Journal of Heredity 2009:100(2):170–180
doi:10.1093/jhered/esn076
Advance Access publication October 3, 2008

Population Structure and Genetic Diversity of Moose in Alaska

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Abstract

Moose (*Alces alces*) are highly mobile mammals that occur across arboreal regions of North America, Europe, and Asia. Alaskan moose (*Alces alces gigas*) range across much of Alaska and are primary herbivore consumers, exerting a prominent influence on ecosystem structure and functioning. Increased knowledge gained from population genetics provides insights into their population dynamics, history, and dispersal of these unique large herbivores and can aid in conservation efforts. We examined the genetic diversity and population structure of moose ($n = 141$) with 8 polymorphic microsatellites from 6 regions spanning much of Alaska. Expected heterozygosity was moderate ($H_E = 0.483–0.612$), and private alleles ranged from 0 to 6. Both F_{ST} and R_{ST} indicated significant population structure ($P < 0.001$) with $F_{ST} < 0.109$ and $R_{ST} < 0.125$. Results of analyses from STRUCTURE indicated 2 prominent population groups, a mix of moose from the Yakutat and Tetlin regions versus all other moose, with slight substructure observed among the second population. Estimates of dispersal differed between analytical approaches, indicating a high level of historical or current gene flow. Mantel tests indicated that isolation-by-distance partially explained observed structure among moose populations ($R^2 = 0.45$, $P < 0.01$). Finally, there was no evidence of bottlenecks either at the population level or overall. We conclude that weak population structure occurs among moose in Alaska with population expansion from interior Alaska westward toward the coast.

Ungulates are important ecologically, socially, and economically (Regelin and Franzmann 1998; Baskin 2000; Cooper et al. 2002; Gordon et al. 2004), and their evolutionary history and genetics have received much attention (Coltman et al. 2001a, 2001b; Hundertmark et al. 2002a, 2002b, 2003; Bowyer et al. 2003; Wilson et al. 2003; Worley et al. 2004). Previously, genetic research on moose (*Alces alces gigas*) in Alaska has used allozymes and mtDNA analyses (Cronin 1992; Hundertmark et al. 1992; 2002a, 2002b, 2003, 2006) to study phylogenetics and population genetics. However, a fine-scale approach with nuclear DNA markers is needed to better understand population status and dynamics, dispersal, and phenotypic differences among moose in Alaska (Bowyer et al. 2001, 2002: Hundertmark et al. 2002a, 2002b, 2003, 2006). The foraging of moose can alter ecosystem structure and functioning (Molvar et al. 1993), and hence, they are a keystone species (Simberloff 1998). Moose also provide a valuable economic and subsistence resource (Nelson 1973; Snepenger and Bowyer 1990; Ballew et al. 2006). Thus, in order to manage populations in a viable manner, a more comprehensive understanding of dispersal and gene flow is required (Frankham et al. 2002).

Moose arrived in North America <15 000 years ago, dispersing into Alaska via the Bering Land Bridge (Hundertmark et al. 2002a, 2002b, 2003). Today moose occur throughout most of Alaska and in other arboreal regions of North America, Europe, and Asia. During the Pleistocene, unglaciated areas in Central Alaska likely provided an ice-free refugium for moose as they dispersed toward southern portions of North America (Hundertmark et al. 2003). From an evolutionary perspective, moose are recent colonists of Alaska; consequently, genetic structure among moose populations might be difficult to detect. In addition, moose occur between our sample areas. Nonetheless, the distances between moose populations are large and landscape features such as mountains provide obstacles between some populations. Furthermore, moose undertake traditional seasonal movements and exhibit strong fidelity to home ranges and traditional mating and birthing areas (Geist 1963; Houston 1968; Le Resche et al. 1974; Anderson 1991; Ballard et al. 1991; Hundertmark 1998; Bowyer et al. 2002). Other life-history characteristics of moose that may contribute to their genetic diversity and population structure include a polygamous mating system and male-biased

