Foraging behaviour and sexual segregation in bighorn sheep

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ABSTRACT

Like many sexually dimorphic ungulates, bighorn sheep, *Ovis canadensis*, form sexually segregated groups. Nursery groups include females, lambs and subadult males, while adult males form bachelor groups. Previous hypotheses to account for sexual segregation in ungulates have suggested sexual differences in energy requirements, predation risk and social preferences. I tested the hypothesis that differing nutritional demands, due to sexual dimorphism in body size, would lead to different movement patterns and time budgets. If ruminating/foraging schedules differed according to body size, males and females could not synchronize their activities and therefore would segregate by sex. To test this hypothesis, I observed a population of marked bighorns. I recorded the time males and females spent lying, grazing or walking during 8–14 h of focal-animal observations. Initial and final location of groups and steps taken per minute foraging were also noted. Females spent more time foraging and walking and had longer foraging and walking bouts than adult males, but did not differ in numbers of steps taken while foraging. Males spent more time lying than females. Subadult males switched between nursery and bachelor groups and changed their foraging behaviour depending on the type of group they were in. The distance moved was on average almost four times greater for female than for male groups. I suggest that sexual difference in time budgets and movement patterns make it difficult for males and females to stay in the same group and therefore lead to sexual segregation.

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Predator pressure and food distribution are the main forces that lead to sociality and the formation of groups (Hamilton 1971; Ward & Zahavi 1973; Alexander 1974; Bertram 1980; Jennings & Evans 1980; Dehn 1990). Ungulates living in open habitat form groups, and individuals decrease vigilance and increase bite rate with increasing group size (Jarman 1974; Berger 1978; Risenhoover & Bailey 1985a, b; Penning et al. 1993; Molvar & Bowyer 1994). In polygynous ungulates, the sexes form separate groups and are spatially segregated for most of the year (Main & Coblentz 1990; Bon et al. 1992; Main et al. 1996). Sexual segregation is an important problem in the behavioural ecology of ungulates because it is a basic component of their social organization. Although the evolution and the adaptive advantage of sexual segregation are poorly understood, several adaptive hypotheses have been proposed to explain this phenomenon.

Main et al. (1996) classified these hypotheses into three groups: (1) sexual differences in how reproductive strategies affect risk of predation and consequently predator avoidance strategies (reproductive strategy hypothesis;

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Geist 1971; Festa-Bianchet 1988; Berger 1991; Young & Isbell 1991; Bleich et al. 1997), (2) social factors, such as interactions with and preference for same-sex peers, and learning fighting skills (social hypothesis; Clutton-Brock et al. 1987; Bon et al. 1992); and (3) sexual differences in energy requirements and therefore foraging behaviour, choice of habitat types and diet (sexual-dimorphism–body-size hypothesis; Shank 1982, 1985; Seip 1983; Clutton-Brock et al. 1987; Harris & Miller 1995; Main et al. 1996).

Because of their small size, juvenile ungulates are exposed to a greater risk of predation from a greater range of predators than either adult males or adult females. Therefore, females with young may choose sites according to safety from predators rather than quality of the forage (Young & Isbell 1991; Bleich et al. 1997). Males, on the other hand, are larger and therefore less vulnerable to predation than females or young. Large males have a higher reproductive success than small ones, because size is correlated with fighting success and access to females in oestrus (Geist 1971; Clutton-Brock et al. 1982). Because body size is likely to have a greater effect on the reproductive success of males than of females, males might choose sites according to nutritional characteristics rather than safety from predators (Jakimchuk et al. 1987; Main & Coblentz 1990; Miquelle et al. 1992). The

reproductive-strategy hypothesis therefore predicts that sexual segregation should be most pronounced when offspring are most vulnerable to predation.

