Introduction

Why do males of polygynous species, such as ungulates from temperate and northern regions, reduce or even stop foraging during the rut? This phenomenon is somewhat paradoxical, as the rut is a period of great reproductive effort for male ungulates and occurs just prior to winter, the most limiting season in terms of both forage quality and availability (Clutton-Brock et al. 1982; Coulson et al. 2001).

Abstract

In polygynous ungulates, the rut imposes constraints on male time budgets that generate a trade-off between maintenance and reproduction, leading to a reduction in time spent foraging. As mating activities can incur substantial somatic costs, males are expected to spend their ‘non-rutting’ time recovering during the breeding season. If the diminution in time allocated to foraging by males is only a consequence of time budget constraints, males should keep a similar ratio of time spent foraging to lying to that observed in the pre-rut, leading to an overall reduction of these two activities (the ‘foraging constraint’ hypothesis). Alternatively, if males adopt an energy-saving strategy, they should limit energy expenditures by reducing foraging but not lying time, as the energy gains of forage intake may not meet the basal energetic requirements, especially in northern and temperate regions (the ‘energy-saving’ hypothesis). Here, we contrast these two hypotheses by comparing individual daily time budgets of marked adult bighorn sheep rams (Ovis canadensis) and male mountain goats (Oreamnos americanus) during the pre-rut and the rut. Concordant results for both species support the ‘foraging constraint’ hypothesis, as sexually-active males reduced time spent foraging and lying from the pre-rut to the rut because of an increase in time spent in mating-related activities. Bighorn sheep rams also increased time spent foraging when not engaged in mating tactics, providing further support for a ‘maximisation’ of energy intake in the absence of reproductive opportunities. Because there are also known physiological changes that occur during the rut which may cause appetite suppression, for example to produce metabolic compounds linked with olfactory communication (the ‘scent-urination’ hypothesis) or to cope with increased burden of parasites (the ‘parasite-induced anorexia’ hypothesis), further research should aim at simultaneously testing these current hypotheses to better understand rut-induced hypophagia and its effects on the life histories of male ungulates.
A reduction in time allocated to foraging, coupled with an increase in energy expenditures associated with mating-related activities (Mysterud et al. 2004; Pelletier 2005), may therefore cause male ungulates to enter winter in poor body condition (Yoccoz et al. 2002; McElligott et al. 2003), which in turn may lower their short-term survival (Stevenson & Bancroft 1995; Jorgenson et al. 1997) and explain the commonly observed female-biased adult sex ratio in wild populations (Loison et al. 1999). Despite its potentially high fitness cost, rut-induced hypophagia is nonetheless common among male ungulates: *Alces alces* (Miquelle 1990), *Bison bison* (Komers et al. 1994), *Cervus elaphus* (Clutton-Brock et al. 1982), *Dama dama* (Apollonio & Di Vittorio 2004), *Oreamnos americanus*, (Mainguy & Côté 2008), *Ovis canadensis* (Pelletier 2005), *Rupicapra rupicapra* (Willisch & Ingold 2007), as well as in other mammals such as primates and pinnipeds (e.g. Alberts et al. 1996; Coltman et al. 1997).

Few hypotheses have been proposed to explain the reduction in time allocated to foraging from the pre-rut to the rut in polygynous male ungulates (for a review see Mysterud et al. 2008). The ‘foraging constraint’ hypothesis was developed within the framework of optimal foraging theory and predicts that individuals face a trade-off between activities related to reproduction and maintenance (Krebs & Davies 1993). Because the rut is generally short in northern ungulates, time spent in mating activities is thus expected to be favoured at the expense of maintenance activities, i.e. the time spent foraging and lying (Wolff 1998; Pelletier 2005). As the rut is also a period of high energy expenditures (Yoccoz et al. 2002; McElligott et al. 2003), male ungulates are expected to allocate most of their time not engaged in mating-related behaviour during the rut (hereafter referred as non-rutting time) maximising energy intake to partially compensate for the energy spent in mating activities. Therefore, foraging should still occupy a large proportion of the non-rutting time of male ungulates to yield a foraging-to-lying-time ratio (hereafter F/L ratio) similar to that outside the breeding season. Thus males would increase energy intake when not actively engaged in mating activities which could reduce foraging constraints imposed by the reproduction. This hypothesis has also been termed the ‘energy-maximising’ hypothesis (Willisch & Ingold 2007), but here we chose to refer to it as the ‘foraging constraint’ hypothesis as we expected that males should maximise time spent rutting and, when ‘spare time’ is available, should allocate it to foraging activities. In addition, foraging time by breeding males might also be constrained by other biological functions. For instance, time spent foraging may decrease the ability to detect predators and may also limit signalling, i.e. sexual communication through visual signals. These additional factors that can shape the foraging patterns of rutting male ungulates are unfortunately difficult to account for, but may impose trade-offs on time budget allocation to foraging.

