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

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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 with other haplotypes 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 spatial separation of moose lineages in the past. Our results indicate that 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 as *A. a. gigas*. Behavioural and morphological differences between *A. a. gigas* and other forest-dwelling subspecies in North America indicate a need to examine moose management strategies and objectives in southeastern Alaska.

Key words: Alaska, British Columbia, Cordilleran ice sheet, moose, phylogeography, range expansion

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Patterns of diversity and dispersion of mitochondrial DNA (mtDNA) haplotypes are useful for inferring historic population processes (Avise et al. 1987) and have been instrumental in elucidating population and range expansion of moose *Alces alces* since the last Ice Age. Hundertmark et al. (2002a,b) focused on worldwide or intercontinental patterns in the distribution of genetic variance in moose. They addressed hypotheses concerning geographic origin, most recent common ancestor and cladogenesis in moose worldwide and determined that low mitochondrial diversity worldwide was due to bottlenecks induced by climate change and that moose colonized North America from central Asia within the last 15,000 years. Hundertmark et al. (2003) described that colonization process by examining variation in mtDNA from a regional perspective in North America, testing hypotheses about pattern and process of colonization as well as genetic structure within and among subspecies. They found a high degree of regional differentiation and hypothesized that colonization was consistent with a large, central population that founded peripheral populations by rare, long-distance dispersal. Geographic structuring of haplotypes at finer scales within North America, however, has not been addressed, particularly in areas where ranges of subspecies come into contact. We now address a long-standing question concerning the genetic affinity and taxonomy of moose in southeastern Alaska and combine phylogenetic data with fine-scale location data to determine relationships with adjacent populations.

The zone of intergradation between the Alaskan moose *A. a. gigas* and the northwestern moose *A. a. andersoni* occurs in central Yukon Territory (Peterson 1955, Gauthier & Larsen 1985), but the orientation of that zone and its location where it intersects the coast of the Gulf of Alaska, and therefore the subspecific identity of moose inhabiting the southeastern Alaska, USA coast, is uncertain. Klein (1965) suggested that moose arrived recently in southeastern Alaska by migrating down major river corridors draining northwestern British Columbia, Canada, through the coastal mountains that form the international boundary. He identified those moose as *A. a. andersoni*, based on the supposition that they represented a population expansion of that subspecies from interior British Columbia. Conversely, Hall (1981:1101) indicated that moose in the northern half of the southeastern panhandle of Alaska are *A. a. gigas*, and that moose are absent from the southern portion of the panhandle or in neighbouring areas of British Columbia to the east and south.

Irrespective of which race of moose occurs in southeastern Alaska, these large mammals are important for recreational and subsistence hunting (Timmermann & Buss 1998), as well as a valuable resource for the tourism industry (Snepenger & Bowyer 1990). Effective management of moose requires that sufficient numbers of mature bulls be present in the population to ensure a high likelihood of females conceiving during their first oestrus (Timmermann & Buss 1998). Moose in southeastern Alaska are managed under similar strategies as those in the rest of the state, in which an objective of 20-30 adult bulls per 100 adult cows after the hunting season is thought to be sufficient for proper rut synchrony (Schwartz 1998). Yet, mating behaviour of North American moose outside Alaska differs from that of *A. a. gigas* (Bubenik 1987, Bowyer et al. 2003) and management objectives in those regions reflect the need for a higher proportion of bulls in the population to ensure rut synchrony (Crête et al. 1981, Timmermann 1992). Moreover, antler size of *A. a. andersoni* is generally smaller than that of *A. a. gigas* (Gauthier & Larsen 1985, Gasaway et al. 1987) and antler sizes in southeastern Alaska moose are smaller than in other parts of the state (Bowyer et al. 2003), but harvest strategies implemented in southeastern Alaska define legal bulls based on antler sizes expected for *A. a. gigas*. Clarification of relationships of moose in southeastern Alaska with those of adjacent populations of *A. a. gigas* and *A. a. andersoni* via a phylogeographic assessment would not only be instructive for inferring population history of those moose but also would serve as an indirect but feasible method to gain insight into their expected life-history strategies, and can allow evaluation of current management strategies and objectives. Therefore, we examined fine-scale geographic patterns of genetic variation in moose in Alaska and British Columbia to determine if moose in southeastern Alaska exhibited a closer phylogenetic relationship to *A. a. gigas* than to *A. a. andersoni* of northwestern British Columbia.

