ORIGINAL ARTICLE

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Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*

Abstract In sexually dimorphic ungulates, males generally spend less time foraging than females, possibly because of difference in body mass or because of the energetic requirements of lactation. The relationship between body size and foraging time has received little attention at the intra-specific level, because few studies have documented activity budgets for individuals of known size. Bighorn rams are a good model to explore how body mass affects foraging time, because they range in mass from 55 to 140 kg. We examined how the foraging time of bighorn rams varied according to individual characteristics. We observed rams in a marked population and constructed time budgets during the 3 months preceding the rut. We determined ram social rank based on agonistic encounters and collected fecal samples to count lungworm larvae. Time spent foraging was negatively correlated with body mass. After accounting for age differences, larger rams spent less time foraging and more time lying than smaller rams. Among rams aged 6–12 years, dominants spent less time feeding than subordinates, while fecal output of lungworm larvae was negatively correlated with foraging time for rams of all ages. Body mass accounts for much of the individual variation in foraging time, suggesting that sexual dimorphism is important in explaining differences in feeding time between males and females.

Keywords Bighorn sheep · Body mass · Foraging · *Ovis canadensis* · Time budget

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Introduction

Because of allometric effects on energy requirements and foraging behavior, body size has important consequences for the ecology, behavior, population dynamics and evolution of ruminants. Small ruminants have a higher relative metabolic rate than large ones, but large animals require more total energy than small ones. Because total metabolic requirements are allometrically related to body mass while rumen size is isometric with body mass (Demment 1982; Demment and Van Soest 1985; Illius and Gordon 1987), with increasing mass the rumen becomes proportionally larger relative to total metabolic requirements. Large ruminants can therefore keep food in the rumen longer than small ruminants, extracting more nutrients (Demment and Van Soest 1985; Illius and Gordon 1987). Consequently, large ruminants can survive on coarser forage than small ruminants, with profound consequences for population ecology and social organization (Bell 1971; Jarman 1974; Demment and Van Soest 1985).

Bell (1971) suggested that because large herbivores have a greater absolute food requirement than small ones, time spent eating should increase with body size. Relative bite size decreases allometrically with body mass, so that as body size increases, ruminants ingest a smaller proportion of their total daily food requirements with each bite (Illius and Gordon 1987). Thus, because rumen size increases isometrically with body size, to achieve the same level of rumen fill the proportion of time spent foraging may need to increase with body size, to compensate for smaller bite size (Demment and Van Soest 1985; Hudson 1985; Owen-Smith 1988). The daily time budgets of large ruminants are usually assumed to be more constrained than those of small ruminants by the foraging time needed to meet daily requirements (Hudson 1985). Indeed, interspecific comparisons of African ruminants show that daily foraging time increases with body mass (Owen-Smith 1988, 1992). For temperate ungulates, however, Mysterud (1998) showed that active time (that mostly involves foraging) tends to decrease allometrically

with increasing body size. He suggested that larger ruminants may consume lower-quality food, requiring longer rumination time and hence less time spent active (Mysterud 1998; Pérez-Barberia and Gordon 1999).

In accordance with Mysterud's (1998) and Pérez-Barberia and Gordon's (1999) findings, Ruckstuhl (1998) and Ruckstuhl and Neuhaus (2002) found that in sexually dimorphic ungulates, males spend less time foraging than females, and that this sexual difference increases with dimorphism in body size. The activity budget hypothesis for sexual segregation in ungulates, proposed that males and females segregate because of differences in activity budgets (Conradt 1998; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2002). This hypothesis assumes that body mass affects the time spent foraging and ruminating. Sexual differences in time spent foraging, however, could partly be due to the high energetic requirements of lactation (Clutton-Brock et al. 1982b; Komers et al. 1993). To rule out the potential effects of lactation, we need to investigate the relationship between body mass and time spent foraging within a single sex. In many ungulates, young adult males weigh less than half as much as fully-grown males and even within the same age class the range in mass can be over 20% (Pettorelli et al. 2002). Male ungulates therefore provide an opportunity to clarify at the intra-sexual level the shape of the relationship between body size and foraging time. Given the broad support for a negative relationship between body mass and time spent foraging at the intraspecific level, we predicted that at the intra-sexual level small males should spend more time foraging than larger ones.