Another hypothesis developed within the framework of optimal foraging theory and termed the ‘energy-saving’ hypothesis, predicts that male ungulates with time consuming mating tactics should allocate most of their non-rutting time to lying instead of foraging, as the efficiency to assimilate energy (e.g. from poor-quality plants at this period of the year) may fall below the level necessary to reach basal energetic requirements (Willisch & Ingold 2007). More specifically, because male ungulates are likely constrained to maintain a cyclic pattern of forage intake and rumination to assimilate energy (Robbins 1993) and rutting activities possibly disrupt that cycle, males should minimise their energy expenditures by lying more than foraging, as the costs of foraging are potentially greater than the energy gains. This strategy was suggested to explain the greater proportion of non-rutting time spent lying instead of foraging by male Alpine chamois (*Rupicapra rupicapra*, Willisch & Ingold 2007). It could also be adopted by other northern polygynous ungulates, as the rut typically occurs during a period when food is limited and of low quality. Recently, Mysterud et al. (2008) proposed an alternative hypothesis, termed the ‘physical rest’ hypothesis, which also predicts that males should trade foraging time for lying time during the mating season. However, the functional explanation for feeding reduction (or cessation) suggested by this hypothesis is the need for males of a physical rest of muscles to successfully compete for access to females.

Bighorn sheep and mountain goats are highly polygynous and sexually dimorphic alpine ungulates for which activity budgets during the pre-rut and the rut have been previously quantified (Pelletier 2005; Mainguy & Côté 2008). In both species, males decrease foraging time by 42–59% during the rut compared with periods outside the breeding season. Bighorn sheep and mountain goats also share similar mating systems in which dominant males defend one oestrus female at a time (tending tactic), whereas subordinates attempt to obtain matings by pursuing females (coursing tactic; Hogg & Forbes 1997; Mainguy et al. 2008). Thus, these two species
are good models to investigate trade-offs in time budgets of male ungulates in relation to the ‘foraging constraint’ and the ‘energy-saving’ hypotheses, as rutting activities appear incompatible with time spent foraging and lying.

Here, we used daily time budgets of marked male bighorn sheep and mountain goats to assess whether the pattern of foraging time during the rut is more concordant with a strategy of minimising energy expenditures or a consequence of foraging constraints imposed by the breeding season. To do so, we explored the trade-off between foraging and lying time by examining the absolute change in the proportion of time spent in these activities and that of other behaviours from the pre-rut to the rut, as well as the change in the ratio of time spent foraging on time spent lying between periods as suggested by Willisch & Ingold (2007). If males adopt an energy-saving strategy, then only time spent foraging should decrease from the pre-rut to the rut and not the time spent lying. As a result, time spent lying is expected to decrease as time spent rutting increases and the F/L ratio is expected to decrease from the pre-rut to the rut (Willisch & Ingold 2007). Conversely, if foraging patterns are only a consequence of time budget constraints, then the decrease in foraging time from the pre-rut to the rut should be similar to the decrease in time spent lying. Consequently, the proportion of time spent foraging and resting should both be negatively correlated with time spent rutting, and the F/L ratio should remain stable between periods (Willisch & Ingold 2007).

