SEXUAL SEGREGATION IN MOOSE: EFFECTS OF INCISOR MORPHOLOGY, QUALITY OF WILLOWS, AND FORAGING BEHAVIOR

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A

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ABSTRACT

Differences in the jaw morphology of Alaskan moose (*Alces alces gigas*) may relate to sexual segregation. Male Alaskan moose had significantly wider incisor breadths than did females; however, incisor depth did not differ between sexes. Those differences in jaw architecture might relate to the diets of sexes when they are spatially segregated. Moose consume willow (*Salix* spp.) as a fundamental component of their diet. Smaller-diameter twigs were more digestible, had more protein, and contained less fiber than larger-diameter twigs. Conversely, no relation existed between age of twigs and digestibility. Ruminants may segregate spatially because females competitively exclude males. An experiment on foraging behavior, however, rejected that hypothesis. Nonetheless, females fed more selectively and had higher rates of forage intake than did males. Thus, differences in foraging behavior between the sexes still may relate to sexual segregation.

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INTRODUCTION

Resource partitioning between male and female ruminants has been postulated to reduce intersexual competition, and may result from body size and other morphological differences. Polygynous ruminants are among the most sexually dimorphic mammals, and most dimorphic ruminants segregate according to sex when not engaged in mating activities. Although sexual segregation is common among polygynous ruminants, the mechanisms controlling this phenomenon continue to be debated.

Sexual segregation may be driven by competition for forage, and result from differences in feeding behavior that are a consequence of morphological differences between the sexes. Indeed, foraging behavior may be involved in differences in use of space by the sexes. Other reasons also may exist besides competition that keeps sexes segregated spatially outside the mating season. For instance, sexual segregation in bighorn sheep (*Ovis canadensis*) likely resulted from differing reproductive strategies of males and females, and sexual segregation in moose (*Alces alces*) did not result from intersexual competition. Nonetheless, no experiments involving competition were preformed. One experiment that increased population density of white-tailed deer (*Odocoileus virginianus*) failed to support the competition hypothesis, but density of deer was altered by exclusion of predators, which confounded strategies of predator avoidance with foraging behavior by those herbivores. Finally, indirect-competition hypothesis did not explain habitat segregation of red deer (*Cervus elaphus*). Thus, whether the competition hypothesis can explain sexual segregation in browsing ungulates remains uncertain.

There are few data on bite size and incisor breadth for browsers, especially large species such as moose. Moreover, moose and other cervids, with dentition adapted for browsing, sexually segregate for much of the year. Consequently, if differences in morphology of the jaw provide a general explanation for sexual segregation, such differences also must occur in browsing ruminants.

Browse is an important element in the winter diet of moose inhabiting boreal forests, and the diet of Alaskan moose is composed principally of willows (*Salix* spp.) throughout the year. Furthermore, diameter of twigs available to moose for consumption may be a crucial aspect of diet selection by this large browser, because most of the nutrients used by moose are contained in the surface of woody twigs, with hard-to-digest carbohydrates (cellulose and hemicellulose) composing the core. Therefore, as twig diameter of browse increases, the ratio of surface nutrients to the core declines, as does the nutritional value of such forage for moose. Additionally, allometric differences between the sexes of moose might affect their ability to assimilate nutrients. Thus, differences in diet selection may lead to spatial segregation of the sexes.

Sexual segregation may be driven by competition for forage and differences in feeding behavior that result from morphological differences between the sexes. Further study on sexual segregation in ruminants is necessary to fully understand this widespread behavior. Understanding why the sexes segregate is important because it is vital to understanding and predicting distribution, habitat selection, and resource requirements related to reproduction for the sexes. Indeed, sexes of dimorphic ruminants exhibit such differences in habitat selection and diet that they should be managed as if they were separate species. Alaskan moose (*A. a. gigas*) lend themselves well to studying sexual segregation because they are highly sexually dimorphic, select habitat differently, and remain spatially separated for much of the year.

Research on females competitively excluding males has been conducted on a grazer (red deer) and herbivores that feeds principally on forbs (mule deer, and white-tailed deer). Few data on browsers, such as moose, are available to evaluate sexual segregation. Such research is essential because sexually dimorphic browsers segregate, and if competitive exclusion of one sex by the other is a general explanation for sexual segregation, this process must operate in moose. No experimental tests of this hypothesis have been conducted.

I tested hypotheses forwarded to explain sexual segregation among polygynous ruminants, and to predict their habitat requirements, using Alaskan moose as a model. I predicted that if competition was the cause of sexual segregation, adult female moose would competitively exclude adult male moose from mutually preferred forages. Furthermore, such differences in foraging behavior by the sexes may lead to sexual segregation and differential use of habitat and space.

I hypothesized that adult female Alaskan moose would competitively exclude adult males from high-quality areas because males are unable to effectively forage in areas with low availability of suitable quality, but difficult to obtain forage. I approached this hypothesis by testing for differences in the foraging behavior of the sexes in an experimental study on captive moose. I predicted that the foraging behavior of adult female moose would affect the foraging behavior of adult male moose in a manner consistent with hypotheses forwarded to explain sexual segregation.

[1]CHAPTER 1.

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

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 reached an asymptote at 4 years old; however, males did 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,

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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.

Key words: Alaskan moose, *Alces alces gigas*, body mass, growth, incisor breadth and depth, morphology, resource partitioning, sexual dimorphism, sexual segregation

INTRODUCTION

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 e*t 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 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 (*Odocoileus virginianus*; Kie and Bowyer 1999). Morphology of the muzzle still might relate to differential use of habitat 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 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 ($\overline{X}_{\text{adj}} = 31.9 \pm 0.24$ mm) did not have a greater arcade depth ($F_{1,53} = 0.88$, $P = 0.35$) than females ($\overline{X}_{\text{adj}} = 31.6 \pm 0.27$ 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 did 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 mass long after maximal incisor breadth is attained, but maximal predicted body mass and incisor breath were 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 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, affect 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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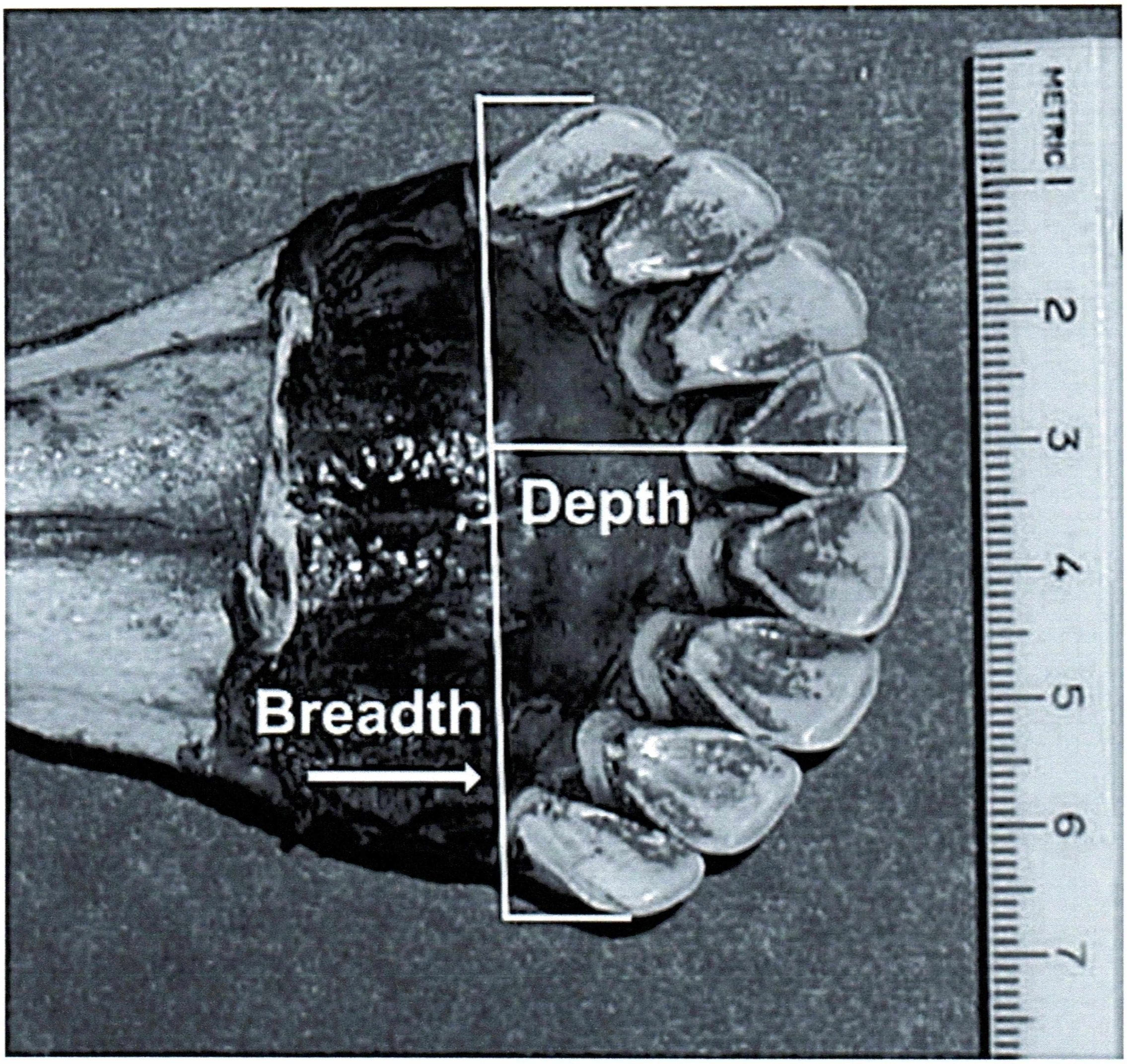

Fig. 1.1. Photograph of the lower mandible of a female Alaskan moose showing the incisor arcade measured to obtain incisor breadth and depth (protrusion). The scale adjacent to the teeth is in centimeters.

