ORIGINAL ARTICLE

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Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex and reproductive status

Abstract We investigated the effects of vegetation biomass, crude protein content of consumed forage, age, sex and reproductive status on bite rates in Rocky Mountain bighorn sheep. We expected higher bite rates and vigilance in lactating females with young and higher bite rates in young growing individuals, than in non-reproducing females or rams. Lactating ewes had higher bite rates than yeld ewes and than subadult or adult rams. Subadult rams had higher bite rates than adult rams or yeld ewes. On recently burned grassland in spring, however, rams had a higher bite rate than adult females, while the contrary was true on control plots and on the burned plots in autumn. Bite rates declined for both ewes and rams from April to September and varied from year to year. While rams of different ages had significantly different bite rates, there was no effect of age on bite rates for ewes. There was no correlation between bite rates and available total biomass or biomass of live vegetation, or the numbers of steps taken while foraging for either ewes or rams. Adult rams had a lower vigilance rate than adult ewes, and vigilance decreased with increasing bite rates for all sheep. Bite rates in bighorn sheep vary greatly according to age, season and vegetation structure. An increase in bite rates during the forage growing season may compensate for higher energy demands during lactation and growth. There is a potential trade-off between foraging and vigilance as vigilance decreased with increasing bite rates.

Keywords Ungulates · Bite rate · Cropping rate · Foraging behaviour

Communicated by A. Cockburn

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Introduction

The aim of our study was to investigate whether forage and individual characteristics affect bite rates in Rocky Mountain bighorn sheep, a sexually dimorphic ruminant. How much food an individual ruminant ingests per day depends on the time spent feeding and the rate at which it can crop forage (Hudson 1985; Spalinger and Hobbs 1992). Although many studies have measured the time spent feeding by ungulates, little is known about individual variability in cropping rates (Bunnell and Gillingham 1985). The limited attention paid to variability in cropping or bite rates may limit our understanding of how individuals may adjust foraging behaviour according to changes in nutritional or energetic requirements, because bite rate may be more flexible than the actual time spent foraging. An individual's bite rate can be affected by many factors such as the quality and biomass of the vegetation, its satiation level and body size, incisor bar width and shape, but also the trade-off between foraging and security from predation, and social conflicts (Arnold 1985; Gross et al. 1993, 1995; Hudson 1985; Illius and Gordon 1992; Lovari and Rosto 1985; Mysterud 1998; Shipley et al. 1994; Wilmshurst et al. 1999). In ungulates, bite size is correlated with the width of the incisor bar (Clutton-Brock and Harvey 1983) but it is most affected by the attributes and quality of the vegetation (Clutton-Brock and Harvey 1983), at least for grazers (Parsons et al. 1994; Pérez-Barberia and Gordon 2001; Renecker and Hudson 1993; Wilmshurst et al. 1999).

The time available for foraging and the bite rate may limit an individual's daily forage intake and therefore affect its body condition, reproductive success and survival. In addition to satisfying its daily food requirements, ruminants in northern or mountain environments must accumulate enough fat during the growing season to reproduce and to survive the seasonal shortage of food during winter (Bruno and Lovari 1989).

Growing animals and lactating females generally have a higher energy requirement than mature or non-reproducing individuals (Robbins 1983). In many ungulate species, they are also considerably smaller than adult males (Owen-Smith 1988; Weckerly 1998). Lactating Nubian ibex (*Capra ibex nubiana*, Linnaeus 1758) females, for example, consume approximately 50% more food per kg of body weight than either adult males or non-lactating females (Gross et al. 1996). In that species, adult males are more than 130% heavier than adult females (Gross et al. 1995). Because there is an upper limit to the time that an animal can forage per day (Hudson and White 1985), increased energy demands should also lead to an increase in cropping rates. Furthermore, bite sizes may be used as a behavioural tool to increase intake rate in grazing animals (Newman et al. 1994). Individual bite rates should therefore be affected by an animal's age, sex and reproductive status. We predicted that bite rates would decrease with age for non-reproducing individuals and would be higher for reproducing females and growing animals than for non-reproducing females or for adult males.