Bon (1991) suggested that sexual segregation should be separated into spatial and social segregation. He argued that social preferences and segregation develop during the ontogeny of young males and females through the formation of same-sex peer groups. Although this hypothesis has not yet been supported by field evidence, Villaret & Bon (1995) found a clear preference for similar-age peer groups in Alpine ibex, *Capra ibex*.

The sexual-dimorphism–body-size hypothesis predicts that females and males will seek habitats with different forage quality. Males are thought to prefer abundant, low-quality forage, while females are thought to prefer high-quality forage to satisfy high energy demands due to gestation and lactation (Main et al. 1996). Although there is some support for the sexual-dimorphism–body-size hypothesis (Beier 1987; Clutton-Brock et al. 1987), several studies have failed to support its predictions (review in Main & Coblentz 1996; Main et al. 1996).

The sexual-dimorphism–body-size hypothesis has principally been tested in terms of sexual differences in diet or habitat choice, but not in terms of foraging behaviour. If the sexes feed on identical diets but with different foraging behaviours, diet and habitat selection studies would tell us little about sexual segregation. I propose that sexual segregation is based on behaviour differences. Sexual segregation could be explained by sex differences in body size that lead to sexual differences in time spent foraging or duration of alternating grazing and lying bouts. Energy requirements and foraging behaviour are affected by body size. Metabolic rate is allometrically related to body weight and mouth size, while rumen volume and gut capacity are isometric with body weight (Jarman 1974; Demment & VanSoest 1985). So, while specific metabolic rate decreases with increasing body mass, gut capacity remains a constant fraction of body mass (Owen-Smith 1988). Therefore, females should have a higher metabolic rate and higher nutritional need per unit body mass than males. Hence, females will have greater food requirements than males relative to their body mass. A large animal has a large rumen and a relatively low rumen turnover ratio, allowing the food to stay longer in the stomach and therefore to be digested more efficiently than in a small animal with a faster rumen turnover rate (Demment & VanSoest 1985; Illius & Gordon 1992). Consequently, males should have longer ruminating bouts than females. For most ungulates for which data are available, females forage longer than males (Owen-Smith 1988). To compensate for high energy demands, females might not only forage longer, but they could also be more selective while foraging than males. If females forage selectively, they should take more steps and cover more ground than males while foraging (Komers et al. 1993).

I propose that differences in time spent foraging and movement rates alone could explain why the sexes segregate. Although this approach fits into the sexual-dimorphism–body-size hypothesis, it is new because it proposes that time spent foraging and movement rates

are the key factors involved in sexual segregation, rather than differences in diet selection. Despite the large number of studies of sexual segregation, apparently only Seip (1983) proposed that differences in time budgets may explain sexual segregation in sexually dimorphic ruminants. Previous work may have failed to look at the possibility that segregation results from differences in time budgets because the required focal-animal samples of marked individuals lasting several hours are very difficult to obtain for wild ungulates.

Rocky Mountain bighorn sheep are mostly diurnal feeders (Sayre & Seabloom 1994), use open habitats, are very social (Geist 1971) and live in groups year-round. Bighorn sheep are sexually segregated for most of the year and form two main types of groups: bachelor groups (mostly adult males) and nursery groups, consisting of adult females, lambs, yearlings of both sexes and subadult males. In my study area some subadult males up to 3 years old stay in female groups (Festa-Bianchet 1991). At 2 years of age males are slightly larger than adult females and at 3 years they are larger than females (Festa-Bianchet et al. 1996). Three-year-old males move to and stay in adult male groups and are rarely seen in female groups (Geist 1971; Festa-Bianchet 1991). I predicted that 2-year-old males should show foraging behaviour closer to that of adult females than to that of adult males because of similarity in body size with females. Three-year-old males with an intermediate body size between adults of both sexes should show a foraging behaviour that is intermediate between that of adult males and adult females. Two- and 3-year-olds sometimes switch between ewe (female) and ram (male) groups (Geist 1971). I propose that if an animal lives in a group, the best strategy would probably be to do as the other group members, to keep up with the group: it would have to move when they do and follow similar time budgets. Consequently, if 2- and 3-year-old males change between male and female groups, they should adjust their foraging behaviour and movement patterns to those of the group they are in. The choice of groups (adult male or female groups) in 2- and 3-year-old males is probably affected by their body size. As they grow older and bigger they should prefer the company of peers of similar body size to be able to forage optimally and this preference should lead to the formation of adult male groups.

