GENETICS, EVOLUTION, AND PHYLOGEOGRAPHY OF MOOSE

Kris J. Hundertmark[1] and R. Terry Bowyer[2]

[1]Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA; [2]Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA

ABSTRACT: Early studies of genetic variation in moose (*Alces alces*) indicated little variation. Recent studies have 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 likely exhibit low levels of heterogeneity 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 a notable ability to adapt to a changing environment, indicating that limited neutral genetic variation may not indicate limited adaptive genetic variation. We conclude that morphological variation among moose worldwide occurred within a few thousand years and indicates that moose underwent episodes of rapid and occasionally convergent evolution. Genetic change in moose populations over very short time scales (tens or hundreds of years) is possible under harvest management regimes and those changes may not be beneficial to moose in the long term. Modeling exercises 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.

ALCES VOL. 40: 103-122 (2004)

Key words: adaptation, *Alces*, convergent evolution, moose, mtDNA, phylogeography, Pleistocene, range expansion

---

Genetics have long had a central role in biological investigations, and provide analytical tools that are applicable across a broad spectrum of investigation. For instance, genetic analysis can provide insights into such diverse investigations as evolutionary histories of species (Avise et al. 1987, 2000), interactions and relationships among populations (Blundell et al. 2002) or individuals (Quellar et al. 1993), evaluation of the success of specific management actions (Vernesi et al. 2002), population and behavioral ecology (Scribner and Chesser 2001), and food habits (Symondson 2002). Recent advances in collection and analysis of genetic data have facilitated more refined approaches to evolutionary and population genetic questions, and our understanding of moose biology has benefited as a result of those advances.

Evolution and taxonomy of moose (*Alces alces*) have been reviewed previously (Peterson 1955; Groves and Grubb 1987; Geist, 1987a,b, 1998; Sher 1987; Lister 1993; Guthrie 1995; Bubenik 1998; Bowyer et al. 2003) and have encompassed aspects of behavior, morphology, paleontology, and genetics, but no review has dealt specifi-

cally with genetics. In this review, our goal is to provide an overview of older studies while focusing on recent advances in genetics and **phylogeography** (see definition in Appendix 1) of moose and the insights they provide.

The broad scope of genetic and evolutionary investigations in species biology would make a complete review of all studies disjointed. Yet, approximately half of all published studies of moose genetics have been published since the comprehensive treatise "Ecology and Management of the North American Moose" (Franzmann and Schwartz 1998) was compiled; thus, we were compelled to present the most complete review possible. In an effort to present a cogent summary of all relevant studies, we have divided this review into 3 parts: (1) assessing genetic diversity, where we review the different types of markers examined in studies of moose genetics and the conclusions drawn from those studies; (2) moose evolution and phylogeography, where we examine the evolutionary descent of moose and processes that have shaped the genetic variation and structure observed today; and (3) genetic effects of harvest, which reviews a small but important body of work composed of management-based modeling that examined effects of various harvest regimes on population and genetic measures.

ASSESSING GENETIC DIVERSITY

One potential difficulty in discussing genetic analyses is the use of specialized terminology. To avoid uncertainty and enhance understanding, we provide a brief glossary of terms used in this review (Appendix 1). Terms defined in the glossary are highlighted in bold in the text at their first usage.

The Allozyme Era

First reports of genetic investigations of moose were published by Braend (1962, cited by Gyllensten et al. 1980), Nadler et al. (1967), and Shubin (1969, cited by Gyllensten et al. 1980), wherein those authors examined electrophoretic variation in proteins from blood serum; no variation in those genetic markers occurred in Scandinavia, North America, and central Russia, respectively. The first study to report genetic variability was Ryman et al. (1977), who examined 1,384 moose from 3 areas of Sweden for polymorphism at 23 **allozyme** loci. That study reported only 1 locus to be polymorphic, however, and only in 1 region. Although they suspected that allele frequencies varied geographically within the 1 variable region, the difference was not statistically significant. Those authors concluded that **genetic drift** associated with a severe population bottleneck (reduction in population size) in Sweden in the 19th century was a probable cause of the observed lack of diversity. Wilhelmson et al. (1978), examining variation in serum proteins, noted no differences between Canadian and European moose. From that evidence, they concluded that moose populations on separate continents had not undergone significant genetic drift despite being separated for thousands of years, implying that **effective population sizes** of moose populations historically had been large.

Wilhelmson et al. (1978) also proposed that historic population bottlenecks in Sweden had not been severe enough to have had an effect on genetic diversity of moose. Gyllensten et al. (1980) conducted extensive screening of a transferrin locus from moose across Fennoscandia and detected a single polymorphism occurring in Norway, Sweden, and Finland. Nonetheless, the polymorphism was present in only 6 of 16 populations and the uncommon allele never exceeded 6% in any population. The authors presented differences in frequency of the uncommon allele as evidence of differ-

entiation of populations geographically, supporting observations of Ryman et al. (1977). Reliance on the occurrence of a single rare polymorphism to demonstrate population subdivision, however, is tenuous at best.

Those early studies and others created an impression among some biologists that certain species, including moose, possessed little genetic variation across the genome. Hypotheses explaining this in evolutionary terms were proposed. Selander and Kaufman (1973) proposed the environmental-grain hypothesis, which stated that large, highly mobile animals exhibited less genetic variability than small, sedentary species. That hypothesis further stated that highly mobile mammals would exhibit greater homogeneity across large areas than more sedentary forms. Other hypotheses proposed that *r*-strategists were less variable than *K*-strategists (Harrington 1985), genetic heterogeneity was greater in species inhabiting broad arrays of habitats compared with habitat specialists (Nevo 1978), or that northern cervids inhabiting boreal forests were less variable than their relatives to the south (Smith et al. 1990).

Analyses of 23 allozyme loci in > 700 individuals representing 18 moose populations in Scandinavia were required to reveal extensive genetic variation in moose (Ryman et al. 1980). Those authors refuted the environmental-grain hypothesis, concluding that large mammals in general, and large cervids in particular, are not naturally monomorphic; previous studies of moose had examined too few loci or individuals to detect variation. Nonetheless, those authors noted that genetic variability in moose was somewhat less than that observed in many other species of mammals (Nevo 1978), but that genetic drift due to small historic population size was a more likely explanation than any specific evolutionary strategy. Thus, genetic drift was once again proposed as being an important factor in determining the structure of genetic diversity. In another comprehensive study, Chesser et al. (1982) examined 1,169 individuals from 4 regions in Sweden for a single polymorphic locus and reported variation in allele frequencies among those regions and, perhaps more importantly, significant variation within 1 of those regions. Detecting variation at geographic scales small enough to be considered within a single population illustrated that structure of moose populations existed at scales smaller than previously imagined, and that vagility was not inconsistent with genetic structuring.

The most recent study of allozyme variation in moose reported extensive variation in a moose population in Alaska (Hundertmark et al. 1992). The level of genetic diversity observed was greater than that reported elsewhere in moose and was similar to levels observed in white-tailed deer, a species known for extensive allozyme diversity (Smith et al. 1984). Hundertmark et al. (1992) hypothesized that lesser levels of variability described in moose from Scandinavia and other regions of North America were attributable to glacial history. All other moose populations studied to that point occurred in previously glaciated terrain that was colonized by moose after retreat of Pleistocene ice sheets. Colonization of previously glaciated areas could have resulted in serial founder events that reduced genetic diversity (Sage and Wolff 1986). Hundertmark et al. (1992) argued that Alaska could have served as a refugium for moose in which genetic diversity could have been maintained because of a large effective population size.

Assessing Variation at the Sequence Level

The first investigation of highly polymorphic molecular markers in moose documented 4 alleles in a **microsatellite**-like

locus in 17 individuals from Sweden (Ellegren et al. 1991). Eight genotypes were reported, which represented a heretofore unthinkable level of polymorphism. Those authors investigated the inheritance of that locus in a 2-generation pedigree and determined that the alleles exhibited Mendelian inheritance. That study and others like it laid the foundation for the explosion of interest in population genetics and phylogenetics based on molecular markers and the polymerase chain reaction (PCR; Mullis et al. 1986).