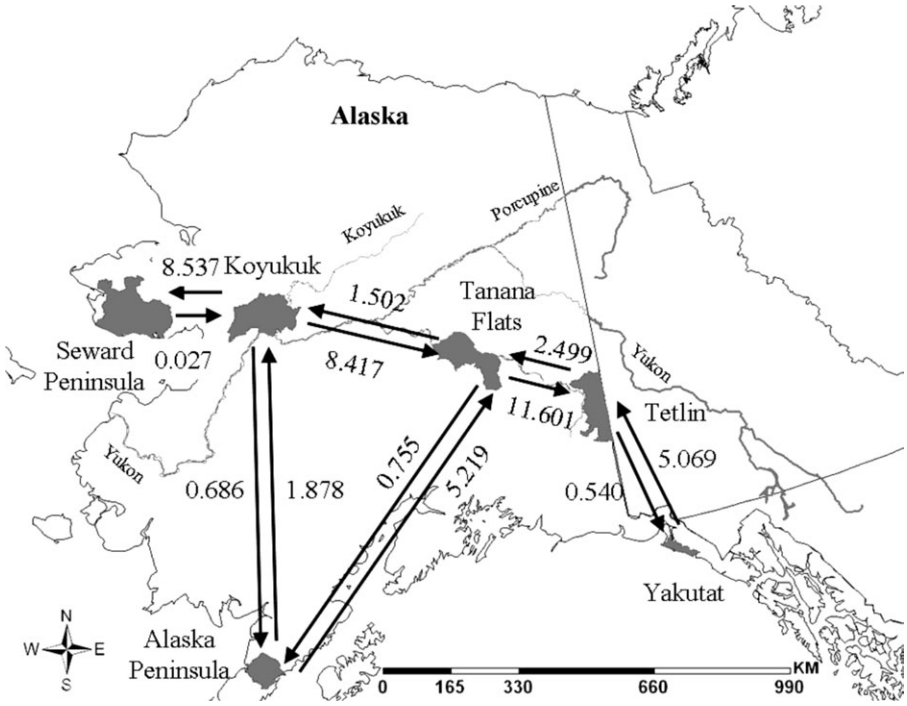

Figure 1. Moose populations used for microsatellite analysis in Alaska, 2003–2005. Population boundaries represent wildlife management units that were our sampling frames. Migration rates (*Nm*) between adjacent populations based on maximum likelihood are indicated.

dispersal (Crête and Helene 1985; Hundertmark 1998). In addition to the influence of behavior, large geographic distances and diverse physical features, including mountain ranges, river drainages, and glaciers, are known to influence moose dispersal in Alaska (Peterson 1955; Le Resche et al. 1974). Last, moose in Alaska are commonly hunted, yielding meat and trophies to sport hunters (Hundertmark et al. 1993), as well as value to subsistence hunters (Ballew et al. 2006). Hunting has been shown to influence genetic diversity and population structure (Coltman et al. 2003; Garel et al. 2007; Proaktor et al. 2007). Genetic diversity also is important because reductions in genetic diversity have been used to explain abnormalities in antler morphology (Hartl et al. 1991; Bowyer et al. 2002), levels of parasite resistance (Coltman et al. 2001a, 2001b), body composition (Hartl et al. 1991; Coltman et al. 2001a), and ultimately survival (Hard et al. 2006; Proaktor et al. 2007).

The objectives of this study were to investigate the genetic structure of moose in Alaska and assess overall levels of genetic diversity. In addition, we sought to estimate effective number of migrants and rates of dispersal between populations, identify potential past bottlenecks, and determine the role that isolation-by-distance has played in shaping moose population structure in Alaska. We hypothesized that Alaskan moose would exhibit population structure with evidence of isolation-by-distance, as documented for moose in Canada (Broders et al.1999), and that populations closer together would experience increased number of migrants between populations (Anderson et al. 2004).

Materials and Methods

Tissue Collection and DNA Extractions

We collected 141 samples of moose from 6 localities within Alaska (Figure 1): Yakutat ($n = 25$), Tetlin ($n = 20$), Tanana Flats ($n = 25$), Koyukuk ($n = 26$), Seward Peninsula ($n = 25$), and Alaska Peninsula ($n = 20$). Samples were composed of both muscle and skin, archived at −80 °C, and extracted with a DNeasy Tissue Kit (Qiagen, Valencia, CA). Tanana Flats and the Seward Peninsula were collected during 2003, Yakutat and Koyukuk samples in 2003 and 2004, Alaska Peninsula sample in 2004, and Tetlin samples in 2004 and 2005. Samples were a mixture of males, females, and individuals of unknown sex, respectively, for Yakutat ($n = 21$, $n = 3$, $n = 1$), Tanana Flats ($n = 4$, $n = 16$, $n = 5$), and the Seward Peninsula ($n = 23$, $n = 2$, $n = 0$). Samples from Tetlin and Alaska Peninsula were all female, meanwhile Koyukuk were all males.

Genotyping

Microsatellite genotyping was performed using 8 primer pairs previously used for moose (Wilson et al. 1997, 2003; Roed and Midthjell 1998; Broders et al. 1999). BM203, Rt1, Rt24, and Rt30 were labeled with HEX dye; BM2830, NVHRT01, NVHRT21, and Rt5 were labeled with 6-FAM. Polymerase chain reaction (PCR) was performed with a total reaction volume of 12.5 μl and contained ~50 μg of genomic DNA, 0.5 μM of fluorescently labeled forward

primer and 0.6 μM of reverse primer, 2.5 mM $MgCl_2$, 1.25 μl of Applied Biosystems 10× buffer B (Applied Biosystems, Foster City, CA; 100 mM Tris–HCl, pH 9.0, 500 mM KCl), 200 μM of deoxynucleoside triphosphates, and 1.0 U of *Taq* DNA polymerase. Bovine serum albumin (1%) was added to optimize PCR for individual loci. PCR cycles were as follows: 94 °C for 2 min, followed by 30 cycles of 94 °C for 30 s, 58 °C for 30 s, and 72 °C for 45 s, and a 30-min final extension at 72 °C. PCR products were visualized on 3% agarose gels stained with 10 μg/μl of ethidium bromide. Allele lengths were determined on an ABI377 DNA sequencer with 36-cm polyacrylamide gels (Cambrex, East Rutherford, NJ; 5% Long Ranger) operated for 2.5 h at 3 kV. We used GENESCAN 3.1 with a 500 base-pair size standard to determine allele sizes. Tetlin moose samples were analyzed by an independent laboratory (Wildlife Genetics International, Nelson, BC, Canada), and a selected set of 3 samples were used to verify compatibility of results. Moose tissues used for this study and not used are archived at the University of Alaska Museum of the North in Fairbanks, Alaska (http://arctos.database.museum/SpecimenSearch.cfm).

