Foraging strategies associated with alternative reproductive tactics in a large mammal

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Abstract

Foraging behaviour plays a key role in growth, survival and reproduction. Male ungulates in temperate environments show seasonal fluctuations in uptake and use of energy, with summer accumulation of reserves later used to sustain the costs of the mating season. To date, however, very little information is available on the foraging behaviour of individuals adopting alternative reproductive tactics. We investigated the year-round foraging strategies of 9 territorial and 10 nonterritorial male Alpine chamois *Rupicapra rupicapra* in the Gran Paradiso National Park (Italy), and discussed them in relation to space use and forage quality. Territorial males showed marked seasonal changes in foraging behaviour, with low values of time spent foraging in spring, followed by an increase in summer, a drop in November and a subsequent increase in winter. The foraging rates of nonterritorial males, on the other hand, showed smaller variation, decreasing gradually from

spring to autumn, and increasing in winter, but with no significant reduction during the November rut. Although in summer territorial males remained at lower elevations than nonterritorial males, faecal crude protein did not show any significant difference between male types. The effort to establish and defend territories (in spring and in November, respectively), may constrain foraging in territorial males, forcing them to compensate by increasing their energy intake over summer. Different levels of vertical movements in the warm months did not affect forage quality, suggesting that territorial males may be selective in the choice of palatable plants. Our results show that different reproductive tactics imply different foraging strategies over the year, which do not seem to depend on forage quality. Different foraging strategies over summer may possibly lead to different body conditions at the beginning of the mating season, which, in turn, could influence individual capability to cope with the costs of mating.

Introduction

In temperate environments that undergo strong seasonal changes in forage quality and quantity, cyclical variations in uptake and use of energy shape a dynamic scenario where foraging behaviour has a clear adaptive value (Apollonio & Di Vittorio, 2004). During the mating season (rut), a common foraging strategy known as rut-induced hypophagia (i.e. reduction in food intake) occurs in male ungulates (e.g. bison *Bison bison*, Bergman et al., 2001; fallow deer *Dama dama*, Apollonio & Di Vittorio, 2004; Bighorn sheep *Ovis canadensis*, Pelletier, 2004; Alpine chamois *Rupicapra rupicapra*, Willisch & Ingold, 2007; Alpine ibex *Capra ibex*, Brivio et al., 2010). Such a strategy, coupled with an increase in energy expenditure due to mating activity, may affect survival in the following winter. The way adult males compete for access to females, however, may differ between individuals (e.g. tending and coursing in Alpine ibex, Willisch & Neuhaus, 2009) and such discrete variations in mating behaviour (alternative reproductive tactics: ARTs) may have different life history trade-offs (Taborsky et al., 2008; Corlatti et al., 2012b). Over the mating season, some individuals may invest more time and energy in costly inter- and intra-sexual interactions, likely increasing current reproductive success to the detriment of survival, whereas others may invest more in foraging, likely improving survival and future reproductive success (Stearns, 1992). In turn, different reproductive tactics may lead to different energetic constraints, hence different trade-offs between reproduction and survival. To date, however, very little information is available about foraging strategies of male ungulates adopting ARTs during the mating season. Pelletier (2004) showed that, in rutting Bighorn sheep, the primary tactic of tending did not constrain foraging more than the secondary one of coursing.

Different levels of rut-induced hypophagia between ARTs may lead to different costs depending on the conditions of males before the rut. Indeed, several authors stress the importance of summer foraging behaviour in acquiring sufficient resources for survival and reproduction (Bruno & Lovari, 1989; Festa-Bianchet et al., 1997; Festa-Bianchet, 1998). Rughetti and Festa-Bianchet (2011), for example, observed that body mass in adult males of Alpine chamois fluctuates greatly throughout the year and peaks just before the mating season, following summer accumulations of fat and muscle mass. Stored energy is then used during the rut (Garel et al., 2011), possibly reducing mortality risks. To our knowledge, however, there are no data on foraging strategies adopted by individuals utilising ARTs outside the rut.