METHODS

Study Area, Animals and Methods

The Sheep River Wildlife Sanctuary is in the foothills of the Rocky Mountains in southwestern Alberta (50°N, 114°W; 1420–1740 m elevation). It is characterized by open south-facing slopes and grassy meadows, intermixed with aspen copses, *Populus tremuloides*, and coniferous forest, mainly white spruce, *Picea glauca*, and lodgepole pine, *Pinus contorta* (Boag & Wishart 1982). Data were collected from April to September in 1994–1996. Observations were made on 51 adult females (17 non- and 34 lactating ewes), 39 adult males, 12 2-year-old, and 18 3-year-old males. All sheep were individually

marked with plastic ear tags and their exact age was known because they were marked as lambs. Females were considered adults at 3 years of age, males from the age of 4. At 3 years of age, females are almost full-grown and they usually have their first or second lamb. Two-year-old females were excluded from the analysis because sample size was too small. Before the age of 4, males are smaller than adult rams; 3-year-old rams are about the same size as ewes or slightly bigger (Festa-Bianchet et al. 1996). Adult bighorn rams are about 50% heavier than females by 4 years of age and sexual dimorphism increases with age at least up to 6 years (Festa-Bianchet et al. 1996). Observations were made with Leica Binoculars (10 × 42) and a Bushnell spotting scope (25–40 × 60 zoom). The sheep were habituated to people and easily observable.

To construct individual time budgets (time spent grazing, lying or walking), one or two observers selected up to 20 marked sheep and observed them for 8–14 h. I used lying time as a measure of ruminating time, because sheep seemed to be ruminating most of the time when lying but it was impossible to assess rumination if sheep faced away from the observer. Time budgets shorter than 8 h were discarded. We attempted to distribute observations over all daylight hours. For each focal animal, the transition time from one behaviour to another was recorded. Behaviour that lasted less than a minute was not recorded. If a sheep changed its behaviour for 1 min or more I considered that it had started a new activity bout. The date, time, location, identity, age and sex of the focal sheep and the number and sex-age classes of animals in the group were noted. I tried to sample the sexes equally across months. This was not always possible as there were fewer females in the study area in summer than in spring or autumn (see Fig. 1 for sample sizes). A total of 12 855 sheep-h of observation were collected.

To measure individual step rate, I counted the numbers of steps each focal sheep took per min grazing. Each animal was observed for 10 times, 1 min per observation session. A total of 140 h of step-rate counts were collected.

To assess the distance travelled by a group during time budgets, I noted the initial and final location as coordinates on a map and calculated the shortest distance between starting and ending points. I then calculated the distance travelled per hour, by dividing the total distance travelled by the hours of observation. If a group travelled but returned to its initial location at the end of the observation period, I calculated the distance travelled as zero. Therefore, I did not measure the total amount of travel, but rather the distance groups travelled away from their original location, which is more pertinent to an understanding of sexual segregation. For example, if females moved to graze somewhere and then returned to the same area, males could remain in the same groups simply by moving in the same general direction but over a shorter distance. If females did not return, males would have to follow female groups to stay with them. Map coordinates noted during time-budget observations were used to assess if ewes and rams were using the same locations.

