INCISOR ARCADES OF ALASKAN MOOSE: IS DIMORPHISM RELATED TO SEXUAL SEGREGATION?

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ABSTRACT: We tested whether incisor arcades of Alaskan moose (*Alces alces gigas*) differed between males and females of known age to examine how allometric differences in jaw architecture might relate to sexual segregation. Lower jaws were collected from moose killed by hunters, and from moose that died of either natural causes or collisions with vehicles. We measured the breadth (width) and the depth (protrusion) of the incisor arcade of moose; age was determined by counting cementum annuli of incisors. Arcade breadth of moose followed von Bertalanffy models of growth, with an asymptote at about 4 years of age for both sexes. Regression models differed for male and female moose; arcade breadth for males was significantly larger than for females. Data from the literature indicated body mass of females also reaches an asymptote at 4 years old. Males, however, do not attain an asymptote in body mass until 8-10 years of age. When incisor breadth was considered relative to asymptotic body mass, incisor breadth of males was less than that of females. Coefficients of incisor breadth relative to body mass, however, scaled similarly for male (0.249) and female (0.260) moose. Incisor depth did not differ between the sexes when depth was corrected for age. Our data indicate that incisor breadth, but not depth, scaled with body mass. Thus, muzzle morphology may exhibit more plasticity than previously thought. We hypothesize that muzzle architecture of moose, as reflected in incisor breadth and depth, relates to the diets of the sexes when they are spatially segregated. Whether incisor dimensions are a cause or consequence of sexual segregation, however, is uncertain.

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Resource partitioning between male and female ruminants has been postulated to reduce intersexual competition (Darwin 1871, Clutton-Brock et al. 1987, Main and Coblentz 1996), and may result from body size and other morphological differences (McCullough 1979; Hofmann 1989; Gordon and Illius 1996; Barboza and Bowyer 2000, 2001). Polygynous ruminants are among the most sexually dimorphic mammals (Ralls 1977, Weckerly 1998), and most dimorphic ruminants segregate according to sex when not engaged in mating activities (Miller and Litvaitis 1992, Miquelle et al. 1992, Main et al. 1996, Bleich et al. 1997). Although sexual segregation is common among polygynous ruminants, the mechanisms controlling this phenomenon continue to be debated (Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997; Barboza and Bowyer 2000, 2001). Sexual segregation may be driven by competition for forage and

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result from differences in feeding behavior that are a consequence of morphological differences between the sexes (Clutton-Brock et al. 1987; Illius and Gordon 1987; Main and Coblentz 1990, 1996).

Although energy requirements of smaller ruminants are proportionally greater to body mass than those of larger species, absolute requirements for energy of larger animals are greater than for smaller ones (McCullough 1979, Van Soest 1994). Clutton-Brock et al. (1987) hypothesized that female red deer (*Cervus elaphus*) competitively excluded males from mutually preferred areas because females were more tolerant of low biomass of plants. Similarly, Main and Coblentz (1996) suggested that competitive exclusion of males by females occurred for Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) feeding mostly on forbs. Illius and Gordon (1987) further postulated that the differential scaling of incisor breadth and metabolic requirements in relation to body mass might be a cause of spatial segregation in grazing ungulates. This hypothesis, however, was not supported by incisor breadths of black-tailed deer (*O. h. columbianus*; Weckerly 1993), or an empirical test on the role of competition in sexual segregation of white-tailed deer (*O. virginianus*; Kie and Bowyer 1999). Morphology of the muzzle still might relate to differential use of habitats by male and female ruminants, however, without requiring competitive exclusion of one sex by the other.

Morphology of the skull and mandible likely reflect requirements of feeding selectivity (Spencer 1995, Brashares et al. 2000), but few studies have focused on the relationship between structure of the incisor arcade and forage selection (Gordon and Illius 1988). Variation in bite mass from grass swards was related more closely to breadth of the incisor arcade than to body mass in captive sheep and goats (Gordon et al. 1996). Pérez-Barbería and Gordon (1999), however, did not detect significant differences in incisor breadth between the sexes in free-ranging Soay sheep (*Ovis aries*).