The Alpine chamois is a mountain-dwelling ungulate widely distributed along the massifs of central Europe and New Zealand (Corlatti et al., 2011). Female chamois and their kids live in herds, while adult males tend to live solitary for most of the year, but clump together during the rut (November, in Europe) (Krämer, 1969). Chamois sexes are nearly monomorphic: only body weight shows a certain degree of dimorphism, yet highly seasonal, rapidly declining from about 40% before the rut to about 6% in January (Garel et al., 2009; Rughetti & Festa-Bianchet, 2011). This, together with the unbiased sex-specific survival (Corlatti et al. 2012a) and the compensatory body growth observed for young males (Rughetti & Festa-Bianchet, 2010) suggests the occurrence of a conservative mating system, such as a weak polygyny or oligoginy. Whatever the level of polygyny, behavioural observations showed that, during the rut, different reproductive tactics may occur: some males (i.e. territorials) patrol a relatively small area in which they try to keep females and chase away intruders, whereas other males (i.e. nonterritorials) display following behaviour and territory intrusions (von Hardenberg et al., 2000; Corlatti et al., 2012b; Corlatti et al., 2013). ARTs, in adult male chamois, do not seem to be related to age or physical features and their maintenance within populations may be favoured by several internal and external factors (Corlatti et al., 2012; Corlatti et al., 2012b). Among the others, energy acquisition before the mating season may play an important role in the individual capability to cope with the costs of reproduction (McElligott et al., 2003).

In this paper, we investigate the year-round foraging behaviour of territorial and nonterritorial male chamois. We expected that both tactics would show rut-induced hypophagia, but foraging rate of territorial males during the rut should be lower than that of nonterritorial males, because of their time investment into territory defence (Corlatti et al., 2013). Von Hardenberg et al. (2000) showed that territorial defence begins well before the rut, as early as springtime. We therefore expected that foraging rates in territorial males would be constrained more than in nonterritorial males already in spring. If so, we would expect territorial males to compensate by drastically increasing their

foraging rates during summer. Finally, Lovari et al. (2006) showed the occurrence of alternative spatial strategies in male chamois, which may be associated with ARTs: migrant males, in summer, inhabit larger home ranges at higher elevations than do resident males. Vertical movements towards higher elevations, in turn, might be advantageous in terms of forage quality, because of the higher nutritive value of vegetation (Mysterud et al., 2001). If territorial males remained at lower elevations in summer (von Hardenberg et al., 2000), compared to nonterritorial males, they may be forced to feed on lower-quality forage that, in turn, may cause an increase in foraging rates.

Methods

Study site and population

The study site (upper Orco Valley, Gran Paradiso National Park –GPNP–, Western Italian Alps, 45°26'30'' N, 7°08'30'' E) covers ca. 10 km^2 at 1,800 to 3,000 m a.s.l.. The area has a dry continental climate; the mean yearly rainfall in the study site is about 1,096 mm and mean temperatures vary between -3.7 °C in winter and 13.1 °C in summer (La Morgia & Bassano, 2009). Meadows of coloured fescue *Festuca varia* dominate the south-facing slope, whereas the north-facing slope is characterised by the presence of larch *Larix decidua* woods and patches of alder shrubs *Alnus viridis*.

The chamois population, protected since 1922, shows densities of ca. 20 individuals/km^2 in the study site (Corlatti, unpublished data) and is regulated predominantly by winter starvation (Peracino & Bassano, 1987). Chamois diet in the study site indicates a preference for herbaceous plants during the summer months, with a prevalence of gramineous species (La Morgia & Bassano, 2009). Between February 2010 and March 2011, 19 adult males were darted with a combination of xylazine and ketamine. For all animals, we estimated age (relative to May 2011) by counting horn rings (Schröder & von Elsner-Schack, 1985). In addition, we equipped them with individually recognizable GSM-GPS Pro-Light collars (Vectronic Aerospace GmbH, Berlin) and ear tags. We assume that Alpine chamois behaviour was not affected by radio-collars as shown by Nussberger and Ingold (2006). The sedative effect was reversed by an injection of atipamezole (Dematteis et al., 2009). On average, the entire procedure took less than 40 minutes and was always performed with a veterinarian present. These methods are in line with Italian law.

