Alaska Department of Fish and Game Division of Wildlife Conservation December 2003

Molecular Genetic Approaches in Wildlife Management

Kris J. Hundertmark

Research Final Performance Report 1 July 2000–30 June 2005 Federal Aid in Wildlife Restoration Grants W-27-4 and 5, ended in W-33-1 Project 1.54

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PROJECT TITLE: Molecular Genetic Approaches in Wildlife Management

PRINCIPAL INVESTIGATOR: Kris J. Hundertmark

COOPERATORS:

FEDERAL AID GRANT PROGRAM: Wildlife Restoration

GRANT AND SEGMENT NR.: Initiated W-27-4, ended W-33-1

PROJECT NR.: 1.54

WORK LOCATION: Kenai Moose Research Center, Soldotna

STATE: Alaska

PERIOD: 1 July 2000 – 30 June 2005

I. PROBLEM OR NEED THAT PROMPTED THIS RESEARCH

As consumptive and non-consumptive demands on Alaska's wildlife resources become greater the Division of Wildlife Conservation will need to manage those resources more intensively. To manage populations more intensively requires more comprehensive information about the biology of populations and species. Currently, information is gathered through survey and inventory activities as well as research projects, the latter usually using marked animals to study movement patterns, habitat use, and population identity. These activities provide much useful information on which to base management decisions; nonetheless, they provide only a snapshot of conditions at the time of data collection. The biology of populations and species is dependent as much or more on historical events as it is on current events, and those historic processes can be inferred from analysis of genetic data. Furthermore, advances in molecular techniques now permit genetic characterization of individuals from small samples of tissue, including hair, feces and bone. That ability can aid management efforts through increased application of forensics, population size estimation, and parentage assessment. Collection and analysis of genetic data can enhance Alaska's wildlife management programs by providing comprehensive information about population structure and history, and by providing new research and management tools for understanding the dynamics of wildlife populations.

II. REVIEW OF PRIOR RESEARCH AND STUDIES IN PROGRESS ON THE PROBLEM OR NEED

The rapid development of molecular genetic techniques over the last 30 years has created an impressive suite of potentially powerful tools for application to resource management issues (Smith et al. 1976, Strobeck and Beech 1992, Smith and Rhodes 1993, Sunnucks 2000). For example, the discovery of short tandem repeats (microsatellites) in the nuclear genome provides us with large numbers of highly polymorphic, neutral markers for animal and population identification. Microsatellites can be amplified via the polymerase chain reaction (PCR), which permits them to be used even when small amounts of tissue are available. Those desirable characteristics (high polymorphism and ease of amplification) have generated a revolution in population genetics analysis, including new theoretical approaches for improving statistical inference from those data (Luikart and England 1999).

Opportunities extend beyond the traditional scope of game management and encompass diverse aspects of wildlife biology (Queller et al. 1993, Paetkau and Strobeck 1994, Paetkau et al. 1995, Taylor et al. 1994, Craighead et al. 1995, Pemberton et al. 1996), and as molecular techniques, ease of application, and costs improve it is virtually certain that molecular genetics will become as important to wildlife management as the radiocollar is today. Recent compilations of theoretical and applied studies in molecular genetics demonstrate the immense potential of this discipline for addressing conservation issues (Berry et al. 1992, Real 1994, Avise and Hamrick 1996, Smith and Wayne 1996, Goldstein and Schlotterer 1999). Some potential applications of genetic techniques are listed in Appendix A, as are specific research and management projects within Alaska that could benefit from a genetic component. Alaska has two primary advantages as a natural laboratory for genetics research. First, it has natural ecosystems still in place. Second, those ecosystems exist over a large enough spatial scale that topics at the individual, population, metapopulation, or regional scale can be addressed. Given our history as a national leader in basic and applied research, a conservation genetics program would be a fitting addition to our conservation efforts.

III. APPROACHES USED AND FINDINGS RELATED TO THE OBJECTIVES AND TO PROBLEM OR NEED

1. Create and maintain a permanent frozen tissue bank and associated database.

A frozen tissue collection was maintained at the Soldotna office of Alaska Department of Fish and Game, consisting mostly of moose tissues. Currently, those moose tissues are on loan to a graduate student at the University of Alaska Fairbanks for her dissertation work on population genetics of Alaska moose.

2. Determine suites of nuclear and/or mitochondrial markers suitable for analysis at the individual and population levels for selected species.