The advent of PCR represented one of the truly significant advances in the history of molecular biology and genetics. The process allows in-vitro amplification of DNA from miniscule amounts of starting material (theoretically as little as 1 molecule of DNA) to provide sufficient quantities for analysis. No longer were researchers required to sacrifice animals to acquire sufficient quantities and types of tissues for genetic analyses because any nucleated cell held the complete genetic complement of the individual. PCR offered unsurpassed access to the genome, and researchers soon applied that to study genetics of moose.

Mikko and Andersson (1995) conducted the first analysis of functional loci in an analysis of variation in the major histocompatibility complex (MHC) in moose from Sweden and Canada. The MHC is a family of genes important in immune system function, and low levels of diversity of MHC alleles have been interpreted as indicators of lost evolutionary potential and increased susceptibility to pathogens (Hedrick 1994). Mikko and Andersson (1995) noted very low levels of MHC variation in both Swedish and Canadian moose. Moreover, those authors documented similarity among alleles between continents and inferred the existence of a bottleneck in an ancient moose lineage prior to divergence of European and Canadian lineages. Mikko and Andersson (1995) applied a **molecular clock** to **DNA sequence** variation in the **control region** of **mitochondrial DNA** (mtDNA) to date the time of divergence of Swedish and Canadian moose, which they estimated at 165,000-350,000 years ago.

The time since divergence of European moose also was analyzed by Ellegren et al. (1996). They assessed variation in **minisatellite** loci of Swedish moose and concluded that normal evolutionary processes could have generated the amount of variation observed within 10,000-50,000 years after a severe bottleneck. Their implication, therefore, was that the estimate of divergence provided by Mikko and Andersson (1995) was too old by perhaps 1 order of magnitude. Surprisingly, the two data sets are not inconsistent; indeed, they show similar levels of variation considering differences in evolutionary rates among marker types. The differences in estimates for date of divergence relate more to the evolutionary rate estimates used than to differences in genetic variability.

Microsatellite loci were first described for moose by Wilson et al. (1997) and Røed and Midthjell (1998). Broders et al. (1999) demonstrated the utility of microsatellites for assessing population structure in moose by assessing consequences of founder events in Canada. Heterozygosity in 3 populations founded by few individuals decreased from 14-30% compared with the source population. Broders et al. (1999), in assessing variability of moose on the island of Newfoundland, Canada, demonstrated that 2 consecutive founder events reduced heterozygosity by 46%. Although they could not discern any decrease in fitness as a result of the decrease in diversity, the authors questioned the long-term viability of those moose populations. Nonetheless, levels of diversity in neutral microsatellite loci were not indicative of diversity in functional loci in moose (Wilson et al. 2003).

The Future

Microsatellites have replaced allozymes as the most widely used molecular marker for assessing nuclear genetic diversity, and will be the choice of geneticists for the foreseeable future (Bruford et al. 1996). There are problems, however, with analysis of microsatellites because the ways in which they mutate into new forms are not entirely understood (Hancock 1999). In the future, a new type of analysis called single nucleotide polymorphism (SNP, pronounced "snip") may replace microsatellites for some applications (Fries and Durstewitz 2001, Brumfield et al. 2003). This new technology allows a single nucleotide site to be queried for presence of a particular nucleotide and presence or absence can be converted to a binary code. Current technology (so-called "real-time PCR" and "DNA chips") allows for fast and accurate examination of many individuals and SNPs, but we must await the development and characterization of marker loci before broad application of this new family of molecular markers can be considered.

MOOSE EVOLUTION AND PHYLOGEOGRAPHY

Origins of Modern Moose

Moose (*Alces alces*) are a young species in the evolutionary scheme of large mammals. The genus *Alces* first appears in the fossil record 2 million years ago (Thouveny and Bonifay 1984) and fossils attributable to *A. alces* are first recorded approximately 100,000 years ago (Lister 1993). Those dates are very recent considering that the subfamily Odocoileinae, to which moose belong, diverged from other deer lineages 9-12 million years ago (Miyamoto et al. 1990).

Paleontological evidence indicated Europe as the place of origin of the genus *Alces* (Lister 1993). The genus never was diverse, with only one species present in the fossil record at any particular time. Yet, the species assumed to be the precursor to *A. alces*, the broad-fronted moose (*A. latifrons*) was distributed across Eurasia and into northwestern North America for a time before becoming extinct in Beringia at the end of the Pleistocene (Guthrie 1995). Thus, the widespread distribution of modern moose and its immediate ancestor indicate a degree of evolutionary success despite a paucity of species diversity.

Up to 8 subspecies of moose are recognized worldwide (Fig. 1); 4 in Eurasia and 4 in North America (Peterson 1955). That number is open to question, however. Geist (1987a, 1998) contends that there are 2 predominant types of moose in the world: American and European, following the convention of Flerov (1952). To the former type he assigns all North American moose as well as eastern Asian subspecies *A. a. burturlini* and *A. a. pfizenmayeri*. He based his opinion primarily on morphology and noted similar geographic divisions in taxonomy among reindeer and caribou (*Rangifer tarandus*) and red deer and North American elk (*Cervus elaphus*; Geist 1998). He further contended that those morphological types should correspond to subspecies designations. Therefore, Geist (1998) recognized *A. a. alces* of Europe and *A. a. americana* in eastern Asia and North America. He also suggested that *A. a. americanus* has precedence under nomenclatural conventions as the proper name for the east Asian-North American subspecies. He referred to *A. a. cameloides* in northern China, Mongolia, and southeastern Russia as part of a primitive fauna native to that region and recognized that subspecies as a valid taxon although he also refers to it as an American-type moose (Geist 1998:230).

The 2-types hypothesis is supported to some degree by karyotype (Boeskorov 1996, 1997) and some data on mtDNA (Mikko

and Andersson 1995). Most Eurasian moose have a karyotype of 2N = 68, whereas North American moose have 2N = 70. That difference derives from a Robertsonian translocation of 2 acrocentric chromosomes into a single metacentric chromosome or vice versa. Although that chromosomal polymorphism originally was thought to separate Eurasian and North American moose (Groves and Grubb 1987), the 2N = 70 form was recently discovered in eastern Asia (Boeskorov 1996, 1997). Similarly, a length mutation (insertion-deletion, or indel) within the control region of mtDNA originally was described as discriminating between North American and European moose (Mikko and Andersson 1995), but subsequent investigations documented that indel in moose from Eastern Asia (Hundertmark et al. 2002b, Udina et al. 2002). Although the precise geographic distributions of those polymorphisms in karyotype and mtDNA

