe Bay region (Shideler and Hechtel 2000; Fig. 1). Oil exploration and production has been ongoing in the Prudhoe Bay region since the 1970s, and potential impacts of this development may include disturbance and mortality caused by humans (Shideler and Hechtel 2000, National Research Council 2003). Mortality may occur when bears are killed from collisions with vehicles and in defense of human life and property. Mortality from hunting harvest may also increase when bears regularly use human food and garbage, habituate to human activity, and become less wary of people.

Elevated levels of mortality and population reductions can reduce genetic variation in grizzly bear populations under some conditions. For example, grizzly bears in the Yellowstone National Park region have a small population size (<1,000 animals, Harris and Allendorf 1989) and are geographically isolated from other grizzly bears (Miller and Waits 2003), which may have resulted in a relatively low level of genetic variation (Paetkau et al. 1998*a*, Waits et al. 1998*a*). Loss of genetic variation can

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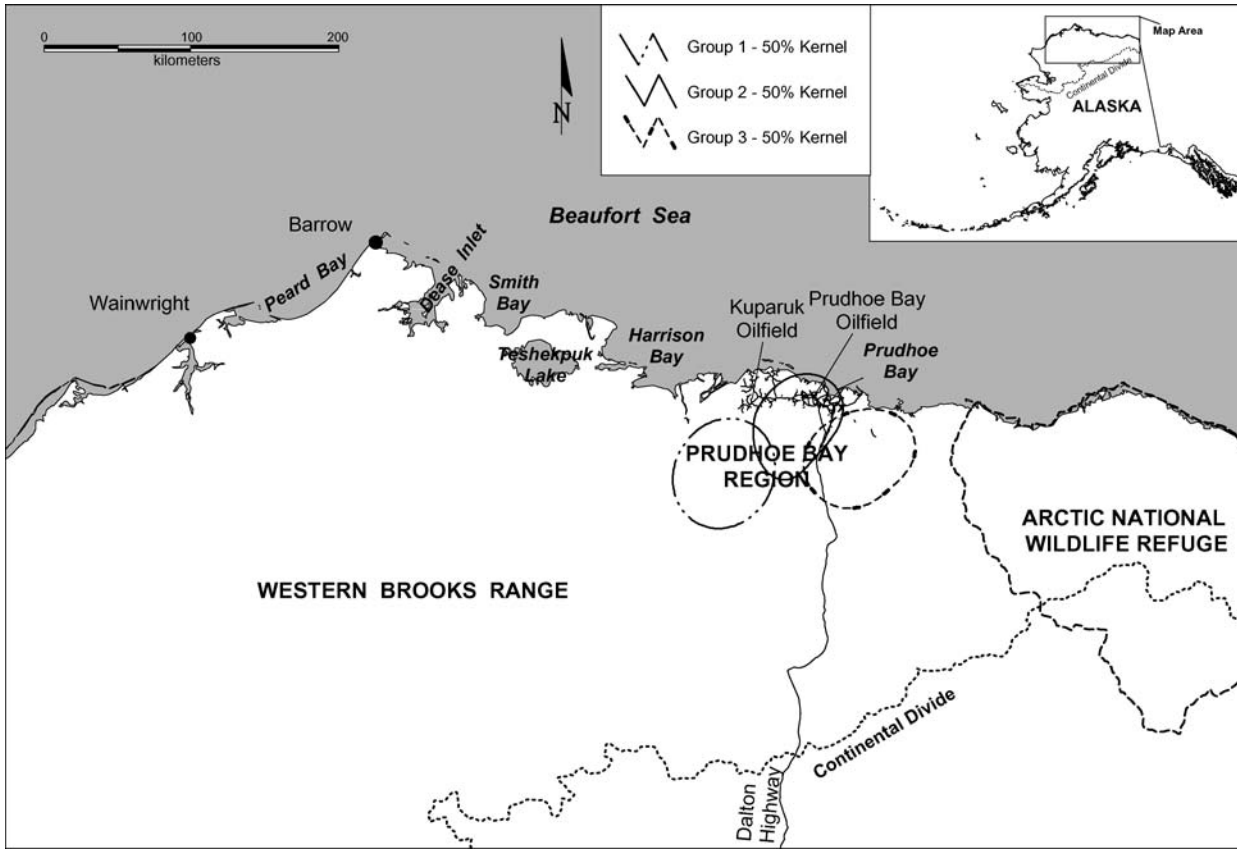

Fig. 1. Map of northern Alaska's Prudhoe Bay region, neighboring western Brooks Range and Arctic National Wildlife Refuge, from which grizzly bears were sampled, 1990–2002. The polygons represent the areas in which 50% of the field observations of members of a group occurred.

result in problems such as inbreeding depression that are associated with small, isolated populations (Charlesworth and Charlesworth 1987, Crnokrak and Roff 1999), including populations of brown bears (Laikre et al. 1996). Therefore, monitoring levels of genetic variation and population structure in grizzly bear populations can provide useful information for managers (Miller and Waits 2003).

Cronin et al. (1999) showed that grizzly bears in the Prudhoe Bay region have high levels of genetic variation and gene flow with bears in adjacent areas. This study included analysis of mitochondrial DNA (mtDNA) and microsatellite DNA variation of bears born prior to 1994. However, the ecology of the area was changed during the late 1990s when bears' access to garbage was restricted after a fence was erected around the dump and bear-proof dumpsters were installed in the oil fields. There was increased mortality of bears from hunting and from defense of human life and property and following these actions, and there are concerns about impacts on the population from this increased mortality (National Research Council 2003). A long-term ecological study of grizzly bears in the oil field region was implemented (Shideler and Hechtel 2000) to provide information for impact assessments and adaptive management as conditions change, as in the 1990s. Because genetic impacts can accompany demographic impacts, as described above for grizzly bears in the Yellowstone region, monitoring genetic variation was included as a component of this study. In this paper we describe the continuation of this genetic monitoring program initially reported by Cronin et al. (1999). We analyzed the same 14 microsatellite DNA loci used in the earlier study and increased the sample size by 42 bears from the Prudhoe Bay region. We also compared bears in the Prudhoe Bay region with those in adjacent regions. Our objectives were to quantify genetic variation and family-level relationships of grizzly bears in the Prudhoe Bay region and to assess

genetic differentiation of bears in the Prudhoe Bay region with bears in adjacent undeveloped areas. This information will contribute to a better understanding of the population dynamics of grizzly bears on the North Slope of Alaska and provide baseline information for assessing impacts of human developments in the Prudhoe Bay region.

