Management and Conservation Note

Genetic Structure and Evidence of a Local Bottleneck in Moose in Sweden

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ABSTRACT The moose (*Alces alces*) is the most intensely managed game species in Sweden. Despite the biological and socioeconomical importance of moose, little is known of its population genetic structure. We analyzed 132 individuals from 4 geographically separate regions in Sweden for genetic variability at 6 microsatellite loci. We found evidence of strong substructuring and restricted levels of gene flow in this potentially mobile mammal. F_{ST} values were around 10%, and assignment tests indicated 3 genetically distinct populations over the study area. Spatial autocorrelation analysis provided a genetic patch size of approximately 420 km, implying that moose less than this distance apart are genetically more similar than 2 random individuals. Allele and genotype frequency distributions suggested a recent bottleneck in southern Sweden. Results indicate that moose may be more genetically divergent than currently anticipated, and therefore, the strong hunting pressure that is maintained over all of Sweden may have considerable local effects on genetic diversity. Sustainable moose hunting requires identification of spatial genetic structure to ensure that separate, genetically distinct subpopulations are not overharvested. (JOURNAL OF WILDLIFE MANAGEMENT 72(2):411–415; 2008)

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KEY WORDS *Alces alces*, bottleneck, conservation genetics, game species, genetic variation, spatial autocorrelation, spatial genetic structure.

The moose (*Alces alces*) is the most intensely managed game species in Sweden. Moose occur over most of the country and the population is large, numbering 300,000–400,000 animals during the summer. Currently, around 100,000 animals are harvested annually by hunters. During the 19th century, however, the population was considerably smaller, periodically comprising only a few thousand individuals (Hermansson et al. 1975). Despite the biological and socioeconomical importance of the species, relatively little is known of the population genetic structure of the moose in Sweden.

Current moose management is not based on identification of genetically distinct biological populations. Rather, hunting pressure is determined by estimates of the number of animals within geographic areas that coincide with villages and land properties. Depending on the true genetic structure of moose this type of management strategy may result in overharvest of particular populations or population segments (cf. Laikre and Ryman 1996, Harris et al. 2002, Laikre et al. 2005).

The moose has the potential for moving large distances and thus, gene flow over Sweden may be considerable. However, early allozyme studies of moose in Scandinavia indicated significant genetic heterogeneity over short geographic distances (Ryman et al. 1977, 1980; Reuterwall 1980; Chesser et al. 1982; Baccus et al. 1983). Levels of genetic variation were low, though, with only 2–5 polymorphic allozyme loci, and this lack of variability precluded fine scale genetic studies. Further, low variation at major histocompatibility complex (MHC) loci was suggested to reflect either a bottleneck or reduced selective pressure at MHC due to the solitary habits of the moose (Ellegren et al. 1996).

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We used 6 microsatellite loci for a pilot study of 132 moose collected from 4 geographically separated regions in Sweden. Our objective was to investigate 1) whether these markers provide enough variability to delineate substructuring, 2) degree of divergence and substructuring among and within these 4 regions, and 3) possible indications of bottlenecks.

STUDY AREA

Muscle tissue samples we used were collected by hunters during the annual hunt in 1980 and had been stored in a frozen tissue bank at the Division of Population Genetics, Department of Zoology, Stockholm University. For each killed animal the hunter marked the location of kill on a map provided with each tissue collection container and protocol. Marks were subsequently digitized and transformed into geographic coordinates. Our 4 investigated counties covered approximately 3,000–25,000 km^2 each, and geographic distance among them varied between 200 km and 800 km (Fig. 1). Dominating tree species for all counties were Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and annual precipitation was 500–1,000 mm. There were no apparent natural barriers to moose migration among the 4 counties. We analyzed 132 individuals for our pilot study, 50 from each of the 2 counties of Västerbotten and Kronoberg and 16 individuals each from the counties of Gävleborg and Stockholm (Fig. 1a). We chose these samples to reflect genetic patterns over short as well as long geographic distances.

