Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic

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Mate guarding is the primary mating tactic used by dominant males of many species of ungulates. Guarding males are thought to forage less during the rut than do nonguarding males, possibly leading to greater fitness costs. I observed bighorn rams foraging during the pre-rut and the rut. I compared how coursing (an alternative mating tactic) and tending (a form of mate guarding) affected the foraging behavior of bighorn rams over the rut, to test whether foraging was more constrained by mate guarding than by coursing. All adult males spent less time feeding during the rut compared with the pre-rut. The decrease in time spent feeding, however, was independent of mating tactic. Contrary to expectation, individual rams observed both coursing and tending spent less time foraging when coursing than when tending. For young rams, the time spent in rutting activities was correlated with individual pre-rut mass, indicating that males either modify their behavior according to available metabolic reserves or adjust the energy devoted to rutting activities to the level of expected benefits. Mate guarding does not appear to constrain foraging more than coursing. The costs of male reproductive behavior may depend more upon individual effort than on the particular tactic adopted. *Key words:* bighorn sheep, feeding constraint, *Ovis canadensis*, rut. *[Behav Ecol]*

Mate guarding is the primary mating tactic used by dominant males in several polygynous ungulates (bison, *Bison bison*: Komers et al., 1992; bighorn sheep, *Ovis canadensis*: Hogg, 1984; Dall sheep, *O. dalli*: Geist, 1971; Soay sheep, *O. aries*: Stevenson, 1994; red deer, *Cervus elaphus*: Clutton-Brock et al., 1982). Mate guarding involves monitoring and following a female's movements, courting her, and defending her against other males, who may either challenge the guarding male (Hogg, 1984) or attempt to mate using "sneaky" tactics. A male can guard one (consort) or several females (harem defense), depending on female distribution (Clutton-Brock, 1989). Mate guarding is more successful than are alternative tactics (Coltman et al., 2002, Hogg and Forbes, 1997, Pemberton et al. 1992) but may impose a greater energetic cost by reducing the time available for foraging and by increasing energy expenditures (Alberts et al., 1996). Here I compare the time spent foraging by rutting bighorn rams using tending or coursing tactics, to determine if either tactic involves a greater foraging constraint that could lead to higher reproductive costs.

It is often proposed that males involved in mate guarding incur greater fitness costs than do other males (Alberts et al., 1996; Clutton-Brock et al., 1982; Geist, 1971; Yoccoz et al., 2002), because the expected reduction in feeding during the rut may cause them to enter the winter in poor condition and be more likely to die from predation, disease, or starvation (Bobek et al., 1990; Geist, 1971). Although a decrease in time spent feeding during the reproductive season has been associated with mate guarding for several mammals (e.g., baboons, *Papio cynocephalus*: Alberts et al. 1996; bison: Komers et al., 1994a,b; Dall sheep and bighorn sheep: Geist, 1971; red deer: Clutton-Brock et al., 1982), no study has directly tested whether a reduction in foraging is specific to mate guarding or is common to all reproductive tactics. Such a test should compare time spent foraging by individuals adopting different reproductive tactics, and ideally by the same individual when adopting different tactics, not simply compare time budgets of mate-guarding males with those of males not involved in reproductive behaviors (Alberts et al., 1996).

Alternatively, if individuals adopt the mating behavior best suited to their own characteristics (Komers et al., 1994a, McElligott et al. 2003) or to their environment (Yoccoz et al., 2002), there may not be differences in energetic constraints between individuals. If there are wide differences in individual quality among males, the best individuals may be dominant and in superior body condition at the beginning of the rut and may adopt mate guarding without incurring an important reproductive cost (McElligott et al., 2003). In this case, coursing may be costlier than is tending, because males using the coursing tactic would be low-quality individuals doing the best of a bad job.