Materials and methods

Between 1990 and 2002 we collected tissue samples (ear tissue and blood during live-captures, muscle from hunter-kills) from 72 bears captured by biologists (Shideler and Hechtel 2000) and 6 bears killed by hunters in the Prudhoe Bay region of Alaska. The samples included 40 males, 35 females, and 3 (hunter-kills) with unidentified sex. Thirty-six of the bears were analyzed previously (Cronin et al. 1999) and 42 of the bears were new. Mother–offspring and sibling relationships of some bears were identified from field observations. Ages of bears were determined by counting cementum annuli in excised vestigial premolar teeth (Matson et al. 1993). Genotypes for 14 microsatellite DNA loci (Table 1) were determined for the 78 bears with the laboratory methods described previously (Paetkau et al. 1998*a*, Cronin et al. 1999). Genetic variation (mean number of alleles per locus, *A*, observed heterozygosity, H_o, and estimated heterozygosity, H_e) was quantified with the Microsatellite Toolkit computer program (Park 2001). Exact tests of Hardy-Weinberg equilibrium were done with the GENEPOP program (Raymond and Rousset 1995), and F_{is}, a measure of heterozygote deficiency or excess (Weir and Cockerham 1984), was calculated. Analysis of linkage disequilibrium of the 14 microsatellite loci was also done with GENEPOP.

Pair-wise relatedness indices (r_{xy}, Queller and Goodknight 1989) between bears were determined with the Kinship 1.1.2 computer program (Goodknight Software, Rice University, Houston, Texas, USA). Potential parent–offspring genetic relationships were determined with the Kinship program and the CERVUS program (Marshall et al. 1998). First, pair-wise comparisons of all bears were made to determine whether they shared at least one allele per locus, and hence were not excluded as parent–offspring. Sharing one allele per locus does not verify a parent–offspring relationship, but indicates it is possible. Bears that shared at least one allele per locus were considered non-excluded. We then considered non-excluded pairs as potential parent–offspring only if the parent was alive and old enough to breed at the time of conception of the offspring. Previous studies suggest that for grizzly bears in northern Alaska, females and males begin breeding at 4 and 8 years of age, respectively (Craighead et al. 1995*a*, Cronin et al. 1999, Shideler and Hechtel 2000). To assess the likelihood of parentage, we calculated LOD scores (the sum of log likelihood ratios at each locus) for potential parent–offspring pairs with CERVUS. The potential parent–offspring pair with the highest LOD score includes the most likely parent. We calculated delta scores (the highest LOD score minus the second highest LOD score) and the 0.8 and 0.95 statistical confidence levels for the delta scores. LOD scores were calculated separately for potential fathers, potential mothers, and non-excluded pairs that did not meet the age–sex criteria as potential parents. For calculations involving potential father–offspring pairs with a known or suspected mother, we included the mother's genotypes in the analysis. Thus, we identified potential parent–offspring pairs with field observations and genetic data considering non-exclusion and likelihood. With this information we constructed a putative pedigree of related bears in the Prudhoe Bay region.

In addition to the pair-wise analysis of relatedness and parentage among individual bears, we calculated the probability of exclusion of parentage for the population with the CERVUS program. This is the probability that 2 unrelated individuals drawn at random from the population would be expected to have alleles in common at every locus (Paetkau and Strobeck 1998). We also calculated the probability of identity of individuals (the probability that 2 bears shared the same genotypes at all 14 loci, Paetkau et al. 1998*a*) and the probability of identity of sibs (Waits et al. 2001) with the GIMLET computer program (Valiere 2002). The latter is a conservative estimator of the probability of identity of individuals that addresses problems associated with microsatellite analyses (Waits et al. 2001).

We compared genetic variation (mean *A*, H_o, H_e) of bears in the Prudhoe Bay region with data reported by others (Craighead 1994; Craighead et al. 1995*a*; Paetkau et al. 1997, 1998*a*, D. Paetkau personal communication) for bears in the adjacent western Brooks Range and Arctic National Wildlife Refuge (ANWR). These areas do not have industrial developments, but the bears are subject to varying levels of hunting. Genotypes for bears in the ANWR and western Brooks Range are available for 8 of 14 microsatellite loci we used on bears in the Prudhoe Bay region (loci: G1A, G1D, G10B, G10C, G10L, G10M, G10P, G10X, Table 1). Differences in heterozygosity were compared among these 3 areas with

Table 1. Genetic variation measures for 14 microsatellite DNA loci, including number of alleles (*A*), allelic richness, observed heterozygosity (H_o), expected heterozygosity (H_e), and F_{is} in grizzly bears in 3 regions of northern Alaska. Data for the Arctic National Wildlife Refuge and western Brooks Range are from Craighead (1994), Craighead et al. (1995*a*), Paetkau et al. (1997, 1998*a*), and D. Paetkau (Wildlife Genetics International, Nelson, British Columbia, Canada, personal communication).

	Region		
Locus	Prudhoe Bay (n = 78)	Arctic National Wildlife Refuge (n = 24)	Western Brooks Range (n = 148)
Locus G1A			
A	9	8	8
H_o	0.844	0.792	0.764
H_e	0.742	0.834	0.729
F_{is}	−0.1381	0.0521	−0.0481
Locus G10B			
A	9	8	9
H_o	0.756	0.792	0.791
H_e	0.798	0.819	0.767
F_{is}	0.0527	0.0343	−0.0304
Locus G10C			
A	8	7	7
H_o	0.679	0.667	0.784
H_e	0.770	0.692	0.743
F_{is}	0.1182	0.0379	−0.0544
Locus G1D			
A	10	8	10
H_o	0.846	0.917	0.878
H_e	0.816	0.874	0.848
F_{is}	−0.0376	−0.0498	−0.0361
Locus G10L			
A	7	3	6
H_o	0.526	0.625	0.662
H_e	0.627	0.547	0.671
F_{is}	0.1632	−0.1462	0.0129
Locus G10M			
A	7	6	7
H_o	0.731	0.708	0.743
H_e	0.756	0.744	0.701
F_{is}	0.0333	0.0487	−0.0611
Locus G10P			
A	9	7	8
H_o	0.769	0.958	0.791
H_e	0.800	0.843	0.793
F_{is}	0.0393	−0.1401	0.0034
Locus G10X			
A	6	6	6
H_o	0.744	0.750	0.784
H_e	0.722	0.754	0.744
F_{is}	−0.0302	0.0060	−0.0538
8-locus totals			
A (SD)	8.13 (1.36)	6.63 (1.69)	7.63 (1.41)
Allelic	6.99 (1.32)	6.46 (1.43)	6.82 (1.05)
Richness (SD)			
H_o (SD)	0.7369 (0.0176)	0.7760 (0.0301)	0.7745 (0.0121)
H_e (SD)	0.7540 (0.0213)	0.7635 (0.0376)	0.7495 (0.0194)
F_{is}	0.0230	−0.0168	−0.0335
Locus CXX20			
A	9		
H_o	0.632		
H_e	0.684		
F_{is}	0.0770		
Locus MU50			
A	8		
H_o	0.782		
H_e	0.821		
F_{is}	0.0477		
Locus MU59			
A	11		
H_o	0.461		
H_e	0.527		
F_{is}	0.1787		
Locus G10H			
A	13		
H_o	0.538		
H_e	0.649		
F_{is}	0.1707		
Locus G10J			
A	5		
H_o	0.590		
H_e	0.696		
F_{is}	0.1540		
Locus G10O			
A	6		
H_o	0.590		
H_e	0.643		
F_{is}	0.0838		
14-locus totals			
A (SD)	8.36 (2.13)		
H_o (SD)	0.6777 (0.0142)		
H_e (SD)	0.7204 (0.0214)		
F_{is}	0.0596		

