Sexual segregation in moose *Alces alces*: an experimental manipulation of foraging behaviour

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We studied Alaskan moose *Alces alces gigas* to test the hypothesis that sexual segregation among polygynous ruminants is the result of competitive exclusion of males by females. We first examined differences in foraging behaviour between sexes, and then tested whether foraging by females influenced subsequent browsing by males, an outcome necessary to postulate competitive exclusion of males by females. Our experiments during the winter of 1999 and 2000 were made on captive moose at the Kenai Moose Research Center, Alaska, USA. Twig diameters of Barclay 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; bite size can not be invoked as an explanation for sexual segregation. Moose of both sexes overcompensated by consuming more second-year growth when feeding on smaller twigs compared with larger ones, ostensibly to adjust for lower nutritional returns in smaller twigs of current annual growth. We modelled the intake rate of moose browsing on willow with multiple-linear regression. The best model included sex, body mass of moose and density of twigs, but not shape of willows. Females had higher bite rates and rates of forage intake than males, and generally took smaller bites of greater variability. Thus, the differences in foraging behaviour between the sexes may relate to sexual dimorphism and allometric differences in digestive morphology, and ultimately to spatial segregation of sexes, as proposed by the gastrocentric hypothesis. No difference, however, occurred in the rate of intake between the sexes foraging on previously browsed willows, which resulted in our rejection of the hypothesis that selective foraging by females could lead to competitive exclusion of males.

Key words: Alaskan moose, competitive exclusion, feeding behaviour, foraging, sexual segregation, willow

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

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 & Hundertmark 1993). Indeed, Kie & Bowyer (1999) and Bowyer, Pierce, Duffy & Haggstrom (2001b) 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, the causes of the phenomenon continue to be debated (for reviews see Miquelle et al. 1992, Main et al. 1996, Bleich et al. 1997, Barboza & Bowyer 2000, 2001). Hypotheses forwarded to explain sexual segregation have included mechanistic approaches related to differential activity patterns of sexes (Conradt 1998, Ruckstuhl 1998), but whether differences in activity or synchrony are a cause or a consequence of sexual segregation is uncertain (Barboza & Bowyer 2001). Clearly, no aspect of the current hypotheses concerning activity patterns explain the spatial separation of sexes outside the mating season (Barboza & Bowyer 2001), which is a common occurrence among polygynous ungulates (Bleich et al. 1997).

The sexes of ungulates may exhibit dietary, habitat and spatial segregation (Kie & Bowyer 1999, Mysterud 2000); hypotheses forwarded to explain why sexes segregate must thus address the widespread occurrence of this phenomenon. We confine our study to postulates that potentially explain an ecological difference between the sexes. One prominent hypothesis maintains that such segregation is driven by differences in feeding behaviour, 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 & Gordon 1987, 1992, Main & Coblentz 1996).

Clutton-Brock et al. (1987) proposed that female red deer *Cervus elaphus* competitively excluded males from mutually preferred areas. In their study, females foraged more selectively than males and were postulated to be more tolerant of a low biomass of plants. Likewise, Main & Coblentz (1996) suggested that female mule deer *Odocoileus hemionus*, feeding mostly on forbs, competitively excluded males. Illius & Gordon (1987) further postulated that differential scaling of incisor breadth and metabolic requirements with body mass might be a cause of spatial segregation in grazing ungulates. Spaeth, Hundertmark, Bowyer, Barboza, Stephenson & Peterson (2001) also noted differences in the breadth of the incisor arcade between the sexes of a large browser, the Alaskan moose *Alces alces gigas*. Weckerly (1993), however, failed to obtain supportive evidence for aspects of this hypothesis (e.g. differences in incisor breadth) between the sexes of black-tailed deer *O. h. columbianus*. One problem in resolving questions concerning sexual segregation is that hypotheses are not mutually exclusive (Bleich et al. 1997). We maintain that an experimental approach is necessary to test the fundamental assumptions of the hypothesis relating to sexual segregation and competitive exclusion of males by females. Moreover, investigating mechanisms involved in the examination of foraging behaviour is an essential first step in sorting the potential causes of why sexes spatially segregate.

Accordingly, we examined the different characteristics of twigs and browse architecture on foraging behaviour by sexes of adult moose, under the assumption that this might lead to sexual segregation. Further, 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, an outcome necessary for females to competitively exclude males.

Material and methods

Study area

The Moose Research Center, a facility operated by the Alaska Department of Fish and Game, is located on the Kenai Peninsula (61°N, 151°W), about 65 km northeast of Soldotna in south-central Alaska, USA. The facility consists of four 2.6-km^2 enclosures constructed of 24 km of woven-wire fence, 2.4 m in height. In addition, the facility includes five small enclosures (holding pens of 1-6 ha), and a scale house for weighing moose. Three adult female moose and three adult male moose, which had been accustomed to handling by the researchers, were used in the feeding experiments. The moose were 5-8 years old with a substantial overlap between males (5, 7 and 8 years) and females (5, 6 and 7 years).

Annual precipitation on the Kenai Peninsula ranges within 40-50 cm with most of it falling as snow in winter and rain in spring or autumn (Schwartz & Franzmann 1991). Annual snowfall ranges within 140-165 cm (Oldemeyer & Regelin 1987), and temperatures are moderated by the influence of the Pacific Ocean. The mean annual temperature is 1°C, and ranges within -30-21°C (Schwartz & Franzmann 1991).

Sampling procedures

We immobilized the captive moose at close range (~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 the moose used in the feeding trials (Stephenson, Hundertmark, Schwartz & Van Ballenberghe 1993, 1998). We determined maximum thickness of rump fat and whether moose were pregnant via ultrasonography (Stephenson et al. 1993, 1998, Keech, Stephenson, Bowyer, Van Ballenberghe & Ver Hoef 1998, Keech, Bowyer, Ver Hoef, Boertje, Dale & Stephenson 2000) using an Aloka model 500 portable ultrasound device (Aloka, Inc., Wallingford, Connecticut, USA). We also measured breadth of the incisor arcade for the immobilized moose using methods described by Spaeth et al. (2001). At completion of the 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).