Parasites and social status may also affect foraging behavior. Parasite infection decreases food intake in domestic lambs (Kyriazakis et al. 1996, 1998). Bighorn sheep (*Ovis canadensis*) are infected by lungworms (*Protostrongylus* spp.) whose prevalence in our study population is 100% (Festa-Bianchet 1991). The effects of these parasites on food intake are unknown. Ram social rank determines access to females during the rut (Hogg 1984, 1987). If dominance is energetically costly (Creel et al. 1996), dominant rams may have higher food requirements than subordinates. Furthermore, dominance is correlated with testosterone levels (Pelletier et al. 2003), an androgen thought to increase basal metabolism (Buchanan et al. 2001) and therefore food requirements.

Here, we investigate the effects of individual characteristics on the foraging behavior of bighorn rams during the autumn pre-rut when they form large bachelor groups. At that time of the year, seasonal body growth is complete and rams are at peak body condition, but vary in mass from 55 to 140 kg. We examined the relationship between time spent feeding and body mass, expecting a negative trend as predicted by the sexual difference in foraging found in many species. We also expected that high social rank and heavy parasite loads would increase the time spent feeding because both could increase daily energetic requirement (Creel et al. 1996; Bonneaud et al. 2003).

Methods

Study area

We studied bighorn sheep in the Sheep River Provincial Park, Alberta (50°40′N, 114°35′W, elevation 1,450–1,700 m). Since 1981, more than 90% of the sheep have been marked with ear tags, mostly when aged 4–6 months. Therefore, we could identify all individual rams over the 3 years (2000–2002) of this study, and their exact age was known.

Activity budgets

Ram activity budgets were collected from September to November. Group size was recorded at the beginning and at the end of each observation period, by observers located at least 75 m away. Observations were made with Leica binoculars (10×42) and Bausch and Lomb spotting scopes (15×45 zoom). As described by Ruckstuhl (1998), we constructed activity budget from marked focal animals (Altmann 1974) by noting their times of transition between different behaviors (resting, foraging, moving, standing and interacting socially), over continuous periods lasting from 6 to 10 h. Because rams were habituated to observers, highly gregarious, and seldom moved more than a few hundred meters during observations, we could monitor behavior transition times of up to ten focal animals within a group. Activity budgets were collected by one or two observers each year and the first author collected most of these data in all years. We tested for an observer effect by including observer as fixed factor in a linear mixed model including ram's identity as random term for 317 activity budgets for which the observer was known and found none ($F_{3,270}$=2.06, p=0.11).

Bighorn sheep are very rarely active at night outside the rut (Sayre and Seabloom 1994; K. Ruckstuhl, unpublished data), therefore our sampling procedure provides an accurate estimate of daily time spent foraging. We could not directly measure the time spent ruminating. While they are lying, rams appear to ruminate most of the time, but rumination can only be detected if the mouth is visible to the observer. Because rams almost never ruminate while standing, it is reasonable to assume that time spent ruminating increased with time spent lying. We used the proportion of time spent lying as an indication of rumination time, but the correlation between lying and rumination needs to be investigated. In the three years of the study 348 time budgets were constructed for 45 different rams for a total of 2,630 sheep-hours. We calculated from the activity budget the proportion of time an animal spent in each behavior, and used this proportion as the dependent variable.

Dominance hierarchy

To assess male social rank we recorded interactions ad libitum from September to mid-November, a time referred to as the 'pre-rut', during which rams establish dominance relationships (Geist 1971). Six agonistic behaviors were noted among rams aged 2 years and older: front kick, rubbing, frontal clash, butt, no contact displacement, and homosexual mount (Hogg 1984, 1987). A total of 261 interactions were observed in 2000, 737 in 2001 and 741 in 2002, involving respectively 46%, 60% and 57% of all possible ram dyads. The linearity of the hierarchy was tested based on an interaction matrix produced by Matman 1.0 (Matrix Manipulation and Analysis, Noldus; de Vries et al. 1993), as explained by de Vries (1995, 1998).

Parasite count

Fecal samples collected from marked sheep were dried and stored in paper bags. The number of lungworm larvae per gram of dry feces was counted using the Beaker technique (Forrester and Lankester 1997).