A previous study on the same bighorn population reported that males and females did not differ in faecal crude protein, an indirect measure of forage quality (Ruckstuhl et al. 2000). Any sexual difference in bite rates is therefore not due to sexual differences in the quality of forage selected. Nevertheless, as the vegetation and the available forage biomass are presumed to be important factors affecting cropping rates in ungulates (Renecker and Hudson 1993), we expected bite rates to vary with season and between years. Bite rates should be high early in the season when newly growing forage has low biomass but is easily digestible, and lower later in the summer when forage biomass is high, but of lower quality. As newly growing forage on grassy meadows in our study area is usually sprouting under a dead layer of previous growth (Ruckstuhl et al. 2000), it can be difficult to assess bite rates on new forage as new growth is ingested simultaneously with the old standing crop. To obtain patches with only newly emerging forage and to study the effects of an increase in forage quality, we burned grassland plots and studied differences in bite rates of male and female bighorns when feeding on burned and control plots.

While feeding, animals must also be vigilant to avoid predation, leading to a trade-off between foraging and alertness (Bergman et al. 2001; Hudson and White 1985; McNamara 1990). We predicted that an individual's vigilance should decrease with increasing bite rate, as these behaviours may be mutually exclusive (but see Illius and FitzGibbon 1994, who proposed that ungulates could remain vigilant while chewing vegetation and therefore pay no cost for vigilance). Lambs are more vulnerable to predation than adults. For example, in our study area adults are unlikely to be preyed upon by coyotes (*Canis latrans* L.), but coyotes regularly prey on lambs. Therefore, we expected lactating females to be more vigilant than non-reproducing females or males, as mothers may need to be more vigilant to prevent predation on their offspring.

Methods

Data sampling

We observed bighorn sheep in the Sheep River Wildlife Sanctuary, in south-western Alberta (lat. 50° N, long. 114' W; 1,420–1,740°m elevation). Forage in the Sheep River Wildlife Sanctuary is abundant throughout the year, and the vegetation consists mainly of open grassy meadows, with low species diversity, intermixed with aspen (*Populus tremuloides*) copses (for more details see Boag and Wishart 1982).

Observations lasted from April to September in 1994–1996. All sheep were individually marked with plastic ear tags and their exact ages were known because they were marked as lambs or yearlings. Observations were made with binoculars (10×42) and a spotting scope (25–40×60). The sheep were habituated to people and most observations took place at distances of 30–100 m.

To measure bite, step, and vigilance rates, a focal foraging sheep was selected randomly from a group. The individual was then observed 10 times each for 1-min focal samples. One-minute focal samples were followed by an interruption of a few seconds to record data on a spreadsheet. If the animal itself interrupted feeding (biting vegetation) for more than 30 s the observation was discarded and the animal re-sampled or data collection resumed once the individual restarted or continued foraging, until ten 1-min samples were collected. During each of these ten minute-long episodes of focal observation, the number of bites, steps (a forward motion with either of the front legs was counted as a step) and vigilance postures were counted. A bite consisted of gathering vegetation with the muzzle followed by an upward jerking movement of the head. Sheep were considered to be vigilant when they interrupted foraging and raised their head above shoulder height (Frid 1997). While sheep could simultaneously take steps and forage or take steps and be vigilant, they could not be vigilant and bite vegetation at the same time. These two behaviours are therefore mutually exclusive. However, within a 1-min observation, sheep could show other behaviours such as standing and chewing, grooming, scratching the ground etc. For a 1-min focal sampling to count the individual had to spend the majority of that 1-min foraging; otherwise the observation was discarded. This procedure was adopted because we were interested in measuring bite, step and vigilance rate during foraging bouts. The rate then refers to the number of occurrences of these behaviours per time interval. Such sampling methods are commonly used to measure rates of specific behaviours (Martin and Bateson 1993).

Observations were distributed over all daylight hours, although analyses revealed no effect of the time of the day on bite, step or vigilance rates. A total of 147 h of observation data was collected during three consecutive field seasons, counting bite rates of 126 adult and 36 subadult ewes and 68 adult and 40 subadult rams.