Territorial vs. non-territorial males

The distinction between territorial and nonterritorial males was based on the framework developed by Corlatti et al. (2012b). For the rutting season 2011, we assumed that territorial males would have a higher site fidelity and win more intra-sexual interactions than nonterritorial males. Site fidelity

was estimated from individual home ranges (90% Fixed Kernel) calculated in in R 2.15.2 (R Development Core Team, 2012), kernel-smoothing the data for each individual track with the plug-in bandwidth selector ('hpi') developed by Wand & Jones (1995). To estimate home ranges, we used high-quality GPS locations (with at least 4 satellites and Dilution of Precision values <10) (Lewis et al., 2007). For each male, the rate of intra-sexual interactions won was calculated as the proportion between number of interactions won and total number of interactions, collected during hourly sessions of observation ad libitum (Altmann, 1974). The focal animal was considered involved in intrasexual interactions if he displayed direct or indirect forms of aggressiveness (Corlatti et al., 2013) towards one or more males.

Both parameters were combined in a matrix and we used the Mahalanobis distance, a measure that can account for correlations in the data set and for objects at different scales (Mahalanobis, 1936), to perform multivariate hierarchical clustering (Everitt et al., 2011) in R 2.15.2 (R Development Core Team, 2012). Following the analysis, 9 males with small home ranges (median = 4.63 ha) and high values of intra-sexual interactions won (median = 1) were classified as territorials, whereas 10 males were classified as nonterritorials (median home range = 20.34 ha; median value of intra-sexual interactions won = 0.04).

Data collection

To investigate monthly variations in time spent foraging, each month from March 2011 to February 2012 we observed between 16 and 19 marked chamois (median = 17) with binoculars and spotting scopes from at least 50 m distance to avoid disturbance. We registered the animal's behaviour using scan sampling at 5-minute intervals (i.e. we recorded the animal's behaviour every 5 minutes) (Altmann, 1974) for 2 hours each month (1 h in the first half of the month, 1 h in the second half; the two observations were always separated by at least one week). Observations were conducted during daylight hours, at different times of the day: morning (144 h), noon (132 h), afternoon (136 h). Behavioural categories included: foraging, lying down (which typically includes rumination), moving, standing, interactions with males or females (cf. Lovari 1985), others (i.e. all the activities that could not be classified into any of the previous categories).

To investigate space use, for each individual we calculated a mean monthly elevation from March 2011 to February 2012 using GPS positions with at least 4 satellites (3D) and DOP (Dilution Of Precision) values lower than 10 (Lewis et al., 2007), collected every 11 hours (ca. 60 fixes/month/individual). Additionally, we collected faecal samples to indirectly obtain monthly forage quality by near infrared reflectance spectroscopy (NIRS) (Stuth et al., 2003), a standard method to determine protein, fibre and fat content (reviewed in Dixon & Coates, 2009). Once a

month we collected approximately 20 g of wet faeces from the observed chamois between March 2011 and February 2012 ($N = 186$). Collared individuals were observed until release of faeces, and scats were collected within 10 min. Within 10 h of collection in the field, they were stored in plastic bags at −20 °C until analysis. Before analyses, faecal samples were dried in an oven (Memmert Schwabach, Germany) at 60 °C for 48 h and then ground with a grinder A11 basic (Ika, Germany). For calibration of the NIRS analyses, 86 of the 186 faecal samples were chemically analysed using standardised methods for crude protein, crude fat, crude ash and dry matter (Nehring, 1960). ADF (acid detergent fiber) and Lignin were determined by Van Soest detergent analyses (Otzelberger, 1983) and evaluated by cross validation. The remaining 100 samples were analysed using a FT-NIR Spectrometer MPA (Bruker Optik, Ettlingen, Germany) with an integrating sphere in diffuse reflection. All samples were analysed in a rotating cup with a diameter of 50 mm three times. The spectrometer was equipped with software OPUS 5.5 with the additional packages OPUS/LAB and OPUS/QUANT (2005, Bruker, Ettlingen, Germany). We determined the following parameters: dry matter, protein, fat, ash, ADF and lignin. Nitrogen free extracts (NFE) were computed by subtracting lignin from ADF (Otzelberger, 1983). In this study, we used percentage of crude protein as an index of forage quality (see Gálvez-Cerón et al., 2013).