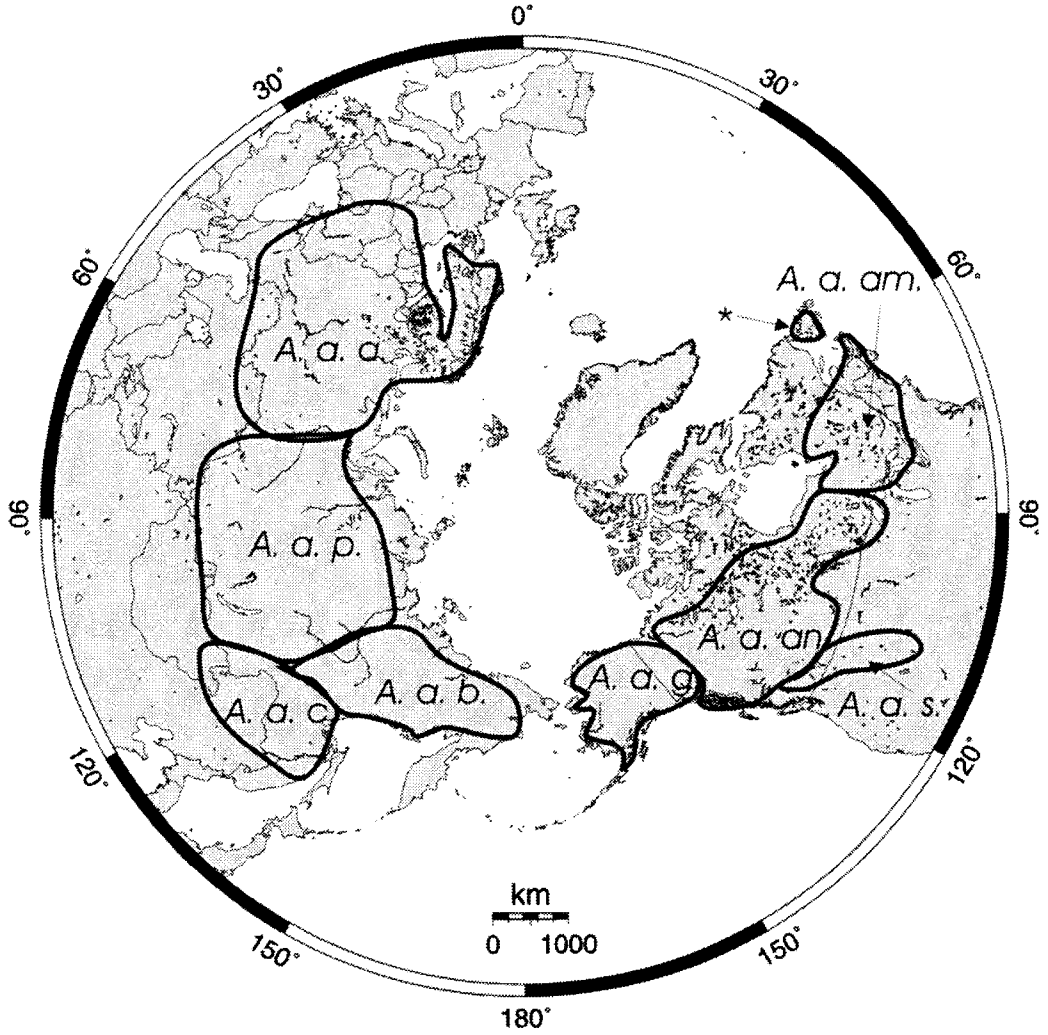

Fig. 1. Approximate ranges of 8 subspecies of moose worldwide. *A. a. a.* = *A. a. alces*, *A. a. p.* = *A. a. pfizenmayeri*, *A. a. c.* = *A. a. cameloides*, *A. a. b.* = *A. a. burturlini*, *A. a. g.* = *A. a. gigas*, *A. a. an.* = *A. a. andersoni*, *A. a. s.* = *A. a. shirasi*, *A. a. am.* = *A. a. americana*, * = introduced population in Newfoundland.

length are not well described, they seem to correspond geographically with a zone of intergradation in east-central Asia, similar to that proposed for American and Eurasian types of moose (Flerov 1952, Geist 1998). More work is needed to determine the extent of that geographic correspondence and to determine if it coincides with subspecies boundaries. Moreover, the question of reproductive viability of the two chromosomal races must be addressed. Indeed, Boeskorov (1997) has proposed that the chromosomal races are different species and Groves and Grubb (1987) have identified them as "semispecies." We caution, however, that chromosome numbers may be a poor designator of species among large mammals (Bowyer et al. 2000).

Hundertmark et al. (2002b) tested the 2-types hypothesis by examining the distribution of genetic variance of mtDNA among and within different hypothetical population structures. Those authors sampled moose throughout their worldwide distribution and arranged them into either 2 groups (corresponding to the 2-types hypothesis) or 3 groups corresponding to continent of origin (Asia, Europe, and North America). They then examined the distribution of genetic variance within and among or between groups, predicting that the correct structure would minimize within-group variation and maximize among-group variation. Percentage of total variation observed among the 3 groups was slightly greater than variation between the 2 groups (61.5% vs. 58.1%), and variation among populations within groups was minimized in the 3-group comparison (21.6% vs. 28.8% in the 2-group comparison). Therefore, Hundertmark et al. (2002b) concluded that mtDNA data provided no support for a 2-type over a 3-type hypothesis. That finding can be visualized by a phylogenetic tree constructed from haplotypes originally reported by Hundertmark et al. (2002b, 2003), which shows North American moose as distinct from both Asian and European forms (Fig. 2).

Ancient Bottlenecks and the Mother of All Moose

Moose worldwide exhibit little variation in a fragment of the mitochondrial cytochrome-*b* gene (Hundertmark et al. 2002a). Cytochrome *b* is useful for constructing mammalian phylogenies (Irwin et al. 1991) and a paucity of variation in moose indicated a recent common ancestry likely due to a severe bottleneck that affected all extant lineages (Hundertmark et al. 2002a), which is in agreement with the findings of Mikko and Andersson (1995). Analysis of variation within the mitochondrial control region, which evolves at a much faster rate than cytochrome *b* (Lopez et al. 1997), was

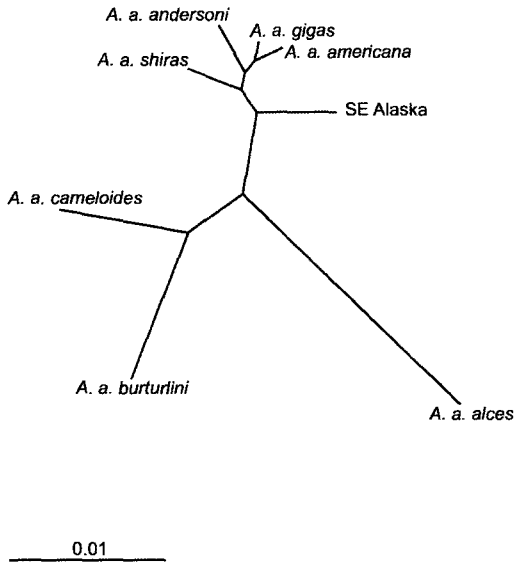

Fig. 2. Unrooted phylogenetic tree of moose populations and subspecies worldwide, with the exception of *A. a. pfizenmayeri*, using F_{ST} as the distance measure [data from Hundertmark et al. (2002b, 2003)]. Note the distinct positions of the 3 Eurasian subspecies and North American moose, which do not support an hypothesis of 2 or 3 races of moose worldwide.

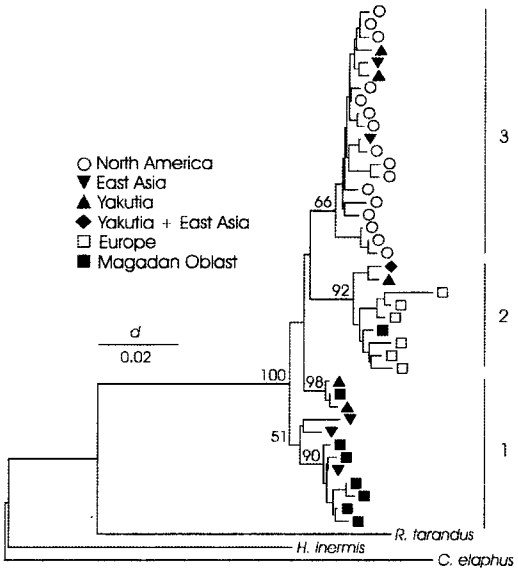

Fig. 3. A phylogenetic tree of haplotypes of the mitochondrial control region of moose. Symbols indicate region of origin, with black symbols indicating Asian origin. Distinct clades or phylogroups are indicated on the right. From Hundertmark et al. (2002b).

necessary to reveal significant levels of variation in moose and subsequently geographic patterns were revealed.