Barclay willows *Salix barclayi*, which were of similar size, age and structure, were cut from nearby forests on the Kenai Peninsula (Spaeth, Bowyer, Stephenson, Barboza & Van Ballenberghe 2002) to establish 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 & Bowyer 1997, Molvar, Bowyer & Van Ballenberghe 1993, Bowyer & Neville 2003) had no effect on our experiments. We cut a sample of the willows, measured all current annual growth at the bud scale scar, dried them in an oven at 55°C and weighed the current annual growth to obtain diameter-mass and length-mass regressions (Telfer 1969, Bowyer & Bowyer 1997, Weixelman, Bowyer & Van Ballenberghe 1998, Bowyer et al. 2001b). 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.

To help quantify foraging behaviour by moose, we calculated the relative change in bite size (RCBS) in relation to the diameter of willow twigs at the bud scale scar in the following way: RCBS = mean bite size - mean twig diameter at the bud scale scar/mean twig diameter at the bud scale scar.

The RCBS 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). We assessed the potential bias from a lack of independence between independent and dependent variables in assessing that relationship (i.e. both independent and dependent variables included twig diameter) using principle-axis regression (Sokal & Rholf 1969).

We used weighted regression analysis (Neter, Kutner, Nachtsheim & Wasserman 1996) to examine effects of moose body mass 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 the analyses we weighted each individual moose by the inverse of the variance in intake rate, bite rate or mass of willow consumed.

Prior to the feeding trials, moose were fed a pelleted ration (Schwartz, Regelin & Franzmann 1985) *ad libitum*, and had access to birch *Betula* spp., aspen *Populus* spp., and willow *Salix* spp. that we placed in the largest (6 ha) of the five smaller enclosures. Willows are the preferred forage of Alaskan moose (Bowyer & Bowyer 1997, Molvar et al. 1993, Weixelman et al. 1998, Van Ballenberghe, Miquelle & MacCracken 1989). Moose at the research centre, however, had limited access to willows in their large enclosure, and browsed the shrubs readily when available. Consequently, we offered willows that were weighed before and after moose fed upon them to the moose immediately prior to each experiment. Feeding of pre-trial willows successfully moderated the feeding rate by captive moose to the feeding rate of free-ranging moose (Molvar et al. 1993, Bowyer & Bowyer 1997, Weixelman et al. 1998, Bowyer et al. 2001b). The addition of pre-trial willows probably had little effect on the nutrition of moose because of the low mass of willows fed, and had no effect on our feeding experiment because male and female moose were treated identically. Indeed, the mean mass (± 95% CI) of pre-trial willows consumed by both moose sexes was similar at both 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 (~3 by 15 m). Moose were randomly selected and allowed to enter the pen and browse on the willows until a moderate (22-50%) or high (51-78%) removal of twigs was obtained. The levels of forage removal were estimated by the observer to be consistent with the browsing intensity on willows in studies of free-ranging Alaskan moose (Molvar et al. 1993, Bowyer & Bowyer 1997, Weixelman et al. 1998, Bowyer et al. 2001b). Time spent feeding and number of bites were recorded for each moose by the observer, and each trial was filmed with a video camera. Post-feeding measurements of diameter at the point of browsing and the percentage of leaders browsed were determined for willows, and the total biomass removed was obtained by weighing the shrubs prior to and after each feeding trial. Willows browsed by a female moose were then offered to a male moose. In a similar manner, other willows browsed by females were also presented to other females. This procedure was repeated at both levels of browsing intensity (moderate and high). The experiment was terminated by removing the willow when most (ca 95%) current annual growth had been foraged upon by moose. That consumption of browse by moose took a mean (± SE) of 128 ± 8.7 seconds 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 behaviour for free-ranging moose because, under these experimental conditions, even large branches of each plant would have been stripped of bark or consumed entirely because willows were the only forage in the experimental pen.

We assessed the architecture of willows used in foraging experiments by placing a 1-m^2 grid with 100 cells (each 10 x 10 cm) directly above each willow. We visually estimated the top 85% of willow twigs (current annual growth) and counted the total number of twigs and the number of twigs per cell (density). We calculated the CV of twig density (an index of the distribution of twigs across the sampling grid) and the proportion of cells that contained ≥ 1 twig. We assessed the reliability of the 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 number of twigs we counted in the grid cells. That value ($\bar{x}$ = 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 two rastor-based indices of shape for willows offered to moose during the foraging experiments, both based on perimeter (p_{ij}) to area (a_{ij}) ratios (McGarigal & Marks 1995). We selected rastor-based measurements because our sampling grid and cells within that structure were square. The shape index (SI) was defined as:

$$\mathrm{SI} = 0.25p_{ij}/\sqrt{a_{ij}}.$$

A shape index of 1 was a square, and it increased as the shape became more irregular. The fractal dimension (FD) was calculated as:

$$\mathrm{FD} = 2\ln(0.25p_{ij})/\ln a_{ij}.$$

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 & Marks 1995).

We used multiple regression analysis to evaluate the effects of willow characteristics on moose foraging behaviour. We controlled for multicollinearity in multiple regressions by eliminating one of any pair of independent variables with the absolute value of r ≥ 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 the resulting models with adjusted multiple coefficients of determination (R^2_{adj}), Mallow's Cp statistic and Akaike information criteria (AIC; SAS Institute 1987).

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

The experimental design to assess rebrowsing of willows involved pairings of three adult male and three adult female moose, which included female-male (i.e. females foraging prior to males) and female-female combinations by two levels of browsing intensity (moderate and high) with three replications each for a total of 72 feeding trials. We acknowledge that the number of test animals was small, and that our design traded-off the number of animals (although we used all existing hand-raised adult moose) against the need for replication, and to make a large number of detailed measurements on moose and their forage necessary to control statistically for differences amongst individuals. Accordingly, we analysed data on rebrowsing of willows by sexes of moose with multivariate analysis of covariance (MANCOVA; Johnson & 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 behaviour. Sex, level of browsing intensity (moderate or high) and their interaction were main effects in that statistical model. An $\alpha = 0.05$ was adopted for all statistical tests.

