Allegato 2b_4

Contrasting alternative hypotheses to explain rut-induced hypophagia in territorial male chamois

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Published in: ETHOLOGY, 120 (2014): 32-41

Abstract

Male ungulates in temperate environments often show a severe reduction in time spent foraging during the mating season. Several hypotheses have been put forward to explain this phenomenon but, so far, no study investigated the proximate mechanisms underlying rut-induced hypophagia in ungulates using alternative mating tactics (AMTs). Between the prerut and postrut of 2011 and 2012, we collected data on activity budgets, parasite burden and androgen levels of territorial and non-territorial male Alpine chamois *Rupicapra r. rupicapra* in the Gran Paradiso National Park (Italy). We aimed to investigate if AMTs showed similar reduction in time spent foraging during the mating period, and test the predictions underlying alternative hypotheses that may explain rut-induced hypophagia. Only territorial males showed a significant reduction in time spent foraging during the rut; the lack of correlation between proportion of time spent foraging and androgen metabolites or parasite burden did not fully support the physiological and the parasite hypotheses, while the foraging constraint, the energy-saving and the physical rest hypotheses could not be discounted. Territorial males decreased the time spent lying down from the pre-rut to the rut, but not their foraging to lying down ratio. During the mating period, we found negative correlations between time spent foraging or lying down and time spent rutting. Our data suggest that territorial males' behaviour is more consistent with the foraging constraint hypothesis, than with the energy-saving hypothesis previously suggested. Yet, during the rut territorial males did not maximise their foraging time, and the optimisation of their energy balance could rather depend upon feeding on relatively high-quality plants. This suggestion –possibly named 'forage-quality hypothesis'– now requires further investigations. This work showed that alternative mating behaviours may underlie different patterns of foraging strategies: we suggest that tests of alternative hypotheses to explain rut-induced hypophagia within ungulate populations should not ignore the occurrence of AMTs.

Introduction

Rut-induced hypophagia, the reduction of time spent foraging during the mating season, is commonly observed in male ungulates in temperate environments (e.g. American bison *Bison bison*, Bergman et al. 2001; fallow deer *Dama dama*, Apollonio & Di Vittorio 2004; Bighorn sheep *Ovis canadensis*, Pelletier 2005; Alpine chamois *Rupicapra rupicapra*, Willisch & Ingold 2007; Alpine ibex *Capra ibex*, Brivio et al. 2010). Pelletier et al. (2009), however, pointed out the 'somewhat paradoxical' nature of this behaviour, as it may potentially affect the overwinter survival for males that already sustain great energy expenditures.

To explain why so many ungulate species do employ such a strategy, different authors tested or proposed as many different hypotheses, all with distinctive behavioural and physiological predictions (reviewed in Brivio et al. 2010). The foraging constraint hypothesis (FCH) assumes that time dedicated to mating activity would increase to the detriment of time spent foraging and lying down, as found in bighorn sheep and in mountain goat *Oreamnus americanus* (Pelletier 2005; Pelletier et al. 2009). The energy-saving hypothesis (ESH), suggested by Willisch & Ingold (2007) for male Alpine chamois, assumes that a drop in digestive efficiency during the rut may bring males to primarily allocate non-rutting time to resting, rather than to foraging. The physical rest hypothesis (PRH) proposed by Mysterud et al. (2008), also suggests that non-rutting time would be primarily devoted to resting, but mainly to recover from physical stress imposed by mating activities. The increase in testosterone levels during the rut often observed in ungulates (e.g. in American bison, Mooring et al. 2004), while promoting male reproductive effort (Knapp 2003) may trigger appetite suppression (Newman et al. 1998). According to the physiological hypothesis (PH), hypophagia may be mediated through hormonal changes (Suttie & Simpson 1985), as suggested to occur in moose *Alces alces* (Miquelle 1990) and, possibly, in fallow deer (Apollonio & Di Vittorio 2004). Finally, the parasite-induced anorexia hypothesis (PAH) proposed by Mysterud et al. (2008) postulates that immunosuppression during the rut would bring males to avoid eating to reduce further ingestion of parasites. No study has examined simultaneously all predictions to explain rut-induced hypophagia, for example collecting data on activity budgets, physiological traits and parasite burden. Yet, disentangling the contribution of different hypotheses could help to explain foraging time reduction during the mating season (Pelletier et al. 2009).