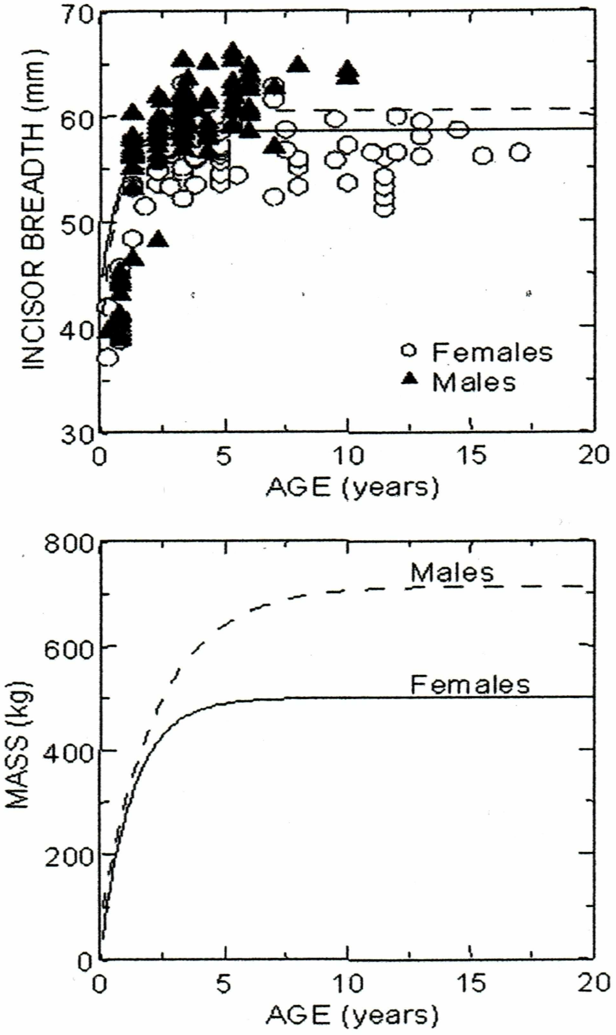

Fig. 1.2. Relationship between breadth of the lower incisor arcade for 98 male (dashed line) and 88 female (solid line) Alaskan moose (above), and the relation between body mass and age (below). von Bertalanffy equations for incisor breadth and age were: $Y = 60.95((1-0.333)^{-1.53(x + 0.012))\wedge 3}$ for males, and $Y = 57.17((1-0.333)^{-1.39(x + 0.26))\wedge 3}$ for females . The relation between body mass and age was from Schwartz *et al.* (1987).

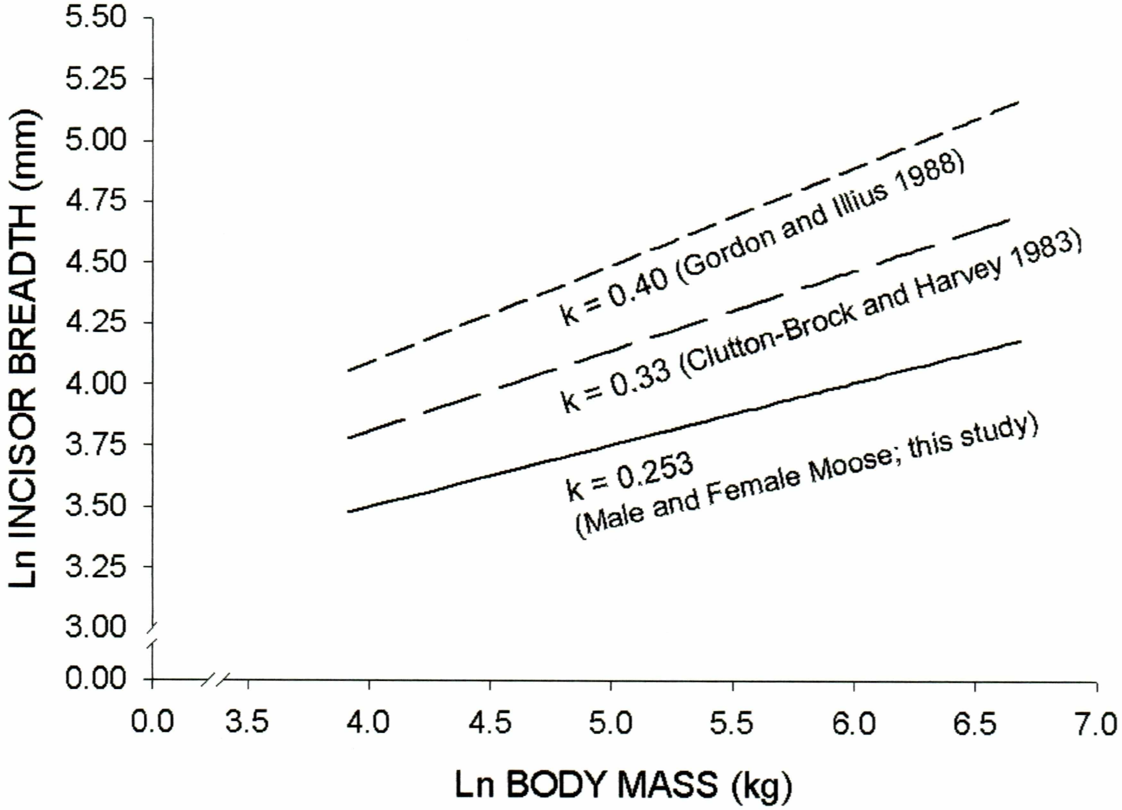

Fig. 1.3. Relationship between incisor breadth and body mass for ruminants, in general (Clutton-Brock and Harvey 1983, Gordon and Illius 1988), and for Alaskan moose. Data on body mass of moose were from Schwartz *et al.* (1987). This result indicates that browsers posses a narrow muzzle compared with other ruminants, especially grazers.

[1]CHAPTER 2.

NUTRITIONAL QUALITY OF WILLOWS FOR MOOSE: EFFECTS OF TWIG AGE AND DIAMETER

ABSTRACT

Alaskan moose (*Alces alces gigas*) consume willow (*Salix* spp.) as a fundamental component of their winter diet. We collected Barclay willow (*S. barclayi*) from 5 nearby sites (15-80 m apart) on the Kenai Peninsula, Alaska, USA, during winter 1999-2000. We tested whether diameter or age of twigs was more important in determining nutritional quality of willows for moose. We sampled older (2 and 3 years old) and current-annual growth for 2,012 twigs from 15 discrete branches of willows to determine in vitro dry matter digestibility (IVDMD), protein content, and fiber content. We tested for differences in forage quality as affected by diameter of twigs, age of twigs, collection site, tannin content, and their interactions. Likewise, we estimated digestible energy of twigs, and tested for differences between diameter of twigs, age of twigs, and collection site. Smaller-diameter twigs had higher IVDMD, protein content, and lower fiber content ($P < 0.001$). An inverse relationship occurred between the age of twigs and protein content ($P < 0.001$), with older aged twigs containing less protein. Accordingly, age of twigs was negatively related to fiber content ($P = 0.002$). Conversely, no relation existed

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between age of twigs and IVDMD ($P = 0.34$). Tannin content varied between sites ($P < 0.001$), and age of twigs ($P = 0.04$), with older twigs possessing more tannins than younger ones, but no difference occurred between diameters of twigs ($P = 0.48$). Digestible energy differed between diameter of twigs ($P = 0.02$), age of twigs ($P = 0.02$), and collection site ($P < 0.001$). Thus, structural components of the twig to support growth were more important in affecting digestibility, whereas age of the twig was more influential in determining nitrogen and tannin content. Those observations are crucial in understanding quality of diet and bite-size selection by moose. Why moose forage on a particular plant or select specific twigs from that plant may provide further insights into the mechanisms controlling foraging behavior.

Key words: Alaskan moose, *Alces alces gigas*, digestibility, digestible energy, Kenai Peninsula, nitrogen, nutrition, *Salix*, twig age, twig diameter, structural carbohydrates, tannin, willows

INTRODUCTION

Browse is an important element in the winter diet of moose (*Alces alces*) inhabiting boreal forests (Peek 1974, 1998; Joyal 1976; Ludewig and Bowyer 1985; Renecker and Schwartz 1998). Indeed, the diet of Alaskan moose (*A. a. gigas*) is composed principally of willows (*Salix* spp.) throughout the year (Risenhoover 1989; Van Ballenberghe et al. 1989; Miquelle et al. 1992; Van Ballenberghe 1993; Bowyer et al. 1998, 1999). Furthermore, diameter of twigs available to moose for consumption may be a crucial aspect of diet selection by this large browser (Vivas et al. 1991, Bowyer and Bowyer 1997).

Most of the nutrients used by moose are contained in the surface of woody twigs, with hard-to-digest carbohydrates (cellulose and hemicellulose) composing the core (Schwartz and Renecker 1998). Therefore, as twig diameter of browse increases (e.g., the diameter at the point of browsing), the ratio of surface nutrients to the core declines, as does the nutritional value of such forage for moose (Hjeljord et al. 1982, Schwartz and Renecker 1998). In winter, adult moose eat forage that contains levels of crude protein below maintenance, and dry-matter intake necessary to meet nitrogen requirements is difficult to attain (Schwartz and Renecker 1998). Furthermore, the role that tannins play in forage selection is complex, and may affect foraging by herbivores (Zelter 1970, Reid et al. 1974, Bryant and Kuropat 1980, Kumar and Singh 1984, Leslie and Starkey 1987, Robbins et al. 1987, Bryant et al.1991, Jantheikki 1996). For instance, leaders of new growth in birch (*Betula* sp.) were heavily defended by secondary compounds, which altered foraging behavior by snowshoe hares (*Lepus americanus*; Bryant et al. 1994).

During winter, moose may be protein as well as energy limited; hence, forage selection should favor young twigs with smaller diameters. Moose eat twigs older than first-year growth, but data on the nutritive value of those older twigs are sparse (Cowan et al. 1950). Indeed, diet quality for herbivores likely involves a preference for species of plants, as well as specific parts of plants (Janzen 1979).

There is increasing evidence that moose play a fundamental role in the structure and function of boreal ecosystems (Pastor and Naiman 1992, Molvar et al. 1993, Bowyer et al. 1997, Kie et al. in press); however, much remains to be learned about their foraging ecology. Gaining insights into why moose forage on a particular plant or select specific twigs, or diameters of twigs, from that plant is critical to understanding the mechanisms controlling foraging behavior.

We tested for differences in forage quality as affected by diameter of twigs, age of twigs, site, tannin content, and their interactions. We also examined the digestible energy content (DE) of twigs, and tested for differences between age of twigs and diameter. We hypothesized that larger twigs would have a lower nitrogen content, be less digestible, have more fiber, and have a lower tannin content than smaller twigs. Likewise, we also predicted that older twigs would have lower nitrogen content, be less digestible, have more fiber, and possess lower tannin content than younger twigs. Furthermore, we hypothesized that dietary energy and protein would change with size and age of browse, and that small changes in browse chemistry might alter availability of protein and energy for moose.

STUDY AREA

We sampled twigs of willow (*Salix barclayi*) at an elevation of 275 m along a roadside located on the Kenai Peninsula, near Ninilchik, Alaska, USA, (60° N, 149° W) during winter 1999-2000. The Kenai Peninsula is characterized by a maritime climate influenced by its proximity to the Pacific Ocean (Weixelman et al. 1998). Annual precipitation ranges from 40 to 50 cm with much of that occurring as snow in winter and rain in spring or autumn (Schwartz and Franzmann 1991). Annual snowfall ranges from

140 to 165 cm (Oldemeyer and Regelin 1987). The mean annual temperature is 1° C, and ranges from – 30 to 21° C (Schwartz and Franzmann 1991).

We began sampling in early December after willows had become dormant and had lost their leaves. Moose migrated from higher elevations across out study site to lower-elevation valleys as winter snowfall accumulated. Thus, much of the willow in this area was unbrowsed, or only lightly browsed. Sampling was completed in late February, and samples were stored between 0 and -25° C until analyzed.