Control region **haplotypes** of moose can be divided into 3 clades, or haplogroups (Fig. 3). The basal haplogroup (i.e., the group that diverges first from the base of the tree) is entirely Asian, which suggests that those are the oldest moose haplotypes. The two other haplogroups are primarily European and primarily North American, although some Asian haplotypes occur in both. The distribution of haplogroups on a worldwide scale illustrates the age of continental assemblages of haplotypes (Fig. 4). The Yakutia area contains moose from all 3 haplogroups. The Russian Far East contains both European and Asian haplogroups, but not North American, and both Europe and North America contain only 1 haplogroup each. Therefore, Yakutia can be identified as the area from which all extant moose lineages were derived, i.e., it is the oldest extant moose population that has been sampled.

Yakutia probably was the center of a single moose population during the last ice age, or at least was the location of the only population to provide descendants of modern moose. Moose would have been restricted in their distribution because the cooler climate in Asia at that time would have resulted in a shift of boreal forest habitat to the south. That habitat could have shifted only so far southward, because of prominent mountains running east-west, which would have formed an effective barrier to further movement to the south (Hewitt 1996).

During the last ice age, there were 2 periods of maximum glacial advance, termed the lower and upper pleniglacials. Those episodes occurred at approximately 62,000 and 20,000 years ago, respectively (Fulton et al. 1986). Boreal forest habitats in Asia would have shifted to the south during those cooling episodes and would have been compressed against the northern slopes of moun-

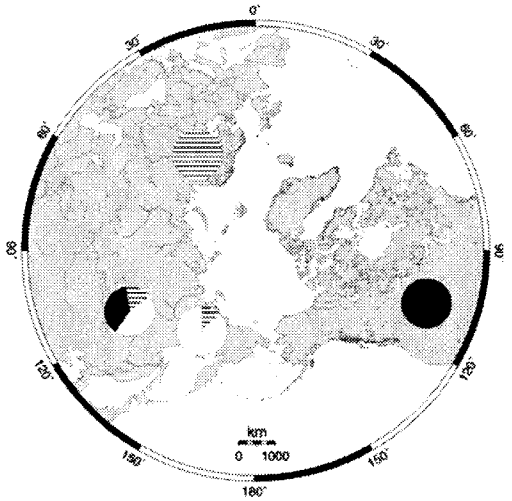

Fig. 4. Distribution of mitochondrial haplogroups worldwide. Note that moose from the Yakutia area have the most diverse composition and that moose from North America do not share haplogroups with moose from Russian Far East.

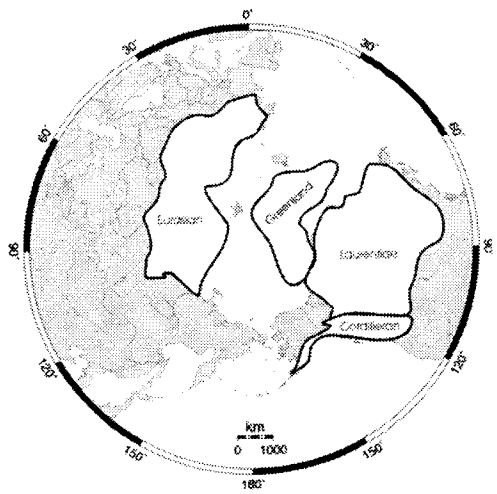

Fig. 5. Glacial coverage during the last glacial maximum, superimposed on a map of present-day sea level. Note that the Bering land bridge between North America and Asia would have been exposed during the glacial maximum due to lower sea levels. Names of major ice sheets are provided.

tain ranges. During subsequent warming intervals, moose habitat would have spread to the north, allowing moose populations to expand (Guthrie 1995). Unlike North America, much of Eurasia was not glaciated during those periods (Arkhipov et al. 1986), providing potential dispersal routes across the continent (Fig. 5). The process of latitudinal shifts of range associated with episodes of climate change results in decreases of existing genetic diversity (Hewitt 1996) and leaves characteristic signatures in the genome of modern moose.

Moose in Eurasia underwent 2 distinct, recent population expansions (Hundertmark et al. 2002b). Any other historic population processes preceding those expansions are not detectable because low population sizes eliminated much of the genetic variation present in the pre-bottleneck populations, and hence no signature from those times exists in the present genome. By applying a molecular clock to those expansion data, Hundertmark et al. (2002b) estimated that the expansions occurred approximately 59,000 and 14,000 years ago. When expansion times of moose are overlaid on a profile of global temperature change for the last ice age (Jouzel et al. 1987), population expansion is correlated with warming trends following the pleniglacials (Fig. 6). Consequently, the evolution and geographic distribution of moose seems to have been affected substantially by climate change, particularly climate reversals associated with the late Pleistocene and early Holocene.

Coming to America

Cronin (1992) analyzed subspecific variation in North American cervids using restriction fragment length polymorphisms (**RFLP**) of mtDNA. Despite analyzing 32 moose sampled from different regions of North America, he documented no variation among haplotypes from that continent. In comparison to other North American cervids, the lack of variation among subspecies of moose was interpreted as an indica-

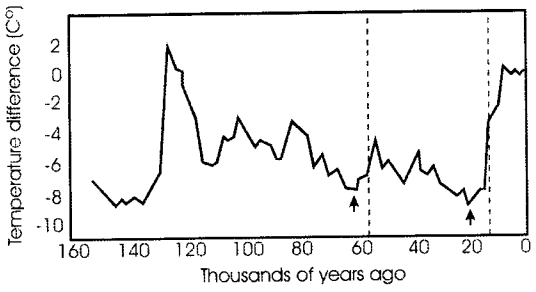

Fig. 6. Representation of mean global temperatures during the last 160,000 years relative to mean temperature in 1900. Negative temperature differences indicate periods colder than today. The 2 glacial maxima of the last ice age are indicated by arrows. Estimated dates of moose population expansion are indicated by dashed lines and correspond to periods of warming associated with glacial retreat and northward advance of the boreal forest in Eurasia. Temperature profile adapted from http://gcrio.ciesin.org/CONSEQUNCES/winter96/article1-fig3.html.

tion of a recent common ancestry, consistent with colonization of the continent after the retreat of ice sheets from the last ice age (Cronin 1992). Similarly, no variation was detected within a fragment of cytochrome *b* in North American moose compared with slight variation in Eurasia (Hundertmark et al. 2002a).

Moose populations in North America were established as a result of a single entry into the continent, and that entry occurred during the population expansion of moose 14,000 years ago at the end of the last ice age, just before the closure of the Bering land bridge (Guthrie 1995, Hundertmark et al. 2002b). A recent entry into North America is the only conclusion that is consistent with limited variation in the mtDNA control region both within North America and between North America and Eurasia. If moose had existed in 4 separate refugia in North America during the last ice age, as suggested by Peterson (1955), or had entered North America from Asia more than once, a more distant common ancestor would be indicated. The timing of the entry is supported not only by genetic data but also by the distribution of suitable moose habitat at the end of the last ice age. The cold, dry grassland habitat that prevailed in Beringia for most of the last ice age was unsuitable for moose and was replaced by boreal forest only within the last 14,000 years (Guthrie 1995).

Evidence from mtDNA variation also indicates that North American moose did not originate in Beringia, as some have speculated (Cronin 1992, Geist 1998), or recolonize the Russian Far East from North America (Coady 1982). Moose in North America are not closely related to moose on the western side of the Bering Strait (Russian Far East). If those moose were once part of the same population recently separated by the flooding of the Bering land bridge, we would still expect to find similarity in composition of mtDNA haplotypes. As noted previously, North American subspecies are distinct from European and Asian subspecies (Fig. 2) and none of the Asian haplotypes in the North American haplogroup were found in the Russian Far East. All haplotypes found in the Russian Far East (Magadan Oblast) are restricted to haplogroup 2 (Fig. 3), which contains all European haplotypes. A likely colonization scenario entails closely related moose from central Asia colonizing both Europe and North America.