For a correct interpretation of the behavioural and physiological predictions underlying alternative hypotheses to explain rut-induced hypophagia, it is important to identify those individuals, or groups of individuals, that actually show reduction in time spent foraging during the rut, and those that do not. Within ungulate populations, the occurrence of discrete patterns of mating behaviour (alternative mating tactics: AMTs) is quite common (Isvaran 2005). The life history theory predicts that individuals that invest more time and energy in costly inter- and intra-sexual interactions will likely increase current reproductive success to the detriment of survival, while individuals that invest more in foraging may improve survival and future reproductive success (Stearns 1992). As a result, different mating tactics may involve different energetic constraints and, possibly, different levels of rut-induced hypophagia. Although very little information is available on this issue, Pelletier (2005) showed that, in rutting bighorn sheep, the primary tactic (tending) did not constrain foraging more than the secondary one (coursing). More recently, however, Corlatti et al. (2013) showed that in Alpine chamois only territorial males seem to experience a strong reduction in time spent foraging during the mating season. Nevertheless, to our knowledge no study investigated the contribution of behavioural and physiological predictions underlying different hypotheses to explain hypophagia in ungulates using AMTs.

The Alpine chamois is a nearly monomorphic ungulate, dwelling on the Mountain massifs of Europe, Turkey and New Zealand. Its highly seasonal body mass dimorphism (from about 40% before the rut to about 6% in January and 4% in spring: Garel et al. 2009; Rughetti & Festa-Bianchet 2011) together with the unbiased sex-specific survival (Bocci et al. 2010) and the compensatory body growth observed for young males (Rughetti & Festa-Bianchet 2010) suggests a conservative mating system, such as weak polygyny. Behavioural observations confirmed the occurrence of alternative mating tactics, i.e. territorial and non-territorial males (von Hardenberg et al. 2000).

Between the prerut and postrut of 2011 and 2012, in the Gran Paradiso National Park (Italy) we monitored 22 marked territorial and non-territorial male chamois, for which we collected data on activity budget, testosterone level and parasite burden, making it possible to test simultaneously all the available hypotheses to explain reduction in time spent foraging. Despite the lack of morphological differences between territorial and non-territorial males, Corlatti et al. (2012) showed that the former invest more time rutting than the latter, suggesting the possibility for different life history trade-offs. Consequently, our main hypothesis was that only territorial males would experience hypophagia during the mating season (see Corlatti et al. 2013). If so, we aimed to investigate whether territorial male chamois would nonetheless adopt an energy-saving strategy, suggested by Willisch & Ingold (2007), or another strategy of energy optimization, by testing all the behavioural and physiological predictions underlying different hypotheses (FCH, ESH, PRH, PH, PAH) in the framework proposed by Brivio et al. (2010). These predictions explore: a) the variation in time spent lying down and b) the variation in foraging / lying down ratio between the pre- and postrut. Moreover, during the mating period they explore the correlations between: c) time spent foraging and time spent rutting; d) time spent lying down and time spent rutting; e) time spent foraging and parasite burden; f) time spent foraging and testosterone levels.

Methods

Study site and population

The study area in the upper Orco Valley (Gran Paradiso National Park –GPNP–, Western Italian Alps, 45°26'30" N, 7°08'30" E) extends over ca. 10 km^2 between 1,800 and 3,000 m a.s.l. The climate is continental, with mean yearly rainfall of about 1,096 mm and mean temperatures between -3.7 °C in winter and 13.1 °C in summer (La Morgia & Bassano 2009). The valley is oriented west to east, with a south-facing slope dominated by meadows of coloured fescue *Festuca varia*, and a north-facing slope characterised by the presence of larch *Larix decidua* woods and patches of alder shrubs *Alnus viridis*. The chamois population of the GPNP has not been hunted since 1922, and currently it shows densities of about 20 individuals / km^2 in the study site (L. Corlatti, unpublished data). The main limiting factor is likely winter starvation, whose severity may change according to sex, age and winter harshness (Rughetti et al. 2011). Other ungulate species present in the study site, with lower densities, are Alpine ibex and roe deer *Capreolus capreolus*.

Between February 2010 and November 2012, twenty-two adult male chamois were darted by the personnel of the Park with a mixture of xylazine and ketamine. Age was estimated by counting horn rings (Schröder & von Elsner-Schack 1985). Each male was equipped with individually recognizable GSM-GPS Pro-Light collars (Vectronic Aerospace GmbH, Berlin) and ear tags. Nussberger & Ingold (2006) showed that Alpine chamois behaviour is not affected by radio-collars. The sedative effect was reversed by an injection of atipamezole (Dematteis et al. 2009). The entire procedure usually took less than 40 minutes and was always performed with the assistance of a veterinarian. These methods are in line with Italian law.