Our study area was a plateau along the sides of an unpaved road that ran east from Ninilchik for approximately 21 km. The roadside was surrounded by boreal forest dominated by white spruce (*Picea glauca*). Willows ranged in size from 1-3 m in height. Our sampling site was adjacent to the road (3-20 m from the snowburm) 16 km from Ninilchik. There was no overstory cover, and patches of dense growth of willows characterized the understory. Shading affects nutritional quality of willows (Hjeljord et al. 1990, Bø and Hjeljord 1991, Molvar et al. 1993); however, the willows we selected were shaded only slightly by a few trees, thereby minimizing that complication. Likewise, this area exhibited little variation in slope, or exposure. Finally, easy access allowed us to sample large quantities of willow in a relatively small area.

METHODS

We sampled an area along a roadside approximately 155 m long that included 5 distinct patches of willows located 15–80 m apart. All stems with abundant twigs (>15 leaders) were cut from the plant at snow level, labeled, and transported to the laboratory for subsequent analysis. Three stems (containing numerous leaders) from each of 5 sites were selected haphazardly for nutritional analyses; the remainder of the branches was withheld for a related experiment on feeding behavior of moose. Current annual growth (1-year-old), 2-year-old growth, and 3-year-old growth were measured with dial calipers to the nearest 0.1 mm at the bud scale scar, and pooled according to diameter and age classes. Twigs were categorized according to diameter: small (0.8 to 2.9 mm) and large (3.0 to 4.9 mm). This classification was based on previous studies of twig selection by foraging moose (Molvar and Bowyer 1994, Bowyer and Bowyer 1997, Stephenson et al. 1998, Weixelman et al. 1998), and availability of diameter and age classes of twigs available to us for sampling.

Samples of twigs from each site were pooled for each age class and diameter category, oven dried to constant mass at 55° C, and then ground with a Wiley mill (1-mm screen). All nutrients were assayed on the basis of dry mass (DM). In vitro dry matter digestibility (IVDMD; Tilley and Terry 1963) was determined for each sample. Fresh rumen inoculum for the digestion trial was obtained from 1 captive reindeer (*Rangifer tarandus*) that was fistulated, and held at the Robert G. White Large Animal Research Station of the University of Alaska Fairbanks (UAF). We conditioned the reindeer to a diet of willow by adding a mixture of approximately 12 g ground willow and 500 ml water directly into the rumen (via canula) every 2-3 days for 18 days. The Forage Quality Analysis Laboratory at UAF performed IVDMD, nutrient analyses, and tannin assays, with duplicates for selected samples. Detergent analysis (Van Soest et al. 1991) was used to determine structural composition of plant cells (percentage dry weight of neutral-detergent fiber [NDF], acid detergent fiber [ADF]), ash of acid extracted fiber and lignin. Fiber fractions were used to derive estimates of cell contents (DM-NDF), hemicellulose (NDF-ADF) and cellulose (ADF-lignin). Nitrogen was determined with an elemental analyzer (Model # CNS 2000, Leco, St. Joseph, MI) and expressed as crude protein based on the assumption of 6.25 g protein per g nitrogen (Robbins 1993). Soluble carbohydrates such as starch were estimated as the difference between cell contents and crude protein, with the assumption that lipid content of winter browse was negligible (Robbins 1993).

Tannins were extracted in ethanol (50% v/v) at 95° C, and assayed by the method of Folin-Dennis (Martin and Martin 1982) to determine the tannin content of willow samples. Differences in nutritional quality of twigs from age classes and diameter categories were compared with multivariate analysis of variance (MANOVA), with measures of forage quality as dependent variables, and age and diameter of twigs, and their interactions as main effects.

Gross energy available in twigs was calculated with caloric values for protein (24.89 kJ/g), soluble carbohydrates (17.48 kJ/g), hemicellulose (17.82 kJ/g), and cellulose (17.49 kJ/g) from Blaxter (1989). Fractional digestibility of cell wall components (cellulose and hemicellulose) was calculated from IVDMD by assuming that DM of protein and soluble carbohydrate were 60% digestible. Digestible-energy content (DE) of twigs was estimated by combining gross energy and DM digestibilities of each fraction.

RESULTS

Overall, MANOVA revealed effects of site, twig age, and twig diameter on nitrogen content ($F_{9, 69} = 49.86$, $P < 0.0001$), IVDMD ($F_{9, 69} = 7.83$, $P < 0.0001$), and tannin concentration ($F_{9, 69} = 7.01$, $P < 0.0001$) of willows; no interactions occurred between site or twig characteristics ($P > 0.05$). No difference ($P = 0.45$) occurred for mean nitrogen content of willow twigs among sites (range of means = 5.9-6.2%). Nitrogen content of twigs differed for age classes ($P < 0.001$) and diameter categories ($P < 0.001$) of twigs, with older and larger-diameter twigs possessing lower nitrogen content than younger and smaller twigs (Fig. 1).

There was an effect ($P < 0.001$) of site on IVDMD of willow twigs (range of means = 44.1-47.2%). Likewise, IVDMD was affected by the diameter of twigs, with larger twigs having lower IVDMD than smaller twigs (Fig. 1). Age of twigs, however, was not related to IVDMD (Fig. 1). Little overlap occurred in values when we compared cellulose and IVDMD between large and small diameter twigs (Fig. 2). Conversely, considerable overlap occurred between ages of twigs when cellulose was examined in relation to IVDMD (Fig. 2). These results confirm that cellulose in the core of stems strongly affected IVDMD. Additional measures of forage quality followed a similar pattern with significant differences occurring among age classes and diameter categories of willow twigs, except for ash, which differed neither in age nor diameter, and lignin, which did not vary with age (Table 1).

Variation in mean tannin concentration of willow twigs among sites ranged from 167.30 mg/g to 209.32 mg/g. Similarly, tannin content ($\overline{X}$±SD) varied between ages of twigs (1-year-old = 185.4±41.63 mg/g; 2-years-old = 206.4±42.86 mg/g; 3-year-old = 204.8±41.31 mg/g); 1-year-old twigs had less tannin than 2 or 3 year-old twigs (P = 0.04). Diameters of twigs, however, did not affect tannin content ($\overline{X}$±SD): small diameter = 199.3±40.85 mg/g; large diameter = 192.7±45.15 mg/g ($P = 0.48$).

Estimated gross energy of protein and carbohydrates was similar among all groups and ranged from 13.65 to 15.09 kJ/g. Digestible energy content (DE); however, differed with sites ($P < 0.001$, range of means = 6.99 kJ/g to 7.65 kJ/g), age ($P < 0.001$, range of means = 7.06 kJ/g to 7.54 kJ/g), and diameter ($P < 0.001$, range of means = 7.12 kJ/g to 7.60 kJ/g).

DISCUSSION

Our results indicated that forage quality of willow twigs in winter varied on a relatively fine spatial scale, especially IVDMD, tannin concentration, and estimated digestible energy. The cause of that variation, however, is uncertain, but cannot be attributed to previous browsing, aspect, or shading, which were similar among sites. Other factors related to plant growth (Chapin et al. 1995) that we could not assess, such as temperature, soil nutrients, and soil moisture, may have been responsible for those differences in quality of twigs.

Older twigs of willow had lower nitrogen content than younger twigs. Larger-diameter twigs of willow also had lower nitrogen content than smaller twigs. Protein availability probably declines with absolute content of nitrogen and with tannin concentrations as parts of plants age, for both diameter categories. Similarly, larger-diameter twigs were less digestible; however, age of twigs did not affect IVDMD. Although age of the twig was more influential in determining nitrogen content, structural components of the twig to support growth (twig diameter) were more important in affecting IVDMD (Fig. 1), as revealed in the relation between IVDMD and cellulose (Fig. 2). Although some differences in quality of twigs relative to age and diameter were not large (Fig. 1), such differences may be of importance to foraging herbivores as nutrients are accumulated over time (White 1983).

Importance of winter forage for moose should be viewed in a broad perspective (Weixelman et al. 1998); several factors likely relate to foraging behavior. The browse moose consume in winter is composed largely of willow twigs that have a low content of crude protein (5-7%), which will not meet maintenance requirements (Schwartz 1992), or fully support reproduction (Schwartz et al. 1988). Northern ungulates are in a negative energy balance during winter, and foraging activities principally slow the rate of loss of body reserves (Mautz 1978, Barboza and Bowyer 2001). Some losses of body reserves, however, may be physiologically regulated, because moose voluntarily reduce their metabolic rate and food intake during winter to conserve energy (Schwartz et al. 1988). If nitrogen levels are below maintenance requirements, then IVDMD may become increasingly important for survival of moose in winter.

Shorter retention times in the rumen are correlated with higher-quality diets and longer retention times with lower-quality forage (Schwartz et al. 1988). Rumen microbes ferment soluble sugars and cell solubles rapidly; however, cell walls require much longer to process (Spalinger 2000, Russell and Rychlik 2001). Lignin content also reduces digestibility of forages, as can tannins and other plant secondary compounds (Bryant et al. 1991, 1992).

Secondary plant compounds (i.e., tannins) may play a role in food choice, because browsing vertebrates avoid consuming plant tissues that contain high concentrations of secondary metabolites (Bryant and Kuropat 1980, Palo et al. 1985). Furthermore, tannins are thought to negatively effect digestibility of browse for moose during winter (Bryant and Kuropat 1980, Palo et al. 1985). Estimations of digestibility of woody forage, however, may not need to be adjusted for tannins, because there may be some benefits to ruminants from tannins (Zelter 1970, Kumar and Singh 1984, Leslie and Starkey 1987, Hagerman and Robbins 1993). Reid et al. (1974) postulated that the presence of tannins provided partial protection of proteins from degradation in the rumen, thereby enhancing assimilation of nitrogen. Moreover, Robbins et al. (1987) suggested that reduction of protein digestion caused by tannins may not result from gastrointestinal adaptations, but may be because of the small amounts of tannins in winter browse. The saliva of moose contains large amounts of proline-rich proteins, which may bind tannins and thereby reduce their effects on moose (Hagerman and Robbins 1993, Jantheikki 1996). Furthermore, many of the tannins in willow are linear-condensed tannins that moose bind well, in contrast to other tannins in lower-quality foods, that moose saliva does not bind (Barry and McNabb 1999).

Weixelman et al. (1998) suggested that reduced food availability, quality, and digestibility, combined with the increased energetic costs of foraging during severe weather, should force animals to maximize caloric return per unit energy expended. In addition, there may be twigs that are too small, or too widely dispersed to provide sufficient nutritional value for moose. Relationships between forage digestibility, retention time in the rumen, and rate of intake (Owen-Smith 1982, Van Soest et al. 1991), indicates digestibility is likely to be an important factor in forage selection by ruminants. Those relationships probably affect the size of a bite for moose foraging in winter, because larger bites have poorer nutritional quality (Schwartz et al. 1988). Likewise, risk of predation also may be an important influence on forage selection and size of bites taken by moose (Edwards 1983, Molvar and Bowyer 1994, Weixelman et al. 1998).