If the time devoted to costly behaviors varies substantially among individuals that adopt the same tactic, individual differences in energetic costs of reproduction could be unrelated to mating tactic. Bighorn sheep are polygynous and highly dimorphic (Festa-Bianchet et al., 1996; LeBlanc et al., 2001) seasonal breeders (Geist, 1971). During the rut, rams may use three different mating tactics. Tending is the most successful tactic, but it can be used only by the most dominant ram among those courting an estrous ewe. A tending ram defends a single estrous ewe against other males by fighting, using horn displays, and physically blocking access to the ewe. Tending pairs are often joined by subordinate rams that seek opportunities to initiate coursing chases (hereafter named coursing rams) by approaching the ewe and attempting to separate her from the dominant ram. Often, a coursing chase is initiated by one subordinate ram when another ram distracts the dominant ram with horn butts or other physical threats. When the estrous ewe is separated from the tending ram, a rapid chase will occur, during which coursing ram(s) may force copulations. The chase typically ends when the dominant ram regains its defending position (Hogg, 1984; 1987). Only the alpha male always tends when courting an estrous ewe. Other males will tend if they are dominant to all other rams courting a ewe, but these males

Table 1

Sex-age structure of bighorn sheep present during the rut at Sheep River, Alberta, 2000–2002

				Males by age class (n)					
Year	Females (n)	Males (n)	Lambs (n)	1 year	2 years	3 years	4 years	5 years	6 years and older
2000	39	20	15	1	3	6	1	2	7
2001	37	20	21	6	2	3	3	1	5
2002	19	9	2	1	3	1	1	1	2

Numbers for males and females refer to individuals 1 year of age and older.

switch to coursing if a higher-ranking ram approaches (Hogg, 1987).

The number of rams tending ewes varies with the daily number of estrous ewes, because rams only tend one ewe at a time. Thus, if three ewes are simultaneously in estrus, the three most dominant males will be tending. If only one ewe is in estrus, only the alpha male will be tending and all other males will either course or search for estrus ewes. Individually, tending rams have a much greater reproductive success than do coursing rams, but approximately 40% of lambs are fathered by coursing rams (Hogg and Forbes, 1997). The reproductive success of coursing rams is independent of social rank (Hogg, 2000), and paternities can be obtained by adult rams of any age (Coltman et al., 2002) and, in rare cases, by yearlings (Hogg JT, unpublished data). A third mating tactic, blocking, involves forcing an estrous ewes away from potential competitors. It has been described in other populations (Hogg, 1984), but it was rarely seen in my study area and will not be included in this article.

Here, I address two main questions. First, does tending constrain foraging behavior more than does the alternative mating tactic of coursing? To answer this question, I compared the time spent foraging by tending and coursing rams during three ruts, and compared the time budgets of the same rams when they adopted different mating tactics during the same rut. I predicted that tending should constrain foraging behavior more than does coursing, assuming that the most rewarding strategy (tending) should also have the greatest energy costs. Therefore, I expected that the decrease in time spent feeding from the pre-rut to the rut should be greater for tending than for coursing rams. If foraging constraints were simply a function of the amount of time devoted to rutting activities, however, the decrease in time spent feeding should not be affected by social rank or mating tactic. Second, I determined whether the time spent in rutting activities by young males varies with individual pre-rut body mass.

METHODS

Animals and study area

I studied bighorn sheep in the Sheep River Provincial Park, Alberta (50°40′ N, 114°35′ W; elevation = 1450–1700 m), in 2000–2002. More than 90% of the sheep were marked as lambs, and all rams were individually identifiable (Festa-Bianchet, 1986; Hogg and Forbes, 1997). During the pre-rut season (September–October), males establish a dominance hierarchy through agonistic encounters (Geist, 1971, Pelletier et al., 2003, 2004). Social rank then determines access to estrous ewes during the rut (Hogg, 1984, 1987). The rut occurs

in traditional sites where bighorns are easy to locate and observe, on open habitat within easy reach of a road. Over the 3 years of study, an average of 96.3% of marked rams were seen during each day of observations during the rut (yearly range = 93–99%). The number of sheep present for the rut and the age structure of rams varied over the 3 years of study (Table 1).

After establishing a dominance hierarchy during the pre-rut in September–October, males start to join female groups in mid November, investigating females and showing sexual behaviors. I defined the rut as the period from the first to the last copulation seen. The first copulation was seen from 19–25 November over the 3 years, and the last one about 20 days later.