During our study, only 3 of 13 2-year-old ewes had lambs, while over 90% of ewes 3 years of age and older reproduced. Two-year-old ewes have not completed body growth and may need to forage more than older ewes independent of reproductive status, to satisfy the metabolic requirement for growth (Festa-Bianchet et al. 1996). Ewes were therefore considered adults at 3 years of age or older, and rams at the age of 4. Males younger than 4 years are visibly

smaller than older males. Bighorn rams are about 60% heavier than ewes by 4 years of age and sexual dimorphism increases with age at least up to 6 years (Festa-Bianchet et al. 1996).

Parturition occurs in late May and early June (Festa-Bianchet 1988a). Ewes were classified as pregnant or yeld according to whether or not their udders were visibly swollen or the ewe was seen nursing a lamb. Additionally, each ewe's faeces were collected and frozen in April/May (last month of gestation). Faecal samples of ewes not seen with swollen udders or nursing a lamb were tested for pregnancy by a faecal-based enzyme immunoassay (Borjesson et al. 1996). After parturition, the reproductive status of individual ewes was measured by noting whether or not they nursed a lamb in early summer. A ewe's reproductive status was determined for each month. If her lamb survived to October, the ewe's reproductive status was rated as 1 for each month. If the lamb died before October, her status was rated as zero after the lamb's death (Ruckstuhl and Festa-Bianchet 1998). If the ewe was pregnant but was never seen with a lamb, her reproductive status was rated as 1 in April and May and thereafter as zero.

Statistical analyses

Data were tested for normality (normal probability plots followed by Lilliefors test) and homoscedasticity (Bartlett-Box F) using the SPSS statistics package (Norusis 1993). Means are followed by standard errors (SE). For statistical analyses, we used the average from each of the ten 1-min observations as one data point for each individual per month. We attempted to sample each individual once a month. The month is therefore the unit of replication. However, as not every individual (ID) was resampled each month and year, a problem of pseudoreplication may exist. To test for this, we performed a general linear mixed model with ID as a random model (REML in Genstat 5). The test confirmed that resampling certain individuals more than others did not affect the overall results [the estimated variance component for ID was not significant (estimated variance component=0.01, SE=1.35)]. We therefore subsequently used general linear models (GLM) in our analyses, using SPSS, and did not have to control for pseudoreplication.

We then did an overall analysis of the effects of age, sex, sex-age class, reproductive status and month on bite rate, steps taken and vigilance postures using GLM. Sheep were classified into three sex-age groups: adult ewes, 2- to 3-year-old rams and adult rams. We used non-parametric statistics for small sample sizes or non-normally distributed data. Because distribution of some data was non-normal, we tested for correlations between vigilance rate, step rate and bite rates using Spearman rank correlation tests (Siegel and Castellan 1988).

Experiments and further statistical analyses

Three different grassland plots were burned in April during three consecutive years. We compared bite rates in burned versus control sites. Within each of these areas one side of the site was burned, and the adjacent side left as a control. The burned areas were large enough to attract groups of grazing bighorn sheep: the smallest of the three burns covered an area of 100×50 m, the two other burns covered 150×250 m and 250×500 m respectively. More details on the burns are provided in Ruckstuhl et al. (2000).

To estimate forage quality (percent crude protein) and quantity (biomass of dried vegetation) available to the sheep, vegetation samples were collected from each burn and adjacent control site. At each site, five randomly selected 25×25 cm vegetation quadrats were clipped to ground level twice a month from May to July and once in August and in September, for a total of eight sampling dates (40 random samples/site) each year. Samples were oven-dried at 50 °C, weighed for total biomass, and later analysed for crude protein content with the Kjeldahl method (Robbins 1983). We first tested for a correlation between forage crude protein content, available biomass of forage and bite rates by using a Pearson rank correlation. We then investigated the effect of available biomass

and live vegetation on bite rates in rams and ewes separately using simple linear regressions. Finally, we investigated whether adult rams and ewes differed in the number of bites taken on recently burned compared to control areas in spring, using GLM and Mann-Whitney-U tests (in cases of non-normal distribution of data). The data on bite rates from the experiment were not used in any other analyses.