a pair-wise *t*-test of the means of the arcsine-transformed H_o and H_e values for each locus (Waits et al. 2000). We compared the allelic richness (the numbers of alleles standardized according to sample sizes; El Mousadik and Petit 1996, Petit et al. 1998) among these regions with a pair-wise *t*-test of the means of the values for the 8 loci with the F-STAT program (Goudet 1995). We also quantified genetic differentiation of bears from these areas with pair-wise and overall F_{st} estimates using the GENEPOP program and analysis of molecular variance (AMOVA, Weir and Cockerham 1984, Excoffier et al. 1992).

Results

Genetic variation in the Prudhoe Bay region

Among the 14 microsatellite loci analyzed in 78 grizzly bears in the Prudhoe Bay region, there were 5–13 alleles per locus with a mean number of alleles (A) of 8.36 (Table 1). Allele frequencies for the 14 loci are in the Appendix. No bears had identical genotypes at all 14 loci, the probability of identity of individuals was 1.5×10^{-14}, and the probability of identity of sibs was 5.2×10^{-6}. The observed heterozygosity (H_o) ranged from 0.46 to 0.85 across the 14 loci, with the mean $H_o = 0.68$ (Table 1). The mean expected heterozygosity (H_e) was 0.72 (Table 1). Significant deviation from Hardy-Weinberg genotype distributions occurred for the G10A ($P = 0.016$), G10H ($P < 0.0000$), G10L ($P = 0.0012$), and MU59 ($P < 0.0000$) loci. The G10A locus had more heterozygotes than expected, whereas the other 3 loci had fewer heterozygotes than expected. The other 10 loci were in Hardy-Weinberg equilibrium. Of 91 tests for linkage disequilibrium, 24 (26%) were significant ($P < 0.05$).

Genetic relationships in the Prudhoe Bay region

Parent–offspring relationships were inferred for non-excluded bears sharing at least 1 allele per locus if the putative parent was alive and old enough at the time of conception of the offspring. The probability of exclusion of parentage with neither parent known was 0.9967, and with 1 parent known it was 0.9999, which means that pairs that are not parent–offspring will not share 1 allele/locus >99% of the time. The genetic data identified 1 or both potential parents of 8 sets of twins, 1 set of triplets, and 14 single offspring, for a total of 33 offspring (Table 2, Fig. 2). The relatedness of the potential parent–offspring pairs was close to the expected value of 0.5 (mean $r_{xy} = 0.5166$, SD = 0.0962). In 7 cases, both parents were inferred from the genetic data (single offspring 4, 32, 30; twins 61–62, 15–16, 11–12, 55–52; Fig. 2).

Of the 35 females sampled, 8 were identified as potential mothers (Table 2, Fig. 2). These 8 females and their offspring comprised 28 potential mother–offspring pairs (Table 2), of which 20 were known or suspected from field observations. The ages of these mothers at breeding ranged from 4 to 21 years old, a range similar to those previously reported for Arctic Alaska grizzly bears (Craighead et al. 1995*a*, Cronin et al. 1999). There was considerable variation in the number of offspring produced by females. Female 2 had 8 offspring with 3 or 4 males. Only 7 of female 2's 8 offspring are indicated in Table 2 because there are no genetic data for 1 of them (number 8 was identified as number 2's offspring with field observation). Female 21 had 6 offspring from 4 males, including 2 litters with 1 male (number 20). Female 1 had 4 offspring from 3 males, 1 that was her father (number 20). Female 19 had 4 offspring in 3 litters from unknown males. Female 4 had 2 possible offspring from 1 male, her father (number 20). Females 10 and 38 each had 2 offspring from 1 male, and number 49 had 1 offspring. The mean relatedness of mother–offspring pairs was close to 0.5, as expected ($r_{xy} = 0.5023$, SD = 0.0866).

For 24 of the 28 mother–offspring pairs, the mother was the only female not excluded with the genetic data that was old enough to be the mother. For 4 of the 28 offspring (bears 6, 23, 52, 72), 2 females were not excluded as mothers with the genetic data. However, in these cases, 1 of the females was suspected as the mother from field observation (Table 2) and the other female was excluded for other reasons (Table 3).

The LOD scores of the mother–offspring pairs identified were all positive, indicating high likelihood of correct parentage assignment (Table 2). For 24 of the 28 mother–offspring pairs, the mother we identified had the highest LOD score and was the most likely mother. Sixteen of these 24 pairs had LOD scores at the 0.95 confidence level, 6 had LOD scores at the 0.80 confidence level, and 2 had LOD scores below the 0.80 confidence level (Table 2). Four of the mother–offspring pairs we identified did not have the highest LOD score of the females that were old enough to be the mother but were considered the most likely mother for other reasons. One of these was the only non-excluded mother (number 2) for offspring number 1 and was suspected of being the mother from field observations. The female with the highest LOD score (number 49) was excluded by not sharing at least 1 allele per locus

Table 2. Potential parent–offspring pairs of grizzly bears in the Prudhoe Bay region, Alaska identified with genetic and field data collected 1990–2002.