The premature termination of this project resulted in little progress on this objective. A suite of microsatellite markers developed originally in domestic livestock was tested on moose and was found to describe differences in genetic variation among populations (see Section V, Job 4).

3. Document genetic variation within and among populations of Alaska wildlife for forensic and biological purposes.

During the life of this project, two investigations were conducted concerning levels of variation in introduced population of Alaska cervids. The first, conducted on elk from Afognak Island, demonstrated that the small initial size of the founded population (8 animals) resulted in significant declines in genetic diversity compared with the source population on the Olympic Peninsula, Washington. The fast growth rate of the population after introduction can be identified as a reason that more severe declines in diversity did not occur. Moreover, computer simulations demonstrated that the 68% decline in population size in the early 1990s due to severe winters did not have a significant effect on diversity.

The second project compared genetic diversity in 2 introduced populations of moose, Kalgin Island and Berners Bay. Those findings are described more fully in Section V, Job 4. Both populations showed similar levels of diversity and showed significantly less diversity than moose from Yukon Flats National Wildlife Refuge. The primary conclusion to be drawn from those results is that neither Kalgin Island nor Berners Bay receives significant gene flow from neighboring moose populations. Thus, diversity remains low and the chance of those populations suffering from inbreeding depression is significant.

4. Develop both field and laboratory methods appropriate to conduct molecular-based CMR population analyses.

The premature termination of this project resulted in no progress on this objective.

IV. MANAGEMENT IMPLICATIONS

Alaska has many populations of wildlife that were established as introductions. We are fortunate to have good records for most of those efforts. Unfortunately, those records indicate that many of those transplants were based on too few founders and have resulted in decreased genetic diversity of those populations that are derived from the original transplants. I have demonstrated that the three populations studied under this project all have decreased diversity relative to "normal" populations of their species. Reduced diversity in Kalgin Island and Berners Bay moose is more severe than in Afognak Island elk, most likely because the moose populations do not have the habitat base to increase their population size to the point where genetic drift is not a serious concern. Serious consideration should be given to supplementing these, and possibly other, wildlife populations to improve their genetic diversity.

V. SUMMARY OF WORK COMPLETED ON JOBS IDENTIFIED IN ANNUAL PLAN FOR LAST SEGMENT PERIOD ONLY

Because the principal investigator retired from ADF&G, this project was prematurely terminated. However, some progress on objectives was accomplished during the reporting period.

Job 1. Preparation of a study plan.

This job was not active.

JOB 2: Genetics technique development

In conjunction with activities relating to Job 4, we tested a suite of microsatellite markers for use with moose. These markers were: BL42, BM203, BM1225, BM4513, BM848, BM888, FCB193, Rt1, Rt5, Rt9, Rt24, and Rt30, and were originally described in bovine or reindeer genomes. Those markers were successful in describing variation in moose from 3 distinct populations (see Job 4.)

Job 3. Genetic differentiation of Alaska caribou herds. (in collaboration with Patrick Valkenburg, ADF&G, Fairbanks)

This job was not active.

Job 4. Moose population genetics.

We tested the hypothesis that small population size in certain moose populations would result in decreased genetic diversity. We sampled 21 moose from Kalgin Island and 8 moose from Berners Bay and compared them to genetic characteristics of 27 moose from Yukon Flats National Wildlife Refuge. The moose population on Kalgin Island, in Cook Inlet, was established as the introduction of 6 calves (3 male, 3 female) over a 3-year period from 1957-1959. The population experiences severe fluctuations due to a limited forage base. The moose population in Berners Bay, Southeastern Alaska, was established in 1958 as an introduction of 16 individuals (5 males, 11 females) from the Susitna and Matanuska Valleys. One calf (sex unknown) died shortly after release. The population was supplemented in 1960 with the release of 6 calves (sex and origin unknown). Neither population is completely isolated from adjacent populations but physical barriers probably keep gene flow to a minimum.

We analyzed 11 microsatellite loci BL42, BM203, BM1225, BM4513, BM848, BM888, FCB193, Rt5, Rt9, Rt24, and Rt30, which were analyzed previously from 27 moose from Yukon Flats National Wildlife Refuge. Laboratory work was conducted by Wildlife Genetics International (Nelson, BC, Canada). We expressed allele sizes in number of nucleotides and analyzed allele and genotype frequencies to characterize variability within each population. Parameters examined were mean alleles per locus (*A*), observed heterozygosity (H_0), expected heterozygosity (H_E) based on allele frequencies and assuming Hardy-Weinberg equilibrium, and number of private alleles. Private alleles are those found in only one population.

