GEOGRAPHICAL VARIATION IN ANTLER MORPHOLOGY OF ALASKAN MOOSE: PUTATIVE EFFECTS OF HABITAT AND GENETICS

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ABSTRACT: We assessed antler size of Alaskan moose (*Alces alces gigas*) with respect to the geographic region and dominant vegetation community (taiga or tundra) from which they were harvested from 1968 to 1983. Our retrospective analysis indicated that moose from the Copper River Delta and Alaska Peninsula possessed the largest antlers, whereas those from southeast Alaska, USA, had the smallest antlers. Delta flood plains of the Copper River offer a rich food supply for moose, and browse on the Alaska Peninsula also is plentiful; both areas have mild maritime climates and longer growing seasons than tundra and taiga habitats in interior Alaska—large antlers in those moose populations likely were the result of superior nutrition. After controlling for age, antlers of moose from tundra communities were significantly larger than those inhabiting taiga. Willows (*Salix* spp.), which are an important food for moose, dominate braided rivers and associated riparian areas in tundra habitat, and provide a high-quality and stable food supply over time. Fire and subsequent successional changes dominate taiga landscapes, which results in a variable food supply that is sometimes low in quality and quantity. Again, forage abundance and quality likely play important roles in determining antler size for populations of Alaskan moose inhabiting those plant communities. Nonetheless, antlers of *A. a. gigas* from taiga regions in Alaska, USA, were larger than those of *A. a. andersoni* from similar habitat in northeastern Minnesota, USA, and Saskatchewan, Canada. In addition, moose from tundra habitat on the Seward Peninsula, Alaska, which have colonized that area within the last ~30 years from the boreal forest, possessed antlers intermediate in size between moose inhabiting taiga and tundra. Moreover, moose from forested areas of southeast Alaska, which have a unique mitochrondial DNA haplotype from other subspecies of moose, also had comparatively smaller antlers than other moose in Alaska. Those outcomes indicated that differences in antler size likely have a genetic in addition to a nutritional basis. We hypothesize that differences in antler size of Alaskan moose in relation to habitat may have genetic as well as nutritional underpinnings related to openness of habitat, but more research is needed. Finally, our results on antler morphology, in concert with information on pelage coloration and recent data on genetics, do not support hypotheses concerning a double migration, or eastern and western races of moose, forwarded to explain morphological variation in moose inhabiting the New World. Likewise, we reject the hypothesis that ecotypical differences are primarily responsible for morphological variation in subspecies of moose inhabiting North America.

ALCES VOL. 38: 155-165 (2002)

Key words: age, Alaskan moose, *Alces alces*, antlers, ecotypes, genetics, habitat, morphology, nutrition, size, taiga, tundra

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Size and conformation of cervid antlers are influenced by genetics, age, and nutrition (Goss 1983). How those factors interact to determine antler size and shape, and whether antler morphology characterizes populations or subspecies, however, continues to be debated (Bubenik 1983, Gasaway et al. 1987). For instance, Geist (1998) proposed that that there were eastern and western races of moose (*Alces alces*). Other geographical variation in morphology for subspecies of this large cervid was thought to be nutritional, and such differences were best regarded as ecotypes (Geist 1998). Bubenik (1998), however, hypothesized that smaller-antlered moose inhabiting forested regions (taiga moose) were genetically distinct from larger-antlered moose living in more open areas (tundra moose), and that such distinctions were worldwide. He proposed a double-migration hypothesis for moose entering the New World to explain extant morphological variation (Bubenik 1998).

Peterson (1955) delineated 4 subspecies of moose in North America based on skull morphology, and Bowyer et al. (1991) described pelage and behavioral differences among subspecies. Hundertmark et al. (2003) confirmed those subspecific differences using mitochondrial DNA (mtDNA). Moreover, Gasaway et al. (1987) documented clear differences in antler size among subspecies of moose, allowing the possibility of genetic underpinnings of that variability. Whether such differences are the result of genetics, nutrition, or both factors, however, remain unresolved.