Results

Morphology of moose and willows

Overall, the three adult male moose (weighing 504, 534 and 602 kg) were larger than the three adult females (weighing 429, 504 and 549 kg), although overlap in body mass occurred. Mean male and female body con-

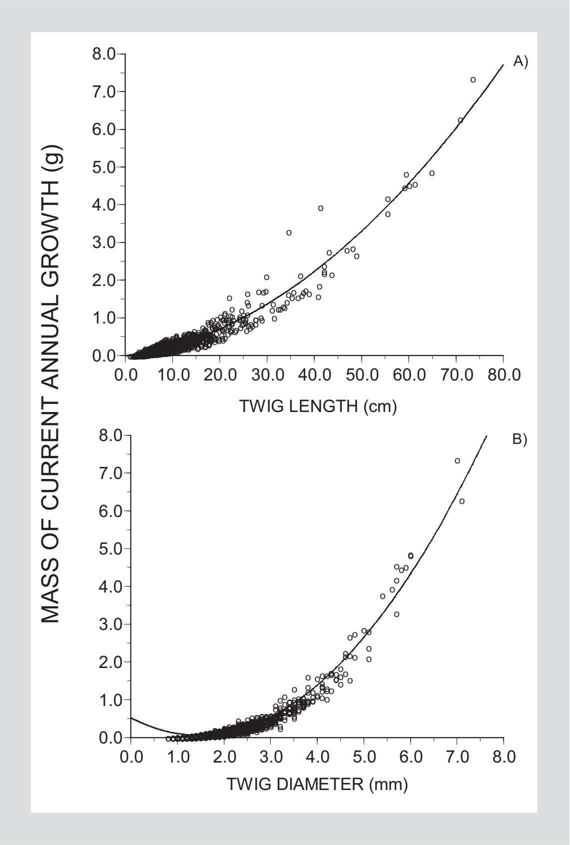

Figure 1. Relations between twig mass and morphology of current annual growth of Barclay willows, on the Kenai Peninsula, Alaska, USA, during the winter of 1999/2000. A) shows the length of twigs (in cm) and mass regression ($Y = 0.013699x + 0.00104x^2$; $r^2 = 0.945$, $P < 0.001$, N = 2,236), and B) the diameter of twigs (in mm) and mass regression ($Y = -0.22315x + 0.14473x^2$; $r^2 = 0.929$, $P < 0.001$, N = 2,236). Lengths were measured from bud scale scar to the tip of current annual growth and twig diameters were measured at the bud scale scar.

dition (as indexed by maximum thickness of rump fat) was 0.93 cm (95% CI = 0.5 cm) and 5.26 cm (95% CI = 2.8 cm), respectively. Males had low rump fat at the start of our experiment in mid-December due to strenuous rutting activities during autumn, but re-feeding following rut resulted in gains in rump fat for most 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 one female gaining (0.2 cm) and the other two losing (1.0 and 1.3 cm) rump fat. Ultrasonography indicated that all females conceived and were pregnant during the feeding experiments, which took place prior to the last third of gestation; one female, however, did not give birth the following spring. Breadth of the incisor arcade was 47.5, 65.8 and 66.9 mm for males and 64.9, 67.8 and 70.7 mm for females. Males had more variable incisor arcades because one male had three outer teeth (both outer canines and one 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 (see Fig. 1). Twig diameter and length reliably predicted mass of current annual growth (see Fig. 1).

Foraging behaviour by sexes of moose

Twig size of current annual growth (as indexed by diameter of twig at bud scale scar; see Fig. 1) affected the size of bites taken by foraging moose when the relationship was examined with respect to absolute (Fig. 2A) and relative size of bites (Fig. 2B). No differences occurred between the sexes of moose (test of slopes; $P > 0.05$). Moose overcompensated (i.e. took disproportionately larger bites) when feeding on smaller twigs of new growth than on older and larger ones (see Fig. 2B). Principle-axis regression confirmed that the results from our simple linear regression analysis was valid (93% variation explained).

Body mass was critical to understanding bite rate, bite size and forage intake by moose. The weighted-regression analysis indicated that bite rate (bites/minute) 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 the relationship was marginally not significant ($P = 0.09$). Body mass (kg), however, did predict bite size (mm) by moose ($Y = 5.032-0.470x$; $r^2 = 0.23$, $P = 0.03$). The weighted regression analysis also revealed positive relationships between body mass (kg) and intake rate (g/second) 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 the missing teeth ($\bar{x} = 0.37$ g/second, 95% CI = 0.29-0.45 g/second) overlapped that of the other males ($\bar{x} = 0.57$ g/second, 95% CI = 0.39-0.75 g/second) and, consequently, did not bias our results markedly. Indeed, body mass rather than the size of the incisor arcade was the primary factor influencing the intake rate of forage by moose.

