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The rutting behaviour of Alpine chamois (*Rupicapra rupicapra rupicapra*) in the Swiss National Park

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Abstract

The Alpine chamois (*Rupicapra rupicapra rupicapra*) is the most abundant alpine ungulate of Europe. Nevertheless, neither the survival strategy nor the mating systems are completely understood by now. The Swiss National Park offers highly protected and undisturbed habitats to Alpine chamois. During the mating season in November 2011 the behavioural pattern of Alpine chamois was studied. We found a higher amount of time spent in rut-specific activities in males than in females, which means males were interacting, moving and standing plainly more than females. Females spent more time in feeding, whereas we clearly noticed hypophagia in males. This begs questions as in other studies rut-induced hypophagia has been observed only in territorial males. Because of the extraordinary dry and warm weather in November 2011 the rut was taking place in high altitudes. Therefore, we suspect having observed particularly non-territorial males as territorials are keeping their mating ground in lower altitudes. Thus, we raise the assumption that non-territorial males show rut-induced hypophagia too as soon as they get reproduction opportunities and therefore increase their rutting activity. This could support the theory of males skipping their feeding/reproduction tactic on a short term basis (e.g. get “spontaneous territorial males”). Indeed, these hypotheses underlie further investigations. However, we did not observe marked individuals and individual alternative mating tactics in males could not be considered which we, however, highly recommend in such research projects, as well as involving data of VHF/GPS transmissions and data about population densities.