There also may be effects of sex on foraging behavior. Male Alaskan moose weigh about 40% more than females (Schwartz et al. 1987), and males likely take a larger bite than females (Miquelle et al. 1992, Bowyer et al. 2001, Spaeth et al. 2001). This observation, combined with the hypothesis of Barboza and Bowyer (2000, 2001) concerning differences in forage-passage kinetics between male and female ruminants, indicate differences between the sexes also my play an important role in diet selection. Differences in foraging behavior of the sexes in relation to forage availability and plant architecture require further study.

Decreases in digestible-energy content of willow twigs with age and diameter reflect declining proportions of crude protein and cell contents as the matrix of the plant cell wall increases in concentration. Differences in digestible-energy content of twigs may be directly related to the food intake required in winter. Schwartz and Renecker (1998) calculated a daily intake of digestible energy in moose during November as 975 $kJ/kg^{0.75}$. Based on our calculations, consumption of 1-year-old twigs with small diameters would require a mean (±SD) daily intake of 124±9 gDM/kg$^{0.75}$ body mass, whereas intakes of 3-year-old twigs with large diameter subtend intakes that are 15% grater at 141±8 gDM/kg$^{0.75}$. That increment in digestive load would increase gut fill and influence passage rate. Changes in digestive function associated with energy demand may feedback on processes of forage selection at the level of plant and twig, and consequently affect foraging behavior of moose.

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Table 2.1. Forage quality (% dry mass) for 1-year-old, 2-year-old, and 3-year-old growth, and for small (0.08 – 2.9 mm) and large (3.0 – 4.9 mm) categories of twig diameter for Barclay willow, Kenai Peninsula, Alaska, USA, winter 1999-2000. Composites of 15-25 twigs were combined in each sample. Sample sizes for age and diameter categories were: 1-year-old, small ($n = 27$); 1-year-old, large ($n = 9$); 2-years-old, small ($n = 13$); 2-years-old, large ($n = 10$); 3-years-old, small ($n = 5$); and 3-years-old, large ($n = 15$).

	Age					
	1-year-old		2-years-old		3-years-old	
Variable[a]	$\overline{X}$	(SD)	$\overline{X}$	(SD)	$\overline{X}$	(SD)
Acid-detergent fiber						
Small	39.68	(2.44)	40.60	(2.37)	42.33	(2.24)
Large	32.39	(2.78)	42.60	(3.37)	44.54	(3.00)
Neutral-detergent fiber						
Small	47.98	(2.93)	49.97	(2.16)	52.97	(2.24)
Large	53.54	(3.39)	54.81	(3.98)	55.82	(3.33)
Ash of acid extracted fiber						
Small	0.35	(0.12)	0.30	(0.08)	0.33	(0.05)
Large	0.31	(0.11)	0.30	(0.09)	0.31	(0.09)

Derived lignin				
	Small	21.64 (1.57)	21.47 (1.98)	20.89 (1.06)
	Large	19.28 (2.01)	18.09 (1.03)	19.56 (1.73)
Derived hemicellulose				
	Small	8.31 (1.01)	9.37 (0.67)	10.64 (0.24)
	Large	11.15 (1.16)	12.21 (0.60)	11.28 (0.73)
Derived cellulose				
	Small	17.68 (1.62)	18.83 (1.05)	21.02 (1.89)
	Large	22.79 (2.69)	24.22 (2.79)	24.67 (2.40)

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[a] MANOVA indicated that significant differences in forage quality occurred among different age classes and diameter categories ($P < 0.01$) for all variables, except for ash of acid extracted fiber (age: $P = 0.56$; diameter: $P = 0.15$) and derived lignin (age: $P = 0.27$).

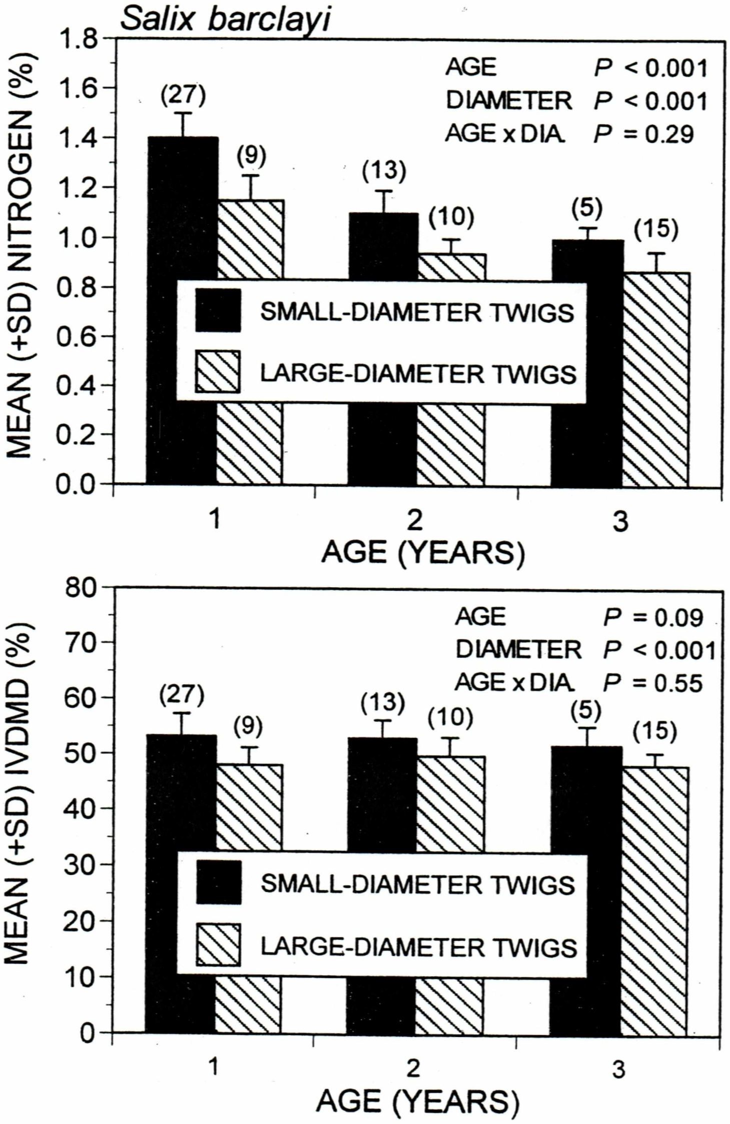

Fig. 2.1. Nitrogen content (top) and in vitro dry matter digestibility (bottom) of small-diameter and large-diameter stems in relation to age of Barclay willow (*Salix barclayi*), Kenai Peninsula, Alaska, USA, winter 1999-2000.

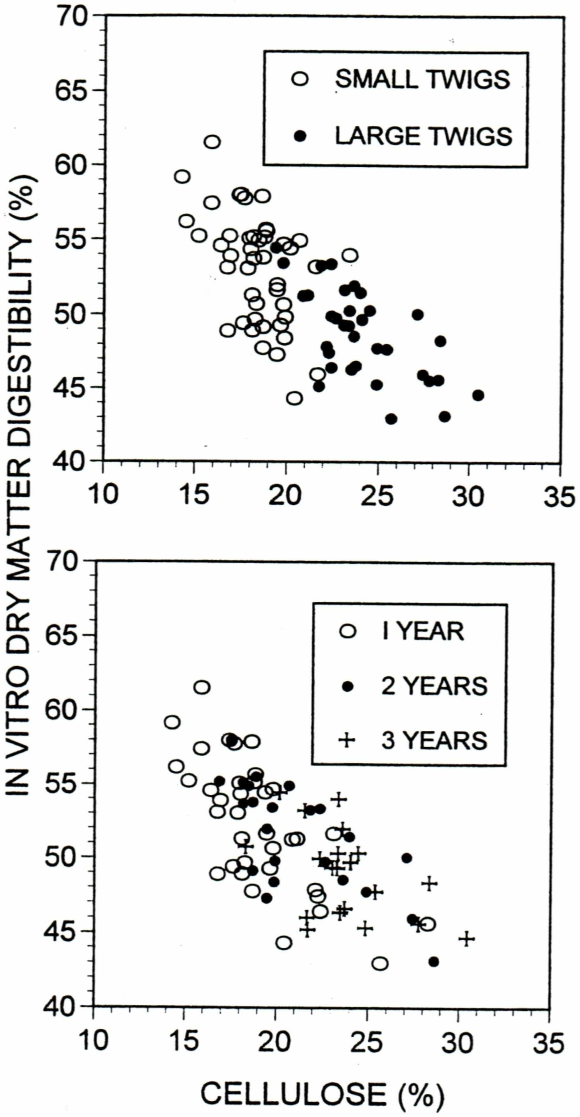

Fig. 2.2. In vitro dry matter digestibility and cellulose content of small-diameter (0.8 – 2.9 mm) and large diameter (3.0 – 4.9 mm) stems (top), and of age (bottom), of Barclay willow (*Salix barclayi*), Kenai Peninsula, Alaska, USA, winter 1999-2000.

[1]CHAPTER 3.

SEXUAL SEGREGATION IN MOOSE: AN EXPERIMENTAL TEST OF FORAGING BEHAVIOR

ABSTRACT

We studied Alaskan moose (*Alces alces gigas*) to test the hypothesis that sexual segregation among polygynous ruminants was the result of competitive exclusion of males by females. We first examined differences in foraging behavior between sexes, and then tested whether foraging by females influenced subsequent browsing by males. All experiments used captive moose at the Kenai Moose Research Center, Alaska, during winter 1999-2000. Twig diameters of willows (*Salix barclayi)* affected bite sizes taken by foraging moose, independent of sex, when that relationship was examined with respect to absolute or relative sizes of bites. Moose overcompensated when feeding on smaller twigs compared with larger ones, ostensibly to adjust for lower nutritional returns in smaller twigs of current annual growth. We modeled intake rate of moose browsing on willow with multiple-linear regression. The best model included sex, mass of moose, and density of twigs; shape of willows did not enter that model. Females had higher bite rates and rates of forage intake than males, and took generally smaller but variable bites. Thus, differences in foraging behavior between sexes may relate to sexual dimorphism and

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[1] Spaeth, D. F., R. T. Bowyer, T. R. Stephenson, and P. S. Barboza. In review. Sexual segregation in moose: an experimental test of foraging behavior. Journal of Mammalogy.

ultimately spatial segregation of sexes. No difference, however, occurred in rate of intake between sexes rebrowsing willows, which resulted in our rejecting the hypothesis that selective foraging by females could lead to competitive exclusion of males.

Key words: Alaska, *Alces alces*, competitive exclusion, feeding behavior, foraging, moose, *Salix barclayi*, sexual segregation, willow

INTRODUCTION

Differential use of space by males and females occurs among numerous organisms (Bowers and Smith 1979; Freeman et al. 1976; Storer 1966), including ruminants (Bowyer 1984; Bowyer et al. 1996; Clutton-Brock et al. 1987; Kie and Bowyer 1999; McCullough et al. 1989). Further, resource partitioning between sexes of the same species has been postulated to result from intersexual competition (Clutton-Brock et al. 1987; Darwin 1871; Main and Coblentz 1996) related to body size and other morphological differences (Barboza and Bowyer 2000, 2001; Jenks et al. 1994; McCullough 1979). Polygynous ruminants are among the most sexually dimorphic mammals (Loison et al. 1999; Ralls 1977; Weckerly 1998), and many of those dimorphic species segregate according to sex when not engaged in mating activities (Bleich et al. 1997; du Toit 1995; Main et al. 1996; Miquelle et al. 1992).