Kalgin Island and Berners Bay moose showed a similar, and low, level of genetic diversity as measured by all parameters (Table 1). Yukon Flats moose exhibited greater diversity than either Kalgin Island or Berners Bay moose (Table 1). Of note is the count of 17 private alleles in the Yukon Flats population compared with 2 and 1 in Berners Bay and Kalgin island, respectively. Those data indicate that both Kalgin Island and Berners Bay populations have suffered from population bottlenecks in the past and continue to show the effects of those reductions in population size. If the Yukon Flats population can be considered as representative of typical moose population in Alaska, the low levels of variation seen in Kalgin Island and Berners Bay populations are indications that neither population experiences significant immigration from neighboring moose populations. That inference is important for two reasons. First, it means that any growth in those populations must come from resident animals. Second, the potential for inbreeding depression is significant, which could lead to decreases in fitness. Antler asymmetry is already common among Kalgin Island moose.

Job 5. Brown bear genetics.

This job was not active.

Job 6. Assess inbreeding in elk from Afognak and Raspberry Islands (in collaboration with Larry van Daele, ADF&G, Kodiak)

A manuscript, "Genetic effects of translocation in a population of Roosevelt elk (*Cervus elaphus roosevelti*) in Alaska," was finished, describing the results of this job. (See Appendix for abstract.)

Job 5. Molecular-based CMR Technique Development

This job was not active

Job 6. Prepare annual and final reports.

This final report was prepared.

VI. ADDITIONAL FEDERAL AID-FUNDED WORK NOT DESCRIBED ABOVE THAT WAS ACCOMPLISHED ON THIS PROJECT DURING THE LAST SEGMENT PERIOD, IF NOT REPORTED PREVIOUSLY

None

VII. PUBLICATIONS

- Hundertmark, K. J., and L. J. Van Daele. In prep. Genetic effects of translocation in a population of Roosevelt elk (*Cervus elaphus roosevelti*) in Alaska. To be submitted to Conservation Genetics by 1/15/2004
- Hundertmark, K. J., R. T. Bowyer, G. F. Shields, C. C. Schwartz, and M. H. Smith. In review. Colonization history and taxonomy of moose (*Alces alces*) in southeastern Alaska inferred from mtDNA variation. Submitted to Wildlife Biology.
- Hundertmark, K. J. and R. T. Bowyer. 2003. Genetics, evolution and phylogeography of moose. Alces 39: in press.
- Hundertmark, K. J., R. T. Bowyer, G. F. Shields, and C. C. Schwartz. 2003. Mitochondrial phylogeography of moose (*Alces alces*) in North America. Journal of Mammalogy 84:718-728.

- Hundertmark, K. J., G. F. Shields, R. T. Bowyer, and C. C. Schwartz. 2002. Genetic relationships deduced from cytochrome-*b* sequences among moose. Alces 38:113-122.
- Bowyer, R. T., K. M. Stewart, B. M. Pierce, K. J. Hundertmark, and W. C. Gasaway. 2002. Geographical variation in antler morphology of Alaskan moose: putative effects of habitat and genetics. Alces 38:155-165.
- Hundertmark, K. J., G. F. Shields, I. G. Udina, R. T. Bowyer, A. A. Danilkin, and C. C. Schwartz. 2002. Mitochondrial phylogeography of moose (*Alces alces*): late Pleistocene divergence and population expansion. Molecular Phylogenetics and Evolution 22:375-387.

VIII. RESEARCH EVALUATION AND RECOMMENDATIONS

Based upon the limited amount of work conducted prior to the premature termination of this project, it is apparent that some populations of Alaska's wildlife that were established as introductions need to be supplemented to increase their genetic diversity. Further study of population genetics of wildlife associated with studies designed to identify inbreeding depression should be conducted.

The frozen tissue collection should be loaned permanently to The Museum at the University of Alaska Fairbanks to be managed as part of their frozen tissue collection.

IX. PROJECT COSTS FROM LAST SEGMENT PERIOD ONLY

Federal Aid share 33,585 State share 11,195 =Total 44,780

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APPROVAL DATE: _____

X. LITERATURE CITED

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	Yukon Flats	Kalgin Island	Berners Bay
Alleles per locus	5.2 (1.8)	2.9 (0.8)	3.1 (0.9)
Но	0.67 (0.12)	0.46 (0.2)	0.53 (0.30)
Не	0.65 (0.12)	0.46 (0.2)	0.52 (0.25)
Private alleles	17	1	2

Table 1. Enidices of genetic diversity in three moose populations from Alaska based on analysis of 11 microsatellite loci.