Introduction

The rutting behaviour (mating behaviour) of the Alpine chamois (*Rupicapra rupicapra rupicapra*) has been discussed within several research projects for the last few years (Krämer 1969; Meile & Bubenik 1979; von Hardenberg et al. 2000; Willisch 2001; Lovari et al. 2006; Willisch & Ingold 2006, Corlatti et al. 2012). To understand life history trade-offs and the key factors which are responsible for the existence of a species it is highly important to understand the mechanisms of reproduction. In addition, studies on mating systems in different habitats can provide information on ecological factors determining the diversity between and within species (von Hardenberg et al. 2000). The Alpine Chamois is the most abundant alpine ungulate of Europe and the Near East and was also introduced to New Zealand (1907; Corlatti et al. 2011). The rut takes place mainly in November, while females show highly synchronised oestrus over a few days in the second half of November (Krämer 1969) which has also an impact on the intensity of the rutting behaviour of males (Corlatti et al. 2012b). Although no genetic studies about siring have yet been published (Corlatti et al. 2012a) the Alpine chamois is suspected to be polygynous. This assumption arises from behavioural observations (Krämer 1969) as well as several facts which underline this hypothesis, e.g. the almost monomorphic sexes. Only close to the mating season males weigh around one third more than females, whereas this difference shrinks back during the rut (Rughetti & Festa-Bianchet 2011). Rughetti & Festa-Bianchet (2010) observed a compensatory body growth for young males. In addition, the Alpine chamois is an extraordinary long-lived species (males 21 years, females 22 years at the Swiss National Park, Corlatti et al. 2012a) and the survival rates of the sexes are almost identical (Corlatti et al. 2012a). But in fact, the apparently unique survival strategy of this species is not yet fully clear. The trade-offs between survival, sexual dimorphism and the mating system underlie further scientific investigations (Corlatti et al. 2011). Nor are the mating systems itself completely understood by now (Corlatti et al. 2012b). Bocci et al. (2010), Rughetti & Festa-Bianchet (2011) and Corlatti et al. (2012) are talking about the adoption of a “low-risk strategy” by males. Some recent studies describe different tactics which may be found in rutting males: A part of the males are showing territoriality (territorial or resident males) whereas others are wandering around, following females and, thereby, occasionally penetrate the territories of territorial males (non-territorial or migrant males, median home range 20.34 ha in Corlatti et al. 2013) (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012b, 2013). The former guard a relatively small mating ground (median home range 4.63 ha in Corlatti et al. 2012b) in which they try to hold up females during the rut and chase away competitors. The different ways on which individual males try to get reproduction opportunities are called alternative mating tactics (AMT's; Corlatti et al. 2012b) or alternative reproductive tactics (ART's; Oliveira 2008; Corlatti et al. 2013), respectively and are closely linked to alternative spatial as well as foraging strategies of males and different life history trade-offs (Corlatti et al. 2011). By now it is not known whether these alternative behaviour patterns are being learned or genetically encoded (Corlatti et al. 2011) and whether a certain strategy is a short-term-tactic and can be changed or adapted year by year or whether it is an individually fixed characteristic (Corlatti et al. 2012b). However, the territories of territorial males are occupied in springtime already (von Hardenberg et al 2000; Corlatti et al. 2013). On one hand, the maintenance of such a territory involves certain expenditures of energy. On the other hand, due to a potentially greater access to females, it can offer higher mating advantages (Corlatti et al. 2012b). Clutton-Brock (1984), Stearns (1992) and Corlatti et al. (2012, 2013) suggest that a greater investment in rutting effort, e.g. spending more time in inter- and intrasexual interactions, may increase the current reproduction. But this, in turn, could be disadvantageous for future reproduction or survival because these individuals invest less time e.g. in foraging. According to Clutton-Brock (1984) in many iteroparous organisms individual differences in breeding effort and success are positively related to survival. However, Corlatti et al. (2013) showed that different reproductive tactics are associated with different foraging strategies over the whole year. Territorial males spent low values of time in foraging during spring, showed an increase in summer, a drop during rut and again an increase in winter. Willisch & Ingold (2007), Corlatti & Bassano (2013) as well as Corlatti et al. (2013) described the hypophagia during the mating season (rut-induced hypophagia) in Alpine chamois as a common foraging strategy (reduction in time spent foraging due to rutting activity) especially for territorial males (Corlatti et al. 2013). But Corlatti & Bassano (2013) elaborate that, although such males forage less, they forage a certain amount of time on relatively high-quality plants. Thus, Corlatti & Bassano (2013) advance the "forage quality hypothesis" which, however, requires further investigations (e.g. whether this behaviour reflects a selective diet or a characteristic of the territories). At the SNP Filli & Campell (2006) suppose the chamois at Il Fuorn to be able to extend the period of high-quality forage intake by migrating to the north-exposed slopes. However, Corlatti et al. (2013) explain fluctuations in the energy-intake and -output of males all year round, while accumulating reserves in summer to sustain the costs of the rut in November. Therefore, the different strategies of spatial behaviour and of reproduction, again, mean also different energetic constraints and different trade-offs between survival and reproduction. It is suspected that the body conditions of males at the beginning of the rut could be variable owing to different foraging strategies over summer (Corlatti et al. 2013). Furthermore, Corlatti et al. (2012b) advance the “stress of dominant” hypothesis, which suggests that individuals which behave in an energetically higher expensive way like territorial males (thus getting better reproductive opportunities) are more stressed, show higher hormone metabolite levels as well as a higher parasite burden. By explaining these relationships they could prove the existence of a life history trade-off among these factors and, in addition, they showed how the mechanism underlying this trade-off is mediated by androgens. Regarding to the age Corlatti et al. (2012b) and Corlatti & Bassano (2013) identified no significant differences between males following the territorial- or non-territorial-strategy. They showed that even adult males often follow the non-territorial-tactic, whereas the age of territorial males varied between 5.5 and 9.5 years. In Corlatti & Bassano (2013) males up to at least 12 years were participating to the rut actively. Considering the weak sexual dimorphism as well as the wide behavioural repertoire (31 behavioural patterns have been described to date; Krämer 1969; Lovari 1985; Corlatti et al. 2012) not either ART’s seem to be related to physical features: Corlatti et al. (2012b) suggest that to reach dominance and mating advantages intensive aggressive behaviours are much more relevant than any physical qualities like horn lengths or body mass.