Constructing ram time budgets

Activity budget were collected from September to mid December, as described by Ruckstuhl (1998). Although four observers were involved over the 3 years of study, I collected 47% of time budgets. Sheep were observed from at least 100 m to avoid possible effects of observers on behavior. Only males that were present during both the pre-rut and the rut were included in the analyses. Overall, a total of 569 activity budgets were obtained for 28 different rams 1 year of age and older observed in at least 1 year and up to 3 consecutive years. To construct activity budgets during the pre-rut, the time of transition from one behavior to another was recorded during continuous focal-animal observations (Altmann, 1974) lasting 6 to 10 h. Because rams are highly gregarious and bachelor groups very stable, when observing a group it was possible to monitor from two to 10 rams simultaneously, as described by Ruckstuhl (1998, 1999). Five types of behavior were recorded: foraging, lying, moving, standing, and interacting. Lying typically involved rumination, but we could not quantify rumination directly. Standing was a motionless posture and included vigilance. Interactions included aggressive encounters with other males and courtship of females. During the rut, ram group cohesion broke down; rams frequently switched groups, and it became impossible to monitor more than one ram at a time. Therefore, we collected three to six 1-h focal watches of single rams each day of the rut, during which we continued to record transition times from one behavior to another. To test whether the two methods used to estimate foraging time led to similar results, I randomly sampled between 3 and 6 single h of observations from 10 pre-rut activity budgets with average duration of 8 h (range = 7–10 h). The proportion of time spent foraging estimated by random 1-h samples was highly correlated with the estimate based on the entire activity budget (3 h: $r = .69$, $p = .03$; 4h: $r = .88$, $p < .01$; 5h: $r = .90$, $p < .01$; 6h: $r = .97$, $p < .01$). Focal watches were distributed over all daylight hours (from approximately 0830–1630) and were conducted every day during the rut.

Sheep were observed for a total of 1267 sheep-hours during the pre-rut, averaging 28.2 h ($\pm$SE = 1.93 h) of observations for each male each year. During the rut, 1279 sheep-hours of observations were recorded, for a mean of 27.33 h ($\pm$SE = 1.68 h) per ram each year. I calculated the number of minutes each male spent foraging, lying, moving, standing, or interacting, and then divided it by the total observation time for that ram to estimate the proportion of time it devoted to each behavior. I used that proportion as the dependent variable for statistical analyses.

To estimate the proportion of time spent coursing and tending during the rut, males were located at least three times a day, either by actively searching for them or by noting their tactic when they first appeared within view during observations of other sheep. We attempted to obtain observations at

regular intervals (morning, midday, and afternoon). Because an average of 96% of males were seen during each day of observations, this sampling method provided a good estimate of the use of different mating tactics by individual rams over one rutting season. Rams behavior was recorded as tending, coursing, blocking, investigating anestrous ewes, or searching for estrous females. I estimated the proportion of time a male was involved in rutting activities as the sum of all reproductive behaviors divided by the total number of observations for each ram.

Dominance hierarchy and mating tactic

During the pre-rut, interactions were recorded ad libitum to assess male social rank. Six agonistic behaviors were noted: front kick (always by a dominant to a subordinate), rubbing of the preorbital gland on the horn of a dominant, frontal clash, horn butt on the body of a subordinate, noncontact displacement from a bedding or foraging site, and homosexual mount (for detailed descriptions of each behavior and their relevance in determining social rank, see Geist, 1971; Hogg, 1984, 1987). Interactions were observed for 46% of the possible dyads among 21 rams during the pre-rut in 2000, 60% for 23 rams in 2001, and 57% for 27 rams in 2002. Interaction matrices were constructed by using Matman 1.0 (Matrix Manipulation and Analysis, Noldus; de Vries et al., 1993) that first tests the linearity of the matrix and then ranks the individuals on a hierarchy (de Vries, 1995, 1998). The dominance hierarchy was linear in all years (2000: $h' = 0.33$, $p = .003$; 2001: $h' = 0.48$, $p < .001$; 2002: $h' = 0.42$, $p < .001$). Because matrix size varied among years, I transformed social ranks as $[1 - (\text{rank}/Nx)]$, where N is the number of adult males during year x (Côté, 2000). The resulting index of social rank varied from zero (subordinate) to one (dominant). Each time a ram was observed defending an estrous ewe, we recorded it as tending. On average, these rams ($n = 11$) spent 41% of the rut tending estrous ewes (range = 10–84%). One rams was never seen coursing and therefore was excluded from within-ram comparisons. An individual ram would tend an ewe if it was dominant to all other rams competing for that ewe, but would resort to coursing if it was subordinate to one or more of the competing rams. I considered a ram to be "coursing" when it was clearly associated with a consort pair. Coursing includes the time actually spent in coursing chases, attempting to separate the ewe from the tending ram, and remaining near the consort pair presumably looking for coursing opportunities. Males traveling alone or in small groups (two to three males) were considered as "searching."