There are few data on bite size and incisor breadth for browsers (Gordon and Illius 1988), especially large species such as moose (*Alces alces*). Moreover, moose and other cervids, with dentition adapted for browsing, sexually segregate for much of the year (Bowyer 1984, McCullough et al. 1989, Miquelle et al. 1992, Bowyer et al. 1996, Kie and Bowyer 1999, Bowyer et al. 2001). Consequently, if differences in morphology of the jaw provide a general explanation for sexual segregation, such differences also must occur in browsing ruminants. We tested whether there were differences in incisor arcades between male and female Alaskan moose, and how size dimorphism in jaw architecture might affect feeding behavior. We also discussed how morphology of the incisor arcade might relate to sexual segregation in moose.

METHODS

We collected lower mandibles (from diastema forward) of Alaskan moose (*A. a. gigas*) from 4 areas in Alaska, USA, during 1999-2000: Cordova (60° N, 145° W), Kalgin Island (60° N, 152° W), Kenai Peninsula (60° N, 150° W), and Palmer (61° N, 149° W). Jaws collected for each sex and age class varied between areas: Cordova (all adults; male $n = 53$, female $n = 5$); Kalgin Island (adults and juveniles; male $n = 16$, female $n = 17$); Kenai Peninsula (adults and juveniles; male $n = 17$, female $n = 23$); and Palmer (adults and juveniles; male $n = 12$, female $n = 43$). Lower jaws with supernumerary incisors or canines (2 of 192), as well as those missing teeth (4 of 192), were not included in our analyses. We also used photographs of lower jaws containing a