Material and methods

We analyzed a subset of genetic sequences described by Hundertmark et al. (2003), selecting the sequences from individuals collected within Alaska and British Columbia (GenBank accession nos.: AF412335-AF412337, AF412246-AF412250). As opposed to that study, wherein geographic locations of haplotypes within populations were not considered, we plotted collection locations of specimens on a map of the area to determine any within-population patterns of haplotype dispersion. We defined populations based on geographic and political boundaries. All samples collected within the province of British Columbia were considered as one population. Moose from Alaska were divided into two populations, one consisting of moose collected in the southeastern panhandle, and the other representing moose from the remainder of the state. The boundary between the areas was Glacier Bay National Park and Preserve (58°30'N, 136°W; Fig. 1). Specimens representing naturally established moose populations from the Chilkat, Endicott, Stikine and Unuk Rivers as well as Thomas Bay in southeastern Alaska were used in this study. Moose from populations in Berners Bay (58°45'N, 135°W) and Chickamin River (55°50'N, 131°W), which were founded by animals introduced from other areas of Alaska (Burris & McKnight 1973), were not included in our analysis.

Detailed descriptions of the amplification and sequencing processes for mtDNA were provided by Hundertmark et al. (2003). The targeted sequence within the mtDNA molecule was the left hypervariable domain of the control region. That portion of the mitochondrial genome evolves at an extremely fast rate and is useful for constructing phylogenies in cervids (Douzery & Randi 1997), particularly among recently diverged taxa, as well as for studies of intraspecific differences among populations. A portion of the adjoining tRNA^{thr} gene and the entire tRNA^{pro} gene also were included in the analysis.

Phylogenetic relationships among sequences were assessed with a neighbour-joining phylogeny (Saitou & Nei 1987) constructed from p-distances using software PAUP* version 4b10 (Swofford 1999). Topological rigour of the phylogeny was assessed using 1,000 bootstrap replicates of sequence data (Felsenstein 1985). Estimates of variability between regional groupings were computed with the software Arlequin (Schneider et al. 2000) and were expressed as pairwise F_{ST}. Significance of pairwise comparisons was tested using 1,000 bootstrap permutations of data (Excoffier et al. 1992). Numbers of migrants (M) per generation between populations were estimated using Arlequin from pairwise F_{ST} estimates under a model assuming mutation-drift equilibrium and a migration rate that far exceeds mutation rate.

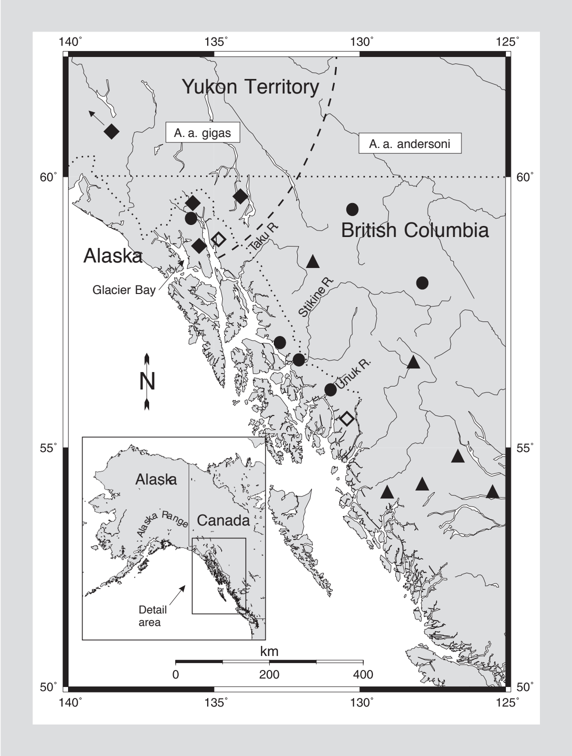

Figure 1. Southeastern Alaska and adjacent areas of Canada; dotted lines indicate provincial and national borders. The symbols represent occurrence of at least one individual of a given haplogroup; haplogroup I (◇), haplogroup II (●), and haplogroup III (▲). The ◆ with the arrow in the upper left corner indicates that all haplotypes from the remainder of Alaska belong to haplogroup I. The ◇ indicate two introduced populations founded by animals collected in areas with haplogroup I that were not sampled for this study. The dashed line indicates our proposed boundary between *Alces alces gigas* and *A. a. andersoni*; the orientation of the boundary in Yukon Territory is speculative and follows Hall (1981).