Moose are a useful species to evaluate effects of nutrition and genetics on antler morphology because antlers of this large cervid have been well studied (Bubenik et al. 1978, Bubenik 1998), including relations with body mass (Sæther and Haagenrud 1985; Solberg and Sæther 1993, 1994; Stewart et al. 2000), age (Sæther and Haagenrud 1985, Stewart et al. 2000, Bowyer et al. 2001), mineral composition (Moen and Pastor 1998), and theoretical interactions of population density, harvest, and genetics (Hundertmark et al. 1998). In addition, differences in morphology among subspecies have been confirmed with genetic analyses (Hundertmark et al. 2002a, 2002b, 2003). Finally, data on age and antler size are available from Alaska, for moose (*A. a. gigas*) inhabiting taiga and tundra habitats, and from northeastern Minnesota, USA, and Saskatchewan, Canada, for another subspecies (*A. a. andersoni*) living in taiga (Gasaway et al. 1987).

We hypothesized that if nutrition was influential in determining antler size, we would find the largest-antlered Alaskan moose (*A. a. gigas*) living in areas where forage was abundant, as well as differences in moose living in tundra compared with those from taiga habitat. Conversely, if genetics were the overriding determinant of antler size, we postulated that the largest difference would be between *A. a. gigas* from taiga and *A. a. andersoni* from that same habitat type. We recognize that these hypotheses are not mutually exclusive, but contend that, in concert with other data on morphology and genetics, we could test ideas concerning the evolution and morphology of subspecies of moose in North America.

STUDY AREA

We subset our data by game management units (GMUs) established by the Alaska Department of Fish and Game, and assigned a habitat type based on the predominant vegetation community in each unit (Fig. 1). Taiga extended from the eastern boarder with Canada westward across the interior; moose harvested in that habitat were from GMUs 12-15, 20-22, and 24. Moose from southeast Alaska inhabited coastal coniferous forests and were har-

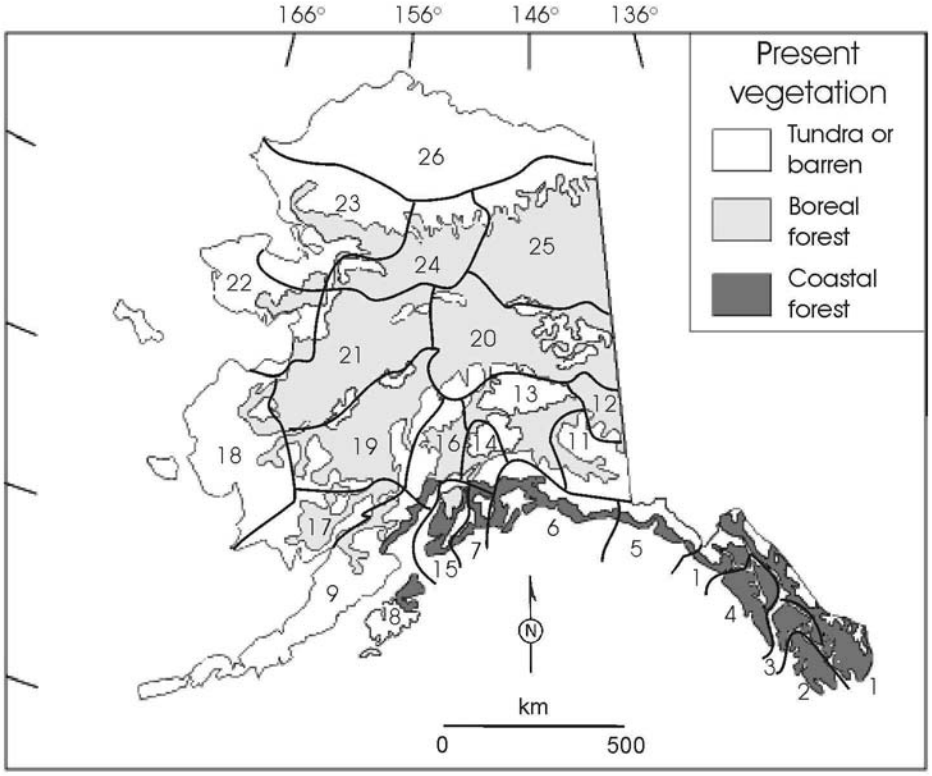

Fig. 1. Map of game management units (GMUs) and vegetation types in Alaska, USA, used in our analysis of antler size of moose (adapted from Albert et al. 2001).