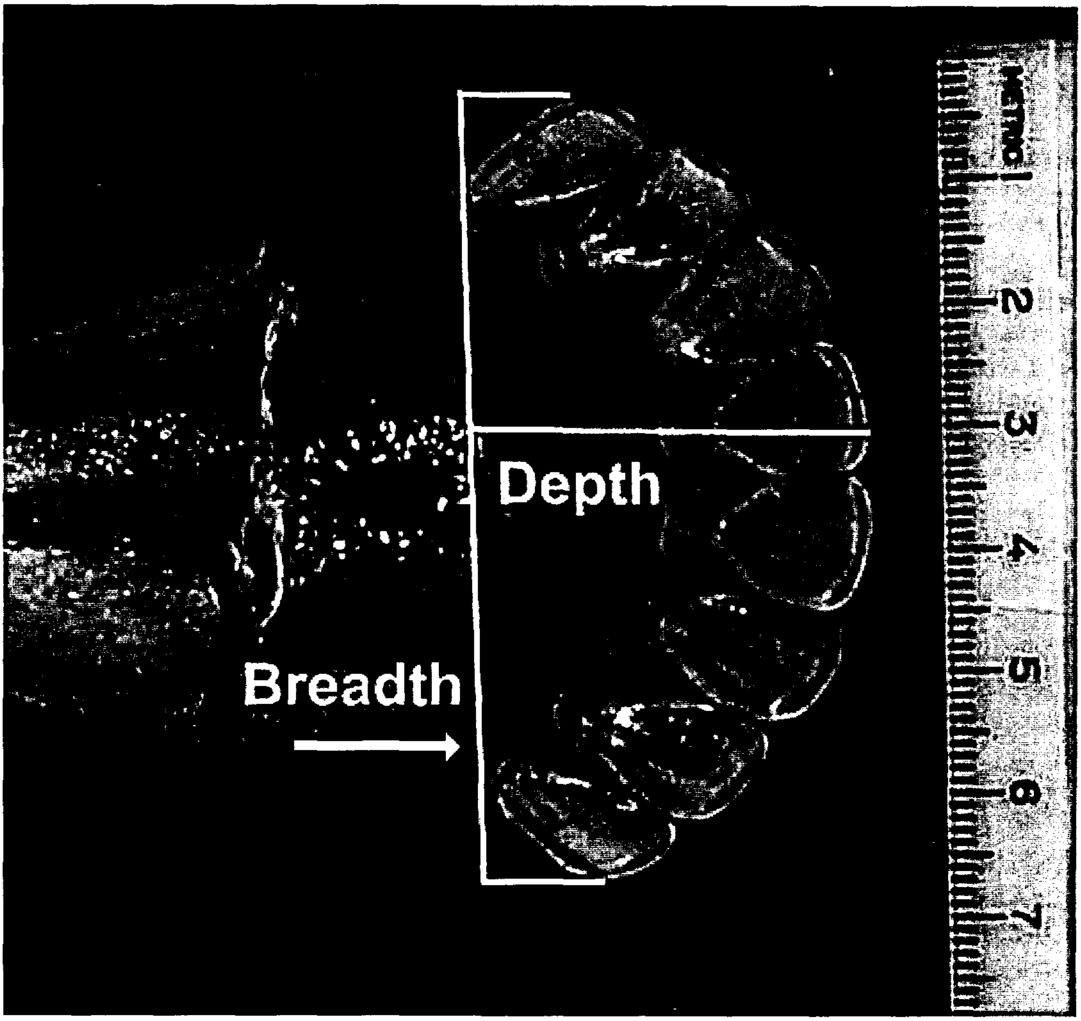

Fig. 1. Photograph of the lower mandible of a female Alaskan moose showing the incisor arcade measured to obtain incisor breadth and depth (protrusion). The scale adjacent to the teeth is in centimeters.

scale to determine incisor breadth (Fig. 1) from 9 older females from the Kenai Peninsula. Photographed jaws were not included in analysis of depth, because of parallax error in that metric. Total sample size, including photographed jaws, was 98 males and 88 females.

Jaws were obtained from moose legally killed by hunters and from animals killed in collisions with either automobiles or trains. Incisor breadth, the distance between the outside surfaces of the incisorform canines, was measured to the nearest 0.1 mm with dial calipers. Depth (protrusion) of the incisor arcade was the perpendicular distance between a line connecting right and left canines and the front of the first incisor (Gordon and Illius 1988, Weckerly 1993), and was measured with dial calipers to the nearest 0.1 mm. We determined age by counting cementum annuli of incisors (Gasaway et al. 1978). Matson's Laboratory (Milltown, MT, USA) performed this analysis for 88 samples, and K. Hundertmark and G. Del Frate counted cementum annuli for 89 jaws. R. Peterson determined ages for 9 moose collected in 1978-79 (those measured from photographs) using similar procedures.

Maximal seasonal weights were assigned to age classes based on data from Schwartz et al. (1987). Those data (Schwartz et al. 1987) relied on small sample sizes, but the relation between body mass and age is well demonstrated for moose (Franzmann et al. 1978, Solberg and Sæther 1994, Stewart et al. 2000). We combined our data on incisor dimensions with data from Schwartz et al. (1987) on body mass of moose to determine allometric relationships and obtain regression exponents to examine scaling among species of ruminants (Clutton-Brock and Harvey 1983, Gordon and Illius 1988).

Incisor breadth and depth were compared for males and females. Data for incisor breadth were fitted to von Bertalanffy equations by nonlinear regression (Zullinger et al. 1984). We used linear regression and ANCOVA (Neter et al. 1985) to examine relationships between incisor breadth and depth, age, and body mass. We examined assumptions of homogeneous variances for regression, and homogeneous slopes for ANCOVA (Neter et al. 1985). Analyses were performed with SYSTAT (1999).

RESULTS

For moose > 1 year old, mean (± SE) depth of the incisor arcade was 32.1 ± 0.24 mm for 85 males, and 31.2 ± 0.32 mm for 71 females. Depth, however, varied inversely with age for males ($Y = 34.16 - 0.549X$, $r^2 = 0.23$, $P < 0.001$) and females ($Y = 32.97 - 0.342X$, $r^2 = 0.21$, $P < 0.001$). ANCOVA, with depth as the dependent variable, age as the co-variate, and sex as the main effect, revealed that males ($\overline{X}_{\mathrm{adj}} = 31.9 \pm 0.24$ mm) did not have a greater arcade depth ($F_{1,53} = 0.88$, $P = 0.35$) than females ($\overline{X}_{\mathrm{adj}} = 31.6 \pm 0.27$ mm). We met assumptions for homogeneous variances and homogeneous slopes for regression and ANCOVA, respectively.