Lack of genetic similarity between moose in Alaska and the Russian Far East is inconsistent with the scenario proposed by Hundertmark et al. (2002b) concerning a colonizing wave of moose traveling from Asia to North America through Beringia. A single wave of moose colonizing North America through Beringia would have left genetically similar populations on either side of the Bering Strait after the Bering land bridge flooded. Yet, ages of subfossil remains of moose from North America indicate clearly that *A. alces* was present in Alaska prior to anywhere else on the continent (Guthrie 1990, Hundertmark et al. 2003), unequivocally supporting an entry through Beringia. One hypothesis that accounts for this seeming paradox is that 1 or both of those populations underwent population bottlenecks shortly after the colonization of North America, and have only recently reestablished populations in those areas, leading to the presence of different genetic lineages in each. Moose in the Russian Far East show evidence of an expansion approximately 1,200 years ago (Hundertmark et al. 2002b) and continue to expand their range toward the Bering Sea (Zheleznov 1993).

Similarly, Alaskan moose show a surprising lack of mitochondrial diversity compared with moose elsewhere on the continent (Hundertmark et al. 2003), which is

indicative of a bottleneck notwithstanding the moderate levels of allozyme diversity reported for Alaskan moose by Hundertmark et al. (1992). Diversity of mtDNA can be reduced to a much greater degree by a bottleneck than diversity of nuclear DNA because mtDNA is 4 times more sensitive to genetic drift due to its haploid, uniparental mode of inheritance (Birky et al. 1983). Simultaneous bottlenecks in moose from both sides of the Bering Strait suggest a widespread causal factor. Recent studies have found evidence of significant biotic effects of climate reversals in Beringia after flooding of the Bering land bridge (Elias 2000, Mason et al. 2001, Anderson et al. 2002). Those effects offer an intriguing mechanism for bottlenecks in Beringian moose populations.

The greatest variation in mtDNA in North American moose occurs within the range of *A. a. andersoni* (Hundertmark et al. 2003). *Alces a. shirasi* from Colorado exhibited no diversity and *A. a. gigas* and *A. a. americana* exhibited very little diversity. If the paucity of mitochondrial diversity in Alaska is due to a bottleneck and recent expansion, those data would be consistent with the serial-founder-events hypothesis of North American colonization (Hundertmark et al. 1992).

The pattern of colonization of North America undoubtedly was influenced by the retreating glaciers and may have had some effect on genetic structure (Hundertmark et al. 2003). Based on the reconstruction of the retreat of the Laurentide ice sheet by Dyke and Prest (1987), we offer the following scenario of colonization. At the last glacial maximum, the Cordilleran and Laurentide ice sheets created an effective barrier between eastern Beringia (Alaska) and other parts of the continent (Fig. 5). As glaciers retreated, a corridor opened on the eastern slopes of the Rocky Mountains allowing passage to the south. By 10,000 years ago, western Canada was ice-free but central and eastern Canada remained covered by the Laurentide ice sheet and large proglacial lakes (Fig. 7). Passage to eastern Canada north of the Great Lakes was impossible at this time and the only dispersal corridor was south of the lakes. By 8,400 years ago, moose arriving in the eastern continent could have dispersed westward north of the lakes, skirting the southern shores of the proglacial lakes to the north, and come into secondary contact with moose from the west once the proglacial lakes receded. Moose in the eastern part of the continent (*A. a. americana*) would have been on the end of a series of founder events, explaining their low mitochondrial variability and the presence of a contact zone between *A. a. americana* and the much more variable *A. a. andersoni* in Ontario between the Great Lakes and Hudson Bay.

Morphological Adaptation

Moose of the Pleistocene and those that entered North America at the beginning of the Holocene were significantly larger than those living today, a trait shared with other northern ruminants (Guthrie 1984). Guthrie (1984) proposed that the reduction in body size was an adaptation to changes in seasonal forage availability that occurred as a result of climate amelioration at the end of the last ice age. The ability of moose to respond to a rapidly changing environment belies the relatively low levels of genetic variation documented by the studies we have reviewed and demonstrates that evolutionary potential is not easily predicted solely by genetic variability but ultimately is determined by the presence of **adaptive genetic variation** and **heritability** of traits that improve fitness (Lynch 1996).

A general reduction in body size is not the only change to occur since the colonization of North America. Moose in

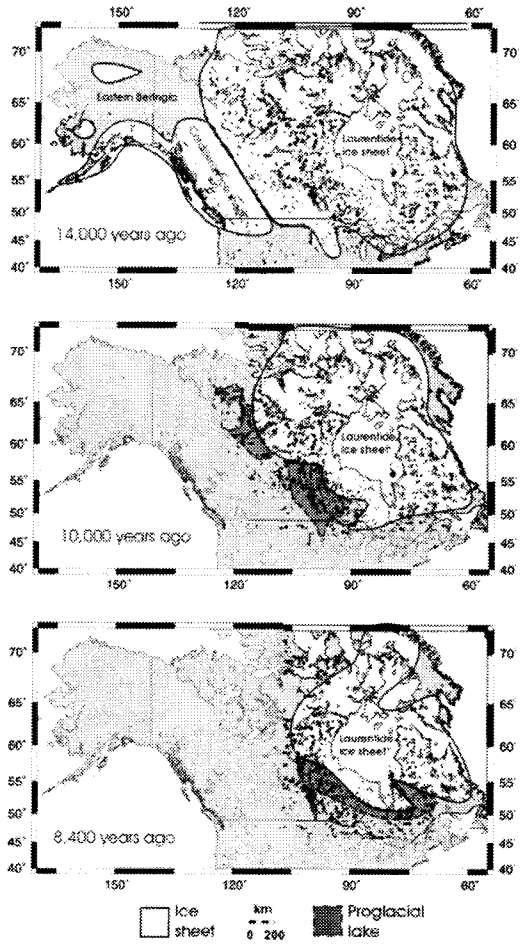

Fig. 7. Coverage of North America by the Cordilleran and Laurentide ice sheets and proglacial lakes at 14,000, 10,000, and 8,400 years ago (adapted from Dyke and Prest 1987).

North America exhibit many differences in behavior and morphology. Alaskan moose are perhaps the most divergent; they exhibit a degree of sociality not observed elsewhere (Molvar and Bowyer 1994) and have more distinctive body markings, also indicative of increased sociality (Bowyer et al. 1991). Molvar and Bowyer (1994) suggested that moose in Alaska have evolved sociality recently as a response to living in open environments. Adaptation to open environments also applies to their mating system, which is harem-based. Harem mating is adaptive in open environments (Hirth 1977) where a male can protect a harem from competitors. Moose elsewhere in North America exhibit a tending-bond system of mating, which is adaptive for forested environments.

Moose in Alaska and Siberia exhibit the largest body size of moose in North America and Eurasia, respectively. The similar appearance of moose occurring on either side of the Bering Strait has caused some investigators to consider them the same subspecies (e.g., Telfer 1984). As moose from those 2 regions are not closely related (Hundertmark et al. 2002a,b), their similarity in size must result from convergent evolution. Both subspecies have adapted to open, northern habitats by increasing body size. Adaptation to open habitats was demonstrated with a multivariate analysis of antler size among moose inhabiting different areas and habitats in Alaska (Bowyer et al. 2002). Those moose inhabiting open habitats (tundra) tended to have larger antlers overall than those living in boreal forest (taiga). Similarly, moose occupying mountainous habitat in the southern portions of their range in North America (*A. a. shirasi*) and Asia (*A. a. cameloides*) are similar; exhibiting small body and antler size (Geist 1998). Bubenik (1998) explained that similarity by proposing a second entry into North America by Asian moose—an entry that bypassed Beringia by traveling along the southern coast of Alaska. Neither genetic nor fossil data support that hypothesis (Guthrie 1990, Hundertmark et al. 2002a,b, 2003).