Body mass

A platform scale baited with salt (Bassano et al., 2003) was used to weigh bighorn sheep. This method allowed multiple measurements of the same individuals over one season. Mass change during the rut was calculated by subtracting mass at the end of the rut from the pre-rut mass for 14 males 1 year and older that were weighed at the appropriate times. Repeated measurements of the same rams during October–November suggested that no mass gain occurred during that time (Pelletier and Festa-Bianchet, 2004).

Data analysis

I used linear mixed effects models (LME; Pinheiro and Bates, 2000) implemented in S-Plus 2000 (MathSoft Inc.) to model foraging behavior over the pre-rut and the rut because I collected repeated measurement of the same individuals over time. Mixed models include ram identity as a random effect and avoid pseudoreplication (Jenkins, 2002; Leger and Didrichsons, 1994; Machlis et al., 1985). For model selection, I used a backward procedure to account for the unbalanced sampling design, beginning with a saturated model including second- and third-order interaction and main effects. I then withdrew terms based on the p value associated with their F ratio value. Because year could have an effect on foraging behavior, I included it as fixed factor in all models before fitting other variables. Because social rank generally increases with age up to about 6–7 years, age and social rank are highly correlated in bighorn rams (Hass and Jenni, 1991); therefore, I could not include both variables in the same model without multicollinearity problems (Glantz and Slinker, 1990). Instead, I used the residuals of the quadratic relationship between age and social rank as an age-independent social rank. Period (pre-rut or rut), age (in years), age-independent rank, and their interactions were fitted as fixed effects.

In the comparison of time budgets for 10 rams that adopted different mating tactics during the same rut, year, mating tactic and age were included as fixed factors. These rams were all aged between 6 and 12 years, when differences in age have little or no effect on social rank (Pelletier F, Hogg JT, unpublished data), and therefore, I did not include an interaction term between age and mating tactic.

Pearson correlations were used to compare time spent in rutting activities with the pre-rut body mass of yearlings and 2-year-old males. I analyzed the two age classes separately to avoid pseudoreplication (Machlis et al., 1985). I used Pearson correlations to compare the change in body mass during the rut with the initial body mass, the proportion of time spent feeding, and the proportion of time involved in rutting activities for rams 1 year and older. Sample size varied between analyses because not all were available for all rams. All proportions were arcsine-square root transformed to approximate a normal distribution (Sokal and Rohlf, 1981).

RESULTS

The proportion of time spent foraging by all rams, including yearlings, was best explained by a model including year, period (pre-rut or rut), age, and an interaction between period and age (Table 2). All males 2 years and older foraged less during the rut than during the pre-rut but did not completely stop foraging (Figure 1). Yearling rams spent a similar proportion of time feeding during the rut and the pre-rut (Figure 1), likely explaining the significant interaction between age and period on time spent feeding (Table 2). There was no effect of age-independent social rank or of its interaction with period on foraging time. Activity budgets of rams involved in different mating tactics are presented in Table 3.