Results

We identified eight haplotypes among 85 moose from Alaska and British Columbia (Table 1). Sequences were organized into three haplogroups (Fig. 2) that were clustered geographically (see Fig. 1). Haplogroup I was composed of two haplotypes differing by a single substitution and was distributed in the main portion of Alaska among 53 individuals. Both haplotypes were found north of the

Table 1. Distribution of the number of control region haplogroups and haplotypes in moose populations in Alaska and northwestern British Columbia. Haplogroups are defined in Figure 1 and letter designations of haplotypes refer to their identity in Hundertmark et al. (2003). 'Alaska mainland' refers to all of Alaska with the exception of the southeastern panhandle.

Haplogroup/haplotype	Alaska mainland	Northern panhandle	Central and southern panhandle	British Columbia	Total
I/A	21				21
I/B	32	7		1	40
II/C		1	12	1	14
II/D			1		1
II/G				1	1
III/E				6	6
III/F				1	1
III/H				1	1
Total	53	8	13	11	85

Alaska Range, which separates interior and northern portions of the state from south-central Alaska (see Fig. 2). Only one haplotype (B) was found south of the Alaska Range in south-central Alaska. Additionally, members of haplogroup I were found in the northern panhandle of southeastern Alaska and in extreme northwestern British Columbia. Haplogroup II was composed of three closely related haplotypes, differing at a maximum of two nucleotide sites, and was the only haplogroup found in central and southern panhandle populations. Two individuals from that haplogroup also were found in British Columbia (see Fig. 1). The remaining three haplotypes, nominally identified as haplogroup III were distributed solely in British Columbia.

Estimates of pairwise F_{ST} between regions were 0.62 between Alaska and British Columbia, 0.66 between Alaska and southeastern Alaska, and 0.29 between southeastern Alaska and British Columbia. Those estimates equate to values of M of 0.26, 0.31 and 1.20 migrants exchanged between populations per generation, respectively. All comparisons were statistically significant ($P < 0.001$), indicating the closer relationship between southeastern Alaska and British Columbia than between either of those populations and Alaska.

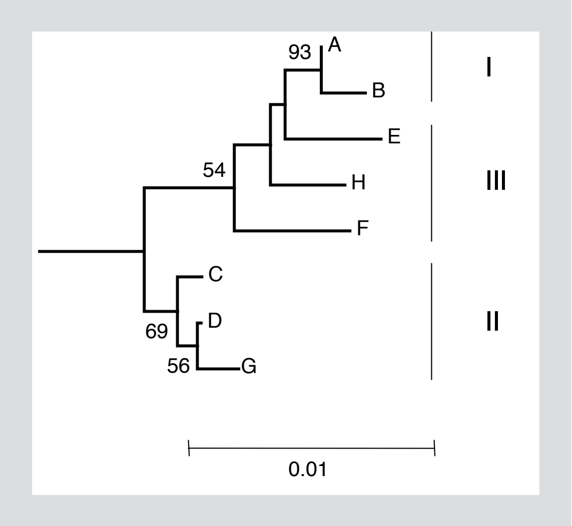

Figure 2. Neighbour-joining phylogeny based on p-distances of mitochondrial control region haplotypes of moose from Alaska and northwestern British Columbia. Haplotype designations refer to Hundertmark et al. (2003). The tree is rooted by sequences from elk *Cervus elaphus* (GenBank accession number Y08207; Douzery & Randi 1997) and caribou *Rangifer tarandus* (GenBank accession number AF414123; Hundertmark et al. 2002), not shown. Reliability scores (percentage support) > 50% for nodes are indicated and were determined by 1,000 bootstrap replicates. Haplogroups (I, II and III) are indicated to the right of the tree.