In this study, we aim to examine the behavioural pattern of Alpine chamois during rut in two protected groups within the Swiss National Park (hereafter SNP). We investigate sex-specific differences and discuss the observational results in the context of the latest scientific findings named above, especially with regard to ART’s and foraging behaviour of males. We predict that (1) the frequency of time spent in rut-specific activities (rutting behaviour, intra- and intersexual interactions, courtship or aggressive behaviour) would be higher in males than in females. Consequently, males would display more time standing and moving (2). Additionally (3), males would show rut-induced hypophagia (highly reduced feeding rate e.g. comparatively to females). Finally, we analyse whether there are differences in behavioural pattern within the two study sites which we, however, do not expect (4). We discuss a comparison of the results with such of similar studies like Willisch (2011), who examined gender-specific differences in rutting behaviour between male and female Alpine chamois at the area of Männlichen Mountain in Wengen, Switzerland or the several studies of Corlatti and Corlatti et al. named above, mostly conducted within the Gran Paradiso National Park, Italy.

Material and methods

Study area

The SNP (170.3km^2) was founded in 1914. It is situated in the Central Alps and is classified as a *category 1a strict nature reserve* by the international Union for Conservation of Nature (Filli & Suter 2006). The Alpine chamois is the only ungulate species which was never extinct or extirpated at the area and since the foundation of the SNP the chamois populations are unmanaged and regulated by natural factors (Filli 1995), whereas predation is on a very insignificant level (no predators presented except the Golden eagle *Aquila chrysaetos*). To date, the number of chamois at the SNP fluctuates between 1000 and 1500 (Filli 1995), whereas the regulation is supposed to be density-dependent (Filli 1995; Lande et al. 2002; Corlatti et al. 2012a). We investigated two groups of chamois: one in the area of the Trupchun valley (Val Trupchun, hereafter TRU) and another in the area of dal Botsch valley (Val dal Botsch, hereafter VdB). The coordinates of the sites from where we conducted observations were 10°04'30.4 E for TRU and 46°35'55.2 N for VdB, respectively. The distance among these sites was around 16km as the crow flies. Filli & Campell (2006) showed an average annual summer home range size at the region of Il Fuorn (where VdB belongs to) of 309 ha for females and 115 ha for males and in TRU 145 ha for females and 163 ha for males, respectively.

Both sites of observation were situated only just above the tree line (2040 m a.s.l. and 2290 m a.s.l., respectively) where extensive patches of low mountain pine shrub can be found. The vegetation is characterised as subalpine to subnival (Landolt 1992) and less than 20% of the terrain is covered by vegetation. Above the patches of low mountain pine a zone of basophile dry meadows with its characteristic "steps of soil tongues" starts, which changes to wind- and frost-resistant but species-poor *Carex firma* -turfs in even higher altitudes. In lower altitudes mountain pine (*Pinus mugo*) and larch (*Larix decidua*) are predominating (Zoller 1995). In TRU chalk beds, marly chalks and marls are predominant whereas dolomite predominates in the region of VdB (Dössegger 1987). The climate is dry continental and precipitations as well as humidity are low. The temperature varies between -30°C in winter and 30°C in summer and the solar radiation is intense (Landolt 1992; Zoller 1995).