**Methods**

**Study Areas and Populations**

Adult (≥2-yr old) bighorn sheep rams were studied over 3 yr (2000–2002) in the Sheep River Provincial Park, Alberta, in the foothills of the Canadian Rockies (50°N, 114°W). More than 90% of the sheep in that population are uniquely marked with plastic ear tags and are of known age, determined at capture by counting horn annuli (Festa-Bianchet 1986; Hogg & Forbes 1997). The area used by bighorn sheep during the pre-rut (from late Sep. until Nov.) and the rut (Nov. to early Dec.) is relatively open, consisting of grassy meadows, aspen (*Populus tremuloides*) patches, and cliffs, which make sheep groups easy to locate and monitor for long-time periods. In this population, the rut has been intensively monitored since 1989 and >96% of males present in the area during the breeding season are seen daily (Hogg & Forbes 1997; Pelletier et al. 2006).

Adult (≥3-yr old) male mountain goats were studied over 3 yr (2004–2006) during the pre-rut (Jun. to Sep.) and the rut (early Nov. to early Dec.) at Caw Ridge, west-central Alberta, in the front range of the Canadian Rockies (54°N, 119°W). This native mountain goat population uses approx. 28 km² of alpine grassy slopes, short cliffs, and open subalpine forests from 1750 to 2170 m in altitude. The Caw Ridge population has been studied intensively since 1989 (Festa-Bianchet & Côté 2008), with ≥98% of individuals aged ≥1 yr individually recognisable since 1993 through ear tags and visual collars. Age is determined by counting horn annuli at capture (Côté et al. 1998). Further details about the Caw Ridge study area and capture procedures can be found in Côté et al. (1998) and Festa-Bianchet & Côté (2008).

**Activity Budgets**

For bighorn sheep rams, time of transition between five types of behaviours was recorded during continuous focal-animal observations (Pelletier 2005) in the pre-rut and the rut. The rut started when the first copulation was observed in Nov. (Pelletier 2005). The five behaviours recorded in each period were: (1) foraging, (2) lying, (3) standing, (4) social (i.e. interactions with males or females) and (5) other, which consisted mostly in moving (i.e. walking or running) but also included any activities that could not be classified in any of the four first categories. Over the 3 yrs, a total of 1047 and 928 sheep-hours of observations were collected (averaging 29.9 and 26.5 h of observation per individual, n = 25 different rams monitored over 1–3 yr) during the pre-rut and the rut respectively. Bighorn sheep rams were located at least three times per day during the rut at regular intervals (morning, noon and afternoon) and observed from at least 100 m to avoid disrupting their behaviour. Each time a ram was monitored, observers watched it for at least 1 h and up to 6 h. Female reproductive status was determined from behavioural observations. Oestrus corresponded to the period when adult females showed receptivity to copulation and typically preceded abandonment by a tending male (Hogg 1984). During each observation, we recorded whether a male was involved in one of the three mating tactics: (1) tending, (2) coursing or (3) blocking (Hogg & Forbes 1997); otherwise it was assigned as (4) investigating when observed in a group of anoestrous females or (5) searching for oestrous females (Pelletier 2005).
This methodology provides a realistic picture of what a male does over the entire rut in terms of both time spent in different behaviours and use of alternative mating tactics, because it samples most of the day for each individual, every day of the mating season. More details on the sampling of time budgets and computation of the proportion of time spent in mating tactics are reported elsewhere (Pelletier 2005; Pelletier et al. 2006).

Individual behaviour of adult male mountain goats was studied using the same five behavioural categories described for bighorn sheep during the pre-rut and the rut, but using scan sampling (Martin & Bateson 1993) at 10-min intervals (Mainguy & Côté 2008) instead of continuous focal observations, as this study was conducted independently of the one at Sheep River. Activity budgets were conducted as long as goats were in sight for a period of at least 1 h and at distances ranging from 200 to 700 m. A total of 1906 and 452 goat-hours of observations were collected (averaging 54.3 and 14.4 h of observation per individual, n = 37 different adult males monitored over 1–3 yr) for the pre-rut and the rut respectively. Because of the sampling method used in mountain goats and as it was not always possible to determine the reproductive status of all females present in a group (i.e. anoestrus or in oestrus), males could not always be assigned to one of the five possible mating situations as in bighorn sheep (i.e. either one of three mating tactics, investigating or searching) and thus, no data were available for the individual repartition of time between tactics in mountain goats. In both species, however, we considered time spent rutting as the total amount of time spent in social activities, standing and other (which consisted mainly in locomotion) during the rut, whereas non-rutting time was defined as the cumulative time spent either foraging or lying. We considered standing and moving as part of ‘active’ rutting behaviours (Maher & Byers 1987; Willisch & Ingold 2007), as these were likely performed in the context of mating activities. For instance, we previously suggested in mountain goats that standing could allow sexually active males to look for potential mates and competitors (Mainguy & Côté 2008; Mainguy et al. 2008), as all the activity budgets that we recorded were conducted in the presence of adult females that were near or in estrus.