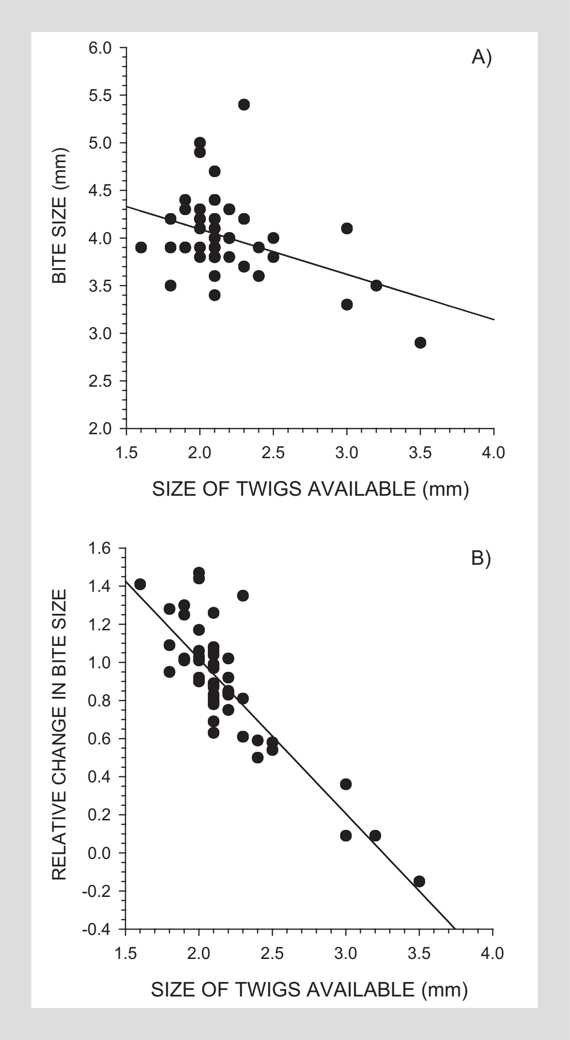

Figure 2. Characteristics of Barclay willow twigs as related to browsing by Alaskan moose at the Kenai Moose Research Center, Alaska, USA, during the winter of 1999/2000. A) shows the point of browsing (bite size) in relation to size of twigs available (diameter in mm at the bud scale scar), and B) the 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 three adult male (N = 18 trials) and three adult female (N = 36 trials) moose. For A): $Y = 5.0419 - 0.4746x$; $r^2 = 0.15$, $P = 0.005$, $N = 54$), for B): $Y = 2.6465 - 0.8133x$; $r^2 = 0.72$, $P < 0.0001$, $N = 54$.

Prior to further modelling of forage intake by moose,

Table 1. Variables available for stepwise multiple regression to explain intake rate by Alaskan moose as related to plant architecture of Barclay willow on the Kenai Peninsula, Alaska, USA, during the winter of 1999/2000. Three adult male (18 trials) and three adult female moose (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. Twig diameter was measured at the bud scale scar.

	Male (N = 18)		Female (N = 36)	
Variable	$\bar{x}$	SE	$\bar{x}$	SE
Intake rate (g/second)				
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 (mm)				
Moderate	2.01	0.06	2.11	0.03
High	2.38	0.17	2.23	0.08
Proportion of cells[a]				
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)[b]				
Moderate	1.52	0.07	1.47	0.05
High	1.42	0.06	1.60	0.10
Fractal (index)[c]				
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

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

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

[c] 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 2. Analysis of intake rate (in g/second) for adult male (N = 3; 18 trials) and adult female (N = 3; 36 trials) Alaskan moose foraging on Barclay willow on the Kenai Peninsula, Alaska, USA, during the winter of 1999/2000. Body mass (in kg) was mean body weight for an individual over the course of the experiment. Twig 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. The overall model was significant ($r^2_{adj} = 0.238$, $P = 0.008$).

Variable	Parameter	F value	P value	Partial r^2
Sex	-0.513	9.41	0.004	0.134
Body mass	0.006	8.51	0.005	0.141
Twig density	0.133	2.32	0.134	0.032

we controlled for multicollinearity by withholding the willow shape index from the multiple-regression analysis; the variable was strongly correlated with the fractal dimension of a plant (r = 0.97). Likewise, we eliminated the total number of twigs which was collinear with both density of twigs (r = 0.64), the diameter of twigs at their bud scale scars (r = -0.65) and excluded the proportion of cells in the grid containing willow twigs because that variable was related to twig density (r = 0.68). We then modelled the intake rate for moose browsing on willow (Table 1). The best model included sex of moose, moose body mass and density of willow twigs (Table 2); the 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 (see Table 2). No other variable was entered into that model ($P > 0.15$). Indeed, the fractal dimension of a willow (i.e. a plant shape index) 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 behaviour of moose were mediated mostly via density of twigs rather than via plant shape *per se*. Even the CV of twig density, which indexed the distribution of twigs across our sampling grid over a willow, did not influence the intake rate by moose ($P > 0.15$).

Effects of previous browsing on foraging behaviour by sexes of moose

The second component of our experimental design was to evaluate foraging behaviour of moose feeding on previously browsed willows. Thus, we investigated the rate of foraging (bites/minute) for male and female moose consuming willows that previously had been browsed at moderate and high levels of intensity using ANCOVA. Diameter of twigs at the bud scale scar was the covariate in the 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 behaviour. The overall outcome was significant ($F_{7, 28}$= 4.09, P = 0.003) and was 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 higher at moderate (10.8 ± 0.02 bites/minute) than at high (9.1 ± 0.08 bites/minute) levels of previous browsing intensity ($P < 0.0001$). Moderate levels of foraging intensity were similar for females (10.8 ± 0.85 bites/minute) and males (10.8 ± 0.89 bites/minute). Females (11.2 ± 0.94 bites/minute), however, foraged at a higher rate ($P < 0.0001$) than males (7.0 ± 0.90 bites/minute) at the high level of previous browsing intensity, indicating that females foraged less efficiently than males at that level.

When we controlled for diameter of twigs at the bud scale scar and included the identity of the individual

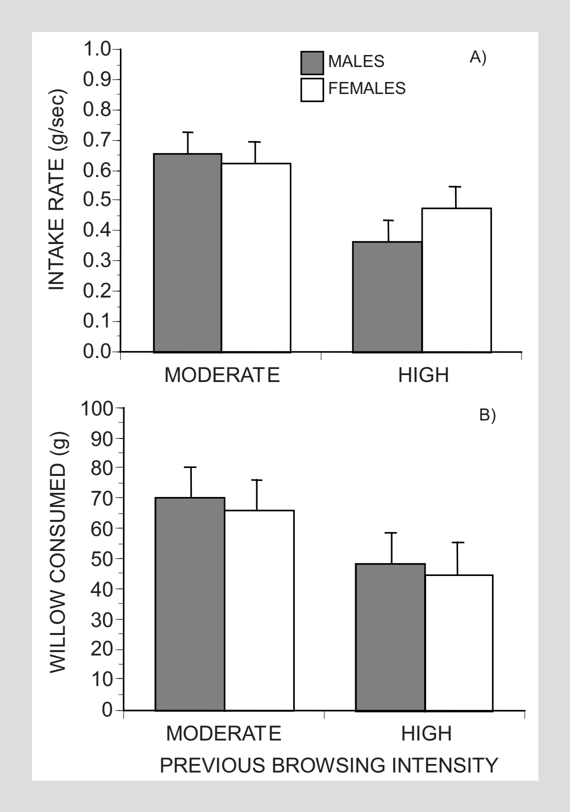

Figure 3. Rebrowsing by three adult male (N = 18 trials) and three adult female (N = 18 trials) Alaskan moose on Barclay willows at the Kenai Moose Research Center, Alaska, USA, during the winter of 1999/2000 expressed as intake rate (A) and willow consumed (B). Analysis of covariance (ANCOVA; forA: $F_{7,35} = 5.66$, $P = 0.0004$, and for B: $F_{7,35} = 1.59$, $P = 0.18$), 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 behaviour) was included, with level of browsing intensity (in A: $P = 0.0034$ and in B: $P = 0.05$) and sex (in A: $P = 0.55$ and in B: $P = 0.71$) as main effects. Adjusted means (+ SE) illustrate the rate of willow intake (A), determined at two 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.

moose, ANCOVA also revealed effects on intake rate (g/second) of willow, as determined by the 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 grams of willow removed were not significantly affected by sex of moose rebrowsing a willow (Fig. 3B). Nonetheless, the level of browsing (moderate or high) significantly affected that variable (see Fig. 3B).