Data Analysis

Data were tested for normality (normal probability plots, Lilliefors test) and homoscedasticity (Bartlett-Box F) using the SPSS statistics package (Norusis 1994). Some sheep were sampled several times and I calculated the mean duration of grazing, resting and walking bouts for each individual each month to reduce pseudoreplication (Machlis et al. 1985; Leger & Didrichsons 1994). I waited at least 1 week between observations on the same individual. Mean duration of grazing and lying bouts were log-transformed and percentages were arcsine square-root transformed (Zar 1984). Mean duration of and percentage of time spent walking and step rates were not normally distributed and therefore were analysed with nonparametric Mann–Whitney U tests. One-way ANOVAS were used to verify whether sex affected the mean duration of activity bouts and the percentage of time spent in different activities, and whether time budgets of young males differed in different types of groups. A two-way ANOVA was used to test the effect of month and sex on the percentage of time adult males and females spent foraging. Multiple comparisons of nonparametric data were done using Mann–Whitney U tests (Siegel & Castellan 1988) with Bonferroni adjusted P values. In the results section means are followed by standard errors (SE). Where nonparametric statistics are applied, the median is given with the interquartile range.

RESULTS

Time Spent Grazing or Lying and Mean Duration of Activity Bouts of Adults

The database included 266 focal observations of females and 354 observations of adult males. Ewes and rams spent at least 80% of the daytime grazing or lying and ruminating. Ewes spent more time grazing than males in all 6 months of observation (Table 1; two-way ANOVA: sex: $F_1=135.13$, $P<0.001$; month: $F_5=45.72$, $P<0.001$, interaction: $F_5=0.96$, $P=0.44$; Fig. 1). Females also had longer grazing bouts than males (one-way ANOVA: $F_{1,620}=18.43$, $P<0.001$). Rams accordingly spent much more time lying and had significantly longer lying bouts than ewes (Table 1; $F_{1,620}=193.5$, $P<0.001$ for time spent lying, $F_{1,620}=21.74$, $P<0.001$ for duration of lying bouts).

Effect of Group Type on Foraging Behaviour of Young Males

Two-year-old males had significantly longer grazing bouts ($F_{1,85}=13.27$ $P<0.001$) and lying bouts in nursery than in bachelor groups ($F_{1,85}=10.05$, $P<0.01$; Table 2). However, 2-year-old rams did not differ in the time spent grazing ($F_{1,85}=2.24$, $P=0.14$) or lying ($F_{1,85}=0.95$, $P=0.33$) with ewes and with adult rams (Table 1). Three-year-olds only changed the duration of lying bouts when they shifted between ewe and adult ram groups ($F_{1,103}=7.45$, $P<0.01$). Grazing-bout duration ($F_{1,103}=0.71$, $P=0.4$) or the percentage of time spent lying ($F_{1,103}=3.48$, $P=0.06$)

Table 1. Mean (±SE) duration of grazing and lying bouts and per cent time spent grazing and lying per observation period (8–14 h) for 2- and 3-year-old bighorn sheep rams in ewe and in adult ram groups, and for adult ewes and rams