GENETIC EFFECTS OF MANAGEMENT

To this point we have discussed distribution of genetic and morphological diversity over space and time in the context of genetic drift and selection for locally adaptive traits. Those patterns are developed over relatively long periods of time and are integral to the process of evolution. Genetic

change also can occur over short periods due to human influences, notably harvest management, and those changes may have unintended and undesirable consequences on individuals and populations (Harris et al. 2002) and therefore are important to recognize.

Although it might be assumed that a well-designed harvest plan acts in a random fashion on genetic makeup of individuals, in reality even a managed harvest can be a highly selective force with measurable consequences in just a few generations (Coltman et al. 2003). Ryman et al. (1981) modeled the effect of different harvest strategies on 2 factors critical in determining the extent of genetic drift and inbreeding in populations: effective population size and **generation interval**, respectively. Hunting strategies were defined by different probabilities of harvest for both juveniles and adult females, and resulted in stable populations with decreased generation intervals and effective sizes compared with unhunted populations. Moreover, temporal changes in genetic diversity differed for different harvest strategies but always decreased. Thus, Ryman et al. (1981) demonstrated that improperly designed harvest regimes can affect genetic characteristics of populations and by extension may have an influence on evolutionary potential. Conversely, Cronin et al. (2001) detected no differences in numbers of alleles or levels of heterozygosity for 5 microsatellite loci among 3 moose populations in Quebec, 1 heavily hunted, 1 lightly hunted, and 1 not hunted.

Another critical factor in management is the effect of harvest on genetic loci underlying characters having a direct effect on reproductive fitness, e.g., antler size in moose. Controlling harvest by defining legal males according to antler size is common in management of North American elk (Thelen 1991) and is a strategy employed in moose management in British Columbia, Canada, and Alaska, USA (Child 1983, Schwartz et al. 1992). In an effort to evaluate genetic effects of the selective harvest system in Alaska, Hundertmark et al. (1993, 1998) modeled moose populations subject to harvest strategies employing different definitions of legal males. They concluded that selective harvest systems could result in allele frequency changes at loci coding for antler characteristics (Hundertmark et al. 1993) and that the position of a population relative to nutritional carrying capacity of the habitat affected the rate of change in allele frequencies (Hundertmark et al. 1998). Those results indicated that limiting harvest to moose with large antlers could cause a genetically based decrease in antler size over time. Such a reduction in adaptive genetic variation runs counter to general conservation goals (Lynch 1996). A stunning example of the effect of harvest on fitness traits was recently reported by Coltman et al. (2003), who documented significant genetic effects on horn size and body mass in bighorn sheep (*Ovis canadensis*) as a result of selective harvest of males with large horns.

Detecting potential changes in genetic composition of moose as they respond to various anthropogenic influences, whether related to management or to changes in the environment, is a difficult task. Nonetheless, it is an important area of investigation and deserves attention. Modeling exercises and studies of genetic variation have not addressed interrelationships of moose populations at fine scales. The effects of management and habitat alteration on processes involved in maintenance of connectivity of moose populations, such as male-mediated gene flow via yearling dispersal are extremely important and should be described. Moose are highly adaptable animals, but the intensive management of moose

populations and the environmental factors influencing their habitat (e.g., wildfire) may have unintended and significant consequences on the moose genome through a change in selective forces. Proper conservation of this species requires that we recognize and avoid that possibility.

ACKNOWLEDGEMENTS

We thank the organizers of the 5th International Moose Symposium for the opportunity to synthesize and present this information. We wish to acknowledge funding support from Federal Aid in Wildlife Restoration through the Alaska Department of Fish and Game as well as the Institute of Arctic Biology, University of Alaska Fairbanks. S. Côté and an anonymous reviewer provided constructive comments for improving the manuscript.

REFERENCES

ANDERSON, P. M., A. V. LOZHKIN, and L. B. BRUBAKER. 2002. Implications of a 24,000-yr palynological record for a Younger Dryas cooling and for boreal forest development in northeastern Siberia. Quaternary Research 57:325-333.

ARKHIPOV, S. A., V. G. BESPALY, M. A. FAUSTOVA, O. Y. GLUSHKOVA, L. L. ISAEVA, and A. A. VELICHKO. 1986. Ice sheet reconstructions. Pages 269-292 *in* V. Šibrava, D. Q. Bowen, and G. M. Richmond, editors. Quaternary Glaciations in the Northern Hemisphere. Pergamon Press, Oxford, U.K.

AVISE, J. C. 2000. Phylogeography: the History and Formation of Species. Harvard University Press, Cambridge, Massachusetts, USA.

_____, J. ARNOLD, R. M. BALL, JR., E. BERMINGHAM, T. LAMB, J. E. NEIGEL, C. A. REEB, and N. C. SAUNDERS. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics 18:489-522.

BIRKY, C. W., T. MARUYAMA, and P. FUERST. 1983. An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. Genetics 103:513-527.

BLUNDELL, G. M., M. BEN-DAVID, P. GROVES, R. T. BOWYER, and E. GEFFEN. 2002. Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. Molecular Ecology 11:289-303.

BOESKOROV, G. G. 1996. Karyotype of moose (Alces alces L.) from northeastern Asia. Proceedings of the Russian Academy of Sciences 329:506-508. (In Russian).

_____. 1997. Chromosomal differences in moose. Genetika 33:974-978. (In Russian).

BOWYER, R. T., D. M. LESLIE, JR., and J. L. RACHLOW. 2000. Dall's and Stone's sheep. Pages 491-516 *in* S. Demarais and P. R. Krausman, editors. Ecology and Management of Large Mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

_____, J. L. RACHLOW, V. VAN BALLENBERGHE, and R. D. GUTHRIE. 1991. Evolution of a rump patch in moose: an hypothesis. Alces 27:12-23.

_____, 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.

_____, V. VAN BALLENBERGHE, and J.G. KIE. 2003. Moose (*Alces alces*). Pages 931 - 964 *in* G.A. Feldhamer, B. Thompson, and J. Chapman, editors. Wild Mammals of North America: Biology, Management, and Economics. Sec-

ond edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

BRAEND, M. 1962. Studies on blood and serum groups in the elk (*Alces alces*). New York Academy of Sciences 97:296-305.

BRODERS, H. G., S. P. MAHONEY, W. A. MONTEVECCHI, and W. S. DAVIDSON. 1999. Population genetic structure and the effect of founder events on the genetic variability of moose, *Alces alces*, in Canada. Molecular Ecology 8:1309-1315.

BRUFORD, M. W., D. J. CHEESMAN, T. COOTE, H. A. A. GREEN, S. A. HAINES, C. O'RYAN, and T. R. WILLIAMS. 1996. Microsatellites and their application to conservation genetics. Pages 278-297 *in* T. B. Smith and R. K. Wayne, editors. Molecular Genetic Approaches in Conservation. Oxford University Press, Oxford, U.K.

BRUMFIELD, R. T., P. BEERLI, D. A. NICKERSON, and S. V. EDWARDS. 2003. The utility of single nucleotide polymorphisms in inferences of population history. Trends in Ecology and Evolution 18:249-256.

BUBENIK, A. B. 1998. Evolution, taxonomy and morphophysiology. Pages 77-123 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

CHESSER, R. K., C. REUTERWALL, and N. RYMAN. 1982. Genetic differentiation of Scandinavian moose *Alces alces* populations over short geographic distances. Oikos 39:125-130.

CHILD, K. N. 1983. Selective harvest of moose in the Omineca: some preliminary results. Alces 19:162-177.

COADY, J. W. 1982. Moose. Pages 902-922 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild Mammals of North America: Biology, Management, and Economics. Johns Hopkins University Press, Baltimore, Maryland, USA.

COLTMAN, D. W., P. O'DONOGHUE, J. T. JORGENSON, J. T. HOGG, C. STROBECK, and M. FESTA-BIANCHET. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426:655-658.