Results

The overall analysis revealed that sheep of different sex-age classes had different bite rates (GLM: model $F_{80, 784}=18.38$, $P<0.0001$; sex-age class $F_{3, 784}=12.30$, $P<0.001$; see below) and that the reproductive status of ewes affected the number of bites taken ($F_{2, 784}=4.56$, $P<0.05$). There were, however, no significant differences according to age, month or year and no significant interaction between different variables (largest $F=1.44$, $P=0.24$). Lactating ewes had higher bite rates than yeld ewes and than subadult or adult rams. Subadult rams had higher bite rates than adult rams and yeld ewes (Scheffé post-hoc tests all $P<0.05$, Fig. 1).

While rams of different ages had different bite rates ($F_{8, 495}=3.31$, $P<0.01$; month $F_{5, 495}=23.57$, $P<0.0001$; $F_{age×month}=1.80$, $P<0.01$) there was no effect of age on bite rates of ewes ($F_{14, 270}=0.38$, $P=0.98$; month $F_{5, 277}=38.92$, $P<0.0001$; $F_{age×month}=0.97$, $P=0.55$, pooled data for lactating and non-lactating ewes; Fig. 2). Bite rates of rams and ewes (all ages pooled) decreased from April to September (rams: $F_{5, 497}=206.27$, $P<0.0001$; ewes: $F_{5, 277}=206.30$, $P<0.001$; Fig. 3) and varied from year to year (rams: $F_{2, 500}=22.47$, $P<0.001$; ewes: $F_{2, 280}=11.58$, $P<0.001$; Table 1).

Interestingly, males took more bites per minute than females on the burned areas (males: 59±1 bites/min, $n=22$, females: 53±2 bites/min, $n=18$; $Z=−2.51$, $P<0.05$)
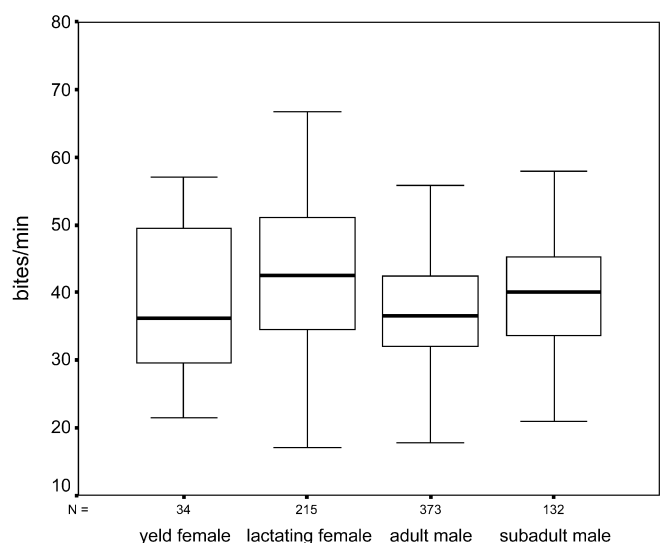

Fig. 1 Bite rates of yeld and lactating ewes, subadult and adult bighorn sheep rams. Displayed are means with interquartile ranges and minima and maxima. *N* Number of 10-min observations

Table 1 Bite rates of male and female bighorn sheep in the years 1994, 1995 and 1996. Listed are means±SE, and number of observations

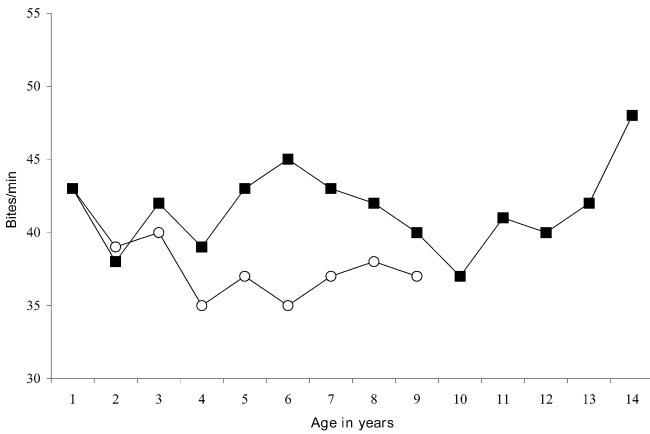| Sex	1994	1995	1996
Female	38.35±0.67 (103)	45.27±1.07 (93)	41.25±1.07 (125)
Male	35.68±0.42 (160)	41.08±0.63 (164)	36.23±0.65 (179)