| | Group type | Bout duration (min) | | % Time | | |
		Grazing	Lying	Grazing	Lying	N
2-year-old rams	Ewes	31±2.0	37±2.4	46±1.7	46±1.7	66
	Rams	20±2.1	26±2.2	41±3.8	50±3.5	20
3-year-old rams	Ewes	28±3.1	43±3.6	43±3.0	49±3.1	29
	Rams	24±1.3	34±1.5	38±1.2	54±1.1	75
Adult ewes	Ewes	37±1.1	36±0.7	53±0.8	39±0.7	266
Adult rams	Rams	29±0.7	40±1.0	38±0.5	53±0.4	35
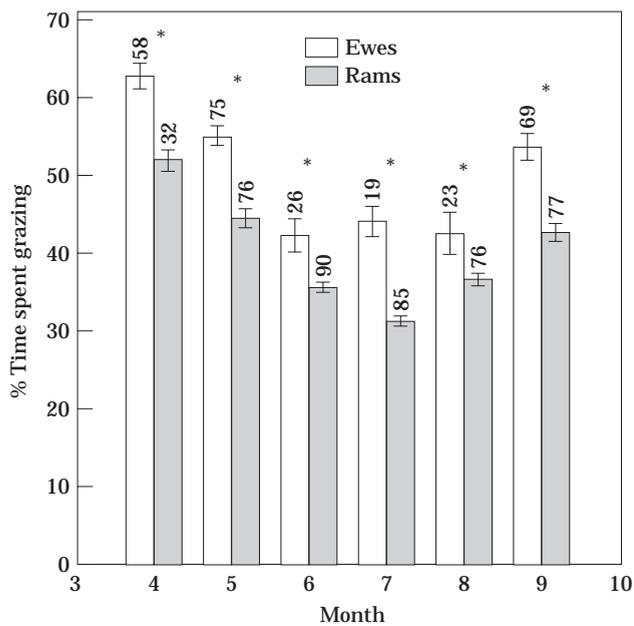
Figure 1. Mean (+SE) per cent time spent grazing by bighorn ewes and rams during 8–14 h of observations. Months 4–9: April–September 1994–1996. Numbers of observations appear above each bar, each month. *$P<0.001$, all pairwise comparisons were made with Mann–Whitney U tests. Adjusted significance level was set at $P=0.008$.

and grazing ($F_{1,103}=2.66$, $P=0.11$) were not affected by group type (Table 1).

Movement Patterns and Sheep Locations

Females spent a median of 0.8% (range 0.2–1.6%; $N=266$) of their time walking compared with a median of 0.4% for males (range 0–1%, $N=354$) ($Z_1 = -4.13$, $P<0.001$). Females also had longer walking bouts than rams (ewes: 2 min, range 1–3 min; rams: 1.2 min, range 1–2 min; $Z_1 = -4.35$, $P<0.001$). Females moved a median of 40 m/h (range 12–75 m, $N=66$ groups) away from their initial location, while males travelled a median of 11 m/h (range 0–50 m, $N=76$ groups). So female groups travelled nearly four times as far as male groups each hour ($Z_1 = -4.2$, $P<0.001$). This result was consistent for all 6 months of observation (Table 2, all comparisons with

P values <0.001, with an adjusted significance level of 0.008, Mann–Whitney U tests). There was no significant difference in the number of steps/min by adult rams and ewes ($Z_1 = -1.86$, $P=0.063$). Ewes ($N=283$ observations) took on average 4.8 (range 3.5–6.5) steps/min, while rams ($N=372$) took on average 5.2 (range 3.8–6.9) steps/min. The step rate of 2- and 3-year-old males did not differ from adult ewes ($Z_{100,1} = -1.5$, $P=0.13$) or from older rams ($Z_{62,6} = -1.6$, $P=0.11$). Two-year-olds took on average 6.3 (range=4.1–8.1) steps/min and 3-year-olds took 5.7 (range 3.8–6.9) steps/min. Ewe and ram groups were found in the same locations most of the time (Fig. 2), except there were a few locations in the southwest portion of the study area preferred by ewes, and some locations in the northwestern and southeastern portions of the study area preferred by rams.

DISCUSSION

Differences in Time Budgets

Bighorn sheep, like most ungulates, spent most of their active time foraging (Hudson 1985). They are mainly active during the day and seldom if ever feed at night (Sayre & Seabloom 1994). Ewes spent more time foraging per observation period, and had longer foraging bouts, than adult rams. Rams accordingly spent more time lying than ewes and had significantly longer lying bouts. Previous studies on a wide range of ungulates also found that females spent more time foraging than males (Bunnell & Gillingham 1985), but long-duration time-budget data on marked individuals of both sexes do not seem to exist, or are based on a few marked individuals. The only other study with a large number of marked individuals was on red deer (Clutton-Brock et al. 1982). Red deer hinds spent much more time foraging than stags during the summer. My study shows a clear difference in foraging behaviour between males and females. What could be the consequences of such differing behaviour for sociality and group structure?