METHODS

We extracted genomic DNA from approximately 25 mg of muscle tissue using the Qiagen DNeasy extraction kit (Qiagen, Inc., Hilden, Germany) according to the manufacturer's instructions. We analyzed genetic variation at 6

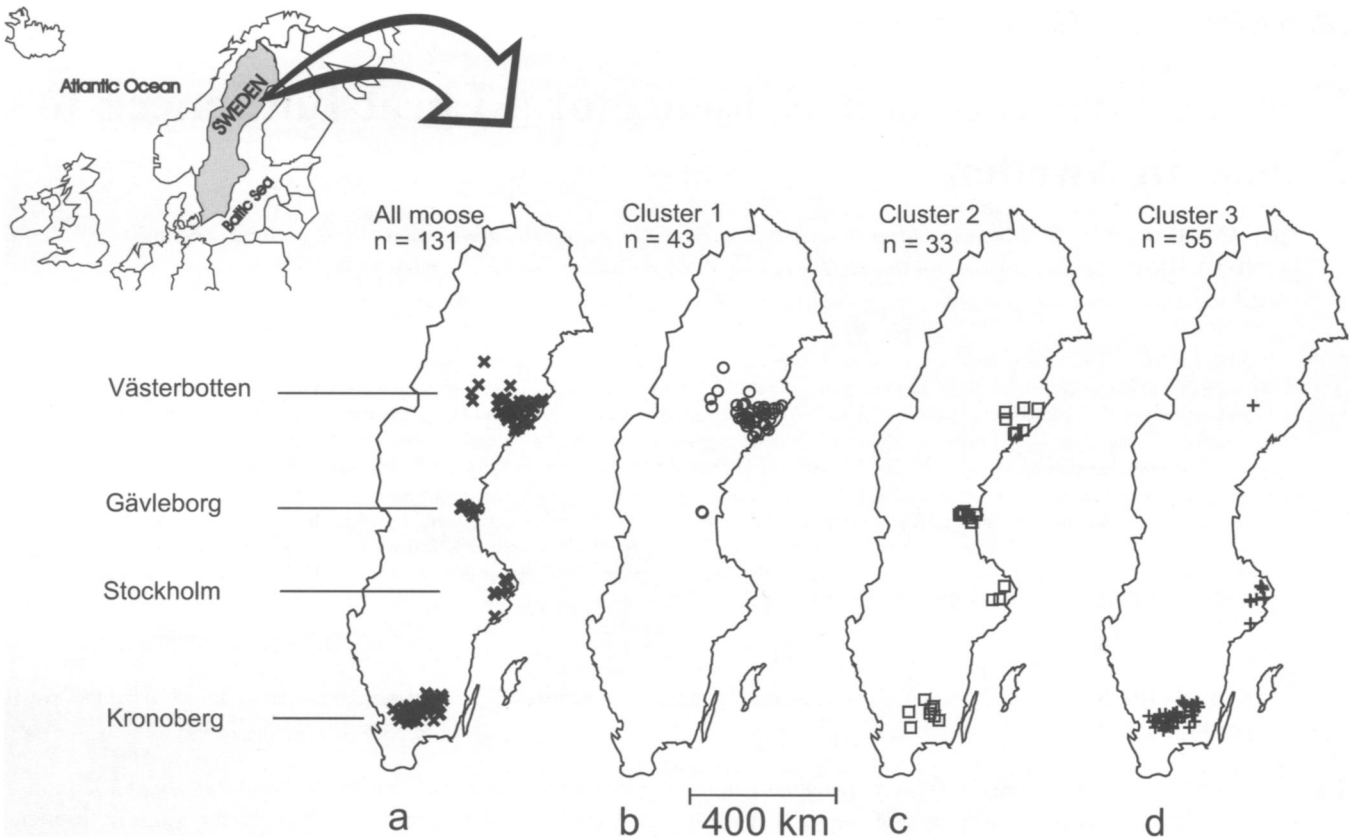

Figure 1. Sampling sites of the 132 moose (we excluded one moose with incomplete geographic coordinates from this analysis) collected by hunters during the 1980 hunt from 4 Swedish counties (a). Plates b–d indicate position of individuals assigned to each of the 3 clusters identified in the STRUCTURE analysis (Falush et al. 2003).

microsatellite loci: McM58, McM130, OarFCB20, RT30, MAF46, and CSSM003 (Swarbrick et al. 1992, Buchanan et al. 1994, Hulme et al. 1994, Moore et al. 1994, Wilson et al. 1997). These microsatellites have previously been shown to detect genetic variation in moose (Wilson et al. 1997, Røed 1998).