vested from GMU 1. Moose killed in the remaining GMUs, which were classified as tundra, included 5, 7, 11, 16-17, 19, 23, and 25-26. We further subdivided our data regionally because habitat in the Copper River Delta (GMU 6) and Alaska Peninsula (GMU 9) differed markedly from other areas. Likewise, we separated data from the Seward Peninsula (GMU 22) because moose had recently colonized that tundra area from nearby taiga.

METHODS

Antler measurements used in our retrospective analysis were collected originally from hunter-harvested moose during 1968-83 across game management units in Alaska (Gasaway et al. 1987). Those measurements were made mostly by employees of the Alaska Department of Fish and Game, who were experienced in gathering such data. Data on antler spread, palm length and width, beam circumference, and number of antler tines were obtained from a subset of data that included associated information on age (*n* = 1,501). Methods used to measure antlers were provided by Gasaway et al. (1987), Stewart et al. (2000), and Bowyer et al. (2001). Age of moose was determined by counts of tooth cementum annuli (Sergeant and Pimlott 1959, Gasaway et al. 1978).

We used principal component analysis (McGarigal et al. 2000) to obtain an overall index to antler size. Principal component 1 (PC1) explained 73% of the variation in measurements of moose antlers; eigenvectors associated with PC1 had similar loadings (0.30-0.35) for the various antler characteristics (Stewart et al. 2000, Bowyer et al. 2001). PC1 exhibited patterns of rapid increase with age from 1 to 6 years old, peaked at 7-11 years, and decreased slightly in moose 12-17 years old, which reflected growth patterns in other antler characteristics (Bowyer et al. 2001). Those results indicated that PC1 provided a reliable measure of the overall size of moose antlers. Moreover, with spread withheld from analysis, PC1 was strongly correlated with antler spread ($r^2 = 0.74$; Bowyer et al. 2001), indicating the usefulness of that measurement in characterizing the size of antlers. Analysis of covariance with PC1 as the dependent variable, age as the covariate, and region of the state or habitat type as the main effect were used to test for differences in antler size; assumptions of homogeneous slopes were met for this analysis (Neter et al. 1985). A posteriori tests between habitats and regions of Alaska were performed with Tukey's HSD (Neter et al. 1985).

Gasaway et al. (1987) used a running 3-year mean to examine differences in antler spread (size) with age among *A. a. gigas* and 2 populations of *A. a. andersoni*. Because we did not have access to the original data for *A. a. andersoni*, we also calculated that same statistic for *A. a. gigas* inhabiting taiga for comparisons with the other 2 populations of forest-dwelling moose. Consequently, no inferential statistics could be applied to those comparisons, and variation in antlers between subspecies and populations was inferred from the magnitude of differences in running means.

RESULTS

Antlers of Alaskan moose (*A. a. gigas*) were characterized by large palms and considerable spread typical of that subspecies. Mean (± SE) of characteristics for 1,501 left antlers were: palm width = 26.9 ± 0.21 cm; palm length = 81.1 ± 0.61 cm; beam diameter = 17.9 ± 0.07 cm; and number of antler tines = 9.0 ± 0.07. Antler spread was 131.3 ± 0.66 cm, and moose averaged 5.4 ± 0.08 years old.

When we controlled for age with analysis of covariance (ANCOVA), clear patterns emerged with respect to the size of antlers (PC1) and geographic regions as well as habitat (tundra and taiga) for Alaskan moose (Fig. 2). The largest-antlered moose occurred on the Alaska Peninsula and Copper River Delta, followed by moose harvested in game management units composed mostly of tundra (Fig. 2), moose inhabiting the Seward Peninsula, those from areas with mostly taiga, and moose from southeast Alaska (Fig. 2). A posteriori tests with Tukey's HSD indicated significant ($P = 0.05$) differences in antler size between all regional and habitat pairings except Alaska Peninsula–Copper River Delta with tundra habitat.