Data Analysis

We first compared absolute changes in daily time budgets according to period (pre-rut and rut), fitted as a categorical fixed effect using linear-mixed models (LMM) with ‘male identity’ fitted as a random term to control for repeated measurements of the same individual (Pinheiro & Bates 2000). As year of observation could have also influenced male activity budgets, we included this variable as a categorical fixed effect in our analyses. Because male age affects time budgets of both species during and outside the rut (Pelletier 2005; Mainguy & Côté 2008), we also included it as a continuous independent variable. We used the overall proportion of time spent in each of the five behavioural categories in each period-year in bighorn sheep as the sampling unit (n = 35 individual-year observations in both the pre-rut and the rut), whereas in mountain goats we used yearly individual means of the proportions of time computed during activity budgets for each period (n = 69 and 66 individual-year observations in the pre-rut and the rut, respectively). The mean proportions of time spent in different behaviours were arc-sin square root transformed to approximate a normal distribution in both species. We also tested the correlation between either time spent foraging or lying with time spent rutting using Pearson correlation tests on transformed proportions. For the computation of ratios, a constant (k = 1) was added to the proportion of time spent foraging and lying in mountain goats to avoid a division by 0 when an individual was not observed to rest or a ratio of 0 when a male was not observe to forage. Consequently, ratios could vary between 0.5 and 2. Ratios were inverse-transformed in mountain goats and log-transformed in bighorn sheep to meet normality before testing for variations between periods. As for absolute changes in the behaviours investigated, F/L ratios were compared between periods when accounting for year of observation and male age using a LMM with ‘male identity’ fitted as a random term. In all analyses, the significance of individual effects was tested by comparing the log likelihood of models with and without the random terms (Steele & Hogg 2003). When the random term was not significant, we present the results of generalised linear models. Finally, in bighorn sheep, we also assessed whether time spent foraging increased with the overall proportion of time a ram was observed investigating and/or (i.e. when not engaged in one of the three mating tactics) using a Pearson correlation test, as more time should be allocated to foraging in the absence of opportunities for reproduction. Proportions of time spent in different mating tactics (or not) were also arc-sin square root transformed prior to analyses. All models were implemented in either
Male activity budgets of bighorn sheep and mountain goats varied greatly from the pre-rut to the rut (Fig. 1), as significant differences were found between periods for each of the behavioural categories considered when accounting for variations in male age and year (Table 1). Both bighorn sheep rams and male mountain goats decreased time spent foraging and lying from the pre-rut to the rut as previously reported (Pelletier 2005; Mainguy & Côté 2008), and increased significantly time spent in the three other behaviours (Table 1 and Fig. 1; that were considered as time spent rutting once regrouped). Bighorn sheep rams also spent more time foraging than lying during both periods (Fig. 1a), whereas adult male mountain goats showed an opposite pattern (Fig. 1b). Bighorn sheep rams decreased time spent foraging, but increased time spent lying and in social interactions with increasing age in both periods, whereas time spent in the remnant behaviours was not affected by age (Table 1). In male mountain