Statistical analyses

To analyse monthly variations of time spent foraging in ARTs, we fitted a generalised linear mixed model separately for territorial and nonterritorial males using R 2.15.2 (R Development Core Team, 2012) in RStudio 0.97.309 (RStudio, 2012) and the function `glmmPQL` ('MASS' package: Venables & Ripley, 2002). We set the number of foraging events recorded in every hour of observation as a response variable, month as a predictor, age and time of the day (morning, noon, afternoon) as covariates. In both models we set animal identity as a random factor and we assumed a Poisson distribution corrected for overdispersion (as the residual deviance of each model was greater than its residual degrees of freedom). Finally, for both models we ran a post hoc test, using the `glht` function (with Tukey contrasts) from the 'multcomp' library (Hothorn et al., 2008), to compare each month with every other month in a pairwise manner. The `glht` function provides a convenient framework to test multiple hypotheses in several parametric models, including linear and nonlinear mixed-effect models (Bretz et al., 2011). Multiple testing with 0.05 significance levels is a very conservative strategy that potentially increases the risk of Type II errors, especially if sample size is small (Quinn & Keough, 2002; Ellis, 2010). Following the advice of Quinn and Keough (2002) and Day and Quinn (1989), given the high number of pairwise comparisons, for multiple testing we adopted a significance level of 0.10. To compare foraging rates between

territorial and nonterritorial males, within each month, we used t-tests for independent samples. Significance level was set at $P = 0.05$; if not specified, all tests are intended as two-tailed.

To compare space use and forage quality between territorial and nonterritorial males, we compared mean elevations and mean values of crude protein within each month (Shapiro-Francia tests confirmed the assumption of normality for both parameters) by means of t-tests for independent samples. Significance level was set at $P = 0.05$; if not specified, all tests are intended as two-tailed. For all t-tests, we used R 2.15.2 (R Development Core Team, 2012) in RStudio 0.97.309 (RStudio, 2012). All graphs show untransformed data, except for the time spent foraging, which was transformed to percentage to facilitate interpretation.

Results

The percentage of time spent foraging by territorial males showed marked seasonal changes (Fig. 1), with low mean values (± 90% Confidence Intervals [CI]) in spring (21% ± 10, in April), followed by an increase in summer (mean of 49% ± 10, in August) (Tukey test April-August: Estimate = -0.869, $Z = -3.087$, $P = 0.081$) and a drop in November (mean value = 9% ± 6; Tukey test September-November: Estimate = 1.645, $Z = 4.266$, $P < 0.01$; difference between October-November was not significant, but showed a large effect size: Cohen's $d = 0.86$, CI = 0.78-0.93, Nakagawa & Cuthill, 2007). After the November rut, territorial males increased their foraging rate (mean of 41% ± 13, in December) (Tukey test November-December: Estimate = -1.517, $Z = -3.880$, $P < 0.01$). Nonterritorial males, on the other hand, showed smaller variations over the year (Fig. 1): the mean percentage of time spent foraging gradually decreased from spring (53% ± 13, in March and 53% ± 13, in April) to autumn (24% ± 11, in October), but no significant reduction was observed during the November rut (21% ± 9). In the following winter, foraging rates increased and reached levels similar to those observed in spring (mean values of 50% ± 15 and 59% ± 14 in January and February, respectively). Foraging rates of territorial males were significantly lower than nonterritorials' in spring (March and April) and November (Table 1), and significantly greater in summer (August and September, Table 1).