We amplified microsatellite loci using a PTC-100 programmable thermal controller (MJ Research, Inc., Waltham, MA) in 15-µL reactions comprising 3 µL DNA extract, 0.64 mM dNTPs, 1× polymerase chain reaction (PCR) buffer (Qiagen), 1.5–4.5 mM $MgCl_2$ (Qiagen), 0.8 µM of each fluorescently labelled primer (Proligo LLC, Boulder, CO), and 0.75 U HotstarTaq (Qiagen). The conditions for the PCR included 10 minutes of denaturation (95° C) followed by 35 cycles of 30 seconds each of 94° C denaturation, 57° C annealing, and 72° C extension, with a final extension period of 30 minutes at 72° C. We separated PCR products on a CEQ 8000 sequencer (Beckman Coulter, Inc., Fullerton, CA) together with a synthetic DNA size standard (400; Beckman Coulter).

We investigated possible indications of scoring problems or occurrence of null alleles using the MICRO-CHECKER software (van Oosterhout et al. 2004). Our sample sizes were small (132 individuals and 6 loci) and we used the POWSIM simulation software to assess whether this material provided sufficient statistical power for our primary goal of revealing population structuring (Ryman et al. 2006, Ryman and Palm 2006). We assessed probability of obtaining a significant result ($P < 0.05$) in contingency tests when sampling 4 populations employing sample sizes corresponding to those from our sampling regions (cf. Fig. 1a).

We used both traditional *F*-statistics (Weir and Cockerham 1984) and individually based approaches that do not require predefined grouping of samples. We used GENEPOP 3.3 (Raymond and Rousset 1995) to quantify spatial genetic heterogeneity and deviations from Hardy–Weinberg proportions within and among the sampled counties, with associated levels of significance (Raymond and Rousset 1995). We calculated allelic richness using the software FSTAT (Goudet 2001).

For the individually based approaches we used likelihood analysis to assess the most likely number of groupings compatible with the observed genotypic distribution using the program STRUCTURE (Pritchard et al. 2000, Falush et al. 2003). We applied GeneClass (Cornuet et al. 1999) for testing the degree to which individuals were assigned to the region from which they were sampled (so-called self-assignment; Cornuet et al. 1999).

Further, we examined spatial autocorrelation between pairs of individuals at different geographic distances using the multiple loci approach described by Smouse and Peakall (1999) as applied in the GenAlEx software (version 5; Peakall and Smouse 2001). The program only allows individuals with a complete genotype for all loci, so we

Table 1. Statistics for microsatellite data (6 loci) by sampling region (Västerbotten, Gävleborg, Stockholm, and Kronoberg) for moose collected during the Swedish 1980 hunt. H is expected heterozygosity. F_{ST} represents the fixation index indicating the amount of genetic differentiation between regions, whereas F_{IT} and F_{IS} quantify the degree of deviation from Hardy–Weinberg expectations in the total material and within regions, respectively (Weir and Cockerham 1984).

Region	n	H	F_{IS}	F_{IT}	F_{ST}	No. of alleles	Allelic richness	No. of private alleles
Västerbotten	50	0.565	−0.039			29	24	3
Gävleborg	16	0.656	−0.005			28	28	0
Stockholm	16	0.608	0.042			23	23	0
Kronoberg	50	0.594	0.031			22	21	0
Total	132	0.640	0.002*	0.109***	0.108***	32		

* $P < 0.05$.
*** $P < 0.001$.

excluded from this analysis 6 individuals with partly missing genotypic data, resulting in a total of 126 moose. We set distance classes at 100 km, resulting in 10 classes corresponding to a total distance of 1,000 km, which covered all pairs of moose in our study with 29–2,215 moose-pairs per class.

To test for indications of bottlenecks we used the program BOTTLENECK 1.2.02 (Cornuet and Luikart 1996), applying the stepwise mutation model (SMM) and the two-phase model (TPM) that combines the stepwise and infinite allele mutation models (Cornuet and Luikart 1996, Piry et al. 1999). For the TPM model we used 95% single-step and 5% multi-step mutations (Piry et al. 1999). We performed tests for heterozygote excess using the one-tailed Wilcoxon test with 10,000 replications (Cornuet and Luikart 1996). We also used the BOTTLENECK program to test whether we could detect mode shifts in allele frequency distributions compatible with a bottleneck in the Västerbotten and Kronoberg samples (for which $n > 30$; Luikart et al. 1998).