Discussion

Concordance of geographic distribution and phylogenetic structure of haplotypes in our sample is indicative of spatial and temporal separation of populations. Such a separation is necessary for the establishment of differences that define subspecies. Our data indicate that there are three separate populations partitioned into two putative subspecies. The pairwise F_{ST} estimates indicate a greater level of gene flow between moose in southeastern Alaska and those in British Columbia than between either of those populations and moose in the main part of Alaska.

Distribution of haplotypes in Alaska showed a geographic structure related to glacial history. The southeastern Alaska-British Columbia area was covered by the Cordilleran ice sheet during the Wisconsinan glaciation (Fulton et al. 1986). That ice sheet extended to the east as far as the Rocky Mountains and during glacial retreat served as the western boundary of an ice-free corridor that may have been used as a movement corridor for moose as they colonized central North America (Geist 1987, Cronin 1990, Bowyer et al. 1991, Hundertmark et al. 1992, Hundertmark et al. 2003). The Cordilleran ice sheet also covered south-central Alaska south of the Alaska Range, but much of the land north of the Alaska Range was ice-free. It is likely that moose colonized habitat north of the Alaska Range during the colonization of the continent and followed that habitat eastward to the corridor leading south. Subsequently, dispersing individuals eventually found suitable habitat in previously glaciated areas.

Moose in southeastern Alaska either migrated up the coast from the south or they arrived via a general movement of moose down the major river corridors from interior British Columbia. Topography of the coast of southeastern Alaska is rugged and dominated by a coastal rain forest of spruce-hemlock *Picea sitchensis-Tsuga heterophylla*, which is not productive habitat for moose (Telfer 1984). Successful dispersal along that coast between river drainages is unlikely. We speculate, therefore, that populations in central and southern southeastern Alaska arose through recent migration down the river valleys from populations in British Columbia, supporting the contention of Klein (1965). Peterson (1955) summarized reports from the late 19th and early 20th centuries that indicated a range expansion of moose from extreme northeastern British Columbia westward toward the coast, which may refer to moose that eventually colonized southeastern Alaska. An exception to this scenario is the population inhabiting the Chilkat River valley in northernmost southeastern Alaska. Moose dispersing into that valley likely originated in the adjacent boreal forest of southwestern Yukon Territory, which is contiguous with the distribution of the Alaskan-like sequences, and the designation of *A. a. gigas*.

The lack of variability within populations of moose in the central and southern panhandle of southeastern Alaska and the low proportion of haplogroup II haplotypes in interior British Columbia is intriguing. The very low haplotype diversity of moose in the central and southern panhandle of southeastern Alaska, combined with the likely lack of genetic interchange between drainages, suggests founding by migrants from one population in interior British Columbia with low haplotype diversity. Considering that the present population in interior British Columbia has high haplotype diversity and is dominated by haplotypes not found currently in southeastern Alaska, we speculate that the diverse composition of the British Columbia population is a result of recent events.

Moose inhabiting the interior portions of northwestern British Columbia exhibited haplotypes that resembled those from coastal Alaska and central North America (Hundertmark et al. 2003). Peterson (1955) reported that moose from the area of the Montana-British Columbia border expanded their range to include southern and central British Columbia early in the 20th century, perhaps aided in their movements by anthropogenic influences on the landscape such as commercial logging. The distribution of haplotypes in southeastern Alaska and northwestern British Columbia, therefore, seems to be a result of admixture that occurred between three expanding populations. We speculate that moose from northeastern British Columbia characterized by haplogroup II haplotypes moved westward and colonized the drainages flowing through the coastal mountains into southeastern Alaska. A second group of moose from the south moved northwestward and was composed of moose with haplogroup III haplotypes. Moose from the north, characterized by a haplogroup I haplotype expanded into the Chilkat Valley in the northern panhandle and there has been some mixing with haplogroup II moose from the east.

Whatever the actual scenario, we believe that the lineage of moose in southeastern Alaska is the remainder of a relict group of moose that split very early from the main colonizing wave. That lineage is distinct from all others in North America (Hundertmark et al. 2003) and is basal in the North American phylogeny, indicating a greater age of the lineage compared with others in North America and closer relationship to moose in Eurasia. Moreover, the limited distribution of that haplogroup indicates that it was not common or was limited to an isolated population.