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

Discussion

Alaskan moose lend themselves well to studying sexual segregation because they are highly sexually dimorphic (Schwartz, Regelin & Franzmann 1987, Bowyer, Van Ballenberghe & Kie 1997, Spaeth et al. 2001), select habitats differently (Miller & Litvaitis 1992, Bowyer et al. 2001b) and remain spatially separated for much of the year (Miquelle et al. 1992).

We used an hierarchical approach to examine the effects of foraging behaviour of moose on sexual segregation. First, we tested whether foraging behaviour 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 the consumption of willows, a critically important food for these large herbivores (Bowyer et al. 1997). 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. Indeed, such competitive exclusion of one sex by the other requires exploitive competition of resources such as willows. Interference competition, which has been documented between species of large herbivores (Stewart, Bowyer, Kie, Cimon & Johnson 2002), will not explain sexual segregation. Interference competition allows the sexes to use the same space at different times and, consequently, does not offer an explanatory mechanism for the spatial separation of the sexes over the long time intervals and spatial scales that has been observed in moose (Miquelle et al. 1992) and other large herbivores (Bleich et al. 1997).

Bite size, body mass and sexual segregation in moose

The inverse relation between size of twigs available and relative size of bite taken (see Fig. 2B) indicated that the size of bite obtained by a moose could not be understood without considering the size of the twig available to feed upon. Moreover, the 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 the available first-year growth was limited (see Fig. 2B). That outcome likely occurred because the current annual growth of willows had a higher nitrogen content than the second-year growth, but it does not rate 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 & Bowyer 2001, Parker, Gillingham, Hanley & Robbins 1999), and small differences in diet quality can be magnified over time (White 1983). Accordingly, moose overcompensated by taking 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, Gross, Spalinger, Hobbs & Wunder 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. Consequently, rather than taking an optimum size of bite (Vivas, Sæther & Anderson 1991), moose probably adjusted the bite size to maximize the quality of the bite obtained (Shipley et al. 1994). Because the sexes of moose did not differ markedly in this regard, bite size is not likely the determinant for spatial segregation of the sexes; a conclusion that was also reached by Weckerly (1993) and Pérez-Barbería & Gordon (1999).

Our data indicated that the three missing teeth from the lower jaw of one male did not bias the interpretation of our foraging experiments, because the incisor breadth of that individual did not affect his intake rate of forage markedly. Further, differences amongst individuals were controlled statistically. Moreover, the effect of that abnormality should have been to reduce foraging efficiency, yet we detected no difference between the sexes in the rate of forage intake. Body mass, not the size of the incisor arcade, was the primary determinant of intake rate of willows by moose.

Several authors (Miquelle et al. 1992, Bowyer et al. 2001b) have suggested that male moose should take larger bites than females, in part because of their slightly larger incisor arcades (Spaeth et al. 2001). We observed generally larger bites by male than female moose rebrowsing willows, but considerable variation occurred between the sexes. Body mass rather than the breadth of the incisor arcade strongly influenced bite size by moose. Nonetheless, the males we used in our experiment probably had not reached their maximal body mass (as heavy as 725 kg), which typically occurs at 8-10 years of age (Schwartz et al. 1987, Stewart, Bowyer, Kie & Gasaway 2000, Spaeth et al. 2001). We caution that males larger than the ones we used in our experiments might take larger bites than we report. 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 the analyses. Moreover, the nutritional state of the animal also likely affected bite size; moose are known to bark strip and consume large stems when physiologically stressed (Telfer & Cairns 1978, Miquelle & Van Ballenberghe 1989, Bowyer, Nicholson, Molvar & Faro 1999a). Again, the physical condition of moose was controlled in our experiment by considering the individuals in our analysis. The critical point is that sexual segregation in free-ranging moose, where spatial separation of the sexes was nearly complete (Miquelle et al. 1992), was reported among the sizes and ages of moose used in our experiment. If competitive exclusion of males by females provides a general explanation for sexual segregation in moose, predicted differences in foraging behaviour between the sexes of our experimental animals rebrowsing willows should have been evident which they were not.

Plant architecture and foraging behaviour by moose

Allometric differences, coupled with differing life-history strategies, between dimorphic male and female ruminants likely result in differential nutrient requirements for the sexes, which in turn influences foraging behaviour and ultimately spatial segregation (sensu Barboza & Bowyer 2000, 2001). Indeed, the differences we observed between the moose sexes initially foraging on willows offer strong support for the gastrocentric hypothesis forwarded by Barboza & Bowyer (2000, 2001); that sex, body mass and twig density contribute to the rate of forage intake (see Table 2). Digestion trials will be required, however, to critically test their hypothesis (Barboza & Bowyer 2001).

Distribution of plants across the landscape (which we can not address with our foraging experiments) and 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 the forage intake by moose. At least for the size and configuration of the shrubs we sampled, shape of plants was comparatively unimportant. Moreover, differences in the 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, which again resulted in higher levels of foraging efficiencies. Our data indicate that the effects of plant shape on foraging efficiency are not independent of the local availability of twigs and should thus not be considered separately. Effects of plant shape on foraging behaviour did not offer a plausible explanation for sexual segregation in moose.