XI. APPENDIX

Appendix 1. Abstracts of publications:

To be submitted to Conservation Genetics

Genetic effects of translocation in a population of Roosevelt elk (*Cervus elaphus roosevelti*) in Alaska

Kris J. Hundertmark^{1,2}* and Lawrence J. Van Daele³

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Abstract

The population of Roosevelt elk (Cervus elaphus roosevelti) inhabiting Afognak Island, Alaska, USA was established by a single introduction of 8 individuals in 1929, and currently contains approximately 1,400 individuals. We examined indices of genetic diversity for 16 microsatellite loci in the Afognak population and compared them to current levels of diversity in the source population of elk from the Olympic Peninsula, Washington, USA to determine effects of translocation on neutral genetic variation. The Afognak population differed significantly (P < 0.0001) from the Olympic population in both allelic and genotypic composition. Estimates of percent loci polymorphic, alleles per locus, number of private alleles, and multilocus heterozygosity were lower in elk from Afognak than in those from Olympic Peninsula. Mean inbreeding coefficients within Afognak (f =0.019) and Olympic (f = -0.006) populations did not differ significantly from zero although a small but significant degree of inbreeding (F = 0.08) was detected among populations. Surprisingly, no evidence of a bottleneck was detected using a test for heterozygosity excess. A statistic testing for a bottleneck signature in the ratio of allele number to allele size range was significant for both founded and source populations, suggesting that the Afognak population has effectively undergone serial bottlenecks. The different outcomes of the tests suggest that their power to detect bottlenecks varies with conditions. In comparisons with other studies of genetic diversity of elk, we provide evidence for generally low heterogeneity among Roosevelt elk.

Alces (in press)

Genetics, evolution, and phylogeography of moose

Kris J. Hundertmark¹ and R. Terry Bowyer²

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ABSTRACT: Until recently, little information about genetics of moose (Alces alces) was available, and the evolution of this species was deduced primarily from morphological and behavioral evidence. Indeed, early studies of allozymes indicated little genetic variation in moose. Recent studies indicated higher levels of variation in nuclear markers; nonetheless, genetic heterogeneity of moose is relatively low compared with other mammals. Similarly, variation in mitochondrial DNA of moose is limited worldwide, indicating low historic effective population size and a common ancestry for moose within the last 60,000 years. That ancestor most likely lived in central Asia. Moose exhibit low levels of heterogeneity worldwide, probably because of population bottlenecks in the late Pleistocene caused by latitudinal shifts in habitat from recurrent climate reversals. A northward movement of boreal forest associated with the end of the last ice age facilitated the northward advance of Asian populations and colonization of the New World, which occurred as a single entry by relatively few moose immediately prior to the last flooding of the Bering land bridge. Despite suffering serial population bottlenecks historically, moose have exhibited remarkable plasticity. We conclude that morphological variation among moose worldwide occurred within a relatively short period and indicates that moose underwent episodes of rapid and convergent evolution. Until recently, few genetic studies directly addressed moose management. Models have demonstrated that harvest strategies can have negative consequences on neutral genetic variation as well as alleles underpinning fitness traits. Biologists should consider such outcomes when evaluating management options.

Submitted to Wildlife Biology

Colonization history and taxonomy of moose *Alces alces* in southeastern Alaska inferred from mtDNA variation

Kris J. Hundertmark, R. Terry Bowyer, Gerald F. Shields, Charles C. Schwartz, and Michael H. Smith

Abstract

We assessed phylogeographic history of moose (*Alces alces*) in southeastern Alaska, USA, by determining their genetic affinity to surrounding populations thereby clarifying their origin and uncertain taxonomic status. Moose from central and southern regions of the southeastern Alaska panhandle were characterized by two mitochondrial haplotypes that were highly divergent from those in the remainder of the state; overlap occurred only in the northernmost area of the panhandle. Moose inhabiting areas of British Columbia, Canada, immediately adjacent to Alaska's panhandle showed high haplotype diversity. A small proportion of those moose shared haplotypes with moose in southeastern and interior Alaska but most possessed haplotypes that were restricted to that region. Association between geographic distribution and phylogenetic structure of haplotypes indicated temporal and spatial separation of moose lineages in the past. Our results indicate there were two separate entries of moose into the region during colonization, likely from different geographic areas. Coastal populations of moose living south of 58° 45' N latitude in southeastern Alaska should be classified as A. a. andersoni rather than A. a. gigas. Behavioral and morphological differences between A. a. gigas and other forest-dwelling subspecies in North America indicate a need to reevaluate management practices in southeastern Alaska.