CRONIN, M. A. 1992. Intraspecific variation in mitochondrial DNA of North American cervids. Journal of Mammalogy 73:70-82.

_____, J. C. PATTON, R. COURTOIS, and M. CRÊTE. 2001. Genetic variation of microsatellite DNA in moose in Québec. Alces 37:175-187.

DYKE, A. S., and V. K. PREST. 1987. Late Wisconsinan and Holocene history of the Laurentide ice sheet. Geographie Physique et Quaternaire 41:237-263.

ELIAS, S. A. 2000. Late Pleistocene climates of Beringia, based on analysis of fossil beetles. Quaternary Research 53:229-235.

ELLEGREN, H., L. ANDERSSON, and K. WALLIN. 1991. DNA polymorphism in moose (*Alces alces*) revealed by polynucleotide probe $(TC)_n$. Journal of Heredity 82:429-431.

_____, S. MIKKO, K. WALLIN, and L. ANDERSSON. 1996. Limited polymorphism at major histocompatibility complex (MHC) loci in the Swedish moose *A. alces*. Molecular Ecology 5:3-9.

FLEROV, K. K. 1952. Fauna of the USSR: Mammals. Vol. 1 no 2. Musk deer and deer. The Academy of Sciences of the USSR, Leningrad. (English translation by the Israel Program for Scientific Translation, 1960, S. Monson, Jerusalem).

FRANZMANN, A. W., and C. C. SCHWARTZ, editors. 1998. Ecology and Management of the North American Moose. Smithsonian Institution Press, Wash-

ington, D.C., USA.

FRIES, R., and G. DURSTEWITZ. 2001. DigitalDNA signatures: SNPs for animal tagging. Nature Biotechnology 19:508.

FULTON, R. J., M. M. FENTON, and N. W. RUTTER. 1986. Summary of Quaternary stratigraphy and history, western Canada. Pages 229-242 *in* V. Šibrava, D. Q. Bowen, and G. M. Richmond, editors. Quaternary Glaciations in the Northern Hemisphere. Pergamon Press, Oxford, U.K.

GEIST, V. 1987a. On the evolution and adaptations of *Alces*. Swedish Wildlife Research Supplement 1:11-23.

_____. 1987b. On speciation in Ice Age mammals, with special reference to cervids and caprids. Canadian Journal of Zoology 65:1067-1084.

_____. 1998. Deer of the World: Their Evolution, Behavior, and Ecology. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

GROVES, C. P., and P. GRUBB. 1987. Relationships of living deer. Pages 3-59 *in* C. M. Wemmer, editor. Biology and Management of the Cervidae. Smithsonian Institution Press, Washington, D.C., USA.

GUTHRIE, R. D. 1984. Alaska megabucks, megabulls, and megarams: the issue of Pleistocene gigantism. Special Publications of the Carnegie Museum of Natural History 8:482-509.

_____. 1990. New dates in Alaskan Quaternary moose, *Cervalces-Alces* – archaeological, evolutionary and ecological implications. Current Research in the Pleistocene 7:111-112.

_____. 1995. Mammalian evolution in response to the Pleistocene-Holocene transition and the break-up of the mammoth steppe: two case studies. Acta Zoologica Cracoviensia 38:139-154.

GYLLENSTEN, U., C. REUTERWALL, N. RYMAN, and G. STAHL. 1980. Geographical variation in transferrin allele frequencies in three deer species from Scandinavia. Hereditas 92:237-241.

HANCOCK, J. M. 1999. Microsatellites and other simple sequences: genomic context and mutational mechanisms. Pages 1-9 *in* D. B. Goldstin and C. Schlötterer, editors. Microsatellites: Evolution and Applications. Oxford University Press, Oxford, U.K.

HARRINGTON, R. 1985. Evolution and distribution of the Cervidae. Biology of deer production. The Royal Society of New Zealand, Bulletin 22:3-11.

HARRIS, R. B., W. A. WALL, and F. W. ALLENDORF. 2002. Genetic consequences of hunting: what do we know and what should we do? Wildlife Society Bulletin 30:634-643.

HEDRICK, P. W. 1994. Evolutionary genetics of the major histocompatibility complex. American Naturalist 143:945-964.

HEWITT, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnaen Society 58:247-276.

HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs 53.

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.

_____, P. E. JOHNS, and M. H. SMITH. 1992. Genetic diversity of moose from the Kenai Peninsula, Alaska. Alces 28:15-20.

_____, G. F. SHIELDS, R. T. BOWYER, and C. C. SCHWARTZ. 2002a. Genetic relationships deduced from cytochrome-*b* sequences among moose. Alces 38:113-122.

_____, _____, I. G. UDINA, R. T. BOWYER, A. A. DANILKIN, and C. C. SCHWARTZ. 2002b. Mitochondrial phylogeography of moose (*Alces alces*): late Pleistocene divergence and population expansion. Molecular Phylogenetics and Evolution 22:375-387.

_____, T. H. THELEN, and R. T. BOWYER. 1998. Effects of population density and selective harvest on antler phenotype in simulated moose populations. Alces 34:375-383.

_____, _____, and C. C. SCHWARTZ. 1993. Genetic and population effects of selective harvest systems in moose: a modeling approach. Alces 29:225-234.

IRWIN, D. M., T. D. KOCHER, and A. C. WILSON. 1991. Evolution of the cytochrome b gene in mammals. Journal of Molecular Evolution. 32: 128 - 144.

JOUZEL, J., C. LORIUS, J. R. PETIT, C. GENTHON, N. I. BARKOV, V. M. KOTLYAKOV, and V. M. PETROV. 1987. Vostok ice core: a continuous isotope temperature record over the last climate cycle (160,000 years). Nature 329:403-408.

LISTER, A. M. 1993. Evolution of mammoths and moose: the Holarctic perspective. Pages 178-204 *in* A. D. Barnosky, editor. Quaternary Mammals of North America. Cambridge University Press, Cambridge, U.K.

LOPEZ, J. V., M. CULVER, J. C. STEPHENS, W. E. JOHNSON, and S. J. O'BRIEN. 1997. Rates of nuclear and cytoplasmic mitochondrial DNA sequence divergence in mammals. Molecular Biology and Evolution 14:277-286.

LYNCH, M. 1996. A quantitative-genetic perspective on conservation issues. Pages 471-501 *in* J. C. Avise and J. L. Hamrick, editors. Conservation Genetics: Case Studies from Nature. Chapman & Hall, New York, New York, USA.

MASON, O. K., P. M. BOWERS, and D. M. HOPKINS. 2001. The early Milankovitch thermal maximum and humans: adverse conditions for the Denali complex of eastern Beringia. Quaternary Science Reviews 20:525-548.

MIKKO, S., and L. ANDERSSON. 1995. Low major histocompatibility complex class II diversity in European and North American moose. Proceedings of the National Academy of Sciences, USA 92:4259-4263.

MIYAMOTO, M. M., F. KRAUS, and O. A. RYDER. 1990. Phylogeny and evolution of antlered deer determined from mitochondrial DNA sequences. Proceedings of the National Academy of Sciences, USA 87:6127-6131.

MOLVAR, E. M., and R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. Journal of Mammalogy 75:621-630.

MULLIS, K., F. FALOONA, S. SCHARF, R. SAKAI, G. HORN, and H. ERLICH. 1986. Specific enzymatic amplification of DNA in vitro: the polymerase chain reaction. Cold Spring Harbor Symposia in Quantitative Biology 51:263-273.

NADLER, C. F., C. E. HUGHES, K. E. HARRIS, and N. W. ADLER. 1967. Electrophoresis of the serum proteins and transferrins of *Alces alces* (elk), *Rangifer tarandus* (reindeer), and *Ovis dalli* (Dall sheep) from North America. Comparative Biochemistry and Physiology 23:149-157.

NEVO, E. 1978. Genetic variation in natural populations: patterns and theory. Theoretical Population Biology 13:121-177.