We caution that our experimental design required willows that initially were unbrowsed to help maintain similarity in the characteristics of willows offered to both sexes of moose. Leaders of current annual growth emerging from previously browsed twigs tend to be larger than for unbrowsed plants, and moose selectively forage on the latter larger leaders (Molvar et al. 1993, Bowyer & Bowyer 1997). Whether such differences in plant architecture produced by regrowth from previously browsed stems would alter the feeding behaviour of moose remains to be tested.

Effects of scale and foraging intensity on sexual segregation in moose

A larger sampling scale (e.g. an area with multiple shrubs or even a landscape) might have yielded results different from the ones we obtained (Bowyer et al. 1996, Bowyer, Stewart, Wolfe, Blundell, Lehmkuhl, Joy, McDonough & Kie 2002, Kie, Bowyer, Nicholson, Boroski & Loft 2002). Such a design, however, would be difficult to control experimentally. We contend that the scale at which we sampled (i.e. the feeding site) was most appropriate for evaluating the foraging behaviour of moose, especially for the controlled experimental design necessary to obtain critical tests of precisely how moose forage. Indeed, bite size influences the use of forage patches by large herbivores, as well as foraging decisions about how long to remain in a particular patch (Gross, Shipley, Hobbs, Spalinger & Wunder 1993, Shipley & Spalinger 1995, Shipley, Bloomquist & Danell 1998, Shipley, Illius, Danell, Hobbs & Spalinger 1999). Further, if females were able to competitively exclude males by feeding more selectively, the foraging site must reflect such competitive interactions for them to be manifest at a larger scale.

A longer temporal scale, which permitted additional foraging, also might have altered our conclusions. Nonetheless, the levels of browsing intensity we obtained in our experiments were similar to the values reported for free-ranging Alaskan moose foraging on willows (Molvar et al. 1993, Bowyer & Bowyer 1997, Weixelman et al. 1998, Bowyer et al. 2001b). Moreover, moderate to high levels of browsing intensity were consistent with what would have occurred if competitive effects on foraging behaviour of males by females were likely. White-tailed deer *Odocoileus virginianus* (Kie & Bowyer 1999) and red deer (Conradt, Clutton-Brock & Thomson 1999) exhibited a greater degree of sexual segregation at moderate than at 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. Allowing females to browse at the usual high levels of intensity would not have been a realistic test of foraging under field conditions in which sexual segregation has been described for moose (Miquelle et al. 1992, Bowyer et al. 2001b).

Competitive exclusion of males by female moose

Body mass, sex of moose and the density of willow twigs predicted the rate of forage intake with females exhibiting higher rates of forage acquisition than males at moderate and high levels of browsing intensity (see Tables 1 and 2). Despite that result, browsing by females did not differentially affect subsequent browsing by males (see Fig. 3). Indeed, females had a disproportional effect on bite rate of other females than of 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 (Schwartz & Hundertmark 1993, Bowyer et al. 1999a, Keech et al. 2000). Differences in foraging behaviour, however, still might reflect disparate nutrient requirements of the sexes related to size dimorphism and differing life-history strategies, which may promote sexual segregation (Barboza & Bowyer 2000, 2001), but not via competitive exclusion.

We acknowledge that other factors not included in our experiment influence foraging efficiency of moose and other large herbivores, including the risk of predation and group size (Edwards 1983, Berger 1991, Bowyer et al. 1997, Molvar & Bowyer 1994, Weixelman et al. 1998, Kie 1999, Bowyer, McCullough & Belovsky 2001a, White, Testa & Berger 2001). Nonetheless, our experimental approach to understanding sexual segregation is among the first of its kind for large browsers. Moreover, we do not foresee how a reduction in foraging efficiency by females in large groups, or those far from concealment cover (Molvar & 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 & Bowyer 1994) does not offer a mechanism for competitive exclusion resulting in spatial separation of the sexes. Indeed, where predation is thought to contribute substantially to spatial segregation of the sexes, females typically occur on poorer-quality ranges with less abundant forage than those occupied by males (Bleich et al. 1997, Bowyer et al. 2001b).

Experimental data addressing competition for large mammals are sparse (McCullough 1979, Kie & Bowyer 1999, Stewart et al. 2002), and we believe that our findings offer unique insights into mechanisms that likely underpin sexual segregation in ruminants. Although our sample included only six moose, we collected the detailed information involving 72 feeding trials necessary to demonstrate that differences in body mass, sex and twig density affected foraging behaviour by moose. Previous browsing by females, however, failed to affect the foraging behaviour of males more than for other females. Females took more bites to obtain an intake rate equivalent to that of males. Thus, female moose took slightly smaller bites, but fed at a higher rate (bites/minute) than did males. Even if the smaller bites obtained by females were of higher quality than the larger bites of males, allometric differences between the sexes likely allow males to do just as well as females on such diets (Barboza & Bowyer 2000, 2001).

When considered in concert with results from field research on free-ranging ruminants, our experimental study offers evidence that competitive exclusion of males by females is not a compelling explanation for sexual segregation. A clear mechanism for females to competitively exclude males was not evident in our foraging experiments. Although our experimental approach yielded clear differences in the manner in which sexes of moose foraged, no disproportional effects of previous browsing by females on males occurred.

Clearly, 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 could be expected (du Toit 1995). Similarly, Miquelle et al. (1992) reported strong segregation of sexes in a population of moose held at low density by predation (Bowyer, Van Ballenberghe & Kie 1998), where intersexual competition was unlikely. Conradt et al. (1999) noted that higher densities of female red deer did not increase sexual segregation, contradicting previous researchers (Clutton-Brock et al. 1987) at that same study site. Kie & 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; the degree of segregation declined with increased population density. Finally, a simple model that increased population density of deer resulted in a decrease in the degree of sexual segregation (Bowyer et al. 2002). 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 the sexes in allometry and nutrient requirements (Barboza & Bowyer 2000, 2001).

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References

Animal Care and Use Committee 1998: Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. - Journal of Mammalogy 74: 1416-1431.

Barboza, P.S. & Bowyer, R.T. 2000: Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. - Journal of Mammalogy 81: 473-489.

Barboza, P.S. & Bowyer, R.T. 2001: Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. - Alces 37: 275-292.

Berger, J. 1991: Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. - Animal Behaviour 41: 61-77.

Bleich, V.C., Bowyer, R.T. & Wehausen, J.D. 1997: Sexual segregation in mountain sheep: resources or predation? - Wildlife Monographs 134: 1-50.