Parent	Sex	Birth year (breeding age[a])	Offspring	Sex	Birth year	Relation from field data	Non-excluded parents	r_{xy}	LOD	Delta
Potential mothers										
1	F	1987 (4)	23	F	1992	Suspected	2	0.5652	6.88	2.19
1	F	1987 (8)	52	M	1996	Suspected	2	0.5997	5.38	1.83[b]
1	F	1987 (8)	55	F	1996	Suspected	1	0.5012	6.16	2.22[c]
1	F	1987 (12)	72	M	1999	Suspected	2	0.4963	3.9	3.48[b]
2	F	1976 (10)	1	F	1987	Suspected	1	0.4962	3.95	2.54[b]
2	F	1976 (10)	6	F	1987	Suspected	2	0.4235	3.72	1.91[b]
2	F	1976 (13)	9	F	1990	Known	1	0.5677	5.01	2.29[c]
2	F	1976 (16)	24	M	1993	Suspected	1	0.4841	5.22	3.89[d]
2	F	1976 (16)	25	F	1993	Suspected	1	0.4356	4.5	4.50[d]
2	F	1976 (16)	27	F	1993	Suspected	1	0.5196	6.38	3.01[c]
2	F	1976 (20)	48	F	1996	Suspected	1	0.3847	3.47	1.41
4	F	1986 (5)	11	F	1992	Known	1	0.6447	6.27	1.48[c]
4	F	1986 (5)	12	M	1992	Known	1	0.6217	6.11	4.06[d]
10	F	1984 (7)	15	F	1992	Known	1	0.3776	5.4	5.40[d]
10	F	1984 (7)	16	F	1992	Known	1	0.4204	4.81	4.81[d]
19	F	1980 (12)	17	F	1993	Suspected	1	0.4242	5.58	5.49[d]
19	F	1980 (12)	18	F	1993	Suspected	1	0.5236	6.68	5.68[d]
19	F	1980 (18)	7	F	1989	Unknown	1	0.5709	8.04	8.04[d]
19	F	1980 (10)	37	F	1991	Unknown	1	0.3209	1.91	1.91[c]
21	F	1976 (9)	4	F	1986	Unknown	1	0.4459	5.17	4.86[d]
21	F	1976 (7)	10	F	1984	Unknown	1	0.5012	5.85	5.85[d]
21	F	1976 (16)	30	M	1993	Known	1	0.6305	8.02	5.00[d]
21	F	1976 (12)	32	F	1989	Unknown	1	0.3789	5.64	2.75[c]
21	F	1976 (21)	61	F	1998	Suspected	1	0.6052	6.67	3.63[d]
21	F	1976 (21)	62	F	1998	Suspected	1	0.5746	8.13	5.48[d]
38	F	1972 (21)	40	M	1994	Unknown	1	0.4636	5.39	5.39[d]
38	F	1972 (21)	41	M	1994	Unknown	1	0.5817	7.28	6.84[d]
49	F	1979 (12)	104	F	1992	Unknown	1	0.5052	7.99	7.47[d]
Mean (SD) mothers								0.5023 (0.0866)		
Potential fathers										
14	M	1981 (10)	15	F	1992	Unknown	1	0.4394	11.65	11.65[d]
14	M	1981 (10)	16	F	1992	Unknown	1	0.5251	8.86	8.86[d]
20	M	1973 (15)	32	F	1989	Unknown	1	0.3837	3.56	3.56[d]
20	M	1973 (22)	52	M	1996	Unknown	1	0.4641	−3.02	N/A
20	M	1973 (22)	55	F	1996	Unknown	1	0.4628	−6.34	N/A
20	M	1973 (12)	4	F	1986	Unknown	1	0.4913	4.48	4.48[d]
20	M	1973 (13)	1	F	1987	Unknown	1	0.6012	10.84	10.84[d]
20	M	1973 (13)	6	F	1987	Unknown	1	0.6334	11.48	11.48[d]
20	M	1973 (18)	11	F	1992	Unknown	1	0.7401	11.07	11.07[d]
20	M	1973 (18)	12	M	1992	Unknown	1	0.7556	9.79	9.79[d]
31	M	1984 (8)	30	M	1993	Unknown	1	0.5041	11.33	11.33[d]
54	M	1986 (11)	61	F	1998	Unknown	1	0.574	11.13	11.13[d]
54	M	1986 (11)	62	F	1998	Unknown	1	0.542	9.01	9.01[d]
Mean (SD) fathers								0.5474 (0.1116)		
Mean (SD) all parent–offspring								0.5166 (0.0962)		

[a]Minimum breeding age of 4 for females and 8 for males (Cronin et al. 1999).
[b]Not the highest LOD score for potential mothers for this offspring.
[c]80% confidence level.
[d]95% confidence level.

with offspring number 1. In 2 cases the sibling (number 6) of the field-identified mother (number 1) had the highest LOD score for offspring numbers 52 and 72. In the fourth case, the mother (number 1) of bear 72 was identified by field observation and had the second-highest LOD score. The female (number 11) with the highest LOD score was dead at the time of conception of number 72 (Table 3).

There is congruence between the relatedness of matriarchal groups identified in the pedigree (Fig. 2) and home ranges (Fig. 1). The polygons on the map represent the area in which the bears in each group were located in 50% of field observations. The bears in group 1 (7, 17, 18, 19, 37) have home ranges centered in the western part of the Prudhoe Bay region and occur in a distinct matriarchal lineage in the pedigree. The bears in group 2 (1, 2, 6, 23) have home ranges centered in the middle of the Prudhoe Bay region and occur in a matriarchal lineage in the central part of the pedigree. The bears in group 3 (10, 15, 16, 21, 32, 46) have home ranges centered in the eastern part of the Prudhoe Bay region, and except for number 46, they occur in a matriarchal lineage on the right side of the pedigree. These data demonstrate overlapping home ranges of females and some of their daughters.

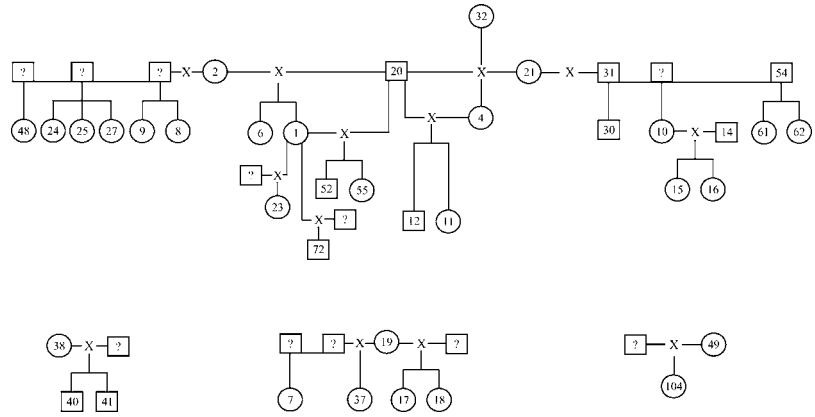

Fig. 2. Pedigrees of related bears in the Prudhoe Bay region of northern Alaska, showing the sample numbers of individual bears (Table 2). Squares denote males and circles denote females, ? denotes unknown fathers, and X denotes a mating relationship.

Of the 40 males sampled, 4 were identified as potential fathers (Table 2, Fig. 2). These 4 males and their offspring comprised 13 potential father–offspring pairs (Table 2), none of which were known or suspected from field observations. There was considerable variation in the number of offspring produced by different males. Male 20 produced the most offspring, including 8 in 5 litters (Table 2, Fig. 2). The data suggest that male 20 mated with 2 of his daughters (4 and 1) to produce 4 offspring in 2 litters (11, 12; 52, 55). The relatedness indices for male 20 and bears 11 and 12 (Table 2) are close to that expected for father–daughter mating (i.e., $r_{xy} = 0.75$). The relatedness indices for male 20 and bears 52 and 55 are of the magnitude expected for non-incestuous parent–offspring relationship (i.e., $r_{xy} = 0.5$). Other potential fathers are males 14 and 54 that each had 2 offspring from 1 female and male 31 that had 1 offspring. The mean relatedness of father–offspring pairs was close to 0.5, as expected ($r_{xy} = 0.5474$, SD = 0.1116).