Body mass

We used a platform scale baited with salt (Bassano et al. 2003) to weigh 21 rams, 8 of which were weighed in different years providing 29 ram-years of mass data. Repeat weighing of the same sheep during October-November suggested that little, if any, mass gain occurred during that time. For all sex-age categories considered, the 95% confidence interval for mean mass gain included zero: 1- and 2-year-old males mean=0.033 kg/day, n=13, CI(−0.031, 0.098), 1- and 2-year-old females mean=−0.017 kg/day, n=7, CI(−0.231, 0.197), adult males mean=−0.024 kg/day, n=7, CI(−0.354, 0.307) and adult females mean=0.003 kg/day, n=31, CI(−0.072, 0.079). Consequently, we did not adjust body mass according to date. For rams weighed more than once we used the average mass.
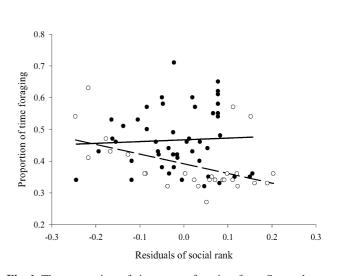
Statistical analyses

Our sampling design included repeated observations of the same individuals. To avoid pseudoreplication (Machlis et al. 1985), foraging time was analyzed using linear mixed effects models implemented in S-Plus 2000 (MathSoft) with ram identity as a random factor. Because year had a significant effect in some analyses, we included it as fixed factor in all models before fitting other variables. To test whether ram identity had an effect on foraging time, we calculated an approximate chi-square statistic equal to twice the absolute difference in log likelihood for the model with and without the random term (ram identity), and then divided the associated p-value by 2 (Steele and Hogg 2003). Because the effect of each individual on the proportion of time spent feeding is assumed to be different, random effects have a distribution rather than a value (Steele and Hogg 2003) and are therefore reported as a standard deviation. Whenever ram identity had a significant effect we included it in our models, thereby avoiding possible biases introduced by pooling our data (Leger and Didrichsons 1994; Jenkins 2002) or by pseudoreplication (Machlis et al. 1985). Age, social rank, lungworm larval count and body mass were fitted as fixed effects. Because social rank is correlated with age (Hass and Jenni 1991), we used the residual of the quadratic regression of social rank on ram age to produce an age-specific measure of rank (referred to as age-specific social rank). Parasite counts were ln-transformed and the proportion of time foraging and lying was arcsin-square root transformed to better approximate a normal distribution (Sokal and Rohlf 1981). Sample sizes vary according to the analysis, as life-history data were not available for all individuals.

Results

For the complete data set, the proportion of time spent foraging was best explained by a model including ram age, lungworm larval count, age-specific rank and an interaction between age and age-specific rank (Table 1). Group size did not affect time spent foraging and was excluded from this model (T-value=−0.005, df=1,357, p=0.89). Age and lungworm count had negative effects on foraging time. Age did not affect the average number of lungworm larvae per gram of dry feces of rams, during the pre-rut the average (±SE) was 137±13 for rams 6 years and older, compared to 105±13 for rams aged 1–5 years. The interaction between ram age and age-specific rank arose because subordinate rams aged 6 years and older spent more time feeding than dominant rams of the same age (Fig. 1). For the 21 rams (29 sheep years) for which we measured body mass, mass had a strong neg-

Table 1 Linear mixed effects model of the proportion of time spent feeding by yearling and adult bighorn rams (*Ovis canadensis*) at Sheep River, Alberta, 2000–2002, giving estimates, standard errors (SE), T statistics and degrees of freedom for terms in the best model. *LPG* number of lungworm larvae per gram of dry feces. Sample size was 307 observations from 43 different individuals. The model explained 23.78% of the variance in time spent feeding. Ram identity had a significant effect (SD=1.02, χ^2=12.04, p<0.001, df=1) and was included as a random term
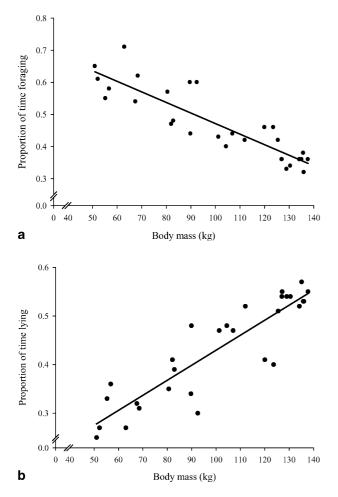
Term	T-value	Estimates (SE)	p	df
Constant	25.33		<0.001	1,258
Year	−3.32		<0.001	2,258
Age	−5.44	−1.15 (0.21)	<0.001	1,258
LPG	−2.35	−0.89 (0.38)	0.019	1,258
Age specific rank	2.35	23.43 (9.96)	0.019	1,258
Age specific rank × age	−2.53	−3.73 (1.47)	0.012	1,258