Behavioural observations

Data collection occurred between 31th of October and 4th of December 2011 at daylight hours between 9 am and 4 pm. During the study approximately one hundred Alpine chamois were present at each observation site, very few of them marked. Data was only recorded from adults. Although we collected data of none-marked animals, the method was basically adapted to the ones chosen in other studies, e.g. Willisch (2001). Alternately, we observed individuals of both sexes over a maximum time period of 30 minutes while constantly noting the time-lengths which they spent for performing a specific behaviour (focal animal sampling, Altmann 1947). A minimum time period was not determined. The expected behaviours have been listed and then categorized and again subcategorized (in advance of the field work, tbl. 1). The behavioural patterns which we categorized and then recorded are in detail described in Lovari (1985), Krämer (1969) and Corlatti et al. (2012). For the recordings we used the hand-held computer *Noldus Pocket Observer XT 10.5*, Model *Psion Teklogix, workabout Pro*[3]. To observe the individuals and estimate their age/gender we used a 20-60x spotting scope from *Swarovsky*. The observation distance ranged from 30 to 1000 metres while trying not to disturb the animals.

Statistical Analyses

We analysed the data by using t-tests for intersexual and local comparisons. The tests were two- tailed and the considered critical p-value was set at 0.05. To get relative time proportions per gender and behaviour category/subcategory we calculated the time shares of the total amount of observation time of three observation days each (totally 21 days). Afterwards, these mean proportions were arcsine square-root transformed to get closer to a normal distribution (Zar 1999). We performed all analyses by using the statistical software R (version R i386 3.0.0, R Development Core Team 2011).

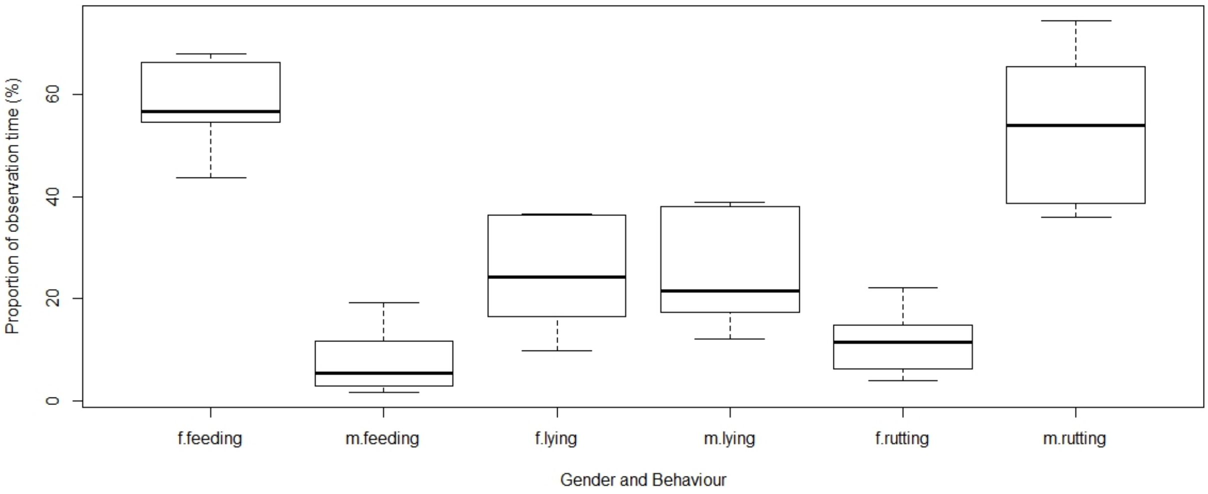
Table 1: Categorized and recorded behavioural patterns

Category	Sub-category	Remarks / Examples
Lying		includes rumination
Standing		only standing, without any other activity and interaction (e.g. rutting activity)
Feeding		snout at vegetation, jerky movements by head
Moving	Walking	slow movement, „in step“, at least two hoofs on ground. On purpose to get from one place to another while not showing any additional behaviour
	Running/Jumping	rapid movement like „trot“, „gallop“ or “jump“. Movement on purpose to get from one place to another while not showing any additional behaviour
Rutting		every conspecific-interaction or reaction of a male/female. Courtship behaviour (e.g. head up), direct (e.g. rush) or indirect (e.g. horning) form of aggression
	Standing	e.g. body–head shake, “Flehmen”, head-up-position of male near female, horning (marking sth.), standing males which obviously are keeping an eye for other males/rivals or females)
	Walking	e.g. male moving to female in head-up-position, male beating or herding female, fleeing or evading male or female
	Running/Jumping	e.g. rush, fleeing or following males like such running after each other to engage each other or to drive the other one out of territory, males running after females
	Other	undefined rutting behaviour, e.g. if movements change too quickly to record (e.g. while interactions)