All 13 father–offspring pairs included the only male old enough to be the father that was not excluded with genetic data. LOD scores support 11 of 13 father–offspring pairs identified (Table 2). These 11 pairs included the most likely father (had the highest LOD score) of the males old enough to be the father, and the LOD scores were at the 0.95 confidence level. The other 2 father–offspring pairs (20 and 52; 20 and 55) had negative LOD scores, despite being non-excluded as parent–offspring.

There were 25 additional pairs not excluded as parent–offspring with the genetic data, but they were excluded for other reasons (Table 3). In 20 cases the potential parent was too young to breed (according to our criteria of minimum breeding ages of 4 years old for females and 8 years old for males) or the pair were siblings. In the other 5 cases, the potential mother was excluded as the parent of the offspring's known littermate, was dead at the time of conception of the offspring, or another bear was known or suspected to be the mother from field observations. The mean r_{xy} of these 25 pairs was 0.5170 (SD = 0.1447), so these bears were probably related in some way. Six of the non-excluded pairs involved males 4–7 years old (5, 12, 20, 47, 70, and 100; Table 3). It is possible these males were the parents, but this would require breeding at <8 years old, so these relationships are tentative.

Twenty-three bears were identified as potential siblings from field observations (Fig. 2, Table 4). This included 8 sets of twins and 1 set of triplets for which parents were identified. Siblings 4 and 32 were in litters in different years from the same parents (the same adults mated in 2 different years). In addition, 2 bears for which no parents were identified were identified as siblings in the field (3 and 5). The mean relatedness of siblings was close to 0.5 as expected ($r_{xy} = 0.5209$, SD = 0.1173). Using the pedigree (Fig. 2), we also identified half-siblings (pairs that share only 1 parent). The mean relatedness of 47 pairs of potential half-siblings

Table 3. Grizzly bears from the Prudhoe Bay region, Alaska that are not excluded as parent–offspring pairs based on genotypes at 14 microsatellite DNA loci but are excluded by age or other reasons.

Bear	Sex	Birth year (breeding age)	Bear	Sex	Birth year	Relation, reason excluded	r_{xy}	LOD	Delta
1	F	1987 (1)	32	F	1989	Age	0.2351	0.82	1.02[a]
1	F	1987 (0)	6	F	1987	Siblings	0.7423	7.27	1.64[b]
1	F	1987 (2)	100	M	1990	Age	0.4921	4.22	5.82[a]
2	F	1976 (11)	3	M	1988	[c]	0.4532	3.23	2.02[b]
3	M	1988 (0)	5	M	1988	Siblings	0.6553	7.66	7.66[d]
3	M	1988 (2)	33	M	1991	Age	0.2768	1	1
3	M	1988 (3)	104	F	1992	Age	0.3325	3.43	3.43[d]
4	F	1986 (2)	32	F	1989	Age	0.5046	4.63	1.02[a]
5	M	1988 (7)	64	M	1996	Age	0.7362	7.5	7.50[d]
6	F	1987 (1)	32	F	1989	Age	0.3238	1.8	1.02[a]
6	F	1987 (8)	52	M	1996	[e]	0.584	5.56	0.18
6	F	1987 (2)	100	M	1990	Age	0.525	4.42	5.82[a]
6	F	1987 (4)	23	F	1992	Suspected aunt/niece[f]	0.6495	6.66	2.19[a]
7	F	1989 (3)	17	F	1993	Age	0.4188	6.43	0.84
11	F	1992 (6)	72	M	1999	[g]	0.6871	7.9	3.48[d]
12	M	1992 (6)	72	M	1999	Age	0.7337	12.1	9.74[d]
23	F	1992 (1)	100	M	1990	Age	0.5566	4.64	5.82[a]
27	F	1993 (2)	100	M	1990	Age	0.5159	5.22	0.58
20	M	1973 (5)	49	F	1979	Age	0.5952	7.17	7.17[d]
47	M	1991 (4)	48	F	1996	Age	0.4148	−1.4	N/A
49	F	1979 (7)	6	F	1987	[h]	0.4409	5.63	1.64[a]
52	M	1996 (2)	72	M	1999	Age	0.4932	3.82	2.46[a]
52	M	1996 (0)	55	M	1996	Siblings	0.4412	1.46	1.46[b]
70	M	1989 (6)	48	F	1996	Age	0.6806	10.53	10.53[d]
100	M	1990 (5)	52	M	1996	Age[i]	0.4371	−3.11	N/A
Mean (SD)								0.5170 (0.1447)	

[a]Not the highest LOD score for potential mothers for this offspring.
[b]80% confidence level.
[c]2 is excluded as mother of 5; 3 and 5 are siblings, so 2 can not be mother of 3.
[d]95% confidence level.
[e]6 is excluded as mother of 55, and 52 and 55 are siblings, so 6 can not be mother of 52.
[f]6 is not excluded as the mother of 23, but field observations suggested that number 6's sibling, number 1, is the mother of number 23, so 6 is 23's aunt.
[g]11 was dead at the time of number 72's conception, so can not be the mother of 72.
[h]49 is excluded as mother of 1, and 1 and 6 are siblings, so 49 can not be mother of 6.
[i]100 is excluded as the father of 55, and 55 and 52 are siblings, so 100 not the father of 55 unless there is multiple paternity. In addition, 100 was young for a male bear to breed.

(excluding those from the mating of number 20 with his daughters numbers 1 and 4) was close to the expected value of 0.25 ($r_{xy} = 0.2371$, SD = 0.1553).

The mean relatedness for the entire sample of 78 bears (3003 pair-wise r_{xy} values) was close to zero (mean $r_{xy} =$ 0.0003, SD = 0.1862). For the entire sample, the large standard deviation compared to the mean reflects a mix of related and unrelated bears. To estimate the proportion of related bears in the sample, we determined the proportion of pair-wise r_{xy} values within 2 standard deviations of the mean for the parent–offspring pairs (Table 2, i.e., $r_{xy} =$ 0.3242–0.7090). We considered this a conservative spread of r_{xy} values of potential first order relatives (expected $r_{xy} = 0.5$). The spread between 2 standard deviations of the parent–offspring mean is close to the actual arithmetic range of r_{xy} values for the potential parent–offspring pairs (0.3209–0.7556, Table 2). Of the 3003 pair-wise r_{xy} values, 159 (5.3%) were within 2 standard deviations of the mean of the entire sample. Only 5 (0.2%) r_{xy} values exceeded the mean plus 2 standard deviations (>0.7090). Two of these high values were for male 20 and his offspring (bears 11, 12) resulting from mating with his daughter, bear 4 (Table 2, Fig. 2). Another high r_{xy} value (0.7423) was for siblings, 1 and 6. The other high values were for non-excluded pairs (pairs 64 and 5; 72 and 12) in which the potential father may

have been too young to breed (Table 3). The other 2,839 (94.5%) r_{xy} values were less than the parent–offspring mean minus 2 standard deviations ($r_{xy} < 0.3242$).