Table 1: Linear models of the effects of period (pre-rut vs. rut), age and year of observation on five behaviours monitored in adult (≥2-yr old) bighorn sheep rams at Sheep River (2000–2002), and adult (≥3-yr old) male mountain goats at Caw Ridge (2004–2006), Alberta, Canada.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Variable</th>
<th>Bighorn sheep</th>
<th>Mountain goats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>β</td>
<td>SE</td>
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<tr>
<td>Foraging</td>
<td>Period</td>
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<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Age</td>
<td>-0.012</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lying</td>
<td>Period</td>
<td>-0.17</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Age</td>
<td>0.009</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Standing</td>
<td>Period</td>
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<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Age</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Social</td>
<td>Period</td>
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<td>0.01</td>
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<tr>
<td></td>
<td>Age</td>
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<tr>
<td></td>
<td>Year</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td></td>
<td>Age</td>
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<td>0.002</td>
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<tr>
<td></td>
<td>Year</td>
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</tr>
</tbody>
</table>

Analyses are based on 70 individual-year observations in bighorn sheep (n = 35 during the pre-rut and 35 during the rut) and 135 in mountain goats (n = 69 and 66 respectively).
goats, only the time spent foraging was affected by age (Table 1), as older males spent less time foraging than younger males. In both species during the rut, time spent foraging (bighorn sheep: \( r = -0.40, p = 0.02 \); mountain goats: \( r = -0.42, p < 0.001 \)) and lying (bighorn sheep: \( r = -0.54, p < 0.001 \); mountain goats: \( r = -0.65, p < 0.001 \)) were negatively correlated with time spent rutting (Fig. 2). In bighorn rams, the F/L ratio increased by 18\% from the pre-rut (1.21 ± 0.09) to the rut (1.43 ± 0.17), but the difference was not significant (\( F_{1,65} = 0.09, p = 0.76 \)) when accounting for year (\( F_{2,65} = 7.1, p = 0.002 \)) and age (\( F_{1,65} = 9.7, p = 0.003 \)). In male mountain goats, the transformed F/L ratio increased by 8\% from the pre-rut (0.87 ± 0.02) to the rut (0.95 ± 0.02; \( F_{1,130} = 6.1, p = 0.01 \)) after accounting for variations in year (\( F_{2,130} = 7.0, p = 0.001 \)) and age (\( F_{1,130} = 5.1, p = 0.03 \)). This significant increase in mountain goats was more pronounced when using the untransformed ratio (which required the removal of five observations during the rut in which the individual did not rest, i.e. causing a division by 0), as it increased by 39\% from the pre-rut (0.87 ± 0.14) to the rut (1.21 ± 0.34). In both species, the F/L ratio also decreased as males aged, concordant with the decrease in the absolute time spent foraging with increasing age. Finally, in bighorn sheep, time spent foraging during the rut increased with an increase in the overall proportion of time spent investigating and searching (\( r = 0.41, p = 0.02 \); Fig. 3) and thus, foraging time decreased when rams were engaged in mating tactics. On the other hand, time spent lying was not correlated with the proportion of time spent in mating tactics (\( r = -0.18, p = 0.30 \); Fig. 3).

**Discussion**

We previously reported that male bighorn sheep and mountain goats decrease substantially the time allocated to foraging during the rut compared with outside the breeding season (Pelletier 2005; Mainguy &
Here, we tested whether males used their non-rutting time to 'maximise' foraging time or, alternatively, lying time as recently shown in male Alpine chamois (Willisch & Ingold 2007). Both species showed a reduction in lying time during the rut compared with the pre-rut, which was also more pronounced than the reduction in time spent foraging in male mountain goats according to the F/L ratio approach. In bighorn sheep rams, the decrease in time spent foraging and lying was similar and thus yielded an unchanged F/L ratio between periods. We estimated that the optimal time relationship between feeding and lying outside the breeding season is on average 1.2:1 for bighorn sheep (Pelletier & Festa-Bianchet 2004) and 0.9:1 for mountain goats (Julien Mainguy & Steeve D. Côté, unpubl. data). In mountain goats, the significant increase in the F/L ratio from the pre-rut to the rut, which was not predicted by either hypotheses, which suggests that non-rutting time is devoted mostly to foraging rather than resting in the species. This trend was also observed in bighorn sheep, which altogether provides further support for the maximisation of forage intake during daytime. The F/L ratio outside the breeding season is, however, strongly age-dependent. For example, in bighorn sheep, the relationship between foraging and lying is 2:1 for yearling males, while it is 0.8:1 for fully grown adults (5 yr and older, Pelletier unpublished data). Time spent foraging and lying during the rut was in both cases negatively correlated with time spent rutting in the two species, suggesting that the trade-off between reproduction and maintenance was not done at the expense of lying time only. Furthermore, in bighorn sheep, rams that spent more time engaged in mating tactics spent less time foraging but not less time lying, suggesting a trade-off mainly between reproduction and foraging during the mating season. Overall, the patterns of foraging behaviour observed in these two polygynous ungulates appear more in accordance with the 'foraging constraint' hypothesis rather than the 'energy-saving' hypothesis. The lack of a significant positive correlation between lying time and the time not engaged in a mating tactic in bighorn sheep rams, however, could also partly support the 'physical rest' hypothesis (Mysterud et al. 2008). This result may indicate that males had to rest throughout the rut, whether engaged or not in a mating tactic. Therefore, the 'foraging constraint' and 'physical rest' hypotheses may not be mutually exclusive and could thus both explain the patterns observed, at least in bighorn sheep rams.