If staying in the same group demands that the animal synchronizes its behaviour with that of other group members, membership in the opposite-sex group would entail lower foraging efficiencies for females that stay in male groups or lower digestive efficiencies for adult males that stay in female groups. Synchronization of foraging

Table 2. Distances travelled (medians and interquartile ranges) in m/h by bighorn sheep ewe and ram groups observed from April to September (1994–1996)

	April	May	June	July	August	September
Ewes	20 (0–87)	60 (34–79)	30 (10–43)	89 (37–116)	26 (13–47)	42 (12–103)
N	12	21	9	6	4	14
Rams	0 (0–37)	12 (0–50)	22 (10–70)	12 (0–50)	0 (0–19)	0 (0–78)
N	4	11	16	18	16	11
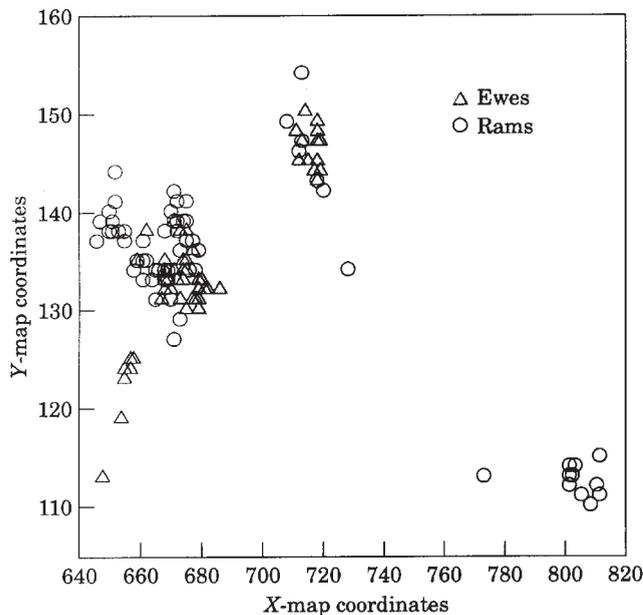
Figure 2. Locations of ewe and ram groups during 143 time-budget observations collected April–September 1994–1996. X- and Y-axes are map coordinates.

behaviour by an individual greatly different in size from the rest of the group would probably result in a cost for that individual. Subadult males changed their behaviour according to the type of group they were in. Two-year-old males changed their activity bout duration when they changed groups. The duration of an activity bout may therefore determine which individuals stay in a particular group. If the duration of lying bouts were very different, some animals would move away while grazing, while others stayed bedded. When 3-year-old males were with ewes, their activity bout durations were similar to those of adult rams, but when they were with adult males, their activity bouts were shorter. This is probably why 3-year-olds were not often seen in ewe groups, as indicated by the low number of time budget observations of 3-year-olds in ewe groups. The same was true for 2-year-olds in adult ram groups. In the same population of bighorn sheep, Festa-Bianchet (1991) found that 60% of 2-year-old and 20% of 3-year-old rams stayed in female groups. That 2-year-old males had short grazing and lying bouts in adult male groups is surprising and difficult to interpret. Because of their body size, 2-year-olds should have longer foraging bouts than adult males, and 3-year-olds should have longer lying bouts than females. There are