Comparison of bears in the Prudhoe Bay region with adjacent areas

The level of genetic variation of the grizzly bears in the Prudhoe Bay region was comparable to that of neighboring areas of the western Brooks Range and the Arctic National Wildlife Refuge (Table 1). These comparisons included 8 of the 14 microsatellite loci described for the Prudhoe Bay region. There was no significant difference ($P > 0.07$) in the mean H_o or H_e between the Prudhoe Bay, ANWR, and western Brooks Range samples. There was a higher mean number of alleles per locus in the Prudhoe Bay region than the western Brooks Range and ANWR, and the mean number of alleles was also higher in the western Brooks Range than in ANWR (Table 1). However, because there was a positive relationship between sample size and number of microsatellite alleles (Miller and Waits 2003, Cronin et al. 2003) we compared the allelic richness (numbers of alleles standardized to the sample size). The mean allelic richness for the 8 loci (Table 1) was not significantly different between the ANWR and the western Brooks Range ($P = 0.209$) or between the western Brooks Range and the Prudhoe Bay region ($P = 0.270$). The mean allelic richness was significantly lower in the ANWR than in the Prudhoe Bay region ($P = 0.017$).

Genetic differentiation was similar in magnitude for samples from the Prudhoe Bay region and the Western Brooks range ($F_{st} = 0.0217$), the Prudhoe Bay region and ANWR ($F_{st} = 0.0196$), and the western Brooks Range and ANWR ($F_{st} = 0.0267$). The overall F_{st} considering all 3 regions was 0.0225. The allele frequencies for the 8 loci analyzed are in the Appendix. These F_{st} values were significantly different from zero ($P < 0.01$), indicating some differentiation of allele frequencies. The AMOVA indicated that 98% of the genetic variation was within populations and 2% between populations ($P < 0.0000$).

Table 4. Sibling relationships among grizzly bears in the Prudhoe Bay region, Alaska, USA from samples collected from 1990 to 2002.

Sibling 1	Sibling 2	Number of loci with shared allele	Relation from field or genetic data	r_{xy}
3	5	14	suspected	0.6553
24	25	11	known mother	0.529
24	27	12	known mother	0.5118
25	27	13	known mother	0.4686
1	6	14	known mother, father	0.7423
11	12	13	known mother, father	0.6451
15	16	12	known mother, father	0.3918
17	18	13	known mother	0.5358
4	32	13	known mother, father	0.5046
9	8	unknown	known mother	No genetic data for 8
52	55	14	known mother	0.4412
61	62	13	suspected	0.51
40	41	13	suspected	0.3149
Mean (SD)				0.5209 (0.1173)

Discussion and management implications

Our data suggest that the bears in the Prudhoe Bay region are part of a genetically variable population that extends across the North Slope of Alaska. All 3 measures of microsatellite genetic variation, H_o, H_e, and A, are high in the Prudhoe Bay region relative to other areas in North America (Table 1, Paetkau et al. 1998*a*). Previous analyses indicate considerable mtDNA variation in the Prudhoe Bay region (Cronin et al. 1999). As a conservative estimate, approximately 5.3% of the bears in the Prudhoe Bay region are first-order relatives, although our results identify several family groups and possible mating between relatives. The mean relatedness of all sampled bears in the Prudhoe Bay region is close to zero, and the mean relatedness of first-order relatives is close to 0.5, as expected (Blouin et al. 1996). Similar values of 0.5 for first-order relatives and zero for non-relatives have been reported for polar bears (*Ursus maritimus*) in Canada (Lunn et al. 2000).

Accurate identification of parent–offspring relationships in natural populations may depend on information other than genetic data (Cronin et al. 1999). Although the genetic data verified non-exclusion for the 20 mothers known or suspected from field observations, in 4 cases the LOD scores indicated a different female was more likely the mother (Table 2). In these cases, field observations allowed identification of the most probable mother. In addition, field data (including age) prevented the potentially incorrect assignment of parent–offspring status to 25 pairs of bears that were not excluded as parent–offspring with the genetic data (Table 3). Some aspects of field data are definitive (age, sex)

while other aspects are only suggestive. For example, females and cubs observed together in the field are suspected of being mother–offspring, but these inferred relationships are not definite because association of non-maternal females and cubs is possible.

In the case of father–offspring, all 13 pairs included only one non-excluded male and 11 of these pairs had positive LOD scores. Two father–offspring pairs (20 and siblings 52 and 55) had negative LOD scores, despite non-exclusion as parent–offspring. If these father–offspring relationships are correctly identified, the negative LOD scores may be due to sharing alleles that are common in the population (Marshall et al. 1998). Alternatively, these may not be father–offspring pairs. These relationships require that male 20 mated with his daughter, number 1, the mother of 52 and 55. The r_{xy} values for 20 and 52 and 55 are 0.46 (Table 2), considerably lower than the 0.75 expected for father–offspring resulting from a father–daughter mating. The negative LOD scores and lower than expected r_{xy} values suggest that male 20 may not have been the father of 52 and 55, despite sharing at least one allele per locus. The other possible father–daughter mating (between 20 and 4) is more likely because the r_{xy} values of the father (20) and offspring (11 and 12) approximate 0.75, and these pairs have positive LOD scores in the 95% confidence range.

In 3 cases involving twins (3, 5; 1, 6; and 52, 55), the genetic data did not exclude one female as a mother of 1 of the twins, but did exclude that female as the mother of the other twin (Table 3). This may indicate that the excluded sibling was adopted by the mother of the non-excluded sibling. Cub adoption has been observed in polar bears (Lunn et al. 2000). However, adoption is questionable in our 3 cases because the sibling pairs had high r_{xy} values typical of full siblings (Table 1), and in 2 of the 3 cases a different female was identified in the field as the probable mother of both twins (Table 2).

Similarly, in another case a male (100) was not excluded as the father of 1 sibling (52), but was excluded as the father of a second sibling (55, Table 3). This could indicate multiple paternity in a litter, which is known to occur in grizzly bears (Craighead et al. 1995*a*), but other factors make this questionable. First, male 100 was probably too young (5 years old) to breed in the conception year of 52 and 55. Second, the r_{xy} values for 52 and 55 (0.4412) are closer to the expected value for full siblings (0.5) than that expected for half-siblings (0.25).