Although bighorn sheep rams and male mountain goats decreased both the time spent foraging and lying from the pre-rut to the rut, they nonetheless attempted to spend time in these maintenance behaviours when less time was required for mating-related activities (e.g. Fig. 3), revealing a trade-off between energy intake and reproduction. It is important to note, however, that foraging time can only provide at best a rough approximation of forage intake and thus energy gain. We chose to use lying time as a surrogate of ruminating time, although males do not necessarily spend all their lying time ruminating. We did this because precise estimates of ruminating time are difficult to obtain in the field, especially for long periods, because it requires the observer to keep permanent eye contact with the mouth of the animal. However, ruminating time is typically correlated with lying time, while the amount of time ruminating when standing is generally negligible. For instance, in bighorn sheep, males...
spend on average 58% of their lying time ruminating based on 399 focal observations of males aged 1 yr and older observed outside the breeding season (K. Ruckstuhl, unpubl. data). It is also worth noting that our study is only concerned with daylight activity budgets and does not cover the full 24-h period. We therefore made the assumption that both bighorn sheep and mountain goats are either not active at night or if they are, their nightly activity patterns are in line with the proportions observed during the day. Previous studies using radio collars equipped with activity sensors suggested that bighorn sheep are inactive at night (Sayre & Seabloom 1994), whereas Alaskan mountain goats appear to greatly reduce ‘active’ time at night (K. White, unpubl. data). Nevertheless, our findings are consistent with results obtained with daily time budgets in bison (Bison bison) showing that males found outside female groups during the rut spent more time foraging and lying than males accompanying females (Komers et al. 1992). Komers et al. (1992) suggested that male bison did so to recover from energy expenditures associated with mating-related activities, which they termed the ‘condition improvement’ hypothesis. In the same species, Wolff (1998) reported that males that tended females in the absence of Challengers spent also more time foraging than males that defended females against other males, supporting the hypothesis of an attempt to gain, instead of saving, energy under time constraints imposed by rutting activities. Daily time budgets collected in bighorn sheep and mountain goats suggest, however, that they do not fully ‘maximise’ energy intake, as males could potentially forage more than they did given, for instance, the large proportion of time spent standing. On the other hand, the reduction in time spent lying from the pre-rut to the rut did not suggest that males were attempting to minimise energy expenditures, as previously observed in male Alpine chamois (Willisch & Ingold 2007). According to focal observations conducted separately from scan sampling in mountain goats, males in consort pairs with oestrous females (i.e. tending) spent as much time lying as the females they tended (16 ± 4% in both sexes, n = 34 consort pairs; Mainguy et al. 2008). Under the energy-saving hypothesis, one could have expected males to rest more than females, as the reproductive costs of males during the rut are potentially higher than those of females. This is likely, as the main costs of reproduction sustained by females occur after the rut and originate mostly from lactation (Clutton-Brock et al. 1989), whereas reproductive costs in males occur only during the rut (Mysterud et al. 2004). Thus, overall, foraging strategies are likely to vary between ungulate species during the rut. For example, Mysterud et al. (2008) recently suggested that male red deer might also be trading foraging time for lying time during the mating season. However, they suggest that males do this to recover from physical expenses and not because their daily feeding cycle is disrupted (Mysterud et al. 2008).