The proportion of time spent foraging by individual rams observed both coursing and tending varied with the tactic adopted (Table 4). Contrary to expectations, these 10 rams spent more time foraging when tending (15.2% ± 2.5 SE) than when coursing (8.2% ± 3.0). During the rut, these rams spent 33% of their time tending (range = 10–77%) and 14% coursing (range = 3–34%). Across all males, however, this difference was small and not significant (Mann-Whitney U test: $z = -1741$, $p = .082$), with tending rams spending only 2% more time foraging compared to coursing rams (Table 3). Independently of mating tactic, there was substantial individual variation in both the time spent foraging (range = 10–47%) and the time devoted to rutting activities (range = 14–84%) by rams 2 years of age and older.

There was a strong correlation between pre-rut body mass and participation in rutting activities for both yearling rams

Table 2

LME model selection of the proportion of time spent foraging by bighorn rams aged 1 year and older, Sheep River, Alberta, 2000–2002

General model: $F = Y + P \times A \times SR$

Variables	F ratio	df	p
$P \times A \times SR$	0.65	1, 532	.422
$P \times A$	4.05	1, 532	.045
$A \times SR$	1.43	1, 532	.232
$P \times SR$	0.11	1, 532	.736
Y	10.47	2, 532	<.001
P	90.51	1, 532	<.001
A	37.52	1, 532	<.001
SR	0.35	1, 532	.553

Selected model = $Y + P + A + P \times A$

Variables	Estimates	SE
Y	—	—
P	−7.84	1.98
A	−1.35	0.43
$P \times A$	−0.72	0.37

Sample size is 569 observations from 28 individuals observed in one or more rutting season, and 23.45% of the variance is explained by the final model. F indicates proportion of time feeding; Y, year, A, age; P, period (pre-rut or rut); and SR, age-independent social rank.
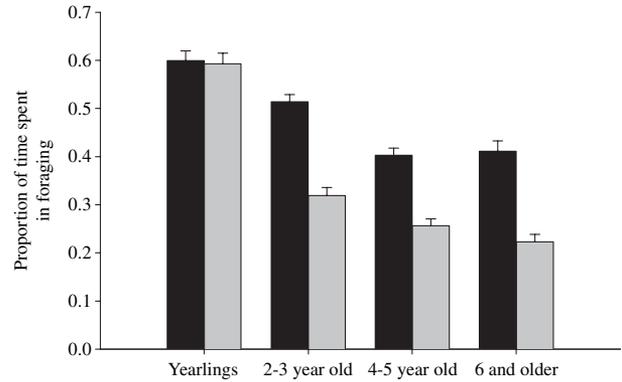

Figure 1
The proportion of time spent foraging ($\pm$SE) by bighorn rams of different age classes during the pre-rut (filled bars) and the rut (shaded bars), 2000–2002, Sheep River Provincial Park, Alberta.

($r = .79$, $n = 8$, $p = .02$) and 2-year-old rams ($r = .85$, $n = 6$, $p = .03$). Participation in rutting activities varied substantially among individuals for both age groups (Figure 2). For rams 3 years and older, there was no relationship between initial mass and participation in rutting activities ($r = .37$, $n = 5$, $p = .54$). Except for yearlings, males of all ages lost mass during the rut (Table 5). Rams lost from 5% to 16% of their pre-rut mass over 15–20 days of rutting. For rams 1 year and older, initial body mass was highly correlated with mass change over the rut ($r = −.97$, $n = 14$, $p < .01$). Mass change over the rut was correlated with the time spent foraging ($r = .88$, $n = 12$, $p < .01$) and with time devoted to rutting activities ($r = −.70$, $n = 12$, $p = .01$) (Figure 3).

DISCUSSION

I quantified the foraging constraints of alternative mating tactics of bighorn rams. Those foraging constraints may affect survival by depleting body reserves just before the winter and therefore could be an important component of reproductive costs. A combination of foraging constraints, injuries from male-male combat, and energetic expenditure for rutting activities has been suggested to explain why the survival rate of ungulate males typically decreases at the age when they start

to be involved in reproduction (Jorgenson et al., 1997; Loison et al., 1999). My results, however, suggest that individual differences in behavior may be more important than are differences in mating tactic in affecting the foraging constraints of reproduction. It is likely that the same pattern exists for reproductive costs. The within-individual comparison suggests that rams show much phenotypic plasticity in their behavior because mating tactic only explains 11% of the variance in foraging behavior.