Four loci were not in Hardy-Weinberg equilibrium in the bears from the Prudhoe Bay region. These loci and others were also out of Hardy-Weinberg equilibrium in populations of Scandinavian brown bears (Waits et al. 2000). Three of these loci (G10H, G10L, MU59) had a deficiency of heterozygotes. Such deviations from Hardy-Weinberg equilibrium may reflect the presence of null alleles, laboratory scoring error, or deviations from random mating (mating of relatives, selection, migration, or population structure). Previous analyses of these loci suggested null alleles are unlikely (Waits et al. 2000), and lab scores were double-checked for all loci. There may be deviation from random mating in our sample for several reasons. With regard to breeding between relatives, evidence suggests father–daughter mating (Fig. 2), although our results indicate a small proportion (<6%) of the bears in the region are first-order relatives. The deficiency of heterozygotes could be due to a Wahlund effect resulting from sampling bears from different subpopulations, but this is unlikely because the deficiency was at only 3 of the 14 loci. In addition, although female philopatry to home ranges may contribute to population structure (Fig. 1), male bears tend to range widely, probably with associated gene flow. It is not known if these microsatellite loci are linked to loci under selection.

We observed significant linkage disequilibrium in 26% of the pair-wise locus tests. The 14 loci we used have been analyzed in other grizzly bear populations, and in some cases linkage disequilibrium is evident but the general conclusion is that these loci are not tightly linked (Paetkau et al. 1995, 1997, 1998*a*, 1998*b*; Waits et al. 2000). Further analyses of linkage are needed to make definite conclusions regarding linkage relationships of these loci.

Genetic differentiation of the samples from the Prudhoe Bay region, the western Brooks Range, and ANWR over a range of approximately 1,000 km ($F_{st} = 0.0225$) is relatively low compared to grizzly bears over smaller geographic distances in other areas. This includes differentiation of grizzly bear populations over approximately 400 km in the northern US Rocky Mountain region ($F_{st} = 0.120$, Miller and Waits 2003) and over approximately 500 km in northern Scandinavia ($F_{st} = 0.139$, Waits et al. 2000). The relatively low F_{st} between the Arctic Alaska regions and the low overall relatedness of the bears in the Prudhoe Bay region suggest that movement of bears results in gene flow across the North Slope of the Brooks Range.

In contrast to the relatively low level of differentiation of microsatellite allele frequencies, maternally-inherited mtDNA haplotype frequencies suggest restriction of female-mediated gene flow between ANWR and the

areas to the west (Talbot and Shields 1996, Waits et al. 1998*b*). Microsatellite markers are bi-parentally inherited and reflect gene flow mediated by males and females. Female grizzly bears have smaller home ranges and lower dispersal than males (Blanchard and Knight 1991, Mace and Waller 1997, Paetkau et al. 1998*b*, Waits et al. 1998*b*, Waits et al. 2000, McLellan and Hovey 2001). In the Prudhoe Bay region, home ranges of 20 adult males averaged 6,704 km^2, whereas the home ranges of 25 adult females averaged 2,560 km^2 (R. Shideler unpublished data). There is also a tendency for related female grizzly bears to have overlapping home ranges (Mace and Waller 1997, Fig. 1, 2). These factors could result in less female-mediated gene flow than male-mediated gene flow and higher differentiation of mtDNA than microsatellite alleles.

Genetic diversity of the bears in the Prudhoe Bay region contrasts with that of bears in the Yellowstone National Park region, where there have also been impacts from human activity (Paetkau et al. 1998*a*, Miller and Waits 2003). Data for the 8 loci available for the 3 North Slope regions (Table 1) for grizzly bears from the Yellowstone region (Paetkau et al. 1998*a*, D. Paetkau, unpublished data) indicate heterozygosities ($H_o = 0.5526$ and $H_e = 0.5545$) significantly lower ($P < 0.01$) than those of the grizzly bears in the Prudhoe Bay region, the western Brooks Range, and the Arctic National Wildlife Refuge (Table 1).

Two factors may contribute to these patterns. First, the grizzly bears in the Yellowstone region are more genetically differentiated from the closest (but geographically disjunct) neighboring bears in the Glacier National Park region ($F_{st} = 0.123$) than are bears in the contiguous Alaska regions ($F_{st} = 0.0225$). Geographic isolation may have contributed to the loss of genetic diversity in the Yellowstone region (Paetkau et al. 1998*a*, Miller and Waits 2003), whereas it appears that genetic variation and gene flow have been maintained across northern Alaska. Second, mortality of grizzly bears following the closing of garbage dumps was considerably higher in Yellowstone Park than at Prudhoe Bay. In the Yellowstone region between 1968 and 1971, 220 grizzly bears were killed after dumps in the Park were closed (Craighead et al. 1995*b*, Miller and Waits 2003). Miller and Waits documented a decline in genetic diversity in the Yellowstone region across the last century due to isolation and low effective population size. One of the contributing factors to low effective population size was the increased mortality to brown bears in the 5 years following the closure of the dumps. Mortality in the Prudhoe Bay region was relatively low. During the 1980s and early 1990s, 6 adult female and 2 adult male bears in the oil field region fed on garbage. These females were conditioned to eating anthropogenic food and had cubs with higher survival to weaning (77%) than did females eating only natural foods (47%). However, food-conditioned sub-adults had a high rate of mortality after weaning (84%). These sub-adults were habituated to humans and were killed in defense-of-life-and-property-situations away from the oil fields (R. Shideler unpublished data). Also, after fencing the garbage dump and installation of bear-proof garbage containers in the oil fields in the late 1990s, 7 bears were killed in 2001 and 2002. The high cub survival and high post-weaning mortality probably balanced each other, and the number of bears in the region did not appreciably change. These impacts were probably not large enough to affect the level of genetic variation of grizzly bears in the region.

The past availability of anthropogenic food in the Prudhoe Bay region has other possible consequences. Our genetic data identify 5 males between the ages of 4 and 7 years old as potential fathers (Table 3). Four of the 6 possible father–offspring pairs involving these males had positive LOD scores at the 95% confidence level, and no other potential fathers were identified. If these males are actually the fathers, they bred at an age younger than previously recorded on Alaska's North Slope (Craighead et al. 1995*a*, Cronin et al. 1999). It is possible that the nutritional status of mothers and their male offspring was enhanced by access to garbage, and this resulted in early maturation of these males. Two of these males were known to have had access to garbage as sub-adults, and 1 of these was the only such male to continue eating anthropogenic food into adulthood. Although we cannot be certain these males bred when younger than 8 years old, the genetic data suggest this may be the case.

Our results suggest that the mortality associated with oil field development has not resulted in loss of genetic variation in the grizzly bears in the Prudhoe Bay region. It is also possible that age at breeding has been reduced due to enhanced food availability. Because actions have been taken to reduce or eliminate access to garbage by bears, such potential impacts can be expected to decline or cease in the future.