Territorial vs. *non-territorial males*

To distinguish between territorial and non-territorial males for the rutting periods 2011 and 2012, we assumed that territorial males would have higher site fidelity and win more intra-sexual interactions than non-territorial males (von Hardenberg et al. 2000; Corlatti et al. 2012). Site fidelity was estimated from individual home ranges (90% Fixed Kernel), using GPS locations with at least 4 satellites and Dilution of Precision values <10 (Lewis et al. 2007). The proportion of intra-sexual interactions won was calculated as the number of interactions won over total number of interactions, collected during hourly sessions of observation *ad libitum* (Altmann 1974). We then combined the two parameters in a data matrix and used the Mahalanobis distance (Mahalanobis 1936) to perform multivariate hierarchical clustering (Everitt et al. 2011) with R 3.0.0 (R Development Core Team 2013) in RStudio 0.97.449 (RStudio 2012). From this analysis, in 2011 nine males were classified as territorials and 10 as non-territorials (see Corlatti et al. 2012). Each of these animals maintained the same tactic in the 2012 rut: this is not surprising, as males are likely to maintain the territory occupied in the previous year (von Hardenberg et al. 2000). In 2012, three other males were observed and sampled: one was classified as territorial, 2 were classified as non-territorials. No significant age difference was detected between territorial and non-territorial males (median=7 years in both groups).

Sampling design

In 2011 and 2012, we collected data (activity budget and faecal samples) over 3 periods: prerut (1 October - 3 November), rut (4 November - 3 December) and postrut (3 December - 31 December), see Corlatti et al. (2012). To construct activity budgets, during each period we observed 14 - 18 marked chamois with telescopes to avoid disturbance, and recorded individual behaviour using scan sampling at 5-minute intervals (Altmann 1974). Each animal was observed for 2 h each period (1 h in the first half of the month, 1 h in the second half, always separated by at least one week), for a total of 194 h of observations. Data collection was conducted during daylight hours, at different times of the day: morning (8 am – 11 am: 60 h), mid-day (11 am – 2 pm: 78 h), afternoon (2pm – 5 pm: 56 h). Behavioural categories included: foraging, lying down (which typically includes rumination), moving, standing, interactions with males or females, other (all the activities that could not be classified in any of the previous categories). The time of observation did not influence foraging (ANOVA: F = 0.848, $P = 0.430$) or lying down (ANOVA: F = 1.153, $P = 0.318$); thus, for each individual we averaged the number of events recorded in the 2 h of observation, to reduce potential issues of zero-inflation.

Over the same periods, fresh faecal samples from marked male chamois were collected to measure androgen metabolites, and to count lungworm larvae. For each observed individual, we tried to collect one fresh faecal sample per period, for an overall of 91 over the two years. Within 10h of sampling, each scat was divided in two fractions and put in separate plastic bags: one for androgen metabolite analysis was frozen at -20 °C, one for counts of parasite larvae was kept refrigerated at +4 °C.

Laboratory analyses

To measure the concentrations of androgen metabolites, we first extracted 0.5 g of each well-homogenized faecal sample with 5 ml aqueous methanol (80%; Palme & Möstl 1997). Androgen metabolite levels were then analysed using a testosterone EIA with sensitivity of 0.3 pg/well and intra- and interassay coefficients of variation of 7.9% and 12.9% (see details in Palme & Möstl 1994). To assess parasite burden, we focussed on lungworm larvae, because their seasonal cycle shows a peak during autumn (Stefancíková et al. 2011). To count larvae, following Thienpont et al. (1979) 2 g of faeces were mixed with a zinc sulphate solution diluted at 33%, and subsequently filtered with a strainer. The two chambers of the McMaster slide were then filled using a Pasteur pipette and counting, performed using a light-optical microscope at 100 magnifications, started 5 min after loading the slide. The sum of all the counted larvae was multiplied by 50 to obtain the number of larvae per gram of faeces.

Statistical analyses

The statistical framework used in this study is similar to that developed by Willisch & Ingold (2007), Pelletier et al. (2009) and Brivio et al. (2010). To test our main hypothesis, we checked for significant variation in time spent foraging between the pre- and postrut in AMTs, fitting linear mixed effect (LME) models separately for territorial and non-territorial males. Prior to analysis, the mean proportion of foraging events (response variable) was arc-sin square root transformed to approximate a normal distribution (Cramer-von Mises tests confirmed normality assumption for both male types. Territorials: W = 0.111, $P = 0.077$; non-territorials: W = 0.086, $P = 0.168$). We then set period, age of the animal and year as fixed factors. Animal identity was fitted as a random factor to account for pseudoreplication. We finally ran a post-hoc Tukey test for periods on LME models of territorial and non-territorial males.