Bowers, M.A. & Smith, H.D. 1979: Differential habitat utilization by sexes of deer mouse, Peromyscus maniculatus. - Ecology 50: 869-875.

Bowyer, J.W. & Bowyer, R.T. 1997: Effects of previous browsing on the selection of willow stems by Alaskan moose. - Alces 33: 11-18.

Bowyer, R.T. 1984: Sexual segregation in southern mule deer. - Journal of Mammalogy 65: 410-417.

Bowyer, R.T. & Neville, J.A. 2003: Effects of browsing history by Alaskan moose on regrowth and quality of feltleaf willow. - Alces 39: In press.

Bowyer, R.T., Kie, J.G. & Van Ballenberghe, V. 1996: Sexual segregation in black-tailed deer: effects of scale. - Journal of Wildlife Management 60: 10-17.

Bowyer, R.T., McCullough, D.R. & Belovsky, G.E. 2001a: Causes and consequences of sociality in mule deer. - Alces 37: 371-402.

Bowyer, R.T., Nicholson, M.C., Molvar, E.M. & Faro, J.B. 1999a: Moose on Kalgin Island: are density-dependent processes related to harvest? - Alces 35: 73-89.

Bowyer, R.T., Pierce, B.M., Duffy, L.K. & Haggstrom D.A. 2001b: Sexual segregation in moose: effects of habitat manipulation. - Alces 37: 109-122.

Bowyer, R.T., Stewart, K.M., Wolfe, S.A., Blundell, G.M., Lehmkuhl, K.L., Joy, P.J., McDonough, T.J. & Kie, J.G. 2002: Assessing sexual segregation in deer. - Journal of Wildlife Management 66: 536-544.

Bowyer, R.T., Van Ballenberghe, V. & Kie, J.G. 1997: The role of moose in landscape processes: effects of biogeography, population dynamics, and predation. - In: Bissonette, J.A. (Ed.); Wildlife and landscape ecology: effects and patterns of scale. Springer-Verlag, New York, USA, pp. 265-287.

Bowyer, R.T., Van Ballenberghe, V. & Kie, J.G. 1998: Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. - Journal of Mammalogy 79: 1332-1344.

Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. & Maier, J.A.K. 1999b: Birth-site selection in Alaskan moose: maternal strategies for coping with a risky environment. - Journal of Mammalogy 80: 1070-1083.

Clutton-Brock, T.H., Iason, G.R. & Guinness, F.E. 1987: Sexual segregation and density-related changes in habitat use in male and female red deer (Cervus elaphus). - Journal of Zoology (London) 211: 275-289.

Conradt, L. 1998: Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? - Proceedings of the Royal Society of London B 265: 1359-1363.

Conradt, L., Clutton-Brock, T.H. & Thomson, D. 1999: Habitat segregation in ungulates: are males forced into suboptimal foraging habitats through indirect competition by females? - Oecologia 119: 367-377.

Darwin, C. 1871: The descent of man and selection in relation to sex. - Murray, London, United Kingdom, 372 pp.

du Toit, J. 1995: Sexual segregation in kudu: sex differences in competitive ability, predation risk, or nutritional needs? - South African Journal of Wildlife Research 25: 127-132.

Edwards, J. 1983: Diet shifts in moose due to predator avoidance. - Oecologia 60: 185-189.

Freeman, D.C., Klikoff, L.G. & Harper, K.T. 1976: Differential resource utilization by the sexes of dioecious plants. - Science 193: 597-599.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E. & Wunder, B.A. 1993: Foraging by herbivores in food-concentrated patches: tests of a mechanistic model of functional response. - Ecology 74: 778-791.

Illius, A.W. & Gordon, I.J. 1987: The allometry of food intake in grazing ruminants. - Journal of Animal Ecology 56: 989-999.

Illius, A.W. & Gordon, I.J. 1992: Modeling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. - Oecologia 89: 428-434.

Jenks, J.A., Leslie, D.M., Jr., Lochmiller, R.L. & Mlechiors, M.A. 1994: Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. - Journal of Mammalogy 75: 1045-1053.

Johnson, R.A. & Wichern, D.W. 1982: Applied multivariate statistical analysis. - Prentice Hall, Inc. Englewood Cliffs, New Jersey, USA, 594 pp.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, R.D., Dale, B.W. & Stephenson, T.R. 2000: Life-history consequences of maternal condition in Alaskan moose. - Journal of Wildlife Management 64: 450-462.

Keech, M.A., Stephenson, T.R., Bowyer, R.T., Van Ballenberghe, V. & Ver Hoef, J.M. 1998: Relationship between blood-serum variables and depth of rump fat in Alaskan moose. - Alces 34: 173-179.

Kie, J.G. 1999: Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. - Journal of Mammalogy 80: 1114-1129.

Kie, J.G. & Bowyer, R.T. 1999: Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. - Journal of Mammalogy 80: 1004-1020.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B. & Loft, E.R. 2002: Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. - Ecology 83: 530-544.

Loison, A., Gaillard, J., Pélabon, C. & Yoccoz, N.G. 1999: What factors shape sexual size dimorphism in ungulates? - Evolutionary Ecology Research 1: 661-633.

Main, M.B. & Coblentz, B.E. 1996: Sexual segregation in Rocky Mountain mule deer. - Journal of Wildlife Management 60: 497-507.

Main, M.B., Weckerly, F.W. & Bleich, V.C. 1996: Sexual segregation in ungulates: new directions for research. - Journal of Mammalogy 77: 449-461.

McCullough, D.R. 1979: The George Reserve deer herd: population ecology of a K-selected species. - University of Michigan Press, Ann Arbor, USA, 271 pp.

McCullough, D.R., Hirth, D.H. & Newhouse, S.J. 1989: Resource partitioning between sexes in white-tailed deer. - Journal of Wildlife Management 53: 277-283.

McGarigal, K. & Marks, B.J. 1995: FRAGSTATS: spatial pattern analysis program for quantifying landscape structure.

- U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technological Report PNW-GTR-351, Portland, Oregon, USA, 122 pp.

Miller, B.K. & Litvaitis, J.A. 1992: Habitat segregation by moose in a boreal forest ecotone. - Acta Theriologica 37: 41-50.