7

Table 1: results of within-months comparisons (independent t-tests) between territorial and nonterritorial male chamois between March 2011 and February 2012 in the GPNP for % of time spent foraging, elevation and % of crude protein. In bold, significant results.

		MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB
% foraging	t	-2.328	-2.851	0.482	0.464	0.387	2.384	2.039	0.444	-2.405	-0.048	-0.328	-0.423
	df	13.826	16.914	15.630	13.247	12.952	14.852	14.715	14.273	15.298	14.765	15.706	12.017
	P	**0.036**	**0.005***	0.637	0.650	0.705	**0.015***	**0.029***	0.664	**0.015***	0.962	0.747	0.679
Elevation	t	0.058	-1.984	-1.890	-2.523	-3.057	-2.272	-2.631	-2.965	-2.016	-3.224	-1.997	-0.719
	df	15.000	14.630	12.921	8.654	12.640	13.451	11.787	9.658	12.017	12.924	11.937	14.177
	P	0.573	0.066	0.081	0.052	**0.009**	**0.040**	**0.022**	**0.015**	0.067	**0.007**	0.069	0.484
% protein	t	-0.926	0.253	0.264		0.710	0.696	1.436	-0.790	2.318	0.343	-0.315	-0.826
	df	8.804	13.371	8.319		9.651	11.999	9.491	11.824	6.609	8.522	13.981	8.965
	P	0.381	0.804	0.798		0.494	0.499	0.183	0.445	0.056	0.739	0.757	0.430

* one-tailed t-test

t-test on crude protein in June was not performed because of lack of data for nonterritorial males

Figure 1: variation of time spent foraging by territorial (closed circles) and non territorial (open circles) male chamois between March 2011 and February 2012 in the GPNP. Values are means ± 90% CIs. Different letters indicate P < 0.10 by post hoc Tukey test for territorials (at the bottom) and nonterritorials (on top). The dashed rectangle indicates the mating season.
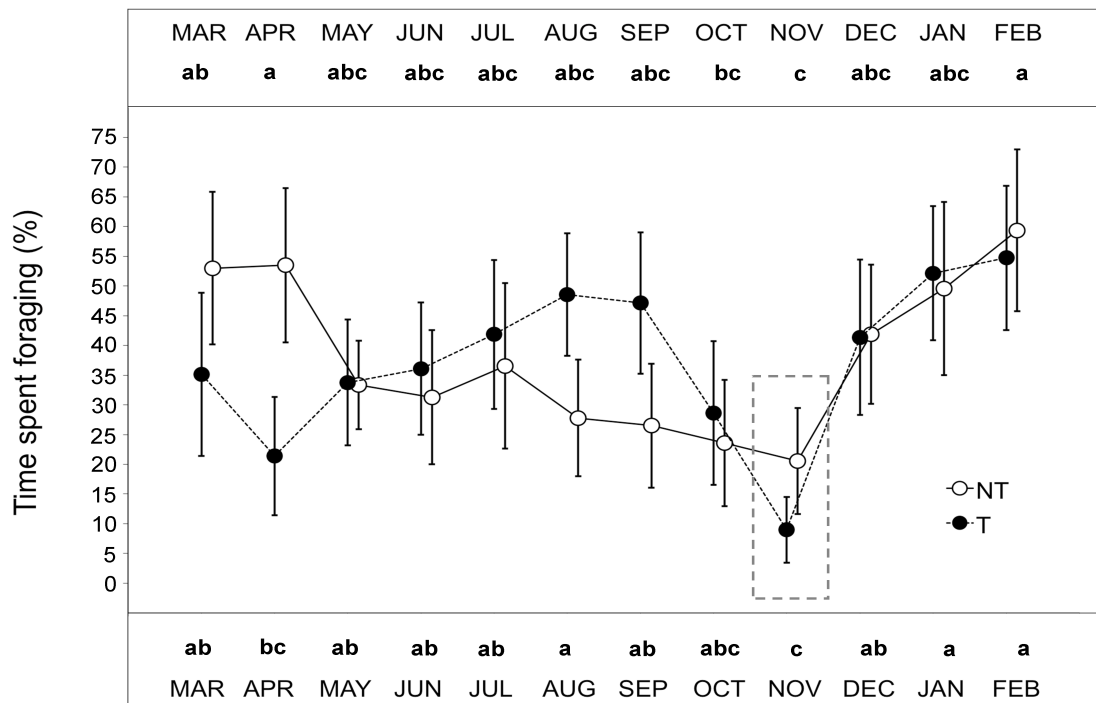
Territorial males remained at significantly lower elevations than nonterritorial males, from July to October (mean values [± 95% CI] between 2017 m ± 128 in July and 2200 m ± 197 in August for territorials, and between 2269 m ± 135 in October and 2527 m ± 151 in September for nonterritorials), and in December (mean values of 1874 m ± 60 and 2043 m ± 83 for territorial and nonterritorial males, respectively) (Table 1, Figure 2). The content in crude protein, however, did not show any significant difference between territorial and nonterritorial males over the year, although in November territorial males showed higher values, and the difference was close to the significance level (mean values [± 95% CI] of 12.3% ± 1.2 and 9.7% ± 1.2 for territorials and non territorials, respectively) (Table 1, Figure 3).