Fig. 2 Effect of age on bite rate in male (*open circles*) and female (*bold squares*) bighorn sheep
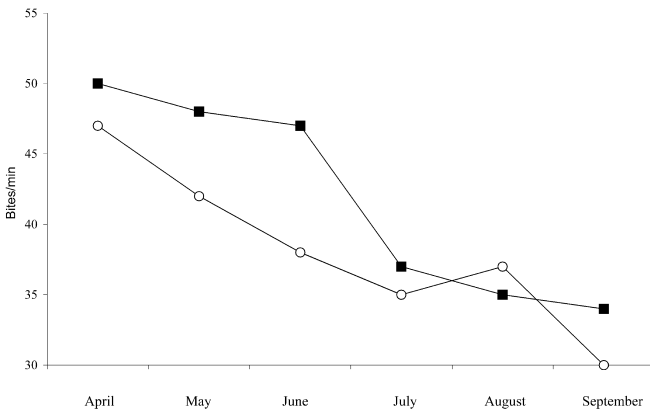

Fig. 3 Bite rates of adult male (*open circles*) and female (*bold squares*) bighorn sheep from April to September (1994–1996)

Fig. 4 Number of alert postures per minute in adult male (*open circles*) and female (*bold squares*) bighorn sheep from April to September (1994–1996)

in spring, but this sexual difference was absent in autumn ($F=2.72$, $P=0.13$). In May, dry weights of vegetation samples taken from 25×25 cm quadrats were on average 10.1±1.1 grams on the burned sites, compared to 34.1+2.0 g for control samples. By mid-August, total biomass of dried vegetation was similar on burned and control sites (both at 37.0±0.8 g/25×25 cm).

There was no correlation between bite rates and available total biomass or biomass of live vegetation for either ewes or rams (Spearman rank order correlation coefficients for ewes: $r_{biomass}=0.07$, $P=0.33$, $r_{live vege}=0.03$, $P=0.69$, $n_{ewes}=184$; for rams: $r_{biomass}=0.01$, $P=0.91$, $r_{live vege}=0.001$, $P=0.89$, $n_{rams}=316$), even when we controlled for year effects (smallest $P=0.18$). Nor was there any correlation between number of bites taken per minute and faecal crude protein (CP) content (ewes: $r=0.01$,
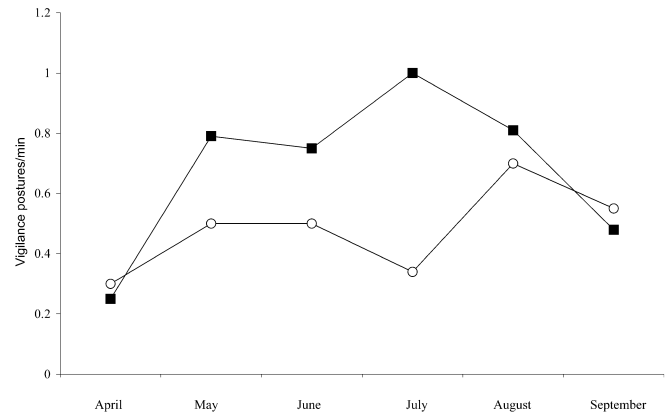
$P=0.97$, $n=47$; rams: $r=-0.13$, $P=0.13$, $n=130$). Contrary to our prediction, there was no correlation between step and bite rates ($r_{Spearman}=-0.002$, $P=0.96$, $n=878$ 10-min observations). This is possibly due to a high variance in bite rates, while step rate remained constant and unaffected by age, sex, reproductive status, month or year (largest $F_{sex}=2.25$, $P=0.13$). Bighorn sheep took on average 5.22±0.10 steps/min while foraging (95% CI=5.11–5.65 steps/min) in all habitats.