Males aged 2 years and older spent less time foraging during the rut compared with the pre-rut, but there was no effect of social rank on the decrease in time spent feeding. Rams did not spend less time foraging when tending than when coursing. On the contrary, males that adopted both mating tactics spent almost twice as much time foraging when tending than when coursing, suggesting that coursing imposes higher foraging constraints than tending. Therefore, tending, which is by far the most successful mating tactic in this population (Hogg and Forbes, 1997) does not involve a greater constraint of foraging time than the less successful alternative tactic of coursing. Indeed, those males that were observed using both tactics incurred a greater reduction in foraging time when coursing than when tending. Thus, despite its lower fitness benefits, coursing may be costlier than is tending. Coursing rams, however, are subordinate to tending rams and therefore have no alternative tactic, other than not attempting to mate. Because dominant rams have a competitive advantage over subordinates at the beginning of the rut, they adopt a mating tactic with a higher payoff, resulting in higher number of offspring (Hogg and Forbes, 1997). The initial competitive advantage of being dominant leads to increasing returns without involving higher foraging constraints (Dobson et al., 1999).

Bighorn rams 2 years and older foraged from 15–20% less during the rut than during the pre-rut, a reduction in feeding

Table 3

Time budgets (% of time $\pm$ SE) of 28 bighorn rams while tending, coursing, or searching for estrous ewes during the rut, Sheep River, Alberta, 2000–2002

Tactic	Foraging	Lying	Moving	Standing	Interacting with males	Interacting with females	Other
Tending	16 ± 0.2	25.0 ± 3.0	6.0 ± 1.0	37.0 ± 0.2	3.0 ± 1.0	13.0 ± 1.0	1.0 ± 0.0
Coursing	14 ± 0.1	13.0 ± 0.2	29.0 ± 3.0	35.0 ± 0.2	2.0 ± 0.1	6.0 ± 0.1	1.0 ± 0.1
Searching	6 ± 0.1	3.0 ± 0.1	63.0 ± 0.2	27.0 ± 0.2	0.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0

Table 4

Linear mixed model selection of the proportion of time spent foraging by bighorn rams that were observed both coursing and tending during the same rut, Sheep River, Alberta, 2000–2002

General model: F = Y + A + TM

Variables	F ratio	df	p
Y	1.91	2, 100	.153
A	0.36	1, 100	.549
TM	10.02	1, 100	.002

Selected model: F = Y + TM

Variables	Estimates	SE
Y	—	—
TM	−8.535	2.730

The data included 114 focal observations of 10 rams, and the final model explained 11.08 % of the variance. F indicates proportion of time spent feeding; Y, year; A, age; and TM, type of mating tactics (coursing or tending).

Table 5

Average mass (kg) of individual bighorn rams of different age class before and after the rut and mass change (±SE) during the rut from 2000–2002, Sheep River, Alberta

Age	Mass before	Mass after	N	Mass change (kg)	SE	% mass change
Yearlings	58.2	59.9	6	1.7	3.3	2.9
2 years	79.5	75.3	3	−4.2	1.1	−5.3
3 years	105.6	90.2	2	−15.4	3.4	−14.6
4 years	113.0	94.9	2	−18.1	3.2	−16.0
6 years	134.2	115.0	1	−19.2	—	−14.3

during the rut, with large rams losing more mass than did small ones. This result is consistent with recent studies that suggest that males adjust their reproductive effort according to their phenotypic quality (McElligott et al., 2003). High-quality individuals can afford the foraging constraints and other energetic costs of competing for mates, whereas low-quality individuals may be better off not attempting to take part in the rut (Clinton and LeBoeuf, 1993; McElligott et al., 2002). Foraging constraints could affect reproductive costs because rams that foraged less during the rut also lost more mass. Rutting activities may be costlier for smaller rams. In another population, Festa-Bianchet et al. (2004) found that as density increased, the larger young rams did not compromise horn growth in favor of maintenance, but the smaller ones allocated relatively fewer resources to horn growth. Therefore, the lower participation in the rut by smaller young rams may be part of a conservative reproductive strategy. Even though reproductive success by coursing rams is unrelated to social rank and presumably also to body mass, it may be very costly for small rams to attempt to mate.