At least two other hypotheses could also explain the reduction in time spent foraging by polygynous male ungulates from the pre-rut to the rut: (1) the ‘scent-urination’ hypothesis (Miquelle 1990) and (2) the ‘parasite-induced anorexia’ hypothesis (Mysterud et al. 2008). The first hypothesis proposes that rutting male ungulates must greatly reduce foraging to produce metabolic by-products in their urine (Miquelle 1991; Whittle et al. 2000). These pheromones would then be involved in intra- and intersexual olfactory communication (Coblentz 1976). For example, in moose (Alces alces; Miquelle 1990, 1991), the scent of urine could provide an honest advertisement of the condition of bulls, as only those in good body condition can afford to produce the scent obtained through the catabolism of fat stores that requires that the animal does not feed during the rut (Whittle et al. 2000). Metabolites produced by the catabolism of body reserves have also been identified in the urine of rutting white-tailed deer (Odocoileus virginianus) bucks (Miller et al. 1998). Testosterone levels, which substantially increase at the onset of the rut in male ungulates (Pelletier et al. 2003; Mooring et al. 2004), could possibly trigger this physiological process by causing appetite suppression (Newman et al. 1998). This hypothesis could thus further explain the complete cessation of feeding during the rut in some ungulates (e.g. Apollonio & Di Vittorio 2004), although many other ungulates, including bighorn sheep and mountain goats, still forage during the rut (e.g. Wolff 1998). The second hypothesis has also been proposed to explain the ‘voluntary’ reduction of food intake in animals, but this time to cope with severe parasite infections (Kyriazakis et al. 1996, 1998; Mysterud et al. 2008). Under the ‘parasite-induced anorexia’ hypothesis, reduced forage intake may allow the host to be more selective in its diet and thus to select forages that either minimise the risk of infection or are rich in anti-parasitic compounds (see Kyriazakis et al. 1998 for a review). This situation is likely as the parasite load per host increases substantially during the rut in several

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species of ungulates (Halvorsen et al. 1985; Pelletier et al. 2005) and high testosterone levels at this period of the year may suppress immunocompetence (Decristophoris et al. 2007). Therefore, males could ‘voluntarily’ decrease their foraging time, and thus intake, to cope with the increase in parasite burden during this stressful period (Mysterud et al. 2008). If this is the case, one should expect a negative correlation between time spent foraging and parasite burden during the breeding period. Thus, both time constraints and physiological changes could account for the reduction of foraging time observed during the rut. The various hypotheses proposed to explaining rut-induced hypophagia have mostly been developed in male ungulates from temperate and northern regions. However, foraging constraints may differ for male ungulates inhabiting tropical regions, as the foraging restrictions (i.e. food availability and quality) may be less severe during the rut at southern latitudes.

In this article, we have shown that rut-induced hypophagia in wild adult male bighorn sheep and mountain goats appeared to result from time budget constraints generated by mating-related activities rather than from an active energy-saving strategy. However, other functional explanations, such as the ‘scent-urination’ hypothesis, could also account for the reduction in time spent foraging by polygynous male ungulates. Further research effort should therefore aim at testing simultaneously multiple hypotheses to quantify the contribution of physiological and behavioural processes to rut-induced hypophagia. The simultaneous collection and comparison of data from activity budgets obtained through field observations (Pelletier 2005; Mainguy & Côté 2008), physiological traits (e.g. plasma testosterone concentrations, Newman et al. 1998), and parasite burden (e.g. nematode egg counts, Decristophoris et al. 2007) prior, during and after the rut may represent an interesting approach to disentangle the contribution of the different potential hypotheses to explain feeding reduction or suppression observed in many temperate and northern ungulates during the rut. This type of research could be more easily achieved in a semi-captive population, as repeated behavioural and physiological samples from different marked individuals are required. Because rut-induced hypophagia is an important component of male reproductive effort, understanding its causes will provide cues on patterns of reproductive effort and ultimately, shed light on the trade-off between current reproduction and survival in wild male ungulates.

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