When we detected a significant decrease in time spent foraging during the rut (either in territorial or non-territorial males), we tested all the behavioural and physiological predictions underlying different hypotheses to explain hypophagia, in the framework proposed by Brivio et al. (2010). We therefore investigated: a) the variation in time spent lying down from the prerut to the postrut, by a post-hoc Tukey test for periods on a LME model. The mean proportion of lying events (response variable) was first arc-sin square root transformed to approximate a normal distribution (Cramer-von Mises test for territorial males: W = 0.052, *P* = 0.477). We then set period, age of the animal and year as fixed factors, and animal identity as a random factor. We then investigated: b) the variation in the ratio between proportions of foraging and lying events (response variable) over time, by a post-hoc Tukey test for periods on a LME model, setting period, age of the animal and year as fixed factors, and animal identity as a random factor. Ratios were computed adding a constant (k = 1) to the proportion of time spent foraging and lying down to avoid a division by 0, and then log-transformed to meet normality assumption (Cramer-von Mises test for territorial males: W = 0.046, *P* = 0.558).

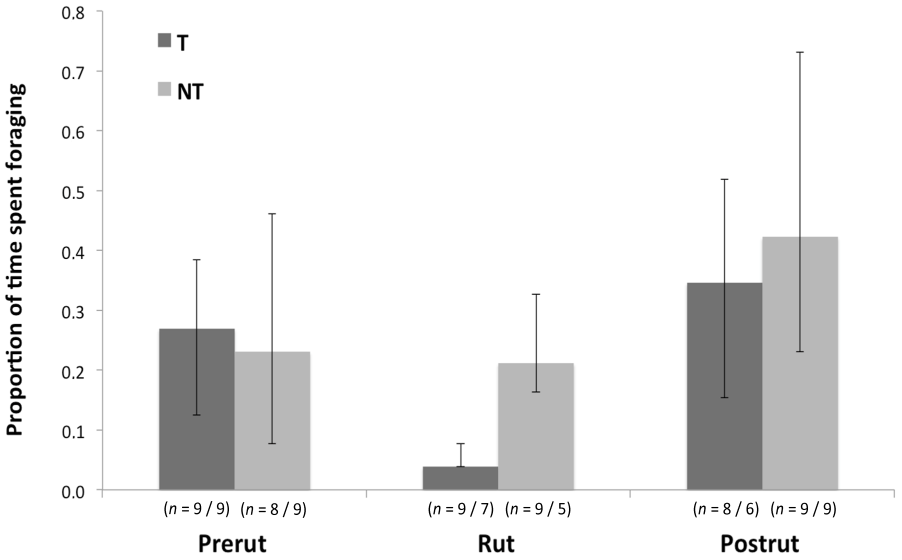
Finally, during the mating period we investigated the correlations between: c) time spent foraging and time spent rutting; d) time spent foraging and parasite load; e) time spent foraging and testosterone levels; f) time spent lying down and time spent rutting. For all relationships, we used Pearson correlation tests on transformed proportions of activity data (Pelletier et al. 2009). To allow comparisons with previous studies (Willisch and Ingold 2007; Pelletier et al. 2009; Brivio et al. 2010), time spent rutting was defined as the total amount of time spent interacting with males and females, moving and standing.

For all statistical analyses, we used R 3.0.0 (R Development Core Team 2013) in RStudio 0.97.449 (RStudio 2012). Linear mixed effect models were built with the function `lme` (‘nlme’ package: Pinheiro et al. 2013). The goodness of fit of every model (homoscedasticity, normality of errors and independence) was checked through visual inspection of residuals. Tukey post-hoc tests were performed using the function `glht` (‘multcomp’ package) (Hothorn et al. 2008).

Results

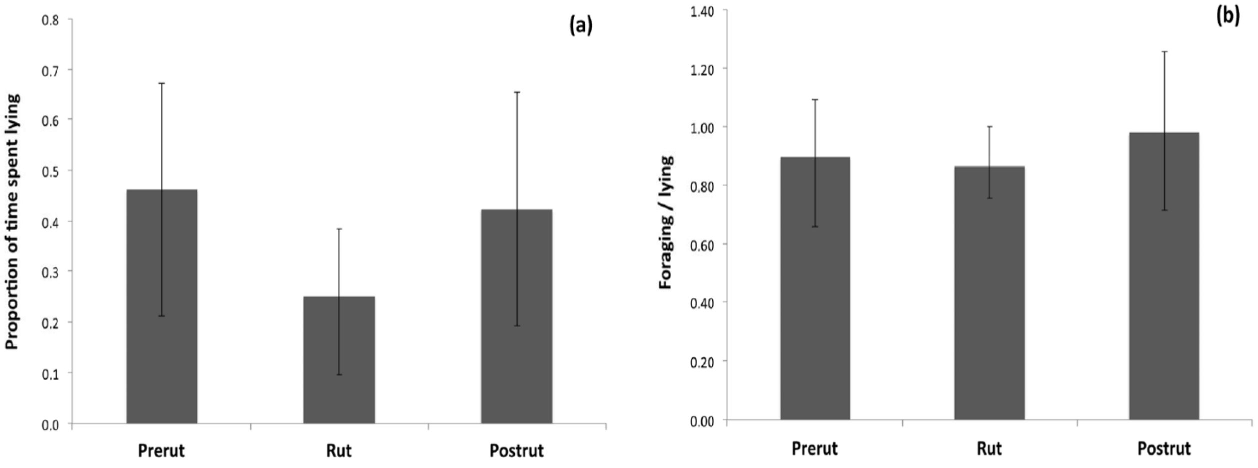
Territorial males spent less time foraging during the rut, compared to the pre- and postrut (prerut: median – Mdn=0.27 [quartile range – QR=0.13-0.38]; rut: Mdn=0.04 [QR=0.04-0.08]; postrut: Mdn=0.35 [QR=0.15-0.52]) (Fig. 1, Table 1). Non-territorial males, on the other hand, did not show rut-induced hypophagia, and increased time spent foraging in the postrut (prerut: Mdn=0.23 [QR=0.08-0.46]; rut: Mdn=0.22 [QR=0.16-0.33]; postrut: Mdn=0.42 [QR=0.23-0.73]) (Fig. 1, Table 1).