Statistical Analysis

All loci were examined for the presence of null alleles and allelic dropout with the software MICRO-CHECKER (Oosterhout et al. 2004). We used GENEPOP (v. 3.4; Raymond and Rousset 1995) to examine Hardy–Weinberg equilibrium (HWE). Also based on individual assignment results, we tested HWE with 2 populations where Yakutat and 1 sample from Tetlin comprised the first population and all others the second population. FSTAT (v. 2.9.3; Goudet 2001) was used to assess linkage disequilibrium (1 680 000 permutations) and calculate expected and observed heterozygosities (Nei 1987), private alleles (El Mousadik and Petit 1996), allelic richness independent of sample size (Goudet 2001), and pairwise F_{ST} statistics (Weir and Cockerham 1984). We performed Bonferroni adjustments for tests that involved multiple comparisons (Rice 1989). We used the methods of Barton and Slatkin (1986) to estimate the effective number of migrants in GENEPOP (Slatkin 1995). We used ARLEQUIN 3.0 (Excoffier and Laval 2005) to perform analysis of molecular variance (AMOVA; 10 000 permutations) and calculate R_{ST} statistics (Paetkau et al. 1995, 1997; Waser and Strobeck 1998) and also to calculate population pairwise differences among the 6 populations. We used a Bayesian approach with BAYESASS 1.2 (Wilson and Rannala 2003) to estimate direction and migration that occurred more recently (i.e., within the last few generations) and rates of dispersal. We believe BAYESASS estimates reflect dispersal, rather than seasonal migration, because the geographic distances among our population comparisons is greater than known migration or dispersal distances for moose (Hundertmark 1998). Furthermore, periods of mating and migration do not overlap temporally for moose in Alaska (Hundertmark 1998). In addition, BAYESASS was used to assess the proportions of individuals assigned to their hypothesized population and to the other populations. To assure consistent and accurate estimates, we varied seed numbers and explored the number of runs needed (i.e., burn-in) to discard before data collection. The burn-in length was set after log-likelihood values peaked. We also varied seed numbers and accepted proposed changes in parameters that were between 40% and 60% of the total iterations (Wilson and Rannala 2003). Finally, we performed 3×10^6 iterations, and a burn-in of 10^6 generations was determined an appropriate number of runs for convergence and stabilization of posterior probabilities with a sampling frequency of 2000.

Maximum likelihood estimate (MLE) and Bayesian estimate of dispersal rates and effective population size were calculated with MIGRATE 2.3 (Beerli and Felsenstein 1999, 2001). The Bayesian approach in MIGRATE differs from that of BAYESASS because estimates from MIGRATE reflect long-term dispersal based on a coalescent approach (Beerli and Felsenstein 1999, 2001), whereas BAYESASS estimates more contemporary migration via a multilocus approach (Faubet et al. 2007). Both MLE and Bayesian approaches allow for asymmetric dispersal and unequal population sizes. Analysis with MLE followed a Brownian-motion model with a Markov chain Monte Carlo (MCMC) repetition of 50 short chains, 25 000 trees sampled, and 250 recorded. Four long chains were analyzed with the same number of trees sampled and recorded as during short chains with a burn-in of 10 000. We used F_{ST} to estimate starting parameters (Θ, $4N_E\mu$) and the number of dispersing individuals per generation ($4N_E m$; Beerli and Felsenstein 1999, 2001; Beerli 2004, 2006). Similar to MLE, Bayesian analysis incorporates a Brownian microsatellite model with a constant mutation rate and F_{ST} to estimate theta (Beerli 2004, 2006). For the Bayesian analysis, we used the estimated theta from the initial run as the starting parameter for the second run (Beerli 2006). Because results were similar between the first and second runs, we did not continue to update the starting parameters.

To test for possible bottlenecks of past populations, we used the program BOTTLENECK with a modified 2-phase model (Garza and Williamson 2001). Parameters for BOTTLENECK were set so that 88% of mutations followed a stepwise mutation model (SMM; Kimura and Ohta 1978), 12% a multistep mutation model, with a variance ($\sigma\_g\hat{}2$) of 9 (Di Rienzo et al. 1994). That variance equates to an approximate mean step size for multistep mutations (Δ_g) of 3 approximately equal to σ_g (Di Rienzo et al. 1994). Significance was determined with a one-tailed Wilcoxon test (Cornuet and Luikart 1996). Although the number of loci used for this analysis was not optimal, it was still within acceptable limits (Cornuet and Luikart 1996).

To test for isolation-by-distance, we performed Mantel tests with FSTAT (Mantel 1967; Smouse et al. 1986; Manly 1991). The geographic distance connecting samples was represented by Euclidean (linear geographic) distances and the ln of Euclidean geographic distance. Genetic distances were calculated with F_{ST}, R_{ST}, and $F_{ST}/(1 - F_{ST})$. To differentiate between the multiple Mantel tests, we calculated corrected Akaike information criterion (AIC) for small

sample sizes (AIC_C), ΔAIC_C, and AIC weights (Burnham and Anderson 2002) in a 2-step process (Spear S, personal communication). With the residuals in FSTAT, we first calculated log-likelihood values by

$$\text{Loglikelihood} = \frac{(n \times \text{number of genetic values}) \times (\log(\text{variance of residuals}))}{2.}$$

Next, we used the resultant log-likelihood to calculate AIC_C values and delta according to the standard AIC_C equations (Burnham and Anderson 2002). With the same geographic and genetic comparisons, we used the statistical program R to perform linear regression (v. 2.5; R development Core Team).