Understanding why sexes of polygynous ungulates segregate is important for understanding and predicting their distribution, habitat selection, and resource requirements related to reproduction and growth (Schwartz and Hundertmark 1993). Indeed, Kie and Bowyer (1999) and Bowyer et al. (2001) suggested that the sexes of dimorphic ruminants exhibited such differences in distribution, habitat selection, and diet that they should be managed as if they were separate species.

Although sexual segregation is widespread among polygynous ruminants, causes of that phenomenon continue to be debated (Barboza and Bowyer 2000, 2001; Bleich et al. 1997; Main et al. 1996; Miquelle et al. 1992 for reviews). One prominent hypothesis maintains that sexual segregation is driven by differences in feeding behavior, which leads to competition, and ultimately results in spatial separation of sexes via competitive exclusion of males by females (Clutton-Brock et al. 1987; Illius and Gordon 1987, 1992; Main and Coblentz 1996).

Clutton-Brock et al. (1987) proposed that female red deer (*Cervus elaphus*) competitively excluded males from mutually preferred areas. In that study, females foraged more selectively than males and were postulated to be more tolerant of low biomass of plants. Likewise, Main and Coblentz (1996) suggested that female mule deer (*Odocoileus hemionus*), feeding mostly on forbs, competitively excluded males. Illius and Gordon (1987) postulated that differential scaling of incisor breadth and metabolic requirements with body mass might be a cause of spatial segregation in grazing ungulates. Spaeth et al. (2001) also noted differences in incisor breadth between sexes of a large browser, the Alaskan moose (*Alces alces gigas*). Weckerly (1993), however, failed to obtain supportive evidence for aspects of that hypothesis (e.g., differences in incisor breadth) between sexes of black-tailed deer (*O. h. columbianus*).

Further study of sexual segregation in ruminants is necessary to fully understand that widespread behavior. Alaskan moose lend themselves well to studying sexual segregation because they are highly sexually dimorphic (Bowyer et al. 1997, Schwartz et al. 1987; Spaeth et al. 2001), select habitats differently (Bowyer et al. 2001a; Miller and Litviatis 1992), and remain spatially separated for much of the year (Miquelle et al. 1992).

We examined differences in characteristics of twigs and architecture of willows on foraging behavior by sexes of adult moose. We predicted that if female moose competitively exclude males from mutually preferred forages, they would do so by feeding more efficiently than males. Thus, we tested whether browsing by females reduced the foraging efficiency (i.e., intake rate) of males more than it did for other females.

MATERIALS AND METHODS

S*tudy area.*—The Moose Research Center, a facility operated by the Alaska Department of Fish and Game, was located on the Kenai Peninsula (61° N, 151° W), ca. 65 km northeast of Soldotna in southcentral Alaska. The facility consisted of 4, 2.6-km^2 enclosures constructed of 24 km of woven-wire fence, 2.4 m in height. In addition, the facility included 5 small enclosures (1-6 ha), holding pens, and a scale house for weighing moose. Three adult female moose and 3 adult male moose, which had been accustomed to handling by researchers, were used in feeding experiments. Moose were 5-8 years of age, with substantial overlap between males (5, 7, and 8 yrs) and females (5, 6, and 7 yrs).

Annual precipitation on the Kenai Peninsula ranged from 40 to 50 cm with most falling as snow in winter and rain in spring or autumn (Schwartz and Franzmann 1991).

Annual snowfall ranged from 140 to 165 cm (Oldemeyer and Regelin 1987). Temperatures were moderated by the influence of the Pacific Ocean. The mean annual temperature was 1°C, and ranged from –30 to 21°C (Schwartz and Franzmann 1991).

Sampling procedures.—We immobilized captive moose at close range (ca. 15 m) with projectile syringes filled with a mixture of carfentanil (2-3 mg) and xylazine (150 mg), propelled by a CO_2 pistol. Following immobilization, we measured nutrient reserves (e.g., rump fat) by ultrasonography to determine the physical condition of moose used in feeding trials (Stephenson et al. 1993, 1998). We determined maximum thickness of rump fat, and whether moose were pregnant via ultrasonography (Keech et al. 1998, 2000; Stephenson et al. 1993, 1998), using an Aloka model 500 portable ultrasound device (Aloka, Inc., Wallingford, Connecticut). We also measured incisor morphology (breadth) of immobilized moose using methods described by Spaeth et al. (2001). At completion of handling, immobilization was reversed with an intramuscular injection of 200-300 mg naltrexone and 400 mg tolazoline. No mortalities occurred. Our project was approved by the Institution Animal Care and Use Committee at the University of Alaska Fairbanks, and was in compliance with procedures adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Willows, which were of similar size, age, and structure, were cut from nearby forests on the Kenai Peninsula (Spaeth et al. 2002) for establishing diameter-mass and length-mass regressions, and for use in feeding trials. Willows exhibited little evidence of browsing; thus, differential regrowth of twigs from previous browsing (Bowyer and Bowyer 1997; Molvar et al. 1993) had no effect on our experiments. We haphazardly cut a sample of those willows, measured all current annual growth at the bud scale scar, dried them in an oven at 55°C, and weighed current annual growth, to obtain diameter-mass and length-mass regressions (Bowyer and Bowyer 1997; Bowyer et al. 2001a; Telfer 1969; Weixelman et al. 1998). We measured the following traits of willows used for browsing trials: number of leaders of current annual growth; diameters of leaders of current annual growth at their bud scale scars; and mass of the intact shrub.

We calculated the relative change in bite size (RCBS) in relation to the diameter of willow twigs at the bud scale scar by: RCBS = mean bite size - mean twig diameter at the bud scale scar/mean twig diameter at the bud scale scar. That value was positive if moose took more second-year growth relative to the size of the bud scale scar in a bite, zero if the bite was at the bud scale scar, and negative if the bite diameter was less than that at the bud scale scar (i.e., the moose consumed only current annual growth). In addition to simple linear regression, we used principle-axis regression (Sokal and Rholf 1969) to analyze the relation of diameter of twigs at point of browsing (bite size) and the derived variable, relative bite size. Hence, we controlled for a lack of independence between independent and dependent variables in assessing that relationship (i.e., both independent and dependent variables included twig diameter).

We used weighted regression analysis (Neter et al. 1996) to examine effects of body mass of moose on intake rate, bite rate, mass consumed, and bite size for twigs of willow eaten during feeding trials, because multiple trials were conducted with individuals, each of which had a similar body mass for trials. Accordingly, in those analyses, we weighted each individual moose by the inverse of the variance in intake rate, bite rate, or mass of willow consumed.

Prior to feeding trials, moose were fed a pelleted ration (Schwartz et al. 1985) ad libitum, and had access to birch (*Betula*), aspen (*Populus*), and willow (*Salix*) that we added to their large enclosure (6 ha). Willows are preferred forage of Alaskan moose (Bowyer and Bowyer 1997; Molvar et al. 1993; Weixelman et al. 1998, Van Ballenberghe et al. 1989). Moose at the research center, however, had limited access to willows in their large enclosure, and ate those shrubs ravenously when available. Consequently, we offered willows to moose immediately prior to each experimental trial; those willows were weighed before and after moose fed upon them. Feeding of pre-trial willows successfully moderated feeding rate by moose, and reduced aggression of moose towards investigators when willows were removed forcibly from pens following trials. Mean (±95% *CI*) mass of pre-trial willows consumed by the sexes of moose was similar at moderate (males = 220.0±59.6 g, $n = 9$; females = 227.0±34.4 g, $n = 27$) and high (males = 191.1±38.8 g, $n = 9$; females = 219.6±26.7 g, $n = 27$) levels of browsing intensity.

Willows were measured and then wired to a post located within a holding pen (ca 3 by 15 m). Moose were randomly selected and allowed to enter the pen and browse on the willows until moderate (22-50%), or high (51-78%) use of twigs was obtained. Time spent feeding and number of bites was recorded for each moose. Post-feeding measurements of diameter at point of browsing and percentage of leaders browsed were determined for willows, and biomass removed was obtained by weighing shrubs at the beginning and end of each feeding trial. Similar levels of browsing intensity on willows have been reported in studies of free-ranging Alaskan moose (Bowyer and Bowyer 1997; Bowyer et al. 2001a; Molvar et al. 1993; Weixelman et al. 1998).

Willows browsed by female moose then were offered to a male moose. In a similar manner, other willows browsed by females also were presented to other females. This procedure was repeated at 2 levels of browsing intensity (moderate and high). The experiment was terminated when most (ca. 95%) current annual growth had been removed. That removal of browse required a mean (±*SE*) of 128±8.7 sec for both sexes. Allowing moose to eat more leaders of growth than at high intensities of browsing would not have provided a realistic test of foraging behavior for free-ranging moose because, under these experimental conditions, even large branches of each plant would have been stripped of bark or consumed entirely.

We assessed architecture of willows used in foraging experiments by placing a 1-m^2 grid with 100 cells, (each 10 by 10 cm), directly above each willow. We visually estimated the top 85% of willow twigs (current annual growth), counted total number of twigs, and number of twigs per cell (density). We calculated the *CV* of twig density (an index to the distribution of twigs across the sampling grid), and the proportion of cells that contained ≥1 twig. We assessed reliability of that count of twigs in the upper 85% of a willow by counting the total number of twigs on a willow in relation to the total twigs we counted in the cells on the grid. That value ($\overline{X}$ = 77%, *SE* = 2.0%) was somewhat lower than our initial estimate of 85%, but provided a relatively consistent measure of forage available to feeding moose.

We also calculated 2 rastor-based indices of shape for willows offered to moose during foraging experiments, both based on perimeter (p_{ij}) to area (a_{ij}) ratios (McGarigal and Marks 1995). The shape index (SI) was defined as: SI = $0.25p_{ij}/\sqrt{a_{ij}}$. A shape index of 1 was a square, and increased as the shape became more irregular. The fractal dimension (FD) was calculated as: FD = $2\ln(0.25p_{ij})/\ln a_{ij}$. Fractal dimensions near 1 had simple perimeters, such as circles or squares; the fractal dimension approached 2 for highly convoluted shapes. Both indices included empty spaces (i.e., cells without twigs) within the perimeter of a willow in their calculation (McGarigal and Marks 1995).

We used multiple regression analysis to evaluate effects of willow characteristics on foraging behavior by moose. We controlled for multicollinearity in multiple regressions by eliminating 1 of any pair of independent variables with the absolute value of $r \geq 0.6$. We also examined final regression models for variance inflation factors (VIF) of independent variables. Values of VIF <10 were considered acceptable (Neter et al. 1996). We used a step-wise procedure for model selection (α to enter and remain = 0.15), and evaluated resulting models with adjusted multiple coefficients of determination (R^2_{adj}), Mallows *Cp* statistic, and Akaike information criteria (AIC; SAS Institute 1987).