two possible explanations for why my results do not confirm this prediction. One is that young males may interact much more with each other in male groups and would therefore interrupt their activity bouts more often, leading to shorter grazing and lying bouts. The other explanation is that young rams in adult ram groups may not have to synchronize their behaviour with those of adult males as much as they would with females, because male groups do not move far while foraging. Subadult males could therefore show very different behaviour and still keep up with bachelor groups, but they would have to synchronize their behaviour with those of moving females to stay within nursery groups. Two-year-old males seemed to synchronize their foraging bouts with those of the group when they were with females, but not when they were with adult males. Three-year-old males, in contrast, did not synchronize their behaviour with those of adult males or females and showed foraging/lying bout durations that were somewhat independent of the group they were in. Because activity bouts were sometimes interrupted by either standing or walking for more than a minute, the actual time sheep spent grazing before lying down (and vice versa) is not necessarily reflected. The percentage of time ewes and rams spent grazing or lying is a better measurement of behavioural differences between the sexes. Indeed, differences in percentage of time spent lying or grazing were in the expected direction. Ewes and rams differed greatly in the percentage of time spent foraging and lying. The behaviour of 3-year-old rams was similar to that of adult rams, while the behaviour of 2-year-old rams was intermediate between that of adults of both sexes. The behaviour of young males provides strong support for the hypothesis that adult males and females segregate because of differences in foraging behaviour. In female groups, 2- and 3-year-olds would have to adjust their behaviour to the rest of the group; and in adult male groups, young rams, which are much smaller than adult rams, might be more vulnerable to predation, either because adult rams take more risks while foraging or because young rams could be easily detected and selected by predators in adult male groups. So the best strategy for young males would be to form a group of similar-age, same-sex peers. Villaret & Bon (1995) found that in Alpine ibex 2- and 3-year-old males sometimes formed groups of their own. In my study area the number of 2- and 3-year-olds was low (two to three per age each year from 1994 to 1996) and they never formed a separate group, but Festa-Bianchet (1991) found that 29% of 2-year-old rams formed peer groups in June in previous years, when numbers of sheep were

higher. Two-year-olds mostly associated with females and only rarely with adult males, while 3-year-olds were mostly in ram groups. For young males that stay in female or adult male groups, there might be a trade-off between predator protection in the group and adjustments/synchronization of their foraging behaviour, which could have a negative effect on their foraging time budgets and energy assimilation. Being in a group was shown to have advantages in terms of predator avoidance strategies: vigilance in mountain goats, *Oreamnos americanus*, and bighorn sheep decreased and foraging efficiency increased with more than five animals in a group (Risenhoover & Bailey 1985a, b). The same pattern was found for domestic (Penning et al. 1993) and Dall's sheep, *Ovis dalli dalli* (Frid 1997). Because there were only two or three subadult rams per year during my study, it might be that their numbers were not sufficiently large to form a group of their own. Therefore 2-year-old males with similar body size and foraging behaviour to that of females should stay in female groups, while 3-year-olds that are closer in their behaviour and body size to adult rams should stay in ram groups, unless they are numerous enough to form a group of their own. Therefore, I would predict that the time at which young rams switch from female to male groups depends on their body size and ultimately their foraging behaviour and movement rates. In larger populations one should see segregation not only by sex but (among males) also by age, as reported by Festa-Bianchet (1991) and Villaret & Bon (1995).

Differences in Time Spent Walking, Step Rates and Movement

Females spent more time walking and had longer walking bouts than males, but rams and ewes did not differ in their step rate. Komers et al. (1993) found that in bison, *Bison bison*, cows had a higher step rate than bulls, and they attributed this difference to higher food selectivity in cows than in bulls. They concluded that differences in step rate lead to temporal but not spatial segregation of the sexes. If step rate was a measure of selectivity, it could be concluded that in my study, rams and ewes did not differ in their forage selectivity. Males and females were observed in the same general locations in the majority of cases (Fig. 2), and protein content in faeces of rams and ewes was not significantly different (unpublished data). Seip (1983) also found no differences in faecal protein of Stone sheep, *Ovis dalli stonei*, ewes and rams, which suggests that ewes were not more selective that rams. Shank (1982), who studied bighorn sheep in winter, found that males and females were spatially segregated, but he concluded that this segregation was not due to diet preferences. Nevertheless, Bleich et al. (1997) found that ewes and rams in desert bighorn sheep, *Ovis canadensis nelsoni*, used the same range year-round but that they differed in their use of vegetation types and plant species when they were segregated, and that rams used areas with higher forage biomass than females. Rams had higher crude protein levels in their faeces than ewes in 2 out of 3 years. It appears that bighorn sheep rams and ewes differ in their habitat and food selection in some areas, but not in others. Therefore, differences in habitat selection are not sufficient as a general explanation for sexual segregation.