We used Bayesian analysis implemented in the program STRUCTURE 2.1 (Pritchard et al. 2000) to infer population structure and explore population assignments of individual moose. To explore population structure, we let the number of populations (K) vary between 1 and 10. After examining various burn-in lengths, we observed that a chain length of 100 000 with 1 000 000 MCMC repetitions was sufficient. A total of 10 simulations were completed for each estimated K. Other parameters included the use of an admixture model and correlated alleles, and no population information was provided (Pritchard et al. 2000). We wished to compare 2 methods to analyze results from STRUCTURE (Pritchard et al. 2000; Evanno et al. 2005). First, to estimate the number of populations, we used the model with the best log-likelihood score and resulted in the highest percentage membership value (q; Pritchard et al. 2000). Second, we analyzed our results according to Evanno et al. (2005), in which the number of populations (K) was plotted against $\Delta K = m|L''(K)|/s|L(K)|$ in which the estimated number of populations identified by the largest change in log-likelihood ($L(K)$) values between estimated number of populations. We used AMOVA in ARLEQUIN to analyze the groups identified by results from the STRUCTURE analysis.

We also made a phylogenetic tree by first using the program MSA (Dieringer and Schlötterer 2003) to calculate Nei's standard genetic distance (corrected for sample size; Nei et al. 1983) with 1000 bootstraps. Then we used PHYLIP (Felsenstein 1989) to construct a neighbor-joining tree, and finally, we used TREEVIEW (Page 1996) to display the tree.

Results

Genetic Diversity and Tests of Disequilibrium

All eight microsatellites were determined to be in HWE, and no linkage disequilibrium was present. Results from MICRO-CHECKER did not indicate the presence of null alleles or allelic dropout. All other tests for HWE and linkage disequilibrium within annual samples within populations were not significant ($P > 0.05$). We did not detect evidence of population differentiation between years. The population with the largest total number of alleles occurred in the Tanana Flats ($n = 31$) and the smallest in the Alaska Peninsula sample ($n = 22$) with a total of 46 alleles detected. Overall number of alleles per locus ranged from 3 (BM2830 and Rt1) to 12 (Rt30). Private alleles occurred in Yakutat (Rt24, $n = 2$; Rt30 $n = 1$, $n = 3$), Tanana Flats (BM2830, $n = 1$; Rt30, $n = 1$), and the Seward Peninsula (NVHRT21, $n = 2$). Koyukuk, Tetlin, and the Alaska Peninsula had no private alleles (Table 1). Expected and observed heterozygosity levels were similar between each other and within a narrow range of moderate values. Expected and observed heterozygosity was greatest in Tetlin and least in the Alaska Peninsula (Table 1). Also, there was no evidence of bottlenecks within populations or when Alaska was tested as a single population. Average pairwise differences within populations were largest for Tetlin and smallest for the Alaska Peninsula (Table 2). Theta values mimicked genetic diversity results with Tetlin the highest and Alaska Peninsula the lowest (Table 3).

Population Structure

Significant structure exists among moose populations in Alaska based on F_{ST} and R_{ST} estimates (Table 2). F_{ST} values ranged from −0.003 to 0.109 and R_{ST} values from −0.010 to 0.125 (Table 2). Estimates with F_{ST} indicated more population structure than with R_{ST}, with 12 versus 4 significant pairwise comparisons, respectively (Table 2). Values of R_{ST} were greater than F_{ST} for only 5 of the 15 pairwise population comparisons (Table 2). Both measures of genetic distance indicated that Koyukuk and the Tanana Flats and Koyukuk and the Seward Peninsula were genetically indistinct (Table 2). Overall F_{ST} (0.055) was greater than R_{ST} (0.039); in addition, F_{ST} was larger for 5 of 8 loci (BM203, BM2830, NVHRT21, Rt24, and Rt30).

Table 1. Sample size, number of alleles (N_A), allelic richness independent of sample size, number of private alleles, expected and observed heterozygosity (H_E, H_O), and F_{IS} averaged over 8 loci and 6 moose populations sampled in Alaska from 2003 through 2005

Population	n	N_A	Allelic richness	No. private alleles	H_E	H_O	F_{IS}
Yakutat	25	4.25	4.040	6	0.554	0.540	0.026
Tanana Flats	25	4.25	4.022	2	0.533	0.540	−0.014
Seward Peninsula	25	4.13	3.880	2	0.550	0.543	0.012
Koyukuk	26	3.75	3.650	0	0.552	0.529	0.042
Alaska Peninsula	20	3.00	2.971	0	0.483	0.455	0.060
Tetlin	20	4.25	4.149	0	0.616	0.569	0.078

Table 2. Population comparisons with F_{ST}[a] values above and R_{ST}[b] values below and average number of pairwise differences within population on the diagonal

	Yakutat	Tanana Flats	Seward Peninsula	Koyukuk	Alaska Peninsula	Tetlin
Yakutat	4.44	0.079***	0.081***	0.069***	0.109***	0.054***
Tanana Flats	0.039	4.26	0.032**	0.014	0.067***	0.051***
Seward Peninsula	0.083**	0.026	4.35	−0.003	0.091***	0.022
Koyukuk	0.125***	0.038	−0.010	4.40	0.078***	0.026***
Alaska Peninsula	0.108**	0.028	0.024	0.005	2.74	0.072***
Tetlin	0.017	0.010	0.036	0.055	0.040*	4.93

[a] Weir and Cockerham (1984).