Vigilance levels varied according to month and sex ($F_{month}=16.91$, $P<0.0001$; $F_{sex}=36.32$, $P<0.0001$, $F_{month*sex}=2.73$, $P<0.001$; Fig. 4). Overall, adult rams had on average a lower vigilance rate (0.58±0.03 alert/min, $n=282$ observations) than adult ewes (0.76±0.04 alert/min, $n=229$ observations for ewes with lams; 0.76±0.08 alert/min, $n=57$ observations for ewes without lambs). Only month, not reproductive status, affected differences in vigilance rates within adult females ($F_{month}=4.86$, $P<0.001$; $F_{reprostat}=0.55$, $P=0.65$; $F_{month×reprostat}=1.49$, $P=0.14$). Vigilance decreased with increasing bite rates for all sheep ($r_{Spearman}=-0.25$, $P<0.001$, $n=878$ observations).

Discussion

Bighorn sheep have variable bite rates, depending on the month of the year, the year, reproductive status and sex-age class. A previous study on the same population of sheep showed that biomass and quality of vegetation also varied among seasons and years (Ruckstuhl et al. 2000). Contrary to our predictions, however, the quantity or quality of the vegetation was not correlated with bite rates. There are several factors which could affect bite

rates within as well as between years. Rainfall and temperature, for example, may both affect bite rates, via the quality or quantity of available vegetation. The structure or height of vegetation may affect handling times, and hence bite rates, as was suggested, for example, for wildebeest (*Connochaetes taurinus*, Burchell 1824), hartebeest (*Alcelaphus buselaphus*, Pallas 1766) and topi (*Damaliscus lunatus*, Burchell 1823) (Murray and Brown 1993). Accordingly, bite rates in our study were higher on burned areas than on control areas in spring, possibly because forage biomass was lower on burns than controls. Bite sizes could therefore have been smaller, resulting in reduced handling times and hence higher cropping rates. Higher cropping rates could also be a strategy used by foraging herbivores to compensate for reduced bite sizes on short swards, as bite sizes and bite rates are usually inversely related (Spalinger and Hobbs 1992). As the season progressed, bite rates decreased for both males and females. Decreasing bite rates are likely related to larger bite sizes on longer swards and a concomitant increase in handling times (Bunnell and Gillingham 1985; Parsons et al. 1994). Spalinger and Hobbs (1992), when modelling herbivore intake rates, also found a negative correlation between bite and intake rate as forage became more abundant. Alternatively, decreasing bite rates could be related to increased selectivity, when forages quality is high (Ferrari et al. 1988). A study by Bleich et al. (1997) on mountain sheep (*Ovis canadensis nelsoni*, Shaw 1804), for example, showed that males and females did select different forages, which led to different levels of crude protein intake. However, there was no indication of higher forage selectivity or sexual differences in faecal crude protein in our bighorn sheep population and forage quality actually decreased as the season progressed.

Bighorn sheep seem to be able to adjust their bite rates to their daily needs, but there seems to be a trade-off between foraging efficiency and alertness, because time spent being vigilant means time lost biting vegetation. Sheep could potentially increase bite rates to spend more time being vigilant, but that was obviously not the case, as bite rates declined with an increase in vigilance rates. Earlier studies on this population of bighorns have shown that both average daily time spent foraging, as well as bite rates, vary seasonally (Ruckstuhl 1998; Ruckstuhl and Festa-Bianchet 1998). While lactating and non-lactating ewes had similar activity budgets and bite rates in spring, lactating ewes had a much higher bite rate than yeld ewes in autumn (Ruckstuhl and Festa-Bianchet 1998). Zebra (*Equus burchelli*, Gray 1823) males and females, which are of comparable body size, and therefore should also have similar bite sizes, show very similar activity budgets but lactating females have higher bite rates than males or yeld females (Neuhaus and Ruckstuhl 2002). The study on zebras and the results on bighorns both point to bite rates being a highly flexible behaviour, which may be opportunistically used to compensate for higher energy demands of growth or reproduction. However, increasing

bite rates may have a cost, such as lower vigilance rates (see above).