Results

In 21 observation days the behavioural pattern of the Alpine chamois was recorded during totally 67 hours (30 hours for females, 37 hours for males). Males spent highly significant more time in displaying rutting activities than females (mean values ± 95% confidence intervals; 55% ± 13 vs. 9% ± 5.2; $t = -6$, $df = 7$, $p = 0.0004$) (Fig. 1).

Figure 1: Percentage of time spent in feeding, lying and rutting/(interacting) (mean proportions of the observation time of three observation days each)



Rutting behaviour consisted either of moving or standing activities, while latter made the most part in each gender (Fig. 3).

Figure 3: Rutting activities of males (left) and females (right)

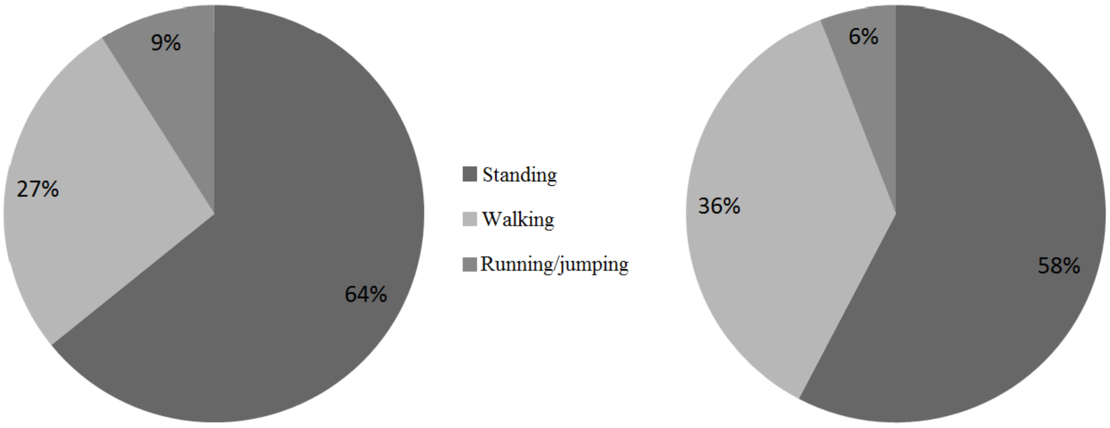
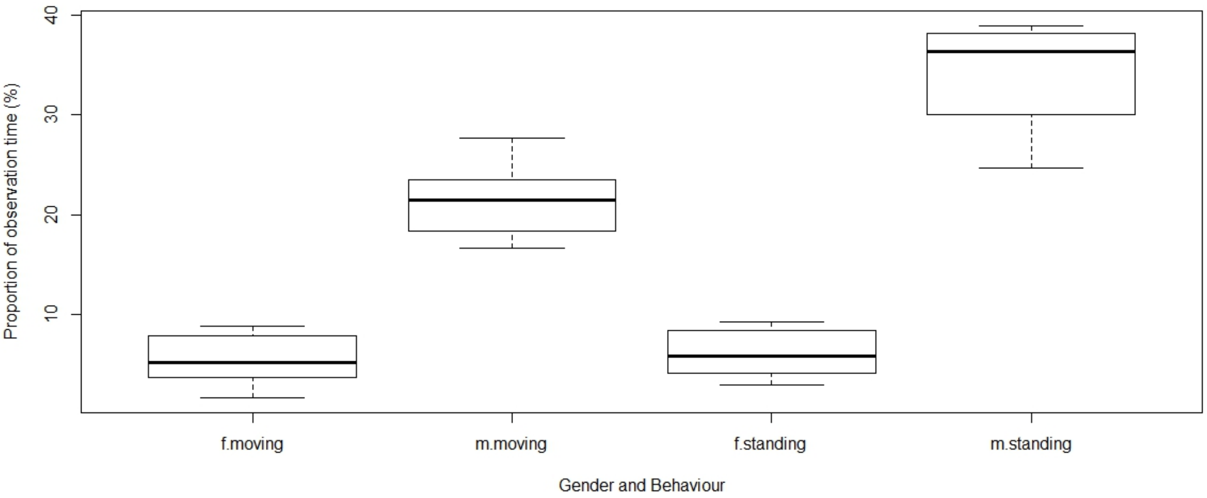