[b] Slatkin (1995).

*Significant at the 5% level; **significant at the 1% level; ***significant at the 0.1% level.

Results of the 2 methods used to analyze output from STRUCTURE were similar, in that both methods indicated that 2 moose populations exist in Alaska. However, we observed bimodal peaks (Figure 2a), indicating a level of substructure with 4 subpopulations. Other studies have observed bimodal peaks, which indicate levels of substructure (Bergl and Vigilant 2007); nonetheless, the height of the peak, which relates to the strength of the observed population structure, indicates that 2 populations are more likely than 4 (Evanno et al. 2005). In concordance, there were also slight plateaus in likelihood values (Figure 2b) when 2 and 4 populations were modeled. The dips in the log-likelihood at populations 7 and 9 (Figure 2b) are due to a phenomenon noted in the STRUCTURE manual when the number of populations is overestimated (Pritchard and Wen 2003). Based on the assignments from STRUCTURE, we tested for HWE with 2 populations, and the population that was predominantly Yakutat was in HWE, but the larger second population was not.

When 2 populations were modeled, 88% and 50% of the moose from Yakutat and Tetlin, respectively, were assigned to one population, whereas 72%, 63%, 73%, and 99% of the moose in the Tanana Flats, Seward Peninsula, Koyukuk, and Alaska Peninsula populations, respectively, were assigned to the second population. Detecting only 2 populations is remarkable given the large geographic distances between populations. For instance, the Alaska Peninsula is >900 km from Tanana and the Seward Peninsula.

Estimates of Dispersal

Estimates of recent dispersal rates differed between the programs used and often produced inconclusive results within a program, especially for Bayesian analyses. BAYEASS performed poorly, and consistent results could not be achieved. Estimates of dispersal differed between Bayesian and MLE methods with MIGRATE (Table 3). Nonetheless, MLE results were more consistent and informative than Bayesian analyses, in which many dispersal estimates resulted in similar values (Table 3). There were several population comparisons with significant asymmetrical rates of dispersal (Figure 1). Based on MLE, Koyukuk was the largest immigration source for 3 of the 6 populations (Figure 1 and Table 3). Furthermore, dispersal out of Koyukuk to the 2 nearby regions sampled (i.e., Tanana Flats and Seward Peninsula) was much greater than dispersal into Koyukuk from these areas (Table 3). The lowest immigration source for 4 of the 6 populations was the Seward Peninsula. The only nonsignificant asymmetrical dispersal was between

Table 3. Comparison of migration rates with MIGRATE (Beerli 1999; 2001) where before the comma are maximum likelihood and after are Bayesian results

		Source					
		Yakutat	Tanana Flats	Seward Peninsula	Koyukuk	Alaska Peninsula	Tetlin
Destination	Yakutat	2.528	0.01, 27.50	0.00, 27.50	2.37, 22.50	2.06, 12.50	0.54, 27.50
	Tanana Flats	1.94, 22.50	1.794	0.00, 17.50	8.42, 17.50	5.22, 27.50	2.50, 27.50
	Seward Peninsula	3.57, 22.50	1.50, 17.50	1.702	0.03, 22.50	1.88, 22.50	1.21, 22.50
	Koyukuk	3.95, 22.50	1.50, 17.50	0.02, 22.50	0.946	1.88, 22.50	1.21, 22.50
	Alaska Peninsula	2.41, 57.50	0.76, 72.50	5.23, 17.50	0.69, 37.50	0.400	1.13, 47.50
	Tetlin	5.07, 27.50	11.60, 37.50	1.60, 22.50	5.99, 32.50	3.20, 22.50	3.092

Column headings are the source population, and row headings are the destination populations. Numbers in diagonal are theta values from maximum likelihood.

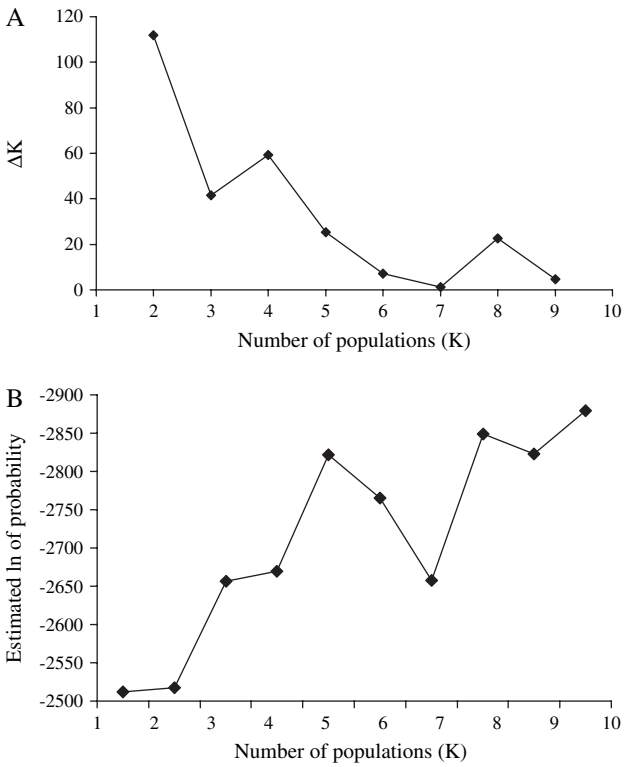

Figure 2. Estimated number of populations (K) from the program STRUCTURE (Pritchard et al. 2000) for moose in Alaska, 2003–2005; (**A**) Rate of change in log-likelihood values ($/K$) for estimated number of populations (Evanno et al. 2005). The maximum $/K$ indicates the most likely number of populations. (**B**) Log-likelihood values for an estimated number of populations (Pritchard et al. 2000). A plateau in likelihood values indicates the most likely number of populations.