PETERSON, R. L. 1955. North American Moose. University of Toronto Press, Toronto, Ontario, Canada.

QUELLAR, D. C., J. E. STRASSMANN, and C. R. HUGHES. 1993. Microsatellites and kinship. Trends in Ecology and Evolution 8:285-288.

RØED, K. H., and L. MIDTHJELL. 1998. Microsatellites in reindeer, *Rangifer tarandus*, and their use in other cervids. Molecular Ecology 7:1773-1776.

RYMAN, N., R. BACCUS, C. REUTERWALL, and M. H. SMITH. 1981. Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. Oikos 36:257-266.

_____, G. BECKMAN, G. BRUUN-PETERSEN, and C. REUTERWALL. 1977. Variability of red cell enzymes and genetic implications of management policies in Scandinavian moose (*Alces alces*). Hereditas 85:157-162.

_____, C. REUTERWALL, K. NYGREN, and T. NYGREN. 1980. Genetic variation and differentiation in Scandinavian moose (*Alces alces*): are large mammals monomorphic. Evolution 34:1037-1049.

SAGE, R. D., and J. O. WOLFF. 1986. Pleistocene glaciations, fluctuating ranges, and low genetic variability in a large mammal (*Ovis dalli*). Evolution 40: 1092 - 1095.

SCHWARTZ, C. C., K. J. HUNDERTMARK, and T. H. SPRAKER. 1992. An evaluation of selective bull moose harvest on the Kenai Peninsula, Alaska. Alces 28:1-13.

SCRIBNER, K. T., and R. K. CHESSER. 2001. Group-structured genetic models in analysis of the population and behavioral ecology of poikilothermic vertebrates. Journal of Heredity 92:180-189.

SELANDER, R. K., and D. W. KAUFMAN. 1973. Genic variability and strategies of adaptation in animals. Proceedings of the National Academy of Sciences of the USA 70:1875-1877.

SHER, A. V. 1987. History and evolution of moose. Swedish Wildlife Research Supplement 1:71-97.

SHUBIN, P. N. 1969. The genetics of transferrins in the reindeer and in the European elk. Genetika 5:37-41. (In Russian).

SMITH, M. H., R. BACCUS, H. O. HILLESTAD, and M. N. MANLOVE. 1984. Population genetics. Pages 119-128 *in* L. K. Halls, editor. White-tailed Deer: Ecology and Management. Stackpole Books, Harrisburg, Pennsylvania, USA.

_____, K. T. SCRIBNER, L. H. CARPENTER, and R. H. GARROTT. 1990. Genetic characteristics of Colorado mule deer (*Odocoileus hemionus*) and comparisons with other cervids. Southwestern Naturalist 35: 1 - 8.

SYMONDSON, W. O. 2002. Molecular identification of prey in predator diets. Molecular Ecology 11:627-641.

TELFER, E. S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces)*. Pages 145-182 *in* R. Olson, F. Geddes, and R. Hastings, editors. Northern Ecology and Resource Management. University of Alberta Press, Edmonton, Canada.

THELEN, T. H. 1991. Effects of harvest on antlers of simulated populations of elk. Journal of Wildlife Management 55:243-249.

THOUVENY, N., and E. BONIFAY. 1984. New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. Nature 308:355-358.

UDINA, I. G., A. A. DANILKIN, and G. G. BOESKOROV. 2002. Genetic diversity of moose (*Alces alces* L.) in Eurasia. Genetika 38:951-957. (In Russian).

VERNESI, C., E. PECCHIOLO, D. CARAMELLI, R. TIEDEMANN, E. RANDI, and G. BERTORELLE. 2002. The genetic structure of natural and reintroduced roe deer (*Capreolus capreolus*) populations in the Alps and central Italy, with reference to the mitochondrial DNA phylogeography of Europe. Molecular Ecology 11:1285-1297.

WILHELMSON, M., R. K. JUNEJA, and S. BENGTSSON. 1978. Lack of polymorphism in certain blood proteins and en-

zymes of European and Canadian moose. Naturaliste Canadien 105:445-449.

WILSON, G. A., C. STROBECK, L. WU, and J. W. COFFIN. 1997. Characterization of microsatellite loci in caribou *Rangifer tarandus*, and their use in other artiodactyls. Molecular Ecology 6:697-699.

WILSON, P. J., S. GREWAL, A. RODGERS, R. REMPEL, J. SAQUET, H. HRISTIENKO, F. BURROWS, R. PETERSON, and B. N. WHITE. 2003. Genetic variation and population structure of moose (*Alces alces*) at neutral and functional DNA loci. Canadian Journal of Zoology 81:670-683.

ZHELEZNOV, N. K. 1993. Historic and current distribution of moose in the northeast USSR. Alces 29:213-218.

Appendix 1. Glossary of specialized terms used in this review.

Term	Definition
Adaptive genetic variation	Genotypic variation at loci that control traits important to fitness, such as morphology, physiology, and behavior.
Allozyme	A gene product (protein) that is distinguished by its migratory characteristics in a gel exposed to an electric field (electrophoresis). Differences among alleles (different variants of the same gene) at allozyme loci relate to amino acid composition and secondary structure of the protein. Only mutations that create proteins with different migratory characteristics are detectable.
Control region	A portion of mtDNA that evolves (incorporates mutations) at a very fast rate, which makes it a valuable marker for examining intraspecific genetic variation. Occasionally referred to as the D-loop.
DNA sequence	The ultimate level of analysis of genetic material. This technique deduces the identity and order of nucleotides in a fragment of DNA. Mutations (nucleotide substitutions) are detectable whether or not they create different gene products.
Effective population size	The size of a standardized population that has the same degree of genetic drift as the population being studied. An ideal population is a closed population of constant size with non-overlapping generations and no variance in reproductive success. The smaller the effective size of a population, the faster it will lose genetic diversity through drift regardless of actual population size. Effective population size (N_e) is almost always a fraction of the true population size (N).
Generation interval	Mean age of all parents.
Genetic drift	Changes in allele frequencies across generations due to random sampling error associated with less than infinite population size.
Haplotype	The haploid equivalent of genotype. Genetic type of an individual when haploid DNA, such as mtDNA, is analyzed.
Heritability	The proportion of variance in the expression of a trait, such as antler size or body size, that is due to genetic effects (as opposed to environmental effects), i.e., the degree to which a trait can be passed on to the next generation.
Microsatellite	Segments of DNA composed of sequence units varying from 2-4 nucleotides in length that are tandemly repeated. Size variation (number of repeated units) defines alleles. Microsatellites are Mendelian in their inheritance, i.e., they are diploid, specific to a site on a chromosome, and occur in either a homozygous or heterozygous genotype.
Minisatellite	Similar to microsatellites except that the repeat units vary from 16-64 nucleotides in length and occur at many sites throughout the chromosomes, thus exhibiting more than 2 alleles per individual and creating complex genotypes of gel banding patterns that resemble bar codes. This is the technique that pioneered genetic fingerprinting.
Mitochondrial DNA (mtDNA)	A circular DNA molecule occurring in the mitochondrion. Unlike chromosomes, which occur in pairs (diploid), mtDNA occurs as a single copy (haploid) because it is inherited only from the maternal line. Therefore, it is not subject to recombination and changes only via mutation. That property makes it particularly useful for tracing lineages through time.
Molecular clock	The assumption that the average rate of mutation for a particular DNA sequence is constant over evolutionary time. If a molecular clock can be assumed, the amount of genetic divergence between populations or species can be converted to time since divergence.
Phylogeography	The study of genetic lineages in a spatial and temporal context, revealing historic population processes and evolutionary histories.
RFLP	Restriction Fragment Length Polymorphism – a section of DNA of known length is digested with restriction enzymes (endonucleases), which cleave DNA at sites with specific target sequences of 4-6 nucleotides. The digested fragments are separated by length (number of nucleotides) using gel electrophoresis and haplotypes are characterized by numbers and sizes of fragments.