Fig. 1 The proportion of time spent foraging from September to November by young and old bighorn rams (*Ovis canadensis*) compared with their age-specific social rank. *Filled circles* and *solid line* indicate males aged 1–5 years, *open circles* and *dashed line* indicate males aged 6 years and older. Residual social rank is the age-specific rank: a negative value represents a ram with lower rank than average for his age, a value of zero is an average rank while positive values indicate rams of higher than average rank

ative effect on foraging time (Fig. 2a). Because ram age and mass were correlated (r =0.91, p<0.001, n=34 ram-years), we examined a model including only age and mass, to determine whether the age effect on foraging time was simply due to the correlation of age and mass. In this model, year was fitted as a fixed effect and ram identity as a random term. The negative relationship between time spent foraging and body mass persisted after accounting for age (Table 2).

Not surprisingly, older rams spent more time lying compared to younger rams (Fig. 2b). Time spent lying was best explained by a model including only body mass as fixed factor. Age did not affect the time spent lying when body mass was accounted for (Table 3). Although rams interacted more frequently as they aged (Kruskal-Wallis, χ^2=28.92, df=2, p<0.001), rams of all age classes

Fig. 2 The proportion of time spent foraging (**a**) or lying (**b**) from September to November by bighorn rams of different body mass, Sheep River Provincial Park, Alberta, 2000–2002

Table 2 Linear mixed effects model of the proportion of time spent feeding by yearling and adult bighorn rams of known body mass, Sheep River, Alberta, 2000–2002, giving estimates, standard errors (SE), T-value and degrees of freedom for terms in the best model. Sample size was 119 observations from 21 individuals and the model explained 47.40% of variance. Ram identity had a significant effect (SD=1.83, χ^2=3.08, $p<0.05$, df=1) and was included as random term

Term	T-value	Estimate (SE).	p	df
Constant	19.04		<0.001	1,94
Year	1.61		0.079	2,94
Age	−2.00	−0.79 (0.40)	0.048	1,94
Mass	−2.94	−0.12 (0.05)	0.004	1,94

spent little time involved in social behavior (0.8% for those aged 1–3 years, 2.0% for rams aged 4–6 years, and 2.9% for rams older than 6 years). Variability in activity budgets between age classes was mostly due to differences in foraging and lying time (Fig. 3).

Table 3 Linear model of the proportion of time spent lying by yearling and adult bighorn rams of known body mass, Sheep River, Alberta, 2000–2002, giving estimates, standard errors (SE), T-value and degrees of freedom for terms in the best linear model. Sample size was 119 observations from 21 individuals and the model explained 37.8% of variance. Ram identity did not have a significant effect (SD=0.001, χ^2=0.01, $p>0.05$, df=1) and was not included in the final model

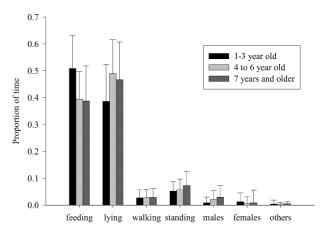| Term	T-value	Estimates (SE)	p	df
Constant	7.138		<0.001	1,114
Year	0.438		0.825	2,114
Mass	3.930	0.158 (0.04)	<0.001	1,114
Age	0.794	0.318 (0.40)	0.429	1,114

Fig. 3 Proportion of time (±SD) spent in seven activities by three age groups of bighorn rams, Sheep River Provincial Park, Alberta, 2000–2002. *Males* indicates the proportion of time males spent in social interactions with other males while *females* refers to the proportion of time spent in social behavior with females

Discussion

We found that large rams spent less time feeding, and possibly more time ruminating, than small rams. Our results agree with the interspecific trend reported by Mysterud (1998) for temperate ungulates, but are opposed to that reported by Owen-Smith (1988, 1992) for African ungulates, where large species spent more time feeding than small ones. Allometric relationships may vary substantially among taxonomic levels. For instance, in vertebrates, fecundity decreases with increasing body size across species (Owen-Smith 1988), but it generally increases with body size within a species (Dobson et al. 1999). The biological implications of body size and of life history traits may therefore differ at the interspecific and intraspecific levels.