Genetic data have been used to identify various population units of bears and other species including evolutionarily significant units (ESU) that share monophyletic mitochondrial DNA, or management units that have some degree of genetic differentiation (Moritz 1994, Waits et al. 1998*b*, Paetkau et al. 1999). Although

genetically based units are appropriate for some applications, practical management units are frequently geographical and based on land use. A national park in the Yellowstone region and an oil field complex in the Prudhoe Bay region require the bears in each area be treated as a management unit regardless of genetic relationships with other areas. Genetic data can aid in management by identifying demographic factors (immigration and emigration in Prudhoe Bay, isolation in Yellowstone) but the management units are frequently based on geography, in addition to genetics, demographics, and other considerations (Cronin 1993, 1997, 2003).

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Appendix I

Allele frequencies, number of alleles (*A*), observed heterozygosity (H_o), expected heterozygosity (H_e), and sample size (*n*) in grizzly bears in 3 regions of northern Alaska, USA. Data for the Arctic National Wildlife Refuge and western Brooks Range are from Craighead (1994), Craighead et al. (1995*a*), Paetkau et al. (1997, 1998*a*), and D. Paetkau (Wildlife Genetics International, Nelson, British Columbia, Canada, personal communication).

Locus Allele	Prudhoe Bay Region, *n* = 78	Arctic National Wildlife Refuge, *n* = 24	Western Brooks Range, *n* = 148
Locus G1A			
180	0.039	0.0417	0.0777
184	0.2143	0.25	0.2432
186	0.026	0.0833	0.0034
188	0.0000	0.0000	0.0068
190	0.0065	0.0000	0.0372
192	0.2078	0.125	0.2128
194	0.4091	0.2708	0.402
196	0.026	0.0833	0.0000
198	0.0519	0.0208	0.0000
200	0.0195	0.125	0.0169
$A/H_o/H_e$	9/0.844/0.742	8/0.792/0.834	8/0.764/0.729
Locus G10B			
140	0.2051	0.1042	0.1655
148	0.0577	0.1667	0.0912
150	0.0128	0.0625	0.0405
152	0.0833	0.1042	0.0236
154	0.0513	0.125	0.0135
156	0.0064	0.0000	0.0439
158	0.0641	0.0417	0.1588
160	0.3397	0.3542	0.4088
164	0.1795	0.0417	0.0541
$A/H_o/H_e$	9/0.756/0.798	8/0.792/0.819	9/0.791/0.767
Locus G10C			
99	0.0064	0.0000	0.0000
101	0.0128	0.0208	0.0068
103	0.2564	0.2708	0.2635
105	0.3397	0.4792	0.3412
107	0.1538	0.0208	0.0405
109	0.0385	0.1042	0.0034
111	0.1667	0.0833	0.25
113	0.0256	0.0208	0.0946
$A/H_o/H_e$	8/0.679/0.770	7/0.667/0.692	7/0.784/0.743
Locus G1D			
172	0.2756	0.125	0.2432
174	0.0705	0.1875	0.0372
176	0.0449	0.125	0.0338
177	0.0000	0.125	0.1419
178	0.1731	0.0208	0.2128
180	0.0192	0.0000	0.0101
181	0.2564	0.1875	0.1047
182	0.0128	0.1042	0.0845
184	0.0833	0.0000	0.0439
186	0.0577	0.125	0.0878
191	0.0064	0.0000	0.0000
$A/H_o/H_e$	10/0.846/0.816	8/0.917/0.874	10/0.878/0.848
Locus G10L			
151	0.0064	0.0000	0.0000
153	0.0128	0.0000	0.0000
155	0.5192	0.5208	0.4764
157	0.3141	0.4375	0.2804
159	0.0256	0.0000	0.0912
161	0.0000	0.0000	0.1318
163	0.0641	0.0417	0.0068
171	0.0577	0.0000	0.0135
$A/H_o/H_e$	7/0.526/0.627	3/0.625/0.547	6/0.662/0.671
Locus G10M			
206	0.1474	0.0417	0.0811
208	0.2885	0.3125	0.4527
210	0.0705	0.1250	0.0541
212	0.0962	0.1250	0.1081
214	0.3590	0.3750	0.2736
216	0.0064	0.0000	0.0000
218	0.0321	0.0208	0.0270
222	0.0000	0.0000	0.0034
$A/H_o/H_e$	7/0.731/0.756	6/0.708/0.744	7/0.743/0.701
Locus G10P			
139	0.0064	0.0208	0.0068
141	0.0256	0.0000	0.0000
149	0.0064	0.0000	0.0372
151	0.3333	0.1458	0.0878
153	0.1859	0.125	0.3446
155	0.1282	0.2083	0.0709
157	0.1795	0.125	0.1959
159	0.0833	0.125	0.0777
161	0.0513	0.25	0.1791
$A/H_o/H_e$	9/0.769/0.800	7/0.958/0.843	8/0.791/0.793
Locus G10X			
129	0.0000	0.0000	0.027
131	0.141	0.1458	0.0541
133	0.0769	0.0417	0.1047
135	0.1154	0.125	0.2095
137	0.4487	0.3333	0.3953
139	0.0000	0.0208	0.0000
141	0.2051	0.3333	0.2095
145	0.0128	0.0000	0.0000
$A/H_o/H_e$	6/0.744/0.722	6/0.750/0.754	6/0.784/0.744
Locus CXX20			
123	0.0132		
127	0.0526		
129	0.5		
133	0.0263		
135	0.0263		
139	0.125		
141	0.0197		
143	0.2237		
145	0.0132		
$A/H_o/H_e$	9/0.632/0.684		

Appendix. Continued.

Locus Allele	Prudhoe Bay Region, $n = 78$	Arctic National Wildlife Refuge, $n = 24$	Western Brooks Range, $n = 148$
Locus MU50			
110	0.1474		
122	0.0385		
126	0.0769		
128	0.1603		
130	0.2692		
132	0.0192		
134	0.0577		
138	0.2308		
$A/H_o/H_e$	8/0.782/0.821		
Locus MU59			
221	0.0066		
223	0.0197		
227	0.6513		
229	0.0658		
231	0.0395		
233	0.0066		
239	0.0855		
243	0.0263		
245	0.0263		
247	0.0658		
249	0.0066		
$A/H_o/H_e$	11/0.461/0.527		
Locus G10H			
221	0.5577		
223	0.0064		
227	0.0385		
229	0.0128		
231	0.0897		
233	0.1795		
235	0.0064		
237	0.0321		
239	0.0064		
252	0.0064		
254	0.0256		
255	0.0256		
257	0.0128		
$A/H_o/H_e$	13/0.538/0.649		
Locus G10J			
78	0.0385		
80	0.4615		
86	0.2051		
90	0.0833		
96	0.2115		
$A/H_o/H_e$	5/0.590/0.696		
Locus G10O			
182	0.2436		
188	0.0321		
192	0.0962		
198	0.5321		
200	0.0064		
204	0.0897		
$A/H_o/H_e$	6/0.590/0.643		