Female groups in my study area travelled on average almost four times the distance travelled by ram groups. Ewes travelled while foraging, but they also moved between foraging bouts. Although ewes and rams did not differ in number of steps per minute while foraging, longer foraging and walking bouts and the longer time spent grazing would lead to a greater number of steps taken by ewes than by rams. If ewes spend on average 445 min (53% of 14 h) of each day grazing and take an average of 4.8 steps/min, while rams spend 319 min (38%) grazing and take 5.2 steps each min, then ewes take a total of 2136 steps compared with 1660 steps taken by males. The difference in numbers of steps alone could lead to spatial segregation unless the ewes move back and forth while foraging. Bleich et al. (1997) concluded that bighorn sheep ewes in their study area chose habitat that was safe from predators, while rams were choosing habitats with high-quality forage. Although my results suggest that it is not necessary to invoke differences in predation risk to explain sexual segregation, it remains likely that sexual differences in habitat selection are affected by predation. It is usually assumed that male ungulates are less vulnerable to predation than females with young or that they take higher risks while foraging (Sukumar & Gadgil 1988; Geist 1971). Indeed, Bleich et al. (1997) found that male mountain sheep used areas with higher predator densities than females. The main predators of sheep in my study area are cougars, *Felis concolor* (Ross et al. 1997), coyotes, *Canis latrans*, and wolves, *Canis lupus*. Coyotes are the most common predators, but only lambs are at risk from coyote predation. Proximity to escape terrain is very important in the habitat choice of female bighorn sheep with lambs, but they must leave the escape terrain to forage (Shannon et al. 1975; Bleich et al. 1997). By moving a lot while foraging, ewes with lambs may be less spatially predictable for predators and could therefore reduce their risk of predation. The greater distance moved by females in this study could therefore be part of a predator avoidance strategy.

A New Approach to Sexual Segregation

Differing predator avoidance strategies and differing time budgets are probably key factors leading to segregation of the sexes. To stay in female groups, males would have to synchronize their movement patterns and foraging behaviours to those of females, with less time lying and ruminating and greater movement rates. For adult males, shorter rumination bouts and less time spent ruminating could lead to a decrease in digestion efficiency and consequently energy assimilation. Therefore it would not be a good strategy for males to adjust their activity budgets to those of females. Females on the other hand need to reduce the risk of predation to lambs. They do so by choosing habitat that is safer from predation than the areas used by males, and by making themselves less predictable by moving more than males. Sexual dimorphism in body size leads to sexual dimorphism in

foraging behaviour. Sexual differences in vulnerability to predators lead to sexual dimorphism in predator avoidance strategies. Therefore, it seems evident that males and females would not benefit from forming mixed-sex groups.

I propose the body-size–predation hypothesis, that the larger males cannot forage with the smaller females due to differences in foraging behaviour (body size effect) and movement patterns (predator avoidance). Therefore the best strategy for adults of each sex is to segregate into different groups. Clutton-Brock et al. (1987) suggested that male and female red deer on Rum segregate because females out-compete males from closely grazed swards of grass due to differences in incisor size. Although this may be true on overgrazed ranges, it does not explain sexual segregation for ungulates in general (see also Bleich et al. 1997). I predict that males and females in sexually dimorphic ungulates would segregate even in the absence of competition for food. Differences in body size that lead to differing foraging behaviours and movement rates could explain why the sexes segregate in the absence of diet or habitat selection, or in environments without predators. In my study, males and females used the same areas, which makes it more evident that behavioural differences alone could lead to the segregation of the sexes. If males and females form different groups because of different time budgets and movement rates, sexual segregation for gregarious ungulates should increase with sexual dimorphism.

Acknowledgments

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