Incisor breadth for male and female moose followed a von Bertalanffy growth model (Fig. 2). Males had significantly wider incisor breadths than did females (asymptotes of 61.0 and 57.2 mm, respectively). Ninety-five percent C.I. did not overlap between the sexes, but the difference in incisor breadth was small (6%). Both females and males reached asymptotes in incisor breadth at about 4 years old (Fig. 2). Females also attained maximal body mass at 4 years of age, but males did not reach that asymptote in body mass until 8-10 years old (Fig. 2). Regressions of incisor breadth on body mass for male ($\ln$ incisor breadth $= 2.52 + 0.249 \ln$ mass, $r^2 = 0.82$) and female ($\ln$ incisor breadth $= 2.44 + 0.260 \ln$ mass, $r^2 = 0.69$) moose were similar.

DISCUSSION

Breadth of incisors increased with age in both sexes of Alaskan moose, but males attained broader incisor arcades (~6%) than did females at maximal body mass (Fig. 2). Van Deelen et al. (2000) reported similar findings for the molar array of white-tailed deer, with males possessing about 4% more surface area than females. An inverse relation existed between incisor depth and age for Alaskan moose. That pattern most likely resulted from increasing tooth wear with age; when we controlled for effects of age, depth of the arcade did not differ between the sexes. Hindelang and Peterson (1994) also demonstrated an increase in tooth wear with age in moose, with a concomitant decline in the "cutting edge" on older teeth.

Maximum predicted mass of male moose is about 40% greater than for females (Fig. 2). Males continue to gain body

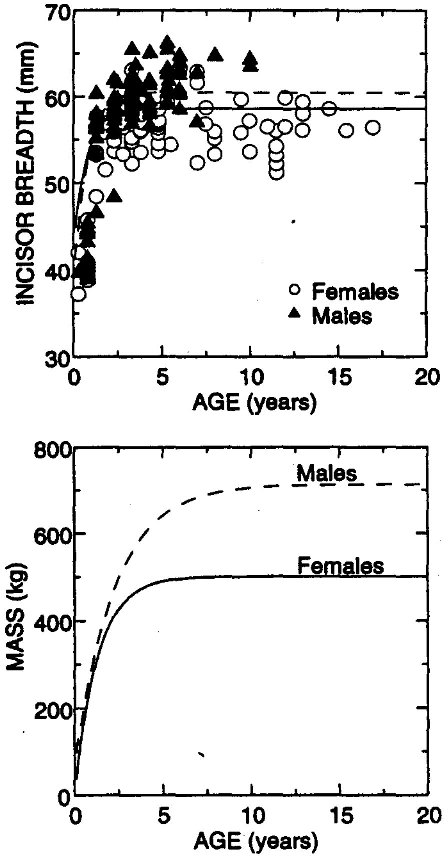

Fig. 2. Relationship between breadth of the lower incisor arcade for 98 male (dashed line) and 88 female (solid line) Alaskan moose (above), and the relation between body mass and age (below). von Bertalanffy equations for incisor breadth and age were: $Y = 60.95((1-0.333)^{-1.53(x+0.012)})^{3}$ for males, and $Y = 57.17((1-0.333)^{-1.39(x+0.26)})^{3}$ for females. The relation between body mass and age was from Schwartz et al. (1987).

mass long after maximal incisor breadth is attained, but maximal predicted body mass and incisor breadth are reached at about the same time in females (Fig. 2). Consequently, at asymptotic body mass, males had smaller incisor breadths relative to their mass than did females. Slopes from regressions of incisor breadth (from this study) on body mass (from Schwartz et al. 1987), however, were nearly identical for males (0.249) and females (0.260), indicating that incisor breadth scaled with body mass in a similar fashion for the sexes. Our result for moose is consistent with the analysis of artiodactyls by Pérez-Barbería and Gordon (2000), which revealed a similar relationship between the sexes for incisor breadth and body mass. Hence, sexual dimorphism alters incisor breadth in an isometric fashion with mass.