Figure 1: Proportion of time spent foraging during the prerut, rut and postrut by territorial (T) and non-territorial (NT) male chamois in the Gran Paradiso National Park (Italy) in 2011 and 2012. Values are medians ± interquartile ranges. In parentheses, the number of animals observed in 2011 and 2012, respectively.



The proportion of time spent lying down by territorial males decreased during the rut (prerut: Mdn=0.46 [QR=0.21-0.67]; rut: Mdn=0.25 [QR=0.10-0.38]; postrut: Mdn=0.42 [QR=0.19-0.65]) (Fig. 2a, Table 1). The ratio between time spent foraging and lying down by territorial males did not vary across periods (prerut: Mdn=0.89 [QR=0.66-1.10]; rut: Mdn=0.86 [QR=0.76-1.00]; postrut: Mdn=0.97 [QR=0.72-1.26]) (Fig. 2b, Table 1).

Figure 2: Proportion of time spent lying down (a) and foraging to lying down ratio (b) during the prerut, rut and postrut by territorial male chamois in the Gran Paradiso National Park (Italy) in 2011 and 2012. Values are medians ± interquartile ranges.



During the rut, the time spent foraging was negatively correlated with the time spent rutting (r = -0.55, d.f. = 14, *P* = 0.026); when accounting for the outlier, its removal did not influence the correlation (r = -0.57, d.f. = 14, *P* = 0.026) (Fig. 3a). Likewise, a negative correlation was found between the proportion of time spent lying down and that of time spent rutting (r = -0.94, d.f. = 14, *P* < 0.001) (Fig. 3b). Foraging time was neither correlated with parasite burden (r = -0.16, d.f. = 13, *P* = 0.564) nor with testosterone metabolite levels (r = -0.04, d.f. = 13, *P* = 0.886).

Figure 3: Proportion of time spent foraging (a) and lying down (b) in relation to proportion of time spent rutting (interacting, moving, standing) during the mating season by territorial male chamois in the Gran Paradiso National Park (Italy) in 2011 and 2012. The removal of the outlier in figure 3(a) did not influence the correlation.