We also compared *A. a. gigas* from taiga habitat in Alaska with *A. a. andersoni* from northeastern Minnesota and Saskatchewan. Comparisons of running means (3 years) for antler size (spread) against age clearly indicated that *A. a. gigas* living in taiga had larger antlers than populations of

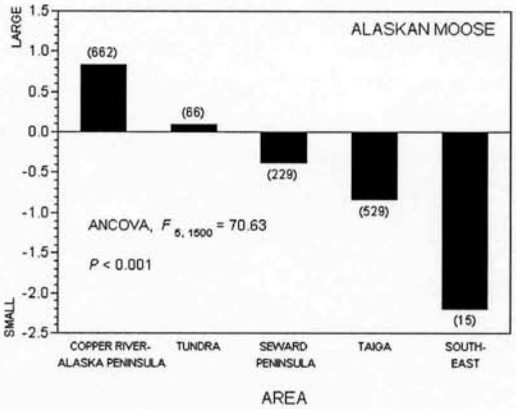

Fig. 2. Antler size of Alaskan moose (*Alces alces gigas*) in relation to habitat and geographic regions in Alaska, USA, 1968-83. Principal component 1 (PC1) indexed overall size, with positive loadings corresponding to larger antlers and negative loadings to smaller ones. Bars represent least-square means corrected for age with analysis of covariance (ANCOVA); sample sizes are in parentheses.

A. *a. andersoni* from similar forested habitat (Fig. 3). Differences in antler size also were evident between the 2 populations of *A. a. andersoni*, with moose from Saskatchewan possessing smaller antlers than those from northeastern Minnesota (Fig. 3).

DISCUSSION

Alaskan moose exhibited clear geographic variation in antler size that likely was related to nutritional differences among habitats. The largest-antlered males in Alaska were from the Copper River Delta and the Alaska Peninsula, although those moose did not differ significantly in size from moose inhabiting tundra (Fig. 2), probably because of high variability in antlers from moose harvested on the delta and peninsula. River deltas are among the most productive of all moose habitats (MacCracken et al. 1997, Peek 1998, Bowyer et al. 2003); browse also is abundant on the Alaska Peninsula, although that area is mostly tundra. Both of those geographically adjacent regions possess maritime climates with less snow and longer growing seasons than other areas of the state, especially interior Alaska (Gasaway et al. 1992, Bowyer et al. 1998, Keech et al. 2000). Snow depth and browse availability are thought to be important factors regulating density and distribution of moose (Coady 1974, Telfer 1978, Telfer and Kelsall 1984, Bowyer et al. 1997). Similarly, larger antlers from Alaskan moose (*A. a. gigas*) living in tundra compared with taiga habitat probably resulted from nutrition rather than genetics; mtDNA haplotypes of moose from mainland Alaska exhibited little variation, indicating a recent range expansion of genetically similar animals (Hundertmark et al. 2003).

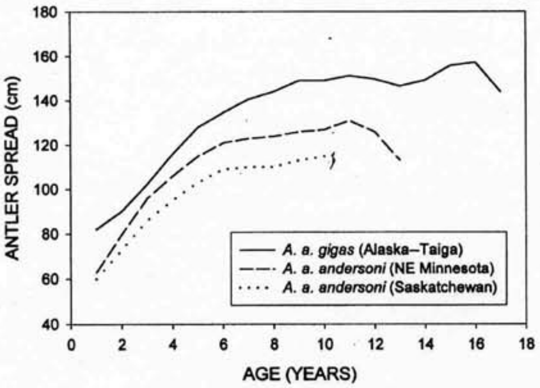

Fig. 3. Antler size (spread) in relation to age for *Alces alces gigas* from taiga habitat in Alaska, USA, compared with *A. a. andersoni* from forested habitats in northeastern Minnesota, USA, and Saskatchewan, Canada. Lines are 3-year running means (adapted from Gasaway et al. 1987).