Fig. 3 shows a higher frequency of indirect forms of aggression than of direct ones. Females and their offspring were often involved just tangentially in rutting activities when a dominant male caused disquiet in the herd, e.g. when he was herding or following an individual at the herd or interacting with another male (e.g. competitor or very young males which were still near their mothers). Then females were watching a certain time what was going on, before they continued feeding. Thus, females and youngsters were affected by rutting males often more indirectly than directly. But when females once were ready for fertilization they were interacting with the dominant male (and sometimes a further competitor) for a longer time. Interactions between competitive males mostly took place outside of the herd. Hence, they did not highly influence the behaviour of the individuals in the herd. Interactions of individuals were observed not only between males and females. Also females were maintaining a certain hierarchy in the herd and were interacting with each other. Finally, whether on reproduction purposes or not, males were moving significantly more than females (21% ± 4 vs. 5% ± 2.7; $t = -9$, $df = 9.9$, $p < 0.0001$), which applies also for the behaviour of standing (34% ± 5 vs. 6% ± 2.5; $t = -12$, $df = 7.5$, $p < 0.0001$) (Fig. 2).

Figure 2: Percentage of time spent in moving and standing (on rutting and non-rutting purposes)



A further significant difference could be detected between males and females in time spent foraging: While males were feeding rarely, females did forage the most part of observation time (mean proportion of observation time 8% ± 6.8 vs. 57% ± 9.3; $t = 10.8$, $df = 8.3$, $p < 0.0001$). No differences occurred between gender in time spent lying (23% ± 8.5 vs. 25% ± 12.2 of observation time each; $t = -0.2$, $df = 12$, $p = 0.85$). The results of the two observation sites TRU and VdB did not differ, neither in time spent feeding ($t = -0.8$, $df = 13$, $p = 0.45$ for males; $t = -1.5$, $df = 14.5$, $p = 0.15$ for females) nor in time spent rutting (incl. standing and moving behaviours; $t = 0.6$, $df = 14$, $p = 0.55$ for males, $t = 0.46$, $df = 15.8$, $p = 0.65$ for females) nor in time spent lying ($t = 0.08$, $df = 12$, $p = 0.95$ for males, $t = 0.56$, $df = 14.6$, $p = 0.58$ for females).