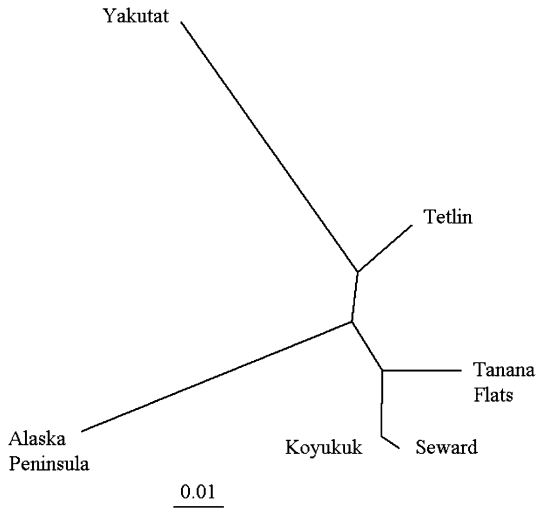

Figure 3. Neighbor-joining tree based on Nei's standard genetic distance (corrected for sample size; Nei et al. 1983) for moose in Alaska, 2003–2005.

Koyukuk and the Seward Peninsula. In the interior, dispersal was eastward with over 4.5× the amount of dispersal into Tetlin from the Tanana Flats than the reverse. There was much more migration toward the recently colonized Seward Peninsula from Koyukuk than in the opposite direction. Estimates that involved the southern populations, Yakutat and the Alaska Peninsula, were more symmetrical but sometimes did not make sense geographically. For example, the primary source of dispersal into and from Yakutat was from the geographically separate Koyukuk area (Table 3).

We do recognize that the sex composition of our sampled populations may influence estimates and direction of dispersal. For example, because our Tetlin is all females, it may appear that Tetlin has little outward dispersal because dispersal in moose is male biased (Crête and Helene 1985; Hundertmark 1998). However, distances between our sampled populations were much greater than expected dispersal distances for moose in Alaska (Hundertmark 1998).

An in-depth exploration of dispersal with STRUCTURE indicated much mixing among Koyukuk and the Seward and Alaska Peninsulas. Within each region, overall inferred ancestry of residents was placed equally among the 3 sample areas. Inferred ancestry in the hypothesized population was slightly larger for the Alaska Peninsula (35%) versus Koyukuk (33%) and the Seward Peninsula (34%). Nonetheless, individual assignments indicated that dispersal is asymmetric, with only one individual in the Alaska Peninsula misassigned, whereas many more were misassigned in Koyukuk ($n = 21$) and the Seward Peninsula ($n = 6$). Of moose misassigned to the Koyukuk sample, the split was similar between the Alaska Peninsula ($n = 10$) and the Seward Peninsula ($n = 11$). In turn, all misassigned moose in the Seward Peninsula were assigned to the Alaska Peninsula. Overall, the various results indicate that dispersal currently occurs especially among the more westward populations with less dispersal to and from Yakutat.

Results from AMOVA indicated that within-population and group variation was minimized with 5 groups comprised of Yakutat, Tetlin, Tanana Flats, and the Alaska Peninsula as independent groups and lastly Koyukuk and Seward Peninsula as a group (among groups 6.07%, among populations within groups −0.25%, and within populations 93.18%). In addition, results from the phylogenetic tree are consistent with F_{ST} estimates (Figure 3).

The best linear regression model used R_{ST} and Euclidean geographic distance (Figure 4). Results from AIC_C scores indicate little difference between genetic distance (61–63), but linear regression indicated large differences between genetic measures with only R_{ST} significant ($P < 0.01$; Figure 4). Mantel tests indicated that isolation-by-distance partially explained observed structure among moose populations ($R^2 = 0.45$; $P < 0.01$). Also, effects of landscape characteristics were indicated because the largest 3 residuals involved Yakutat and the Alaska Peninsula, which are separated from the other populations by mountainous ranges.

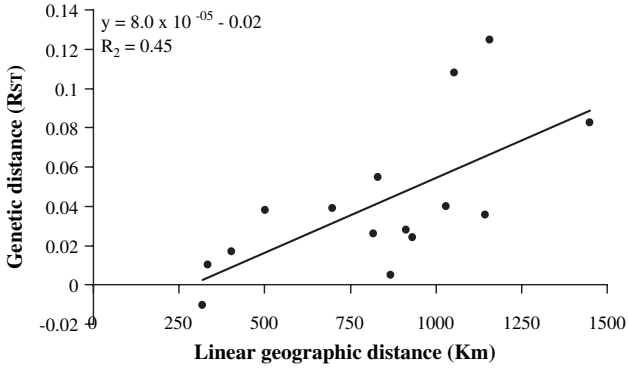

Figure 4. Linear regression of Euclidean (linear geographic) distance versus R_{ST} (Rousset 1997) for moose in Alaska, 2003–2005, indicating isolation-by-distance.