Miquelle, D.G. & Van Ballenberghe, V. 1989: Impact of bark stripping by moose on aspen-spruce communities. - Journal of Wildlife Management 53: 577-586.

Miquelle, D.G., Peek, J.M. & Van Ballenberghe, V. 1992: Sexual segregation in Alaskan moose. - Wildlife Monographs 122: 1-57.

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

Molvar, E.M., Bowyer, R.T. & Van Ballenberghe, V. 1993: Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. - Oecologia 94: 472-479.

Mysterud, A. 2000: The relationship between sexual body size dimorphism in large herbivores. - Oecologia 124: 40-54.

Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. 1996: Applied linear statistical models: regression, analysis of variance and experimental designs. Fourth Edition. - Irwin, Homewood, Illinois, USA, 1127 pp.

Oldemeyer, J.L. & Regelin, W.L. 1987: Forest succession, habitat management, and moose on the Kenai National Wildlife Refuge. - Swedish Wildlife Research Supplement 1: 163-179.

Parker, K.L., Gillingham, M.P., Hanley, T.A. & Robbins, C.T. 1999: Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. - Wildlife Monographs 143: 1-48.

Pérez-Barbería, F.J. & Gordon, I.J. 1999: Body size dimorphism and sexual segregation in polygynous ungulates: an experimental test with Soay sheep. - Oecologia 120: 258-267.

Ralls, K. 1977: Sexual dimorphism in mammals: avian models and unanswered questions. - American Naturalist 122: 917-938.

Ruckstuhl, K.E. 1998: Foraging behaviour and sexual segregation in bighorn sheep. - Animal Behaviour 56: 99-106.

SAS Institute Inc. 1987: SAS/STAT guide for personal computers. Version 6. Cary, North Carolina, USA.

Schwartz, C.C. & Franzmann, A.W. 1991: Interrelationship of black bears to moose and forest succession in the northern coniferous forest. - Wildlife Monographs 113: 1-58.

Schwartz, C.C. & Hundertmark, K.J. 1993: Reproductive characteristics of Alaskan moose. - Journal of Wildlife Management 57: 454-468.

Schwartz, C.C., Regelin, W.L. & Franzmann, A.W. 1985: Suitability of a formulated ration for moose. - Journal of Wildlife Management 49: 137-141.

Schwartz, C.C., Regelin, W.L. & Franzmann, A.W. 1987: Seasonal weight dynamics of moose. - Swedish Wildlife Research Supplement 1: 301-310.

Shipley, L.A. & Spalinger, D. 1995: Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. - Oecologia 104: 112-121.

Shipley, L.A., Blomquist, S. & Danell, K. 1998: Diet choices by free-ranging moose in relation to plant distribution, chemistry, and morphology in northern Sweden. - Canadian Journal of Zoology 76: 1722-1733.

Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T. & Spalinger, D.E. 1999: Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. - Oikos 84: 55-68.

Shipley, L.A., Gross, J.E., Spalinger, D.E., Hobbs, N.T. & Wunder, B.A. 1994: The scaling of intake rate in mammalian herbivores. - American Naturalist 143: 1055-1082.

Sokal, R.R. & Rholf, F.J. 1969: Biometry: the principles and practice of statistics in biological research. - W. H. Freeman and Company, San Francisco, California, USA, 776 pp.

Spaeth, D.F., Bowyer, R.T., Stephenson, T.R., Barboza, P.S. & Van Ballenberghe, V. 2002: Nutritional quality of willows for moose: effects of twig age and diameter. - Alces 38: 143-154.

Spaeth, D.F., Hundertmark, K.J., Bowyer, R.T., Barboza, P.S., Stephenson, T.R. & Peterson, R.O. 2001: Incisor arcades of Alaskan moose: is dimorphism related to sexual segregation? - Alces 37: 217-226.

Stephenson, T.R., Hundertmark, K.J., Schwartz, C.C. & Van Ballenberghe, V. 1993: Ultrasonic fat measures of captive yearling bull moose. - Alces 29: 115-123.

Stephenson, T.R., Hundertmark, K.J., Schwartz, C.C. & Van Ballenberghe, V. 1998: Predicting body fat and body mass in moose with ultrasonography. - Canadian Journal of Zoology 76: 717-722.

Stewart, K.M., Bowyer, R.T., Kie, J.G. & Gasaway, W.C. 2000: Antler size relative to body mass in moose: tradeoffs associated with reproduction. - Alces 36: 77-83.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J. & Johnson, B.K. 2002: Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. - Journal of Mammalogy 83: 220-244.

Storer, R.W. 1966: Sexual dimorphism and food habits in three North American accipiters. - Auk 83: 423-436.

Telfer, E.S. 1969: Twig weight-diameter relationships for browse species. - Journal of Wildlife Management 33: 917-921.

Telfer, E.S. & Cairns, A. 1978: Stem breakage by moose. - Journal of Wildlife Management 42: 639-642.

Van Ballenberghe, V., Miquelle, D.G. & MacCracken, J.D. 1989: Heavy utilization of woody plants by moose during summer in Denali National Park, Alaska. - Alces 25: 31-35.

Vivas, J.H., Sæther, B-E. & Anderson, R. 1991: Optimal twig-size selection of a generalist herbivore, the moose Alces alces: implications for plant-herbivore interactions. - Journal of Animal Ecology 60: 395-408.

Weckerly, F.W. 1993: Intersexual resource partitioning in black-tailed deer: a test of the body size hypothesis. - Journal of Wildlife Management 57: 475-494.

Weckerly, F.W. 1998: Sexual size dimorphism: influence of mass and mating system in the most dimorphic mammals. - Journal of Mammalogy 79: 33-52.

Weixelman, D.A., Bowyer, R.T. & Van Ballenberghe, V. 1998: Diet selection by Alaskan moose during winter: effects of fire and forest succession. - Alces 34: 213-238.

White, K.S., Testa, J.W. & Berger, J. 2001: Behavior and ecologic effects of differential predation pressure on moose in Alaska. - Journal of Mammalogy 82: 442-429.

White, R.G. 1983: Foraging patterns and their multiplier effects on productivity of northern ungulates. - Oikos 40: 377-384.