Discussion

The advanced hypothesis in this study can be supported. The frequency of time spent in rut-specific activities was significantly higher in males than in females (1) and in consequence males spent more time in standing and moving behaviours (2). As the most part of the recorded rutting behaviour in males and females was noticed as “standing”-behaviours, we suspect a higher frequency of indirect forms of aggression which was also conducted in Corlatti et al. (2012). Additionally, we could clearly notice hypophagia in males (3) and, finally, the behavioural pattern of Alpine chamois in VdB was similar to the ones presented in TRU (4). All in all, these results coincide with the ones of similar studies like Willisch (2001) and Willisch & Ingold (2006) who detected also males spending significantly more time in standing, moving and in social activities during the rut than females. In these studies a highly minimised foraging rate could be detected as well (9% of observation time in Willisch 2001, 8% ± 6.8 in this study). Even captive chamois at the Los Angeles Zoo showed a similar behavioural-pattern during mating season: The only adult male has been resting and feeding less and was standing vigilant and engaged in social behaviour more frequently than the others (Forthman & Pappas 2005). But indeed, some critical points and possible shortcomings of this study should be discussed, especially with regard to ART’s. As we did not observe marked individuals ART’s were not considered (differentiation between territorial and non-territorial males). As several behavioural differences are named in the context of individual males following ART’s the effect of the rut could be diluted if all males are considered as the same (Corlatti et al. 2012b). Corlatti et al. (2012) and Corlatti & Bassano (2013) showed a great variability in individual behaviour of males (e.g. territorial males stopped rutting after the most female oestruses occurred whereas non-territorial males increased their rutting-activity afterwards). In particular, ART’s seem to be associated with different foraging strategies (during rut and over the whole year; Corlatti et al. 2013). In Corlatti et al. (2013) only territorial males showed rut-induced hypophagia, whereas non-territorials did not. Our results showed a rather deep mean proportion of the feeding rate of all observed males, despite territorial or not. In Corlatti et al. (2013) the mean value of time spent foraging in territorial males in November was 9% (± 6) and 21% (± 9) in non-territorials. Hence, our results reflect rather the values of territorial than non-territorial males, which would indicate that we observed more territorial than non-territorial males. On one hand this could come from highly more presented territorial males. But this, in turn would be contradictory to the described reaction of Alpine chamois in Lovari et al. (2006) and Corlatti et al. (2012b) to different meteorological conditions during November. These studies suppose that snowfall causes the females moving in lower altitudes, where resident males do have their territories and monopolize mating. But late snowfall would be advantageous for non-territorials as females stay in higher altitudes. Indeed, November 2011 was extraordinary warm and low precipitated (Meteo Schweiz 2011) and the rut happened in high altitudes. This, in turn, indicates that we should have recorded particularly non-territorial males while rutting, as the territorial ones were suspected to be in lower areas (keeping their ground until the end of the season; Corlatti et al. 2012). To proceed on the assumption we observed particularly non-territorial males but, nevertheless, detected very low feeding rates in males, we could raise the assumption that non-territorial males show rut-induced hypophagia too as soon as they increase their rutting activity. This would be in line with the "foraging constraint hypothesis" (reduced foraging time due to intense rutting activities; Corlatti & Bassano 2013; Brivio et al. 2010 in Capra Ibex). Likewise, this would support the theory of males skipping their feeding tactic on a short-term basis (Corlatti et al. 2012b). A further theory could be the one of non-territorial males which would be capable of building a very short-term territory at the current location of the females in the beginning of the rut (when this happens on higher altitudes where no territorial males are dominating). This could be named the theory of the "spontaneous territorial males". Further questions in this context would be whether such spontaneous rutting territorial males would change to forage on relatively high-quality plants too or not (Corlatti & Bassano 2013) and whether they would cope worse with the costs of mating because of different foraging strategies over summer (Corlatti et al. 2013). Furthermore, if we still proceed on this theory, potentially greater mating advantages and a greater frequency of aggressive and courtship behaviour would be suspected also in these non-territorial males and not only in territorial ones (Corlatti et al. 2012). However, further studies are necessary to clarify whether these suggestions may apply or not. Especially long term studies on controlled marked individuals would clarify the questions not answered by now (e.g. Clutton-Brock 1984). These studies should also pay attention to meteorological conditions (Lovari et al. 2006) as well as the current densities of the investigated populations (e.g. density of competitors or local density of females; Corlatti & Bessano 2013). Finally, as our analyses were highly limited in some aspects, we recommend involving data of VHF/GPS transmitters. This could be also recommendable due to the opportunity of involving night-time data as Alpine chamois show activity at night as well (Ingold et al. 1998).

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