Incisor breadth of moose scaled with a projected body mass to $kg^{0.25}$, which was considerably smaller than estimates of $kg^{0.33}$ and $kg^{0.40}$ derived for several species of ungulates (Clutton-Brock and Harvey 1983, Gordon and Illius 1988; Fig. 3). We caution, however, that models developed for interspecific relationships may not hold for intraspecific ones (Barboza and Bowyer 2000). Nevertheless, our results indicate that incisor breadth for moose increases more slowly with mass than for smaller-bodied species. Bite widths, therefore, may grow differentially for large browsers compared with other ruminants, and in a fashion similar to long bones, which may reflect overall skeletal growth. For instance, hind limbs also vary with the exponent of body mass to $kg^{0.26}$ among bovids, and reach maximal size long before asymptotic body mass is attained (Schmidt-Nielsen 1984). Likewise, Franzmann et al. (1978) reported that maximal shoulder height was reached in female moose by 4 years old, but was not attained by males until about 8 years of age.

Width of the incisor arcade in moose may be constrained genetically as are the craniofacial elements of other mammals (Miller and German 1999). Nonetheless, there may be considerable phenotypic plasticity in rates of growth and in the final size of body parts attained by populations within a species. Growth rates, organ size, and body mass respond to periods of restriction and re-feeding in domestic ruminants, with a longer duration of compensatory growth in cattle than in sheep (Ryan et al. 1993a, 1993b). Environmental effects also may

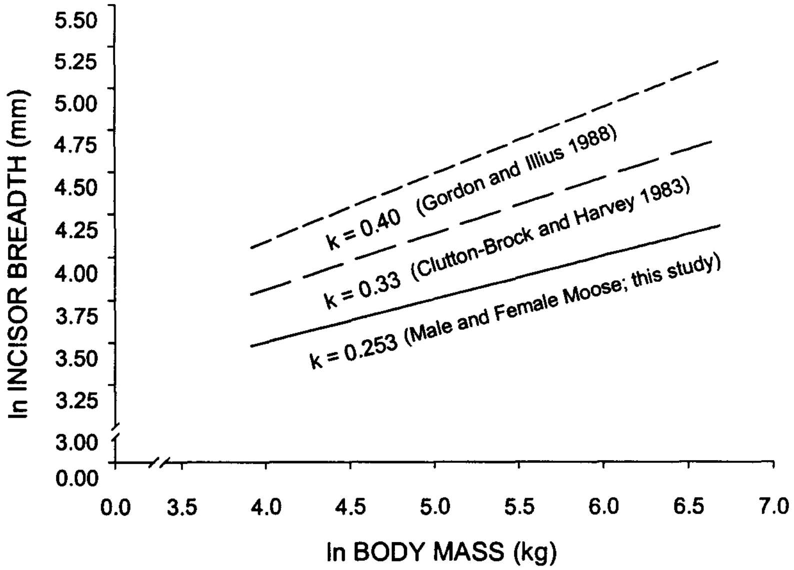

Fig. 3. Relationship between incisor breadth and body mass for ruminants, in general (Clutton-Brock and Harvey 1983, Gordon and Illius 1988), and for Alaskan moose. Data on body mass of moose were from Schwartz et al. (1987). This result indicates that browsers possess a narrow muzzle relative to body mass compared with other ruminants, especially grazers.

result in different patterns of growth of skeletal and soft-tissue between populations and between sexes (Post et al. 1999). Indeed, Hindelang and Peterson (2000) noted differences in mineral densities of metatarsals in male and female moose.