To determine which bites were from a moose that initially browsed a particular willow, and which were from moose that rebrowsed that willow, we used blue food coloring to mark twigs eaten by the initial moose. Consequently, we evaluated whether food coloring placed on willow twigs influenced browsing by moose. We clipped willows to simulate browsing, removing current annual growth, for twig diameters ranging from 2 to 4 mm. We applied blue food coloring to the exposed surfaces of approximately one-half of those twigs remaining on the shrub. We then offered willows to adult moose for consumption. Willows were withdrawn from moose when most ($\overline{X}$ = 72%, *SE* = 0.05%, range = 42-100%) twigs had been eaten. We counted number of marked twigs that remained, and determined number of remaining marked twigs that would be expected, based on no effect on browsing from coloring twigs. We replicated that experiment 13 times using 2 adult male and 1 adult female moose, and used a chi-squared test for goodness-of-fit (Sokal and Rholf 1969) to determine if food coloring affected twig selection by moose. Mean proportion (±*SE*) of twigs marked before consumption by moose was 47.8±0.02%, and mean proportion of marked twigs remaining after browsing was 35.4±0.06%. There was no effect of food coloring on twig selection by moose ($\chi^2 = 3.16$, $P > 0.9$).

The experimental design to assess rebrowsing of willows involved pairings of 3 adult male and 3 adult female moose, which included female-male (i.e., females foraging prior to males), and female-female combinations, by 2 levels of browsing intensity (moderate and high), with 3 replications each, for a total of 72 feeding trials. We analyzed data on rebrowsing of willows by sexes of moose with multivariate analysis of covariance (MANCOVA; Johnson and Wichern 1982), with diameter of willows at the bud scale scar as a covariate. We also included the individual identity of moose rebrowsing a particular willow (a coded variable), which controlled for differences in body mass, fat stores, size of incisor arcades, and other individual differences that might influence foraging behavior. Sex, level of browsing intensity (moderate or high), and their interaction were main effects in that statistical model.

RESULTS

Overall, 3 adult male moose (504, 534, and 602 kg) were larger than 3 adult females (429, 504, and 549 kg), although overlap in body mass occurred. Mean body condition (as indexed by maximum thickness of rump fat) was 0.93 cm (95% *CI* = 0.5 cm) for males, and 5.26 cm (95% *CI* = 2.8 cm) for females. Males had low rump fat at the start of our experiment in mid-December because of strenuous rutting activities during autumn, but re-feeding following rut likely resulted in gains in rump fat for the 3 males (3.7, 4.2, and 0.5 cm) by mid-April. Females exhibited variability in rump fat over the course of the experiment, with 1 female gaining (0.2 cm) and the other 2 loosing (1.0, and 1.3 cm) fat. Ultrasonography indicated that all females likely conceived, and were pregnant during the feeding experiments, which occurred prior to the last one-third of gestation; 1 female, however, did not give birth the following spring. Mean breadth of the incisor arcade was 60.1 mm (47.5, 65.8, and 66.9 mm) for males, and 67.8 mm (64.9, 67.8, and 70.7 mm) for females. Males had smaller and more variable arcades because 1 male had 3 outer teeth (both outer canines and 1 incisor) lacking on his lower jaw.

Strong curvilinear relationships existed between dry mass of willow twigs and their length and diameter available to moose for browsing (Fig. 1). As diameter and length of willow twigs increased, dry mass of current annual growth increased exponentially (Fig. 1). Thus, twig diameter and length reliably predicted mass of current annual growth.

Twig size of current annual growth (as indexed by diameter of twig at bud scale scar; Fig. 1) affected the size of bites taken by foraging moose, independent of sex (test of slopes; $P > 0.05$), when that relationship was examined with respect to absolute (Fig. 2a) and relative size of bites (Fig. 2b). Moose overcompensated (i.e., took disproportionately larger bites) when feeding on smaller twigs of new growth compared with larger ones (Fig. 2b). Twig diameter at the bud scale scar was not completely independent of relative change in bite size of moose in this analysis (Fig. 2b), because the independent variable was used in calculating the dependent variable. Consequently, we also analyzed that relationship (Fig. 2b) using principle-axis regression, which confirmed that our analysis from simple linear regression was valid (93% variation explained).

Body mass was critical to understanding bite rate, bite size, and forage intake by moose. Weighted-regression analysis indicated that bite rate (bites/min) was positively related to body mass (kg) of moose ($Y = 1.477 + 0.030x$). Nonetheless, variability in bite rate was high ($r^2 = 0.054$) and that relationship was marginally not significant ($P = 0.09$). Body mass (kg), however, did predict bite size (mm) by moose ($Y = 5.032 – 0.470x$, $r^2 = 0.23$, $P = 0.03$). Weighted regression also revealed positive relationships between body mass (kg) and intake rate (g/sec) for moose feeding on both unbrowsed willows ($Y = -1.133 + 0.005x$, $r^2 = 0.15$, $P = 0.02$), and previously browsed willows ($Y = -0.931 + 0.003x$, $r^2 = 0.20$, $P = 0.004$). Intake rate of willow for the male with missing teeth ($\overline{X} = 0.37$ g/sec, 95% $CI = 0.29$-0.45 g/sec) overlapped that of other males ($\overline{X} = 0.57$ g/sec, 95% $CI = 0.39$-0.75 g/sec) and, consequently, did not bias our results markedly.

Prior to further modeling forage intake by moose, we controlled for multicollinearity by withholding the shape index for willows from multiple-regression analysis; that variable was strongly correlated with fractal dimension of a plant($r = 0.97$). Likewise, we eliminated total number of twigs, which was collinear with both density of twigs ($r = 0.64$), and diameter of twigs at their bud scale scars ($r = -0.65$). In addition, we excluded proportion of cells in the grid containing willow twigs because that variable was related to twig density ($r = 0.68$). We then modeled intake rate for moose browsing on willow (Table 1). The best model included sex of moose, their body mass, and density of willow twigs (Table 2); examination of residuals and variance inflation factors indicated the model was apt. Sex and mass of moose explained most variation, as revealed by values for partial r^2 (Table 2). No other variable entered that model ($P > 0.15$). Indeed, fractal dimension of a willow (i.e., an index to plant shape) likely did not enter the multiple regression ($P > 0.15$) because shape was inversely related to twig density ($r = -0.56$) and the total number of twigs ($r = -0.27$). Thus, effects of plant architecture on foraging behavior of moose were mediated mostly via density of twigs rather than plant shape per se. Even the *CV* of twig density, which indexed distribution of twigs across our sampling grid over a willow, did not influence intake rate by moose ($P > 0.15$).

The second component of our experimental design was to evaluate foraging behavior of moose feeding on previously browsed willows. Thus, we investigated rate of foraging (bites/min) for male and female moose consuming willows that had been browsed previously at moderate and high levels of intensity with ANCOVA. Diameter of twigs at the bud scale scar was the covariate in that analysis; incorporating individual identity of moose rebrowsing a particular willow controlled for differences in body mass, fat stores, size of incisor arcades, and other idiosyncrasies that might influence foraging behavior. The overall outcome was significant ($F_{7,\,28}$= 4.09, $P = 0.003$) and driven by sex of moose (P = 0.02), level of browsing intensity (P = 0.04), and identity of moose (P = 0.04), with a sex by level interaction ($P = 0.03$). Adjusted means (± *SE*) of bite rate for rebrowsing were increased at moderate (10.8±0.02 bites/min) compared with high (9.1±0.08 bites/min) levels of previous browsing intensity ($P < 0.0001$). Moderate levels of foraging intensity were similar for females (10.8±0.85 bites/min) and males (10.8±0.89 bites/min). Females (11.2±0.94 bites/min), however, foraged at a higher rate ($P < 0.0001$) than males (7.0±0.90 bites/min) at the high level of previous browsing intensity, indicating that females foraged less efficiently (experienced a greater handling time) than males at that level.

When we similarly controlled for diameter of twigs at the bud scale scar, and included identity of individual moose, ANCOVA also revealed effects on intake rate (g/sec) of willow, as determined by level of previous browsing (moderate or high), and individual identity of moose, but not sex of moose that rebrowsed willows (Fig. 3a). Analysis of covariance (ANCOVA) likewise indicated that total grams of willow removed was not significantly affected by sex of moose (Fig. 3b). Nonetheless, level of browsing (moderate or high) significantly affected that variable (Fig. 3b).

We also examined bite size (twig diameter at the point of browsing) of moose rebrowsing willows with the same statistical model we used for analyzing bite rate and forage intake. Adjusted means revealed few differences in bite size between moderate ($\overline{X}_{adj}$ = 4.2mm, 95% *CI* = 4.1-4.4 mm) and high ($\overline{X}_{adj}$ = 4.2 mm, 95% *CI* = 3.9-4.4 mm) levels of previous browsing intensity. Females ($\overline{X}_{adj}$ = 4.0, 95% *CI* = 3.4-4.3 mm) generally took smaller bites than did males ($\overline{X}_{adj}$ = 4.3, 95% *CI* = 4.0-4.5 mm), but there was overlap in 95% *CI.*

DISCUSSION

We used an hierarchical approach to examine effects of foraging behavior of moose on sexual segregation. First, we tested whether foraging behavior of the sexes differed, and how characteristics of animals (e.g., body mass and sex) and the willows they foraged upon (e.g., architecture, density, and size of twigs) affected consumption of willows. Second, we tested whether foraging by females influenced subsequent browsing by males more than for other females—an outcome necessary to postulate competitive exclusion of males by females as a causal mechanism for sexual segregation.

One outcome of our research was unexpected. The inverse relation between size of twigs available and relative size of bite taken (Fig. 2b) was counterintuitive, and indicated the size of bite obtained by a moose cannot be understood without considering the size of the twig available to feed upon. Moreover, amount of current annual growth helped determine how much second-year growth was taken in a bite; moose consumed relatively more second-year growth when available first-year growth was limited (Fig 2b). That outcome likely occurred because current annual growth of willows was higher in nitrogen content than second-year growth, but not higher in digestibility of dry matter (Spaeth et al. 2002). Digestible contents of protein and energy can influence diet selection by ruminants during winter (Barboza and Bowyer 2001; Parker et al. 1999). Consequently, moose overcompensated with larger bites when the opportunity for a high-quality (1 year old) bite was limited. Moose taking an optimum size of bite would have produced a relatively consistent bite size across diameters of available twigs, rather than the inverse relation documented in Figure 2a. Mouth morphology (Spaeth et al. 2001), along with other factors associated with oral processing (Shipley et al. 1994), and larger twigs possessing higher levels of tannins and lower digestibility (Spaeth et al. 2002) probably helped limit the upper size of a bite. The nutritional state of the animal also likely affected bite size; moose are known to bark strip and consume large stems when physiologically stressed (Bowyer et al. 1999a; Miquelle and Van Ballenberghe 1989; Telfer and Cairns 1978). Consequently, the idea that moose take some optimum size of bite (Vivas et al. 1991) can be rejected; the quality of the bite obtained and physical condition of moose likely are important factors regulating bite size.