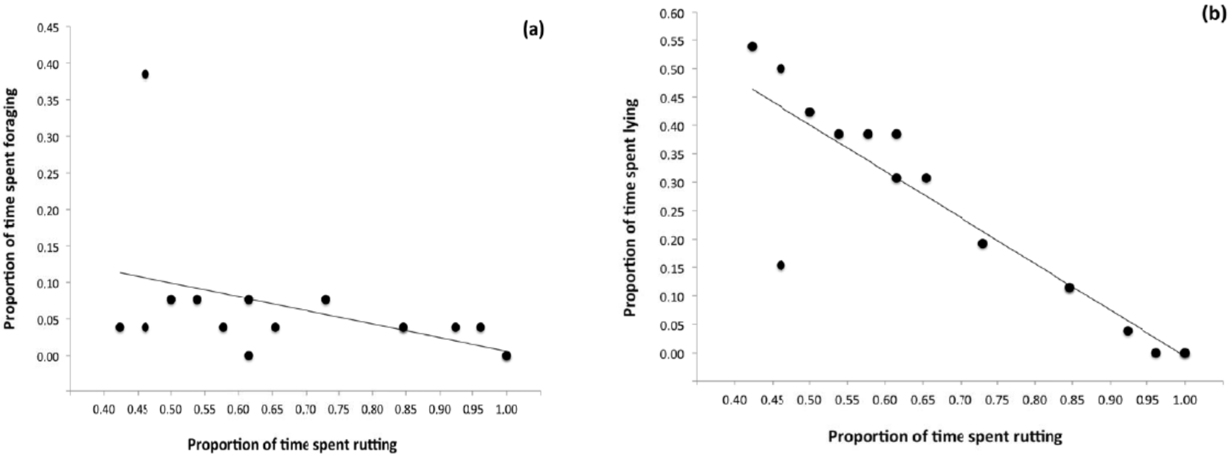
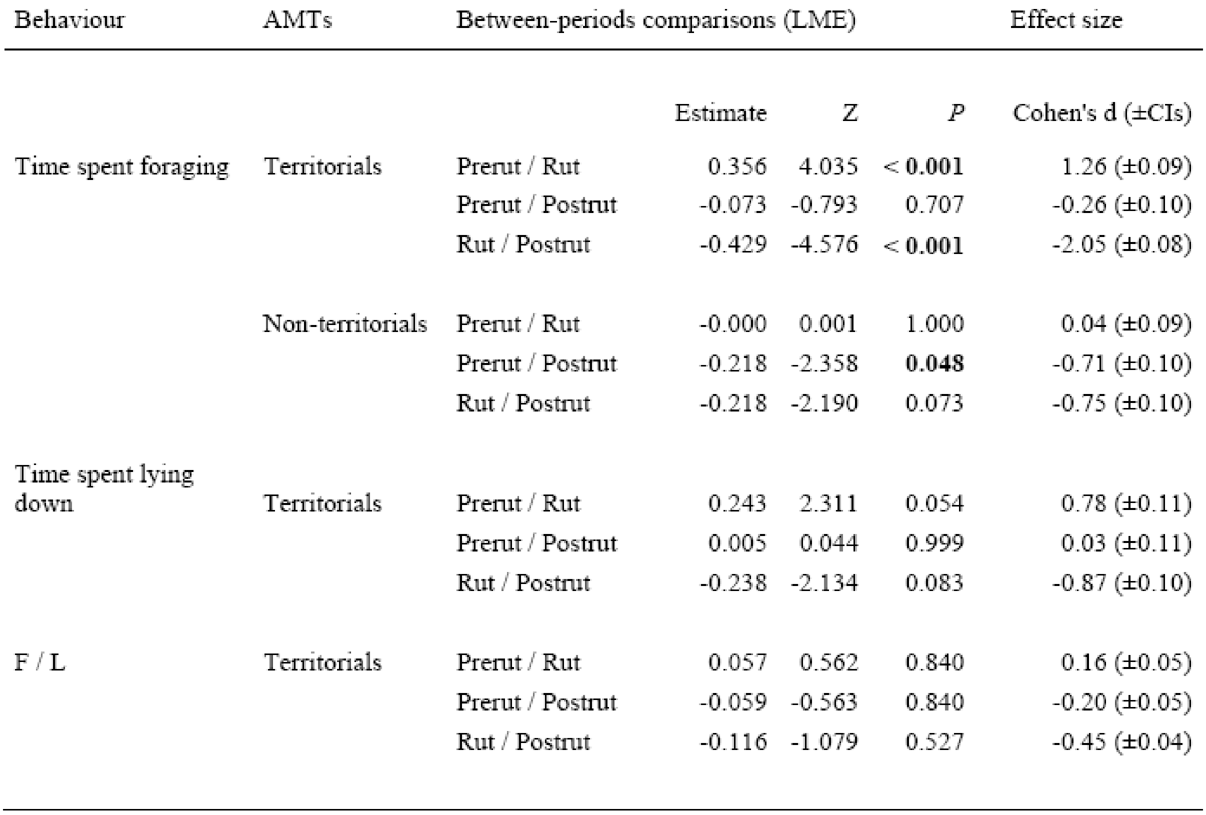


Table 1: Post hoc multiple comparisons of models analysing temporal variation in time spent foraging, time spent lying down and foraging to lying down ratio –F/L– (estimated through linear mixed effect models –LME) and effect sizes (± Confidence Intervals) in territorial and non-territorial male chamois, in the GPNP, in 2011 and 2012.



Behaviour	AMTs	Between-periods comparisons (LME)				Effect size
			Estimate	Z	*P*	Cohen's d (±CIs)
Time spent foraging	Territorials	Prerut / Rut	0.356	4.035	**< 0.001**	1.26 (±0.09)
		Prerut / Postrut	-0.073	-0.793	0.707	-0.26 (±0.10)
		Rut / Postrut	-0.429	-4.576	**< 0.001**	-2.05 (±0.08)
	Non-territorials	Prerut / Rut	-0.000	0.001	1.000	0.04 (±0.09)
		Prerut / Postrut	-0.218	-2.358	**0.048**	-0.71 (±0.10)
		Rut / Postrut	-0.218	-2.190	0.073	-0.75 (±0.10)
Time spent lying down	Territorials	Prerut / Rut	0.243	2.311	0.054	0.78 (±0.11)
		Prerut / Postrut	0.005	0.044	0.999	0.03 (±0.11)
		Rut / Postrut	-0.238	-2.134	0.083	-0.87 (±0.10)
F / L	Territorials	Prerut / Rut	0.057	0.562	0.840	0.16 (±0.05)
		Prerut / Postrut	-0.059	-0.563	0.840	-0.20 (±0.05)
		Rut / Postrut	-0.116	-1.079	0.527	-0.45 (±0.04)