Constraints on foraging time, as well as other energetically costly activities such as long-distance travel to search for females or frequent agonistic encounters, should vary with the intensity of competition for mates, which in turn should be affected by male age structure, operational sex ratio, spatial distribution of estrous ewes, and synchrony of estruses. Because foraging constraints typically result from trade-offs in time budget allocation (but see Miquelle, 1990; Whittle et al., 2000), all mating tactics are likely to impose some costs, which should be higher for the most active individuals

time smaller than that reported for guarding males in other ungulates (Clutton-Brock et al., 1982; Komers et al., 1994b; Miquelle, 1990, McElligott et al., 2003). In those species, males may stop feeding almost completely during the rut and lose up to 40% of their body mass. Bighorn rams only lost up to 16% of their pre-rut body mass, possibly indicating a more conservative reproductive strategy than what has been observed for cervids. Interspecific differences in mass loss during the rutting season could be related to differences in mating system. Tending rams can spend considerable time feeding while guarding an estrous ewe. In mountainous terrain, it is often possible for a tending ram to block all access to an estrous ewe simply by positioning itself on a narrow cliff ledge, where it can spend time foraging. Males that rut on a lek or defend a group of females, on the other hand, may have to constantly display or defend their territories, which could results in higher mass lost.

Young bighorn males appear to adjust their participation in rutting activities to their available energy reserves. For all rams, pre-rut body mass was a good predictor of mass change
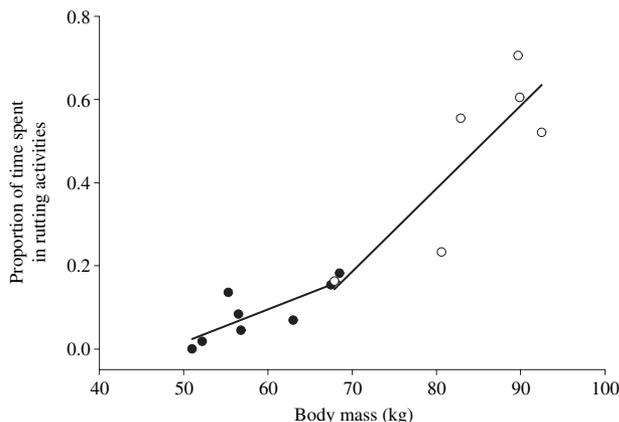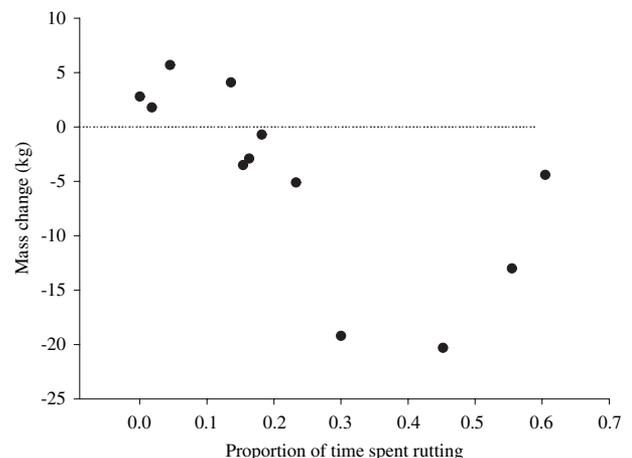

Figure 2
Relationship between pre-rut body mass and the proportion of time spent in rutting activities for yearling (closed circles) and 2-year-old bighorn rams (open circles) in 2000–2002, Sheep River Provincial Park, Alberta.

Figure 3
Mass change (kg) for bighorn rams 1 year and older in relation to the proportion of time spent in rutting activities during the rut from 2000–2002. Data above the dotted line indicate a mass gain;, data below the line indicate mass loss.

independently of the tactics used. Therefore, a male's individual behavior should be a better indicator of reproductive effort than its age or social rank. Moreover, even within a tactic, males showed great variability in reproductive effort. Consequently, for polygynous species, the cost of reproduction for males may not be strongly associated with reproductive success (McElligott et al., 2003).

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