Many areas of tundra are not suitable habitat for moose. Nonetheless, willows (*Salix* spp.), which supply high-quality forage for moose (Peek 1974, Bowyer et al. 1998) and grow along braided rivers and in association with riparian zones in tundra habitat, provide productive areas that are relatively stable through time (Peek 1974, 1998; Bowyer et al. 2003). Erosion, flooding, and ice action keep riparian vegetation in early successional stages and offer locally abundant forage for moose (Peek 1998, Bowyer et al. 2003). Conversely, productivity of the boreal forest is largely dependent upon fire and subsequent regeneration of browse for moose (Peek 1998, Weixelman et al. 1998). Forage production on burns begins declining by 15-20 years following fire, and succession results in forage species becoming much less abundant and of lower quality by 80 years of age (Cowan et al. 1950, Weixelman et al. 1998)—subsequent declines in productivity of moose populations follow those successional patterns in taiga (Loranger et al. 1991). Moose harvested from across taiga habitat in Alaska would have, on average, a less-abundant supply of lower-quality food than those living in tundra. Indeed, less-palatable species such as birch (*Betula* spp.) and aspen (*Populus* spp.) may compose a large component of the diet of moose inhabiting taiga

(Peek 1974, Weixelman et al. 1998).

Moose populations throughout much of Alaska are held at low density by large mammalian carnivores (Van Ballenberghe 1987, Gasaway et al. 1992, Van Ballenberghe and Ballard 1994, Ballard and Van Ballenberghe 1998, Bowyer et al. 1998). Consequently, biases from density-dependent effects on physical condition of cervids (sensu McCullough 1979, Bowyer et al. 1999) and, ultimately, antler size (McCullough 1982, Stewart et al. 2000) would not be expected. Declines in body and antler size, which are positively correlated in cervids (Clutton-Brock 1982, McCullough 1982, Bowyer 1986, Stewart et al. 2000), would be expected with increasing population density relative to carrying capacity (*K*). Those well-documented relationships offer strong evidence against the ecotype hypothesis of Geist (1998). If morphological differences among subspecies were mostly the result of nutrition, then the magnitude of morphological variation observed among subspecies should be present in a population undergoing a rapid change in population size. Although nutritional stunting can occur among cervids, sufficiently large changes in morphology, including differences in pelage markings, within a population undergoing even enormous changes in numbers have not been described (Klein 1968, McCullough 1979). Indeed, we are unaware of a nutritional mechanism that would cause the marked differences in pelage color and behavior described for subspecies of moose in North America (Bowyer et al. 1991). The presence of a white morph in moose that is not an albino, and white females giving birth to reddish-brown young (Franzmann 1981, Armstrong and Brown 1986), strongly support the hypothesis of a genetic component to differences in pelage coloration that cannot be attributed to ecotypes. That same interpretation likely holds for subspecific differences in antlers of moose.

Over the past ~30 years, moose have colonized the Seward Peninsula, which is mostly tundra, from nearby taiga habitat. Those moose possess antlers that are intermediate in size between moose inhabiting tundra and taiga habitats (Fig. 2). Although we believe that the intermediate antler size of moose on the Seward Peninsula likely has nutritional underpinnings, we cannot completely rule out genetics as a cause for that difference because the response in size was neither immediate nor as large as those in other tundra regions of the state (Fig. 2). Subspecies of cervids inhabiting more open terrain tend to be more social, and have larger body and antler sizes, and more conspicuously marked pelage than those from densely vegetated forests (Cowan 1936, Peek et al. 1974, Hirth 1977, Geist 1987, Bowyer et al. 1991, Molvar and Bowyer 1994). More research is needed to determine if antler size was under selection related to more open habitat for moose living on the Seward Peninsula, as well as for moose inhabiting other open landscapes.

Antler conformation for Alaskan moose (*A. a. gigas*) differs from other subspecies in North America in their tendency to exhibit a “butterfly” configuration of main and brow palms (Gasaway et al. 1987, Bowyer et al. 2001). Bubenik (1983) further proposed that in forest-dwelling subspecies (i.e., *A. a. andersoni*, *A. a. shirasi*, and *A. a. americana*) the orientation of palms curved upward to form a dish, whereas in moose from the tundra (e.g., *A. a. gigas*) the palms were comparatively flat. Gasaway et al. (1987), however, rejected that hypothesis by comparing ratios of antler characteristics from various subspecies of moose—few differences existed in the overall shape of antlers. Moose from wooded habitats also were postulated to have a narrower antler spread than those living in tundra (Bubenik et al. 1978, Bubenik 1983).