Discussion

Studies on foraging strategies of ungulates using AMTs are rare. Pelletier (2005) showed that in rutting bighorn sheep, no difference in time spent foraging occurs between males engaged in coursing or tending. Corlatti et al. (2013), however, suggested that foraging time of territorial male chamois may be constrained more than that of non-territorial males, during the mating season. To our knowledge, this is the first study to investigate all predictions underlying different hypotheses to explain rut-induced hypophagia in alternative mating tactics. Our results showed that only territorial males experienced a significant reduction in time spent foraging, while non-territorial males maintained similar levels from the prerut to the rut.

For territorial males, the lack of correlation between proportion of time spent foraging and androgen metabolite levels may not support the physiological hypothesis, even though this hypothesis suggests potential effects of endogenous opiate antagonists (Plotka et al. 1985), which we did not test. Likewise, although androgen levels in territorial males peak during the rut, possibly leading to an immunosuppressive effect and a severe parasite increase (Folstad & Karter 1992; Corlatti et al.

2012), the lack of correlation between time spent foraging and parasite burden argues against the parasite-induced anorexia hypothesis proposed by Mysterud et al. (2008). We acknowledge that hormonal levels and parasite burdens may be exceedingly difficult to assess reliably in field conditions, as they may be influenced by several factors such as time of day, season, number and quality of interactions, as well as individual physical state and life-history stage (Palme 2005; Villanúa et al. 2006). Therefore, even though assessing hormonal levels and parasite burden through faecal samples should reflect roughly their overall levels, it remains an indirect measure to be taken with caution (Palme 2005, Villanúa et al. 2006). According to our data, the foraging constraint, the energy-saving and the physical rest hypotheses remain as the main competitive explanations for the reduction in time spent foraging during the mating season. Territorial males decreased their time spent lying down during the rut, while maintaining similar levels of foraging to lying down ratio from the prerut to the rut (between 0.89 and 0.86, very similar to the 0.9 value suggested by Pelletier et al. 2009 for another goat-antelope, the mountain goat). Time spent rutting was negatively correlated with time spent foraging and time spent lying down. Overall, the behaviour of territorial males during the rut appears more in accordance with the foraging constraint hypothesis, than with the energy-saving hypothesis previously suggested (Willisch & Ingold, 2007). Doubts about the energy-saving hypothesis arise from the hypothesised inability of individuals to 'maintain the basic cyclic pattern of ingesting and ruminating food' (Willisch & Ingold, 2007) to ensure an efficient microbial fermentation in the foregut. The drastic increase of time spent foraging in the postrut (observed in this study and in Willisch & Ingold 2007) contrasts with the hypothesised severe drop in the efficiency of microbial fermentation. From a physiological standpoint, if this were the case, we would expect a more gradual shift towards greater rates of food intake: indeed, 'herbivores such as ruminants and equids that utilize cellulose are poorly suited to rapid increases in food intake and sudden changes in diet composition because those changes may exceed the capacity to maintain homeostasis' (Barboza et al. 2009, p. 270). Moreover, rapid variations of food intake do not allow animals to reduce their basal metabolic rate, because they must maintain the capacity for digestion when feeding resumes (Barboza et al. 2009). Willisch & Ingold (2007) observed a negative relation between age and time spent foraging, as well as between age and foraging to lying down ratio. Most likely, these trends were partly due to age-dependent allocation of resources to reproduction, although the terminal investment hypothesis (Clutton-Brock 1984) hinted at by the authors appears questionable. The Alpine chamois, in fact, is a surprisingly long-lived species (Bocci et al. 2010) and males can actively participate to the rut up to at least 12 years of age (Corlatti et al. 2012), while the animals observed by Willisch & Ingold (2007) were only 3 to 8 years old. On the other hand, age is somewhat related to mating behaviour in chamois, as the onset of territoriality in this species is probably around 5 years of age (Corlatti et al. 2012). This work showed that alternative mating behaviours may well be associated with different patterns and strategies in foraging behaviour: we suggest that tests of alternative hypotheses to explain rut-induced hypophagia within ungulate populations should not ignore the occurrence of AMTs. A possible shortcoming of the present study is its restriction to daylight hours, while Willisch & Ingold (2007) investigated the 24h activity budget. Although very little is known about chamois nocturnal behaviour, observations conducted by the same authors offer some evidence of similar activity budgets between day and night in adult male chamois, indirectly supporting the reliability of data presented in our study. Our results are in line with other studies on mountain ungulates such as bighorn sheep, Alpine ibex and mountain goat (Pelletier et al. 