Taxonomy of moose in southeastern Alaska

Evidence of geographic structure of haplogroups presented here suggests that southeastern Alaska contains two subspecies of moose. We contend that moose north of the latitude of Berners Bay (58°45'N latitude; see Fig. 1) be classified as *A. a. gigas* based on the common lineage they share with moose inhabiting areas to the north. Although we did not have access to samples from Yukon Territory, we can speculate that the boundary extends through central Yukon as depicted by Hall (1981). Moose inhabiting the major river drainages of southeastern Alaska south of Berners Bay are most appropriately considered a separate subspecies. Moose populations in the northern part of the panhandle of Alaska and in extreme northwestern British Columbia carry haplotypes that occurred in both groups and undoubtedly represent a transition zone. A conservative approach to taxonomy would classify moose in central and southern southeastern Alaska as *A. a. andersoni*. That classification could be justified on the assumption of substantive gene flow along the river valleys between moose from southeastern Alaska and British Columbia. Species with strong female philopatry, such as moose (Hundertmark 1998) or white-tailed deer *Odocoileus virginianus* (Purdue et al. 2000), can experience nuclear gene flow through male dispersal without changes in the structure of mtDNA in populations (Paetkau et al. 1998). The geographic association of three lineages in our study area, however, indicates that the lineages were effectively isolated at some time in the past, which may have resulted in divergence justifying separate taxonomic status of moose in southeastern Alaska. Nonetheless, the close affinity between moose in southeastern Alaska and northwestern British Columbia indicates that moose in southeastern Alaska likely share more traits with populations to the east than with populations to the north. Moreover, the potential for gene flow along the coast is much less than the potential for gene flow along river valleys, which would act as a disruptive force against maintaining the coastal populations as a separate taxonomic unit.

Designation of taxonomic units should not be based solely on genetic differences but should also rely on other characters (Cronin 1993). Subspecies of deer have at times been shown to diverge genetically (Smith et al. 1986) whereas other studies frequently fail to show that they do (Hillestad 1984, Cronin 1991, Ellsworth et al. 1994a,b). Ellsworth et al. (1994a) described patterns of genetic differentiation in white-tailed deer that were not associated with recognized subspecific ranges, which those authors interpreted in terms of admixture facilitated by low sea levels along the coastal plain of the southeastern United States during glacial periods. Genetic differences at neutral loci may not fully resolve the taxonomic level of forms involved, such as the South American subspecies of white-tailed deer in Surinam studied by Smith et al. (1986) that has such highly divergent skull morphology that it may actually be a separate species like those described by Molina & Molinari (1999) in Venezuela. Local populations of white-tailed deer show strong spatial heterogeneity and often do not share mtDNA haplotypes over even limited geographical areas in southeastern USA (Purdue et al. 2000). Given the common occurrence of spatial heterogeneity in genetic characteristics in deer, care is needed when using only genetic differences to designate taxonomic forms, and it would be much better if the designation also depended upon other differences. The two recommended subspecies of moose not only differ genetically but in other characteristics as well (Gauthier & Larsen 1985, Gasaway et al. 1987, Bowyer et al. 1991, 2002).

Based on our conclusion that *A. a. andersoni* occurs in southeastern Alaska, we recommend that wildlife managers carefully consider management strategies employed for those populations. Harvest strategies based upon antler phenotypes expected for *A. a. gigas* and management objectives that assume a harem breeding system may not be appropriate for those populations. Further research should be conducted to verify the extent to which moose in southeastern Alaska resemble those in British Columbia both morphologically and behaviourally, but until such studies have been accomplished we recommend caution in setting management objectives.

We document a range extension of moose in northwestern British Columbia and southeastern Alaska. Collection locations of moose from those areas had not been published previously and occurred as far south as the Skeena and Endako Rivers in British Columbia (approximately 54°N latitude; see Fig. 1), as well as the Unuk River, Stikine River and Thomas Bay in southeastern Alaska. Presence of moose in those areas is common knowledge among local people and management agencies but the areas were not included within the range of moose depicted by Hall (1981) or more recently by Karns (1998), and we believe that the true distribution of moose in those areas should be noted. Although moose likely have been present in lower southeastern Alaska for > 100 years (Klein 1965), the species may have colonized the Skeena region of British Columbia relatively recently.

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