Several authors (Bowyer et al. 2001a; Miquelle et al. 1992) suggested that male moose should take larger bites than did females, in part because of their larger incisor arcades (Spaeth et al. 2001). We observed generally larger bites by male than female moose rebrowsing willows, but considerable variation between sexes occurred. Body mass strongly influenced bite size by moose, and males used in our experiment probably had not reached maximal body mass (as heavy as 725 kg), which typically occurs at 8-10 years old (Schwartz 1987; Spaeth et al. 2001; Stewart et al. 2000). We caution that males larger than those we used in experiments might take larger bites than we reported. That potentiality, however, is unlikely to affect our test for differences in foraging between the sexes, because we corrected for body mass (by including the identity of individual moose) in those analyses.

We do not believe that the 3 missing teeth from the lower jaw of 1 male biased interpretation of our foraging experiments, because incisor breadth of that individual did not markedly affect his intake rate of forage. Moreover, the effect of that abnormality should have been to reduce foraging efficiency, yet we detected no difference between sexes in rate of forage intake. That result might have occurred because muzzle size may be as important as breadth of the incisor arcade in determining foraging behavior in ruminants (Pérez-Barbería and Gordon 1999).

A larger sampling scale (e.g., an area with multiple shrubs or even a landscape) might have yielded different results than we obtained (Bowyer et al. 1996, 2002; Kie et al. 2002). We believe, however, that the scale at which we sampled (i.e., the feeding site) was most appropriate for evaluating foraging behavior of moose, especially for the controlled experimental design necessary to obtain critical tests of precisely how moose foraged. Moreover, if females were able to competitively exclude males by feeding more selectively, the foraging site should best reflect those competitive interactions.

A longer temporal scale, which permitted additional foraging, might have altered our conclusions. Nonetheless, we allowed for moderate to high levels of browsing intensity where competitive effects on foraging behavior of males would have been manifested if competitive exclusion were likely. Levels of browsing intensity we obtained in our experiments were similar to values reported for free-ranging Alaskan moose foraging on willows (Bowyer and Bowyer 1997; Bowyer et al. 2001a; Molvar et al. 1993; Weixelman et al. 1998). Moreover, white-tailed deer (*Odocoileus virginianus*; Kie and Bowyer 1999) and red deer (Condrat et al. 1999) exhibited a greater degree of sexual segregation at moderate compared with high population densities. Thus, greater foraging intensity resulting from increased population density for those large herbivores would have occurred under circumstances where sexual segregation was reduced.

Allometric differences between dimorphic male and female ruminants likely results in differential nutrient requirements for the sexes, which in turn influences foraging behavior, and ultimately their spatial segregation (sensu Barboza and Bowyer 2000, 2001). Hence, the distribution of plants across the landscape (which we cannot address with our foraging experiments) and even plant architecture may affect sexual segregation in moose (Bowyer et al. 1997). Nonetheless, our analyses, which incorporated sophisticated metrics of plant shape, strongly indicated that the density of twigs on which to forage was more influential than plant shape in determining forage intake by moose. At least for the size and configuration of shrubs we sampled, shape of plants was comparatively unimportant. Moreover, differences in plant shape we measured were correlated with several variables that were related to the abundance of twigs on which to forage, with simpler shapes having denser twigs that resulted in higher foraging efficiencies. We contend that effects of plant shape on foraging efficiency are not independent of local availability of twigs, and should not be considered separately. Our willows, however, were initially unbrowsed, and leaders of current annual growth emerging from previously browsed twigs tend to be larger than for unbrowsed plants—moose selectively forage on those larger leaders (Bowyer and Bowyer 1997; Molvar et al. 1993). Whether such differences in plant architecture produced by regrowth from previously browsed stems would alter feeding behavior of moose remains to be tested.

Body mass and sex of moose, and density of willow twigs predicted rate of forage intake, with females exhibiting higher rates of forage acquisition than males at moderate and high levels of browsing intensity (Tables 1 and 2). Despite that result, browsing by females did not differentially effect subsequent browsing by males (Fig. 3). Indeed, females had a disproportional effect on bite rate of other females compared with males, especially at high levels of previous browsing intensity. Female-female competition exacerbated via high density is thought to be a primary constraint on reproductive performance in ungulates (McCullough 1979), including moose (Bowyer et al. 1999b). Differences in foraging behavior, however, still might reflect disparate nutrient requirements of sexes related to size dimorphism and differing life-history strategies, which may promote sexual segregation (Barboza and Bowyer 2000, 2001).

We acknowledge that other factors not included in our experiment influence foraging efficiency of moose and other large herbivores, including risk of predation and group size (Berger 1991; Bowyer et al. 1997, 2001b; Edwards 1983; Kie 1999; Molvar and Bowyer 1994; Weixelman et al. 1998). Nonetheless, our experimental approach to understanding sexual segregation is among the first of its kind for a large browser. Moreover, we do not foresee how a reduction in foraging efficiency by females in large groups, or those far from concealment cover (Molvar and Bowyer 1994), would lead to competitive exclusion of males. Increased foraging efficiency of females would be required to produce that result. Similarly, that females with young foraged less efficiently than males (Molvar and Bowyer 1994), does not offer a mechanism for competitive exclusion resulting in spatial separation of the sexes.

Experimental data addressing competition for large mammals are sparse (Kie and Bowyer 1999; McCullough 1979; Stewart et al. 2002); we believe our findings offer unique insights into mechanisms that likely underpin sexual segregation in ruminants. For instance, if feeding by females reduced foraging efficiency (i.e., intake rates) by males more than for other females, then the hypothesis that females have the ability to competitively exclude males would be supported. Conversely, if feeding by females failed to do so, then the competitive-exclusion hypothesis would be rejected. Our experiment clearly demonstrated that foraging by females did not adversely effect feeding by males more than for other females (Fig. 3), at least for the willow shrubs we evaluated. Indeed, previous foraging by females had a greater effect on other females than on males. Indeed, females took more bites to obtain an intake rate equivalent to that of males. Thus, females took slightly smaller bites, but had a greater handling time (bites/min) than did males. Even if the smaller bites obtained by females were of higher quality than larger bites of males, allometric differences between sexes may allow males to do as well as females on such diets (Barboza and Bowyer 2000, 2001).

When considered in concert with results from field research on free-ranging ruminants, our experimental study offers convincing evidence that competitive exclusion of males by females is not a compelling explanation for sexual segregation. Certainly, competitive exclusion of males by females was not operating where male bighorn sheep (*Ovis canadensis*) occupied higher-quality habitats than females (Bleich et al. 1997), or where segregation in lesser kudu (*Tragelaphus imberbis*) was less pronounced during the season when resources were most limiting and, in consequence, high levels of intersexual competition were expected (du Toit 1995). Likewise, Conradt et al. (1999) noted that higher densities of female red deer did not increase sexual segregation. Kie and Bowyer (1999) reported that an experimental increase in population density of white-tailed deer lead to a response that was antithetical to predictions of competitive exclusion—degree of segregation declined with increased population density. Consequently, we believe that competitive exclusion of males by females can be rejected as a general explanation for sexual segregation in ruminants, and recommend that future research be directed at more fruitful avenues of research, including risk of predation (Bleich et al. 1997) and differences between sexes in allometry and nutrient requirements(Barboza and Bowyer 2000, 2001).

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Table 3.1.—Variables available for stepwise multiple regression to explain intake rate by Alaskan moose (*Alces alces gigas*) as related to plant architecture of Barclay willow (*Salix barclayi*) on the Kenai Peninsula, Alaska, winter 1999-2000. Three adult male (18 trials) and 3 adult female (36 trials) foraged on 54 willows, at moderate (≤50% of current annual growth removed) and high (≥51% of current annual growth removed) levels of browsing intensity.

	Male ($n = 18$)		Female ($n = 36$)	
Variable	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Intake rate (g/sec)				
Moderate	1.09	0.23	1.28	0.15
High	0.97	0.25	1.17	0.12
Bite diameter (mm)				
Moderate	3.98	0.15	4.01	0.05
High	3.99	0.26	4.02	0.07
Twig diameter[a] (mm)				
Moderate	2.01	0.06	2.11	0.03
High	2.38	0.17	2.23	0.08
Proportion of cells[b]				
Moderate	0.42	0.02	0.37	0.03
High	0.31	0.04	0.34	0.02

Density (twigs/100 cm^2)				
Moderate	3.54	0.21	3.68	0.19
High	3.35	0.39	3.34	0.20
CV of twig density				
Moderate	59.8	2.26	62.3	1.50
High	63.7	2.29	62.5	1.63
Shape (index)[c]				
Moderate	1.52	0.07	1.47	0.05
High	1.42	0.06	1.60	0.10
Fractal (index)[d]				
Moderate	1.10	0.01	1.09	0.01
High	1.09	0.01	1.11	0.01
Total number of twigs				
Moderate	191.7	13.6	169.5	10.1
High	131.1	22.0	153.0	11.8

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[a] measured at the bud scale scar.

[b] number of cells with twigs/100 cells.

[c] calculated as: $0.25p_{ij}/\sqrt{a_{ij}}$, where p_{ij} = perimeter of a willow, and a_{ij} = area of a willow.

[d] calculated as: $2\ln(0.25p_{ij})/\ln a_{ij}$, where p_{ij} = perimeter of a willow, and a_{ij} = area of a willow.

Table 3.2.—Analysis of intake rate (g/sec) for adult male ($n = 3$, 18 trials) and adult female ($n = 3$, 36 trials) Alaskan moose (*Alces alces gigas*) foraging on Barclay willow (*Salix barclayi*) on the Kenai Peninsula, Alaska, winter 1999-2000. Mass (kg) was mean body weight for an individual over the course of the experiment. Density was the total number of twigs of current annual growth on the willow/m^2. Results are from stepwise multiple regressions ($\alpha = 0.15$ to enter and remain). Akaike Information Criteria (AIC) and Mallow's *Cp* statistic also indicated that this was the best model.