Alces 38:113-122 (2002)

Genetic relationships deduced from cytochrome-b sequences among moose

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ABSTRACT: We studied variation in nucleotide sequences of the mitochondrial cytochrome-*b* gene to assess the phylogeny of moose (*Alces alces*) in general, and the position of North American moose within that phylogeny in particular. We combined North American, Asian, and European haplotypes generated for this study with 3 Eurasian haplotypes obtained from GenBank. No nucleotide variation occurred within moose from North America, whereas 3 haplotypes were present in European moose and 4 haplotypes in Asian moose. Clade structure was consistent over 6 most-parsimonious trees, with Asian haplotypes composing 1 clade, and North American and European haplotypes composing a second, albeit poorly supported clade. Low diversity of nucleotides in cytochrome *b* indicated a recent ancestry among moose worldwide. Existence of 1 North American haplotype is strong evidence of a single, recent entry into the New World via the Bering land bridge, rather than multiple entries through \geq 1 corridors. Furthermore, no phylogenetic support existed for the theory of distinct lineages of European versus Asian-North American moose.

Alces 38:155-165 (2002)

Geographical variation in antler morphology of Alaskan moose: putative effects of habitat and genetics

R. T. Bowyer, K. M. Stewart, B. M. Pierce, K. J. Hundertmark, and W. C. Gasaway

(Abstract unavailable at this time)

Journal of Mammalogy 84:718-728 (2003)

Mitochondrial phylogeography of moose (Alces alces) in North America

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Nucleotide variation was assessed from the mitochondrial control region of North American moose (Alces alces) to test predictions of a model of range expansion by stepping-stone dispersal, and to determine if patterns of genetic variation support the current recognition of 4 subspecies. Haplotypes formed a star phylogeny indicative of a recent expansion of populations. Values of nucleotide and haplotype diversity were low continent-wide, but were greatest in the central part of the continent and lowest in peripheral populations. Despite low mitochondrial diversity, moose exhibited a high degree of differentiation regionally, which was not explained by isolation by distance. Our data indicate a pattern of colonization consistent with a large central population that supplied founders to peripheral populations (other than Alaska), perhaps through rare, long-distance dispersal events (leptokurtic dispersal) rather than mass dispersal via a stepping-stone model. The colonization scenario does not account for the low haplotype diversity observed in Alaska, which may be derived from a post-colonization bottleneck. Establishment of peripheral populations by leptokurtic dispersal and subsequent local adaptation may have been sufficient for development of morphological differentiation among extant subspecies.

Molecular Phylogenetics and Evolution 22:375-387 (2002)

Mitochondrial Phylogeography of Moose (*Alces alces*): Late Pleistocene Divergence and Population Expansion

Kris J. Hundertmark,*^{†1} Gerald F. Shields,^{†‡} Irina G. Udina,[§] R. Terry Bowyer,[†] and Charles C. Schwartz*[¶]

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Sequence variation within the left hypervariable domain of the mitochondrial control region of moose (Alces alces) occurred at low to moderate levels worldwide, and was structured geographically. Partitioning of genetic variance among regions suggested isolation-by-distance as the primary agent for differentiation of moose, and does not support the existence of distinct eastern and western races. Levels of genetic variation and structure of phylogenetic trees indicate Asia as the origin of all extant lineages. A recent coalescence is indicated, with the common mitochondrial ancestor dating to the last ice age. Moose have undergone two episodes of population expansion, likely corresponding to the final interstade of the most recent ice age and the onset of the current interglacial. Timing of expansion for the population in the Yakutia-Manchuria region of eastern Asia indicates that it is one of the oldest populations of moose, and may represent the source of founders of extant populations in North America, which were colonized within the last 15,000 years. The population in Magadan Oblast, Russia, adjacent to the Bering Sea, expanded recently and was not related closely to moose in North America, indicating colonization of that area subsequent to the colonization of the New World. Our data suggest an extended period of low population size or a severe bottleneck prior to the divergence and expansion of extant lineages, and a recent, less-severe bottleneck in Europe. Climate change during the last ice age, acting through contraction and expansion of moose habitat and the flooding of the Bering land bridge, undoubtedly was a key factor influencing the divergence and expansion of moose populations.