Most ewes 2 years of age and older reproduce and nurse young from May to November. Therefore, it was not surprising that age had no effect on bite rates in females, whereas there was an effect in males. The females' high energy demands most likely translate into high bite rates for all ewes older than one. Non-reproducing 2-year-old females may also have high bite rates because of growth and preparation for the first breeding season in the following year. Young males on the other hand need energy to grow and accumulate fat reserves.

There was no correlation between bite rates and the number of steps animals took while foraging, which we interpreted as female bighorns not being more selective foragers than males. Actually, step rates were very constant for all sex-age classes, while time spent foraging varied greatly (Ruckstuhl 1998). Bighorn sheep are mainly grazers (Hofmann 1989; Stelfox 1993); hence, instead of selecting high-quality food, females may opt for a higher intake rate in times of higher energy demands. Although the sexes may have selected different forage plants, females of our study population did not have higher faecal crude protein content than males (Ruckstuhl et al. 2000).

Bighorn sheep are social and live in groups year-round (Geist 1971; Ruckstuhl and Festa-Bianchet 2001). Living in groups is advantageous because of predator detection and dilution effects (Dehn 1990; Rubenstein 1978; Wrona and Dixon 1991). Synchrony of behaviour seems to be an important factor in maintaining group cohesion (Jarman 1974). Synchrony of activity budgets, for example, is highest in groups of animals with similar body sizes (Conradt 1998) and time budgets (Ruckstuhl 1999; Ruckstuhl and Neuhaus 2001). Nursery groups, however, are often composed of animals of differing body size or reproductive status and synchrony of behaviour seems to be lower for red deer (*Cervus elaphus* Linnaeus 1758), bighorn sheep, and Alpine ibex (*Capra ibex ibex*, L.) nursery groups than for similar body-size groups (i.e. bachelor groups) (Conradt 1998; Ruckstuhl 1999; Ruckstuhl and Neuhaus 2001). Synchrony of behaviour may be costly when animals differ in their optimal activity budgets (Conradt 1998; Ruckstuhl 1999). Increasing bite rates, instead of increasing time spent foraging, for example, might be the optimal strategy to compensate for higher energy demands, allowing lactating and non-lactating females to synchronize their activity budgets (Conradt 1998; Ruckstuhl 1999) and maintain group cohesion. Additionally, the constancy in step rates within sex-age classes may be another strategy to maintain group cohesion.

A study on bighorn sheep by Berger (1991) showed that females make a trade-off between foraging efficiency for increased vigilance or security to their offspring, whereas males have higher foraging efficiency and use habitat with higher predator densities than females. As predicted, females in our population were more vigilant

than males most of the time, except during April and September when vigilance rates were similar for both sexes. Most lambs in our study were born in May/June and weaned by October (Festa-Bianchet 1988a, 1988b). It is therefore not surprising that sexual differences in vigilance were greatest when lambs were small and dependent on their mothers (Fig. 4). As reported in a previous study, there was no difference in vigilance rates between lactating and non-lactating females (Ruckstuhl and Festa-Bianchet 1998), which was quite surprising. However, as non-lactating and lactating females were in the same groups, lactating, and possibly more vigilant females might have affected the vigilance rates of non-lactating females.

Vigilance and bite rates were negatively correlated, which means that vigilance either affected bite rates or vice versa. Higher vigilance levels or higher bite rates are therefore both potentially costly for bighorn sheep and more or less mutually exclusive behaviours, contrary to that proposed by Illius and FitzGibbon (1994). Therefore, a trade-off between foraging and predator avoidance seems to exist in these bighorns. Especially females and growing individuals may have to base their decisions to increase bite rates according to daily energy demands, and in the long term, according to perceived predation risks and future reproductive potential. Foraging in groups may, however, allow individuals to increase bite rates at the cost of vigilance due to dilution effects (Dehn 1990).

We conclude that in addition to measurements of bite size (Gross et al. 1993) and total time spent foraging (Ruckstuhl 1998), bite rates could also be an important measure for determining intake rates of ungulates. We further suggest that, for social ungulates, changes in bite rates according to an individual's specific needs could be the main behavioural tool to minimize costs of activity synchronization in a group of individuals with different energy needs.

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