Variable[a]	Parameter	*F* value	*P value*	Partial r^2
Sex	-0.513	9.41	0.004	0.134
Mass	0.006	8.51	0.005	0.141
Density	0.133	2.32	0.134	0.032

[a] The overall model was significant ($R^2_{\text{adj}} = 0.238$, $P = 0.008$)

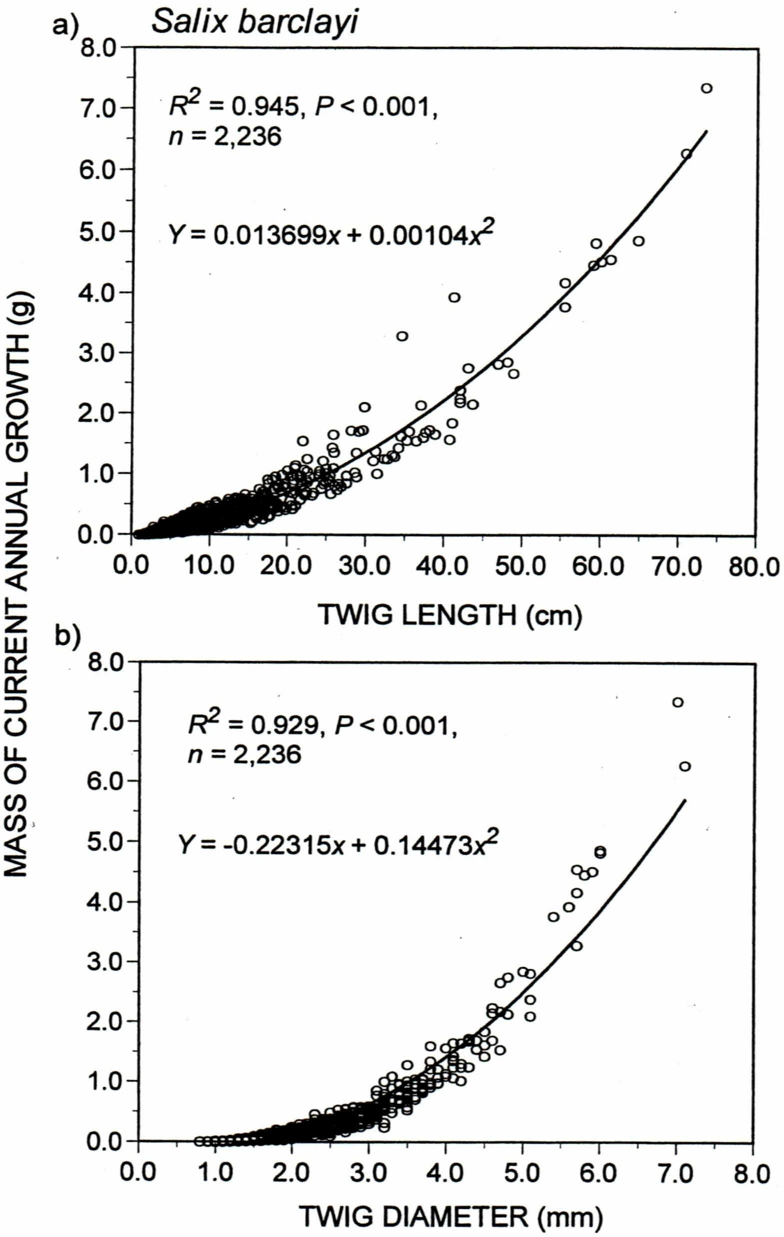

Fig. 3.1.—Relation between twig mass and morphology of current annual growth of willows (*Salix barclayi*), Kenai Peninsula, Alaska, winter 1999-2000: a) length of twigs and mass regression; and b) diameter of twigs and mass regression. Diameters were measured at the bud scale scar, and lengths were measured from bud scale scar to the tip of current annual growth.

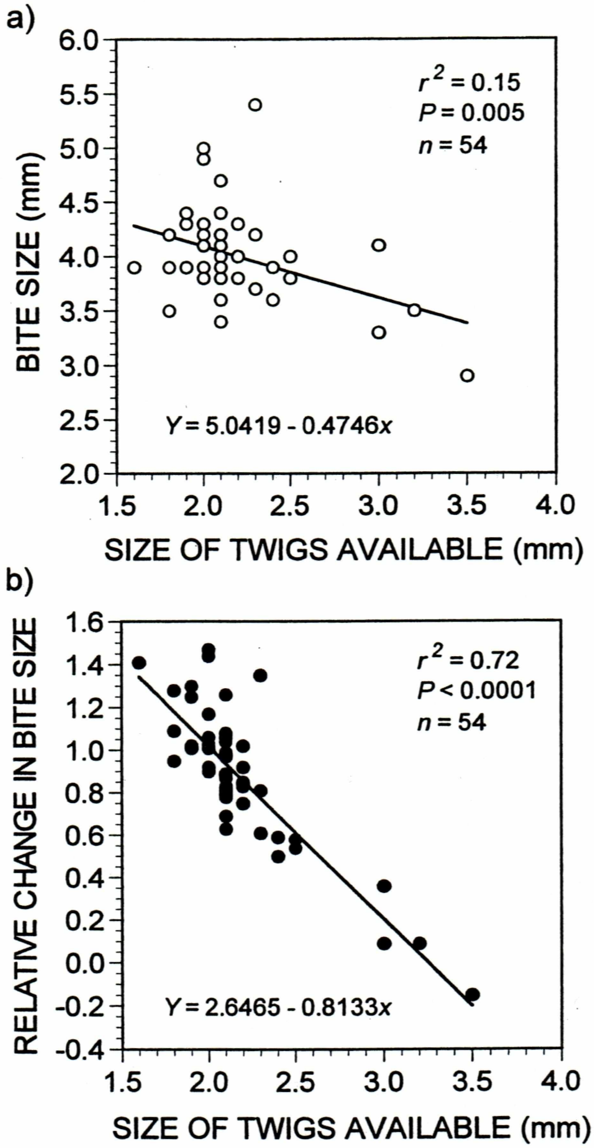

Fig. 3.2.—Characteristics of willow twigs (*Salix barclayi*) as related to browsing by Alaskan moose (*Alces alces gigas*): a) point of browsing (bite size) in relation to size of twigs available (diameter at the bud scale scar); and b) relative change in bite size as related to size of available twigs. Relative change in bite size was calculated as mean bite size minus mean twig diameter available divided by mean twig diameter. Analyses were based on adult male ($n = 3$, 18 trials) and adult female ($n = 3$, 36 trials) moose located at the Kenai Moose Research Center, Alaska, winter 1999-2000.

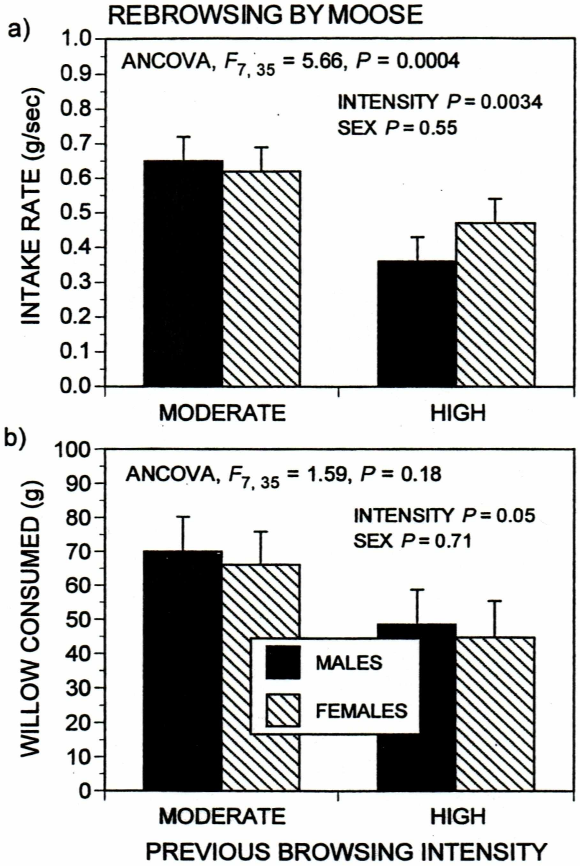

Fig. 3.3.—Rebrowsing by adult male ($n = 3$, 18 trials) and adult female ($n = 3$, 18 trials) Alaskan moose (*Alces alces gigas*), on willows (*Salix barclayi*) at the Kenai Moose Research Center, Alaska, winter 1999-2000. Analysis of covariance (ANCOVA) included diameter of twigs (measured at the bud scale scar) available for browsing as a covariate. Identity of individuals (a coded variable that controlled for mass and physical condition of moose, as well as idiosyncrasies in foraging behavior) was included, with level of browsing intensity and sex as main effects. Adjusted means (+*SE*) illustrate rate of willow intake (a), determined at 2 levels of browsing intensity (moderate ≤50% of 1-year-old twigs browsed; high ≥51% browsed) for both sexes. Total mass of willow consumed (b) was determined for moderate and high intensity of browsing. Measurements of intake and amount of willow consumed were for browsing by males and females after females had browsed previously.

SYNOPSIS AND CONCLUSION

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. Additionally, maximum predicted mass of male moose was about 40% greater than for females. Males continued to gain body mass long after maximal incisor breadth was attained, but maximal predicted body mass and incisor breath were reached at about the same time in females. There may, however, be some limit to incisor breadth, because moose often forage selectively on individual leaders of current annual growth. 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. Browsers, in particular, need to forage selectively on leaders of new growth, which are generally higher in nutrient content than older growth. The width of the incisor arcade in male moose, likewise, was 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, or the kinetics of forage passage.

Forage quality of willow twigs in winter varied on a relatively fine spatial scale, especially IVDMD, tannin concentration, and estimated digestible energy. The cause of that variation, however, was uncertain, but could not be attributed to previous browsing history, aspect, or shading, which were similar among sites. Other factors related to plant growth that I could not assess, such as temperature, soil nutrients, and soil moisture, may have been responsible for those differences in quality of twigs. Older twigs of willow had lower nitrogen content than younger twigs. Larger-diameter twigs of willow also had lower nitrogen content than smaller twigs. Protein availability probably declined with absolute content of nitrogen and with tannin concentrations as parts of plants age, for both diameter categories. Similarly, large-diameter twigs were less digestible; however, age of twigs did not affect IVDMD. Although age of the twig was more influential in determining nitrogen content, structural components of the twig to support growth (twig diameter) were more important in affecting IVDMD, as revealed in the relation between IVDMD and cellulose. Although differences in quality of twigs relative to their age and diameter were not large, such differences may be of importance to foraging herbivores as nutrients are accumulated over time.

The inverse relation between size of twigs available and relative size of bite taken was counterintuitive, and indicated the size of bite obtained by a moose could not be understood without considering the size of the twig available to feed upon. Moreover, amount of current annual growth helped determine how much second-year growth was taken in a bite; moose consumed relatively more second-year growth when available first-year growth was limited. That outcome likely occurred because current annual growth of willows was higher in nitrogen content than second-year growth, but not higher in digestibility of dry matter. Consequently, the idea that moose take some optimum size of bite can be rejected; the quality of the bite obtained and physical condition of moose likely are important factors regulating bite size.

Body mass and sex of moose, and density of willow twigs predicted rate of forage intake, with females exhibiting higher rates of forage acquisition than males at moderate and high levels of browsing intensity. Despite that result, browsing by females did not differentially effect subsequent browsing by males. Indeed, females had a disproportional effect on bite rate of other females compared with males, especially at high levels of previous browsing intensity. Female-female competition exacerbated via high density is thought to be a primary constraint on reproductive performance in ungulates, including moose. Differences in foraging behavior, however, still might reflect disparate nutrient requirements of sexes related to size dimorphism and differing life-history strategies, which may promote sexual segregation. When considered in concert with results from field research on free-ranging ruminants, this experimental study offers convincing evidence that competitive exclusion of males by females is not a compelling explanation for sexual segregation. Consequently, competitive exclusion of males by females can be rejected as a general explanation for sexual segregation in ruminants, and future research should be directed at more fruitful avenues of research, including risk of predation and differences between sexes in allometry and nutrient requirements.