Body-size dimorphism in moose increases mass disproportionately to incisor breadth. There may be some limit to incisor breadth, however, because moose often forage selectively on individual leaders of current annual growth (Bowyer and Bowyer 1997). Perhaps male Alaskan moose have reached that limit for dealing efficiently with browse they consume. Consequently, muzzle size of moose in relation to their body mass may be constrained by a diet high in browse (Houston 1982). Browsers, in particular, need to forage selectively on leaders of new growth, which are generally higher in nutrient content than older growth (Aldous 1945). We hypothesize that width of the incisor arcade in male moose, likewise, is constrained by selective foraging. For example, if male moose took too large of a nonselective bite, they would obtain substantial amounts of low-quality plant parts, especially second and third year growth of trees and shrubs. Selection of food quality ultimately may be constrained by intake rate and factors associated with oral processing (Shipley et al. 1994), or the kinetics of forage passage (Gross et al. 1996, Illius and Gordon 1999, Barboza and Bowyer 2000).

Incisor breadth may not be the most important determinant of bite volume and thereby feeding efficiency in browsing mammals. Increments of bite width are selectively advantageous for grazing mammals, because food is distributed in a single plane. Browsing species contend with a variety of foods distributed in 3 dimensions that must be selected and harvested (Provenza 1995, Hanley 1997). Although bite width may enhance the harvesting rates of moose consuming aquatic plants (Belovsky and Jordan 1981), muzzle length and other cranial features likely relate to obtaining a diet high in browse (Janis and Ehrhardt 1988, Spencer 1995). Nevertheless, breadth of the incisor arcade may affect the ability of moose to forage selectively on individual leaders of browse, or to concentrate their foraging on new growth. This style of feeding might be especially important where browse takes on a hedged appearance and leaders of new growth are clustered together from previous foraging by moose (Molvar et al. 1993).

Our results are in agreement with data presented by Clutton-Brock and Harvey (1983) for red deer, but differ from other studies, which did not find intersexual differences in incisor breadth relative to body mass. For example, our data are not consistent with those presented on incisor breadth of black-tailed deer by Weckerly (1993). This difference raises questions concerning the potential phenotypic variability in the size of the incisor arcade between the sexes. In addition, the sexes of most dimorphic ruminants spatially segregate for much of the year (Bleich et al. 1997). If types and amounts of forage available to the sexes of these large herbivores varied markedly, then there might be selection for changes in muzzle morphology, including the incisor arcade, between the genders. We cannot address phenotypic versus genotypic variation in the architecture of muzzles with our data, but suggest this is a fruitful area for further research.

Clutton-Brock et al. (1987) postulated that male red deer were less tolerant of low plant biomass than were females, and selective foraging by females competitively excluded males from specific areas, thereby causing sexual segregation. Main and Coblentz (1996) also provided supportive evidence for this hypothesis for mule deer by noting that the biomass of nutritious forage was lower on areas occupied by females than for areas inhabited by males. Indeed, Illius and Gordon (1987) suggested that metabolic requirements related to differences in body size between the sexes, including incisor morphology, might cause sexual segregation for many ungulates. Nonetheless, the importance of muzzle architecture in causing competitive exclusion of males by females has been questioned (Pérez-Barbería and Gordon 2000). Despite concerns as to whether the competitive-exclusion hypothesis causes sexual segregation in ruminants (Kie and Bowyer 1999, Pérez-Barbería and Gordon 2000), morphology of the muzzle still may be related to differential use of habitats and, hence, forages consumed by males and females.

Male moose take larger bites than do females (Miquelle et al. 1992, Bowyer et al. 2001). Yet, whether competitive exclusion occurs in large browsers, such as moose, remains to be demonstrated. Other nutritional hypotheses that do not require competitive exclusion may explain sexual segregation among cervids and other large herbivores (Barboza and Bowyer 2000, 2001). Perhaps the habitat, and thereby dispersion and architecture of forage plants into which the sexes segregate, affects some aspects of the morphology of the mouth (Weckerly 1993). We are uncertain whether muzzle shape is a cause or consequence of sexual segregation in ungulates. Architecture of the incisor arcade, however, likely is related to food acquisition in these dimorphic ruminants, and thereby affects many of their life-history characteristics.

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