Figure 2: variation of elevation (m a.s.l.) in territorial (closed circles) and nonterritorial (open circles) male chamois between March 2011 and February 2012 in the GPNP. Values are means ± 95% CIs. The dashed rectangle indicates the mating season.
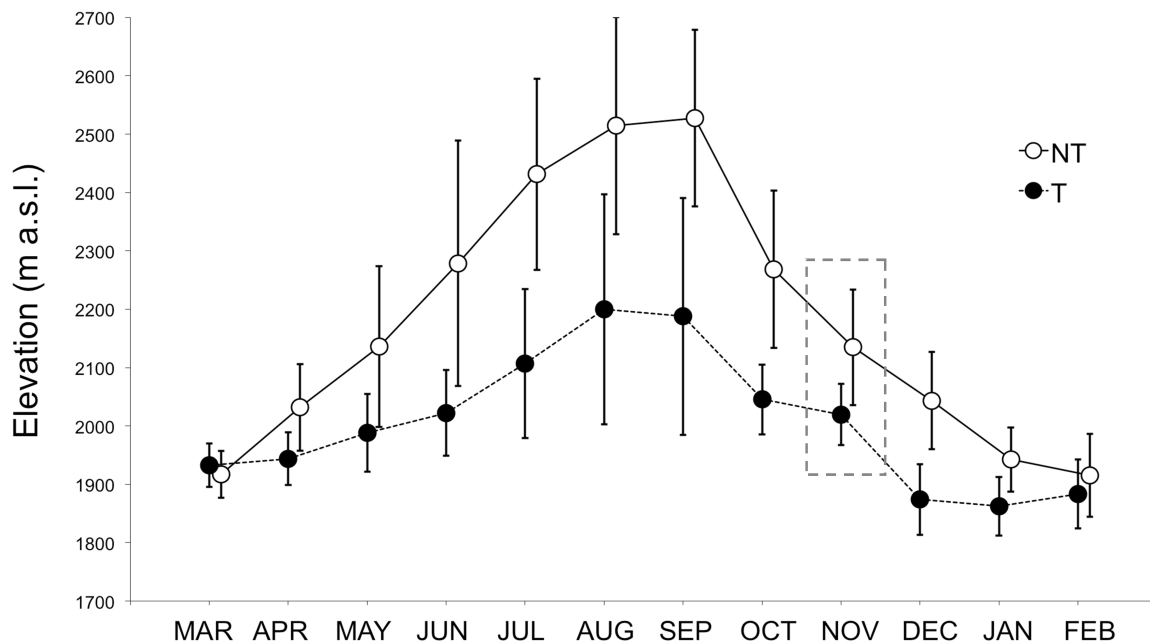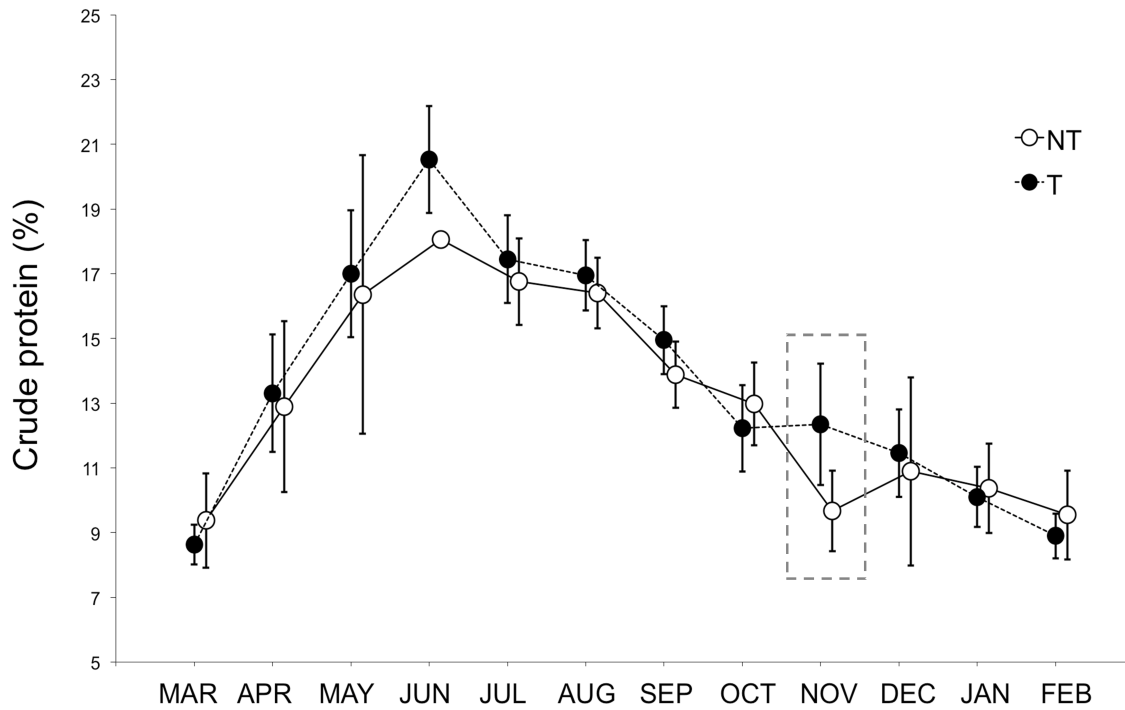
Figure 3: variation of crude protein content (%) in territorial (closed circles) and nonterritorial (open circles) male chamois between March 2011 and February 2012 in the GPNP. Values are means ± 95% CIs. The dashed rectangle indicates the mating season.