RESULTS

We observed 32 alleles at 6 microsatellite loci with 3–8 alleles per locus. Expected overall heterozygosity (H_T) was in the range 0.52–0.78 for separate loci and between 0.57 and 0.66 per sampling region (Table 1). We found no indications of scoring problems or null alleles. The POWSIM analysis showed that statistical power was high for detecting even small levels of divergence (measured as F_{ST}) using our 6 loci with observed allele frequencies and sample sizes. For example, assuming a true F_{ST} of 0.01 among the 4 sampling localities, probability of detecting this amount of divergence with our sample sizes was about 85%.

We found no deviations from Hardy–Weinberg proportions within sampling regions. OarFCB20 in Stockholm was the only locus–sample region combination (out of 24) with significant ($P < 0.05$) deviation from Hardy–Weinberg expectations (representing heterozygote deficiency). We estimated overall F_{ST} as 0.108, and both F_{ST} and overall F_{IT} (0.109) were positive and highly significant (Table 1), which indicates that the Swedish moose population does not constitute a single panmictic unit.

Significant allele frequency differences occurred in all 6 pairwise comparisons among the 4 sampling regions (Table 2). Using a critical $P = 0.001/6 = 0.00017$ for Bonferroni significance, all values remained significant at the 0.001 level.

Our results from the STRUCTURE analysis suggest that the genotypic distribution most likely conforms to 3 populations under the STRUCTURE model assuming genetic exchange among sampling regions and possible occurrence of offspring from matings between individuals from different populations (Falush et al. 2003). Locations of the 3 clusters largely conforms to a northern (Fig. 1b), a central (Fig. 1c), and a southern population (Fig. 1d). Our results are consistent with the GeneClass self-assignment results of 88%, 75%, 63%, and 80% for Västerbotten, Gävleborg, Stockholm, and Kronoberg, respectively.

The correlogram from the spatial autocorrelation analysis intercepts the x-axis at approximately 420 km (Fig. 2), which implies that moose collected at shorter distances are genetically correlated, whereas pairs of moose collected >420 km apart are less genetically similar than 2 randomly selected moose from the total collection.

We observed a significant deviation from genotype frequency distributions expected under mutation-drift equilibrium for the Kronoberg sample (one-tailed Wilcoxon test for H excess $P < 0.05$; Table 3). In this county 5 of the 6 loci showed a heterozygote excess for both the SMM and TPM mutational models, suggesting a recent bottleneck in this region. Kronoberg was also the only sample in which we observed a mode shift in allele frequency distribution (i.e. fewer alleles at low frequency [<0.1] than in intermediate allele frequency classes [e.g. 0.1–0.2]; Luikart et al. 1998).

DISCUSSION

Our results indicate that gene flow may be restricted in moose. Such restricted gene flow may be due primarily to

Table 2. Pairwise genetic differentiation for moose in Sweden (1980) measured as F_{ST} over 6 microsatellite loci and 4 regions (Västerbotten, Gävleborg, Stockholm, and Kronoberg).[a]

	Västerbotten	Gävleborg	Stockholm	Kronoberg
Västerbotten				
Gävleborg	0.122			
Stockholm	0.118	0.099		
Kronoberg	0.115	0.137	0.032	

[a] All $P < 0.001$.

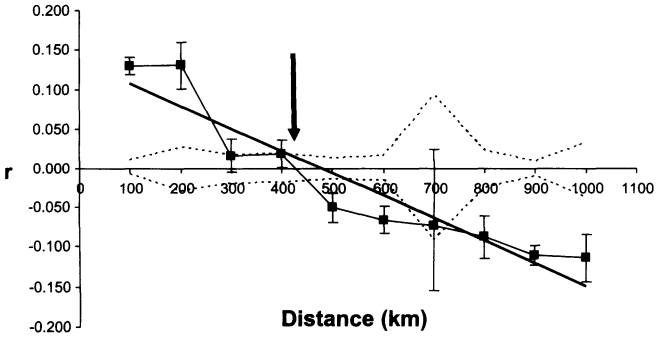

Figure 2. Spatial autocorrelogram for moose in Sweden collected during the 1980 hunt from the 4 counties Västerbotten, Gävleborg, Stockholm, and Kronoberg. Each point represents the autocorrelation coefficient (r) based on 32 alleles with bars indicating 95% confidence interval. The straight solid line is the linear regression fitted to the autocorrelation coefficients ($P < 0.001$). Dotted lines indicate permutated 95% confidence intervals for sampling from the null distribution ($r = 0$). The correlogram intercepts with the x-axis at a distance of approximately 420 km (indicated by the arrow).

the dispersal pattern of moose; although a potentially highly mobile mammal, radiotracking data indicate that moose are philopatric with annual home ranges for females and males of about 14 km^2 and 26 km^2, respectively (Cederlund and Sand 1994).