Gasaway et al. (1987) concluded that if forest-dwelling moose have evolved antlers that are adapted to dense woodlands, they have done so by altering size rather than shape of antlers—a supposition supported by our results (Figs. 2 and 3). Moreover, we hypothesize that differences in antler size between Alaskan moose inhabiting taiga and moose from forested areas of northeastern Minnesota are mostly genetic. Moose from both of those areas are subjected to predation (Peek et al. 1976, Gasaway et al. 1992); consequently, nutrition is not likely the cause of that disparate difference in antler spread (Fig. 3). We further hypothesize that differences between the size of antlers of *A. a. andersoni* from northeastern Minnesota and Saskatchewan may be nutritional (Fig. 3). Such differences would be expected because of more intense predation in the Minnesota population (Peek et al. 1976), and the concomitant increase in physical condition of those moose from being farther away from *K* than moose from Saskatchewan (sensu McCullough 1979, Bowyer et al. 1999).

The hypothesis of Bubenik (1998) that taiga and tundra moose are genetically distinct also can be rejected, as can the hypothesis of Geist (1998) for the existence of eastern and western races of moose. Moose subspecies inhabiting tundra in the Russian Far East (*A. a. buturilini*) possess a different chromosome number (2n = 68) and are not closely related to *A. a. gigas* (2n = 70) from tundra in Alaska (Hundertmark et al. 2002b). Moreover, Alaskan moose, which Geist (1998) places with moose from the Russian Far East, have the same fundamental chromosome number as other subspecies of moose in North America, and are more closely related to other subspecies in the New World than subspecies from Eurasia (Hundertmark et al. 2002b). Similar morphology of *A. a. gigas* and *A. a. buturilini* likely is a result of convergent evolution resulting from living in more open habitats than other subspecies of moose (Hundertmark et al. 2002b).

Differences in antler size between *A. a gigas* from taiga in Alaska, and *A. a. andersoni* from that same habitat in Minnesota and Saskatchewan (Fig. 3), implicate genetics as the cause of such geographic variation. Moreover, moose from forested areas of southeast Alaska recently have been identified as possessing a unique haplotype of mtDNA lacking in other subspecies of moose (Hundertmark et al. 2003). Although we caution that our sample size was small (Fig. 2), males from southeast Alaska also had much smaller antlers than moose from taiga habitat in other regions of Alaska, further indicating that selection operating in isolated populations affects antler size. Consequently, differences in antler size among populations of moose are not completely a result of the type of habitat they occupy. In addition, moose from southeast Alaska may be a unique subspecies. We believe, however, that morphological data presented herein, and genetic data from Hundertmark et al. (2002a, 2002b, 2003) are not yet sufficient to draw that conclusion—more research is needed.

Neither the hypothesis of Geist (1998) nor Bubenik (1998) was supported by our study of antler size in moose. Clearly, both nutrition and genetics are involved in the size and shape of antlers (Williams et al. 1994), but not in the manner proposed by either Geist (1998) or Bubenik (1998). More research is required to understand precisely how nutritional and genetic factors interact, and how they might be related to founder effects during dispersal into new habitat, and how natural selection operates on the size of moose inhabiting more open habitat compared with those living in closed boreal forest. We proposed that studies of DNA microsatellites, which would allow greater resolution of genetic differences among populations (Broders et al. 1999), would be a fruitful next step in resolving this important question.

ACKNOWLEDGEMENTS

We are indebted to those individuals who originally made measurements of moose antlers, and who are properly acknowledged in Gasaway et al. (1987). The Alaska Department of Fish and Game, and the Institute of Arctic Biology at the University of Alaska Fairbanks funded this research. Data on vegetation communities of Alaska were obtained from http://climchange.-cr.usgs.gov/info/lite/alaska/fig1.gif.

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