Discussion

The link between foraging behaviour and the evolution of life history traits is underpinned by the ultimate value of feeding, i.e. to provide energy for growth, survival and reproduction (Cuthill & Houston, 1997). Energy budgets depend upon how efficiently animals allocate their time to various activities that, eventually, will determine individual success in survival and reproduction (Stearns, 1992). In this study, territorial and nonterritorial males presented profound differences in their seasonal foraging behaviour. The former showed marked fluctuations, with a significant increase from spring to summer, a significant decrease during the rut, followed by an increase in winter. The latter, on the other hand, showed smaller fluctuations, and no rut-induced hypophagia –although they do eat a bit less during the time of the rut, when comparing food intake to all other times of the year.

So far, only one study investigated rut-induced hypophagia in ungulates in relation to ARTs (Pelletier, 2004) and found no evidence for differences in time dedicated to foraging between tactics. Studies on fallow deer (Apollonio & Di Vittorio, 2004) and bison (Maher & Byers, 1987) found an age-dependent effect on time spent foraging, with only older males showing hypophagia during the rut, but they do not make any specific reference to ARTs. Our results suggest that

10

different levels of food intake may occur between ARTs, with only territorial males showing hypophagia, which may not be limited solely to the mating season. Von Hardenberg et al. (2000) showed that occupation of territories in male chamois begins well before the rut, as early as springtime. Corlatti et al. (2012b, 2013) reported that territorial males invest more than nonterritorial males in intra- and interspecific interactions during the rut. It seems likely that the effort to establish and defend territories (in spring and in November, respectively) could induce hypophagia –or at least a strong reduction in time dedicated to foraging– in territorial males in different times of the year. The lack of reduction in food intake over the same periods in nonterritorial males, supports this hypothesis. To explain the strategy of energy optimisation underlying rut-induced hypophagia, Willisch and Ingold (2007) suggest that male Alpine chamois may not maximize their energy intake during the rut, rather adopting an energy-saving strategy to optimize their energy balance. This work, however, does not provide information on individual reproductive tactic, possibly leading to undetected different strategies of energy intake between tactics. Further studies are needed to clarify whether their suggestion may apply or not to territorial males, while it seems likely that nonterritorial males, who do not show rut-induced hypophagia, may adopt a different strategy to optimise their energy balance.

Corlatti et al. (2012b, 2013), for the same population, suggest that territorial males –while having a greater mating success– may incur greater costs during the rut, because of greater rates of interactions, higher levels of hormone metabolites and greater parasite levels. In addition to that, different strategies of energy optimisation during the mating season may increase such differences in trade-offs between opportunity for survival and reproduction. McElligott et al. (2003), however, emphasise the role of body condition at the beginning of the rut, which may lead dominant males to adopt mate guarding without incurring important reproductive costs. Unlike many other polygynous ungulates, Alpine chamois show surprisingly high longevity and very similar sex-specific survival rates (Bocci et al., 2010; Corlatti et al., 2012a). Interestingly, our data suggest that territorial and nonterritorial males indeed have different strategies of resource accumulation before the rut. The observed reductions in food intake during spring and autumn may force territorial males to compensate by drastically increasing foraging rates in summer, possibly allowing them to gain enough resources to sustain the costs of mating. Similarly, the observed increase in time spent foraging in winter may reflect the need to accumulate resources to survive the cold season. Whether different tactics of resource accumulation may lead to different body conditions at the beginning of the rut, it is still unclear (but see preliminary data in Corlatti et al. (2013), suggesting little differences between male types in terms of body weight).

Differences in foraging strategies may potentially reflect differences in diet quality. With increasing altitude, there seems to be an increase in the nutritive value of vegetation (Albon & Langvatn, 1992; Van Soest, 1994), which in turn drives the seasonal pattern of ungulate migration towards higher elevations (Oosenbrug & Theberge, 1980; Mysterud, 1999; Mysterud et al., 2001). Territorial males occupied areas at lower elevations, compared to nonterritorial males, during summer. The NIRS analysis of crude protein, however, showed that diet quality of ARTs was not affected by elevation. Chamois can be highly selective in the choice of high-quality palatable plants (Garcia-Gonzalez & Cuartas, 1996). Although lower elevations may provide a higher proportion of lower-quality forage, territorial males may still be able to selectively feed on high-quality forage, possibly compensating hypophagia during the rut. This leads us to reject our last hypothesis, as different foraging rates between ARTs, before the mating season, were not affected by forage quality. In spring, the diet of nonterritorial males showed larger variations in values of crude protein: spatial overlap with dominant, territorial males could force them to adopt a less selective diet. In summer, when overlap is avoided, crude protein variations were much smaller.

Our results show that different reproductive tactics are associated with different foraging strategies over the year, which do not seem to depend on forage quality. Different foraging strategies over summer may possibly lead to different body conditions at the beginning of the rut, which, in turn, could influence individual capability to cope with the costs of the mating season. Data on body weight before the rut, as well as long-term information of tactic-specific survival rates would help investigating the mechanisms underlying the maintenance of ARTs.

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