Our observed overall F_{ST} among sampling regions of 0.11 appears quite large, but also in line with previous observations. For instance, a study of moose in Canada found F_{ST} values of 0.02–0.10 (excluding isolated island populations; Wilson et al. 2003), and similar values have been observed in reindeer, roe deer, white-tailed deer, and elk (Postma et al. 2001, Côté et al. 2002, Doerner et al. 2005, Hicks et al. 2007). Assuming migration-drift equilibrium, $F_{ST} \approx 1/(4N_em + 1)$, where N_e and m are effective population size and migration rate, respectively. With the observed F_{ST} of 0.108 among our 4 regions the number of genetically effective migrants per generation (N_em) would then correspond to only about 2.1 (e.g., Crow and Kimura 1970). Further, the spatial autocorrelation correlogram profile (Fig. 2) largely coincides with expectation under a model of isolation by distance where divergence grows continuously with geographic distance.

Clearly, ours is only a pilot study, and more detailed investigations are required before the primary factors shaping spatial genetic structure of moose in this region can be identified. These factors may include biological characteristics, such as philopatry, but also geographic constructions, such as highways and cities, and the strong hunting pressure that is maintained over all of Sweden.

Previous computer simulations have demonstrated that various regimes for moose hunting may considerably affect the genetically effective population size and generation interval, and thereby the rate of inbreeding and loss of genetic variability (Ryman et al. 1981). The strong genetic substructuring we observed implies that these types of effects may occur locally.

Allele and genotype frequency distributions suggest a recent bottleneck in southern Sweden. This bottleneck is indicated by genotype frequency distributions but does not appear to have strong effects on current levels of variability as measured by gene diversity and allelic richness (Table 1). However, statistical power for detecting differences in the amount of variation may be low and the present material too restricted to reveal possible effects on levels of variation (cf. Leberg 2002). The indicated bottleneck in southern Sweden may reflect founder effects following the recolonization of this area in the beginning of the 20th century, but could also be an effect of a strong hunting pressure over the past decades. A more detailed analysis compromising more individuals and loci is needed to provide a better picture of the recent genetic history of moose in this region.

Table 3. Tests for deviation from heterozygosity expected under mutation-drift equilibrium, potentially indicating genetic bottlenecks within sampling regions (Västerbotten, Gävleborg, Stockholm, and Kronoberg) collected during the 1980 hunt in Sweden. H_E and H_D are the number of loci showing heterozygosity excess and deficiency, respectively. SMM and TPM represent 2 different mutation models (the stepwise mutation model and two-phase model, respectively). P = probability based on one-tailed Wilcoxon test for heterozygote excess (cf. Cornuet and Luikart 1996).

	Heterozygosity excess					
	SMM			TPM		
Region	H_E	H_D	P	H_E	H_D	P
Västerbotten	1	5	0.977	1	5	0.961
Gävleborg	4	2	0.281	4	2	0.281
Stockholm	4	2	0.281	5	1	0.219
Kronoberg	5	1	0.023	5	1	0.016
Total	4	2	0.656	3	3	0.281

Management Implications

Our results indicate that moose in Sweden are more genetically substructured than previously anticipated. To ensure long-term viability and future evolution of moose in this region it is important to maintain within- and between-population variability (Allendorf and Ryman 2002). Management should focus on individual subpopulations to ensure that between-population variation is maintained (cf. Comer et al. 2005, Coulon et al. 2006). Currently, moose are managed in units that are not defined by genetic relationships, which results in a harvest that is not based on the genetic status of separate subpopulations. A strong hunting pressure is maintained all over Sweden, with similar levels of harvest in the 4 regions sampled in our study (approx. 0.2 moose/km^2; Jägareförbundet 2007). Our results indicate that the moose of Kronoberg County have experienced a genetic bottleneck. If current levels of hunting result in small local effective population size this may, in turn, lead to a prolonged bottleneck in this area potentially resulting in local loss of genetic variation. To provide long-term biological sustainability of Swedish moose management, a more thorough delineation of the spatial genetic structure is warranted. Management units should be modified so that management and genetic groupings coincide.

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