Discussion

Population Structure

Ungulates commonly exhibit genetic population structure (Chesser 1991a, 1991b; Mathews and Porter 1993; Wang and Schreiber 2001; Worley et al. 2004). Even though past research has indicated low levels of mtDNA and nuclear diversity in moose (Hundertmark et al. 2002a, 2002b; 2003; Wilson et al. 2003), population structure has been observed for moose with the use of microsatellites (Broders et al. 1999; Wilson et al. 2003). Similar to studies of moose in Canada (Broders et al. 1999; Wilson et al. 2003), our F_{ST} values were larger than R_{ST} estimates, but our estimates were not as large as those from Canada. These results are somewhat surprising because moose are thought to have become established in Alaska prior to becoming established in Canada (Hundertmark et al. 2003) or at least to have become established at similar times. Moreover, although geographic scale of population distribution was similar between those studies there are more geographic barriers to gene flow in Alaska (e.g., the Alaska Range and St Elias Range) that presumably would foster greater population differentiation. Genetic distances between Alaska populations in close proximity (i.e., Seward Peninsula, Koyukuk, and Tanana Flats) were less than a similarly arrayed group of moose populations described by Wilson et al. (2003). Also, the greatest genetic distance observed among Alaska populations were less than those observed by Wilson et al. (2003) despite the great distances and topographic barriers present between the relevant populations in Alaska.

Our results suggest that moose have been established in Canada longer than in Alaska, thereby resulting in more population differentiation and larger F_{ST} values in Canada than Alaska. Furthermore, the range of many of our genetic estimates was narrow (Table 1). For example, F_{IS} values ranged from −0.014 to 0.078, whereas those observed by Wilson et al. (2003) ranged from −0.132 to 0.176. This outcome is consistent with the hypothesis of Hundertmark et al. (2002a), who proposed that moose more recently established a sustainable population in Alaska than in Canada.

Our results demonstrated that population structure does exist in Alaska moose but not at the level expected. This is remarkable given the large geographic distances between areas sampled. The bimodal peaks from STRUCTURE we observed have been reported previously when genetic structuring is subtle (Basset et al. 2006; Bergl and Vigilant 2007). Differences also occurred between F_{ST} and R_{ST} values with F_{ST}, indicating considerably more structure than R_{ST} (Table 2). The major difference among the population comparisons was with the Alaska Peninsula—F_{ST} revealed much more structure. One likely reason for the differences between the 2 results is because of the way F_{ST} and R_{ST} are calculated; F_{ST} incorporates only variance in allele frequencies, but R_{ST} also includes variance in allele size (Balloux and Lugon-Moulin 2002). All samples had private alleles, with the exception of moose from the Alaska Peninsula (Table 1). With the presence of private alleles, allelic frequencies between populations can be dramatically different, whereas variance in allelic size may not be as great. Therefore, F_{ST} would be more affected when population comparisons involve the Alaska Peninsula than would R_{ST}. Both approaches agree that the Yakutat population is distinct from other moose populations in Alaska. F_{ST} and R_{ST} values also indicated moose from west-central Alaska (Koyukuk and the Seward Peninsula) are not separate genetic populations. The lack of differentiation from both methods supports ethnographic data, which maintain that moose filtered into the Koyukuk region from central interior Alaska in the early 1900s and then dispersed into the Seward Peninsula in the 1940s (Nelson 1973).

Previously, STRUCTURE has failed to detect population structure when gene flow is moderate or low ($\leq 5Nm$) or mutation rates are low, whereas traditional F_{ST} and R_{ST} perform much better even when gene flow is high (Nm = 25, Waples and Gaggiotti 2006). Contradictory results between F_{ST} and R_{ST} estimates and the program STRUCTURE are not surprising because F_{ST} and R_{ST} measure differentiation among predefined populations, which is a much easier statistical solution than finding structure without prior population information (Pritchard et al. 2000). Furthermore, the largest differences between maximum likelihood and Bayesian approaches with MIGRATE occurred when migration was large (Beerli 2006). Overall with mixed results or failure to obtain results, our research indicates that moose population expansion is evolutionarily recent and ongoing in Alaska.

Dispersal

One remarkable insight that can be gained from our results is the influence of past glaciers. Interior Alaska provided an ice-free refugium during the Pleistocene era and glaciers during this time have been shown to influence population expansion of moose and numerous other species in Alaska (Klein 1965). It has been hypothesized that a small number of moose remained in Alaska during their progression from

Beringia via the Bering Land Bridge to the rest of North America (Hundertmark et al. 2003). Presumably, the Tanana Flats, Koyukuk, and Tetlin are the 3 oldest populations because they occur in the ice-free corridor when moose traversed across the Bering Land Strait and into North America (Peterson 1955). When the glaciers retreated, it is likely that an expansion of moose followed the retreat and they expanded into previously glaciated regions like Yakutat (Hundertmark et al. 2003) and the Alaska Peninsula. Among these 3 populations, dispersal rates are more asymmetrically biased toward the east (Figure 1). Also supporting this notion is that there are fewer private alleles, which may indicate recent or ongoing gene flow among theses areas. Moose are known to use riparian habitats surrounding rivers in Alaska, and major rivers within our study area corresponded with the east to west dispersal (Figure 1).