2009; Brivio et al. 2010). The foraging constraint hypothesis, however, predicts that animals should maximise energy intake by using their non-rutting time primarily to forage. Our data suggest that territorial chamois do not maximise energy intake, as they could potentially forage more than they actually did (see also Pelletier et al. 2009) and the correlation between foraging and rutting time (Fig. 3) achieved limited explanatory power. In fact, only between 10 and 28% of the non-rutting time was spent foraging, and between 72 and 90% lying down (slightly more than what found by Willisch & Ingold [2007]: between 0.4 and 11.7% of the non-rutting time was dedicated to foraging, about 90% to lying down). Pelletier et al. (2009), however, pointed out that foraging time only provides a rough approximation of energy gain: ideally, one should consider also ruminating time (Moquin et al. 2010), which is difficult to record in the field. Furthermore, to correctly evaluate energy gain, it appears important to investigate not only how much time an animal spends foraging, but also the quality of forage ingested, because even little differences in the nutritive quality of forage may lead to substantial differences in growth of ruminant herbivores (White 1983; Hanley 1997). Data on diet quality in Corlatti et al. (2013), retrieved using Near Infrared Spectroscopy (Gálvez-Cerón et al. 2013) on faecal samples of the same individuals in 2011 showed that, during the mating season, territorial males fed on much higher quality forage than did non-territorial males (crude protein: 12.3% vs. 9.7%, respectively). In addition, despite a consistent decreasing trend in forage quality from June onwards –likely due to plant phenology– the mean percentage of crude protein registered for territorial males during the rut remained similar (but with a slight increase) to that registered in the prerut (12.2%) (Corlatti et al. 2013). Altogether, these data suggest that foraging time is reduced during the rut, due to intense rutting activities, but territorial males –as capital breeders– may use body stores gained in summer (Rughetti & Festa-Bianchet 2011) and, in parallel, allocate a reasonable amount of time to forage on relatively high-quality plants, likely maintaining an efficient microbial fermentation, hence the possibility to readily increase food intake in the postrut and reduce overwinter mortality. If so, we could hypothesise that territorial male chamois during the rut may optimise their energy balance primarily by foraging on relatively high-quality plants, rather than maximizing foraging time, or minimizing energy expenditures. Higher-quality forage may either reflect a selective diet (García-González & Cuartas 1996) or intrinsic characteristics of the territories. This suggestion –that we may name 'forage-quality hypothesis'– now requires further investigations, for example through the analysis of plant quality within territories and in neighbouring areas. Nonetheless, in biology rarely a pattern depends on just one factor, especially when behaviour is concerned: in their study on bighorn rams, Pelletier et al. (2009) suggest that the proposed alternative hypotheses may not be mutually exclusives, but rather concur to explain rut-induced hypophagia. To this end, it is worth noticing that both the physiological and the parasite hypothesis provide possible physiological mechanisms that might underlie any one or more of the other hypotheses, which are different in being descriptions of potentially adaptive strategic trade-offs. The parasite-induced anorexia hypothesis, for example, appears as an additional, more detailed explanation of the adaptive trade-offs (and possibly non-adaptive trade-offs due to parasite manipulation) that could be going on inside territorial male chamois. Despite its relatively small sample size, this study emphasises the importance of evaluating the presence of AMTs within animal populations, and their diet quality, when investigating alternative explanations for rut-induced hypophagia. Different tactics may lead to different amounts of time spent rutting and foraging, likely in interaction with the density of competitors, the local density of females (Isvaran 2005) and meteorological conditions (Lovari et al. 2006). To what extent different patterns of foraging behaviour during the rut may impact on the fitness trade-offs of territorial and non-territorial males, however, is still unclear, and long-term data on marked individuals would be necessary to assess the tactic-specific reproductive success and survival rates.

Acknowledgments

We thank the wardens of the GPNP (especially P. Chabod and P. Guglielmetti) for their help in capturing chamois. We also thank all the students and interns who helped collecting data in the field, E. Ferroglio, S. Béthaz and C. Lorenzetti (University of Turin) for the parasite analysis, R. Palme and E. Klobetz-Rassam (University of Veterinary Medicine Vienna) for the assessment of hormone metabolites. We thank S. Lovari (University of Siena), M. Festa-Bianchet (University of Sherbrooke), J. Herrero (University of Zaragoza) and an anonymous reviewer for helpful comments on earlier drafts of the manuscript. L.C. participated in the capture of all animals, collected data in the field, did the statistical analyses and wrote all drafts of this paper. B.B. participated in the capture of all animals and in writing up this paper.

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