At the interspecific level, there are no fixed constraints on the amount and quality of forage selected by animals, because different species may be adapted to different diets. Typically, larger ruminants are relatively unselective and consume a large amount of coarse forage, while smaller species are more selective and choose food of higher quality (Bell 1971; Jarman 1974; Demment and Van Soest 1985). Consequently a small species may

spend little time foraging because it can rapidly obtain its nutrient requirements by eating high-quality forage. In gregarious animals that must maintain group cohesion, it may be difficult for individuals of the same species and sex to vary their diet according to individual body size. Size-specific diet selection may also be limited by the constraints imposed by species-specific characteristics such as rumen physiology or bite size. In our study, individual body mass varied substantially, with the heaviest rams being almost 3 times the mass of the lightest ones. Because rams seldom formed age-segregated groups (Ruckstuhl and Festa-Bianchet 2001), group foraging imposed a constraint on diet selection as all rams had to forage in the same area. It appears that to obtain sufficient nutrition the younger and smaller males were forced to forage longer than the older and larger ones.

The daily amount of food ingested by an individual ruminant depends on the time it spends feeding, but also on its bite rate (Hudson 1985). Relative bite size decreases with increasing body mass (Illius and Gordon 1987). In bighorn sheep, males aged 1–3 years have faster bite rates than older males (Ruckstuhl et al. 2003). Consequently, it seems inevitable that the rate of food intake during foraging declines with body mass. Despite a more rapid bite rate and larger bite size relative to body mass, our results suggest that small rams must spend more time feeding than larger rams to obtain their nutritional requirements. Small rams likely require more food because they have a high relative metabolic rate. It is unlikely that small rams have high nutritional needs associated with continued body growth, because in autumn sheep do not gain any weight.

Rams with higher fecal output of lungworm larvae spent less time foraging than those with a lower larval count. Anorexia may promote the immune response or allow selection of foods that either minimize the risk of future infection or are high in antiparasitic compounds (Kyriazakis et al. 1998). However, our results on the effect of parasites on foraging time should be taken cautiously because we could not correct for changes in daily fecal production (Sutherland 2003).

Among males 6 years and older, low-ranking rams spent more time foraging then high-ranking ones. This result is consistent with the pattern of larger rams spending less time foraging than small ones, because dominance rank of bighorn rams is highly correlated with body mass (Pelletier and Festa-Bianchet, unpublished data). It is unclear, however, why this relation existed only for older rams. Although social dominance may involve subtle costs, such as higher levels of glucocorticoids (Creel et al. 1996; Creel 2001), in our study those costs did not appear to lead to a substantial increase in time spent foraging during the pre-rut.

Synchronization of foraging behavior by ruminants of widely different body mass is likely difficult, because smaller animals require more daily feeding time than larger individuals. Others studies on bighorns and other ungulates reported similar findings: young bighorn rams spent more time foraging than adult males in spring and summer (Ruckstuhl 1998, 1999), adult male white rhinoceros (*Ceratotherium simum*) spent 5.5% less time foraging per day than subadults (Owen-Smith 1988) while adult male kudus (*Tragelaphus strepsiceros*) foraged for 10% less time than subadult males (Owen-Smith 1998). These findings suggest that in species with multi-year growth one should expected social segregation by age class, because younger individuals will have different time budgets than older and larger ones. Age segregation has been reported in male Alpine ibex (*Capra ibex*) that have substantial age-related differences in body mass (Bon et al. 2001). During our study, all bighorn rams in the population were often all in one group and did not strongly segregate by age, possibly because they were few (27–37) and needed to form large groups for antipredator reasons (Roberts 1996). We expect that age-specific groups should be encountered in larger populations where there will be enough rams to form large age-segregated groups.

Our results are consistent with the idea that ungulates are sexually segregated because of differences in activity budgets (Conradt 1998; Ruckstuhl 1998; Ruckstuhl and Kokko 2002; Ruckstuhl and Neuhaus 2002). Inter-sexual comparisons suggest that sexual dimorphism in size and in time spent foraging are correlated, with males generally foraging less than females (Ruckstuhl and Neuhaus 2002). Red deer hinds (*Cervus elaphus*) spent much more time feeding than stags during summer (Clutton-Brock et al. 1982a), a sexual difference observed for several other species of ungulates (Owen-Smith 1988; Gross et al. 1996). Differences in time budget between the sexes, however, could be attributable to sexual differences other than body size. We found that, within a sex, body mass accounted for much of the variation in foraging time, suggesting that sexual dimorphism is likely important in explaining the difference in feeding time between males and females.

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