In general, moose dispersal is much greater east to west along the interior river corridor than north to south across the Alaska Range, which separates the Yakutat and Alaska Peninsula from interior Alaska populations (Figure 1). However, from Koyukuk, there is clearly dispersal in both directions. Westward dispersal from Koyukuk toward the Seward Peninsula is due to habitat conditions recently becoming more favorable for moose (Chapin et al. 2006), and eastward dispersal is likely due to historic movements along river corridors between Koyukuk and the Tanana Flats (Nelson and True 1887). However, Tetlin has genetic characteristics that slightly distance itself from other interior moose populations (i.e., Tanana Flats, Koyukuk, and Seward Peninsula; Figure 3). We believe that this maybe due to secondary contact with the western Canadian subspecies of moose (*Alces alces andersoni*) that occurs just east of Alaska in the Yukon Territory (Peterson 1955; Gauthier and Larsen 1985). The possibility of contact with moose in the Yukon could also be the reason that this population had the highest within-population pairwise differences (Table 2). Added diversity from Canada could also be the reason why Tetlin had the largest theta value even though it had the smallest sample size (Table 3). This idea is supported by the conclusion of 2 populations recommended by STRUCTURE, one population was composed of Yakutat and Tetlin moose and the second was composed of all other Alaskan moose. Also in the phylogenetic tree, Tetlin is the closest population to Yakutat (Figure 3), and hence, the eastern (Yakutat and Tetlin) moose comprise of a group genetically distinct from the other populations we studied. Also, these 2 populations have the largest allelic richness, which could have been gained from ghost populations (i.e., unsampled populations) in Canada.

Koyukuk is a source for dispersal into many surrounding regions and thus helps maintain gene flow. This is crucial for maintaining genetic diversity and thus reducing negative effects of inbreeding and bottlenecks, while increasing the ability of moose to adapt to their environment (Frankham 2005). Ability to cope with a changing environment is crucial for the sustainability of moose in Alaska given the rapid rate of climate change observed (Bowyer et al. 1998; Chapin et al. 2006). Finally, the maintenance of genetic diversity is needed to mitigate the potential negative effects of hunting (Harris et al. 2002; Coltman et al. 2003; Proaktor et al. 2007). Moose are commonly harvested by sport and subsistence hunters in Alaska (Hundertmark et al. 1993, 1998; Schmidt et al. 2005; Ballew et al. 2006), but a direct test of the effects of hunting on these populations is yet to be conducted.

To provide a better understanding of observed genetic structure, we hypothesized that isolation-by-distance played a role in genetic structure of Alaskan moose because we detected a slight significant positive relationship between R_{ST} and Euclidean geographic distance (Figure 4). The narrow range of AIC_C values indicates that the genetic measure used and transformations of Euclidean geographic distances minimally influence the relationship between geographic and genetic distance. We acknowledge that topography between sample areas is very different, and moose may face impediments that require a convoluted path; nevertheless, the signal of isolation-by-distance with Euclidean geographic paths indicates a strong underlying relationship between geographic and genetic distance. Even though some of our populations are not distinct, previous research was able to detect isolation-by-distance in non-equilibrium populations and when gene flow was high ($Nm > 1$; Slatkin 1993; Matthaeis et al. 2000). Also the effect of ghost or unsampled populations is evident in that the 3 points furthest from the regression line involved the 2 most geographically distant regions: Yakutat or the Alaska Peninsula (Figure 4). However, there was no trend in the residuals. With this new knowledge, research on moose genetics can move forward and use landscape genetics to better explain population structure and gene flow for moose populations in Alaska.

Finally, differences observed between F_{ST} and R_{ST} values can provide valuable insights into the balance between mutation and genetic drift (Hardy et al. 2003). Moose in both Alaska and Canada (Wilson et al. 2003) had higher F_{ST} values than R_{ST} values, which may be due to the downward bias observed with R_{ST} values (Balloux and Goudet 2002). Furthermore, 2 of our 8 loci did not follow the stepwise mutation model, and, when this pattern occurs, R_{ST} estimates may be somewhat inaccurate and in general lower than F_{ST} (Lugon-Moulin et al. 1999; Balloux et al. 2002). Larger F_{ST} estimates are likely because of the relatively recent colonization of Alaska by moose; mutations would be overcome by the affects of migration (Hundertmark et al. 2003). Mutations are the primary basis for R_{ST} values, and it is unlikely they have accumulated within populations in so short a time. This is supported by the lower estimates with R_{ST} versus F_{ST}; consequently, we hypothesize that high levels of gene flow and dispersal are the drivers of genetic population structure for moose. Thus, anthropogenic activities that alter the landscape and changes in habitat associated with climatic warming in northern environments (Serreze et al. 2000; Chapin et al. 2006) are likely to alter the future population structure of moose via population expansion (Darimont et al. 2005) as well as population connectivity.

Funding

Interdisciplinary Graduate Education and Research Training (IGERT) Program of the National Science Foundation and Alaska Experimental Program to Stimulate Competitive Research (EPSCoR; EPS-0092040) at the University of Alaska Fairbanks.

Acknowledgments

We thank G. Stout, K. Persons, D. Young, and K. Kellie (Alaska Department of Fish and Game), Gail Collins (formerly US Fish and Wildlife Service), M. Moran and S. Oehlers (US Forest Service), and anonymous moose hunters in Alaska for providing samples.

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Received April 7, 2008; Revised July 30, 2008; Accepted August 26, 2008

Corresponding Editor: Ernest Bailey