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DIFFERENTIAL SPACE USE AND ENDOPARASITE COSTS OF ALTERNATIVE MALE MATING TACTICS IN ALPINE CHAMOIS

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Abstract

The Northern chamois *Rupicapra rupicapra* is a mountain ungulate with a wide distribution ranging from Western Europe to Asia Minor. Recent studies have investigated alternative male mating tactics, yet still many questions remain unanswered. While some males adopt a territorial behaviour, other animals avoid the effort implied to occupying territories. Territoriality is likely to be associated with greater mating benefits, but also with greater costs. In this study, 19 radio- and GPS-collared males were monitored to investigate relative feeding time, elevation, parasite and hormone metabolite levels. The hypotheses were that territorial males would a) inhabit lower elevations, b) have higher parasite loads, c) have higher levels of stress and d) show greater relative feeding time than nonterritorial males. Generally speaking, e) elevation, mating behaviour and age should influence the mentioned variables. Territorial males used significantly lower elevations, but did not show significantly higher parasite burden, higher faecal androgen metabolite levels, or greater feeding activity than nonterritorials. Nonterritorial males showed a slightly higher level of faecal cortisol metabolites. Only faecal cortisol metabolite values were positively related to elevation. While territorial males pay greater costs for their behaviour during the rut, costs appear low during the summer months, likely due to less competition for resources and to lack of intrasexual aggression.

Foreword

This thesis was written between autumn 2012 and spring 2013, under the supervision of Professor Klaus Hackländer and Dr. Luca Corlatti.

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1 Introduction

The Northern chamois *Rupicapra rupicapra* is an ungulate (Fam. *Bovidae*, Sub-fam. *Caprinae*) that occupies the mountainous parts of Central and Southern Europe as well as Asia Minor. It includes seven subspecies and in Europe, together with three subspecies of the Southern chamois *Rupicapra pyrenaica* it is distributed from the Cantabric Mountains in the West to the Caucasus in the East (MILLER & CORLATTI 2009). The fragmented distribution in Europe is due to the non-continuous distribution of mountainous or adequate habitat (CORLATTI et al. 2011). The Alpine Chamois *R.r.rupicapra* is the most abundant mountain ungulate in the Alps and is found in Switzerland, Austria, Germany and Eastern France, Italy, Slovenia and Liechtenstein (GIACOMETTI et al. 1997 in VON HARDENBERG et al. 2000, AULAGNIER et al. 2008) where it is considered an important game animal. This subspecies has also been introduced to Argentina and New Zealand as well as to the Black Forest and the Vosges Mountains (MILLER & CORLATTI 2009).

Only little morphologic differences occur between sexes, mainly in horn size and – seasonally– in body weight (GAREL et al. 2009, RUGHETTI & FESTA-BIANCHET 2011). The diet is composed mainly by grass and herbs. Shrubs and conifers can play an important role in autumn or winter (even early spring) but they seem to be almost completely neglected in summer (TRUTMANN 2009). The Alpine chamois is mainly found in subalpine and alpine habitats ranging usually between 1500m and 2500m a.s.l., although some populations in Trieste (Italy) or New Zealand live at much lower elevations. The species shows a wide range of social behaviour depending on age, sex, population density and season. While adult males usually spend their summer time as solitary individuals or within small groups of other (younger) males, females are known to live in small to large groups with their young. In autumn, when the rut approaches, large mixed groups appear, although older males still prefer to stay alone. Large groups of both sexes and all age classes can still be observed over the rest of the winter, after the rut, although they are mainly due to the scattered distribution of food resources (MILLER & CORLATTI 2009). While KRÄMER (1969) classifies the Alpine chamois as polygynous, CORLATTI et al. (2011) argue that the weak sexual size dimorphism may hint at a less intense male-male competition, suggesting the occurrence of an oligogynous mating system. The suggested low level of polygyny would be supported by the occurrence of unbiased survival rates for male and female Alpine chamois (CORLATTI et al. 2012), in contrast to the biased survival towards females found in highly polygynous species (e.g. in red deer *Cervus elaphus*, CATCHPOLE et al. 2004).

Moreover, whatever the level of polygyny, the reproductive strategies of male Alpine chamois have not been fully understood so far. COUTURIER (1964) suggests that all males occupy a

territory in early summer which they will defend until the end of the rut. VON HARDENBERG et al. (2000) observed in the Gran Paradiso National Park that some males, while occupying a common winter range, chose exclusive areas over summer and autumn and were more aggressive towards each other in summer than in spring. These findings suggest that territorial males, defending a hotspot for females already before the rut, could have higher reproductive success. However, not all males occupy and defend a territory. CORLATTI et al. (2012) demonstrated the existence of territorial and nonterritorial males. This classification, quite differently to the concept of residentiality used by LOVARI et al. (2006), is clearly from a mating viewpoint, as the investment in territoriality is related to reproduction strategy while residentiality is a mere observation of preference. Both studies suggest a trade-off between mating effort (costs) and mating success (benefits). LOVARI et al. (2006) showed, for twenty-one males in the same population, the existence of resident males (76%, overlapping use of winter and summer ranges, smaller home ranges) and non-resident males (24%, different ranges for winter and summer). These findings lead to the concepts of territoriality and residence. According to KAUFMANN (1983), territoriality aims to provide and assure a supply of limited resources. The positive effects on the individuals' fitness are counterbalanced by time, energy and injury costs of territorial behaviour. On the other hand, LOVARI et al. (2006) use residentiality in the context of animals sharing the same winter and summer ranges, independent whether the defence of territory occurs or not. KRÄMER (1969) suggests that for chamois, monopolised areas are a result of social competition (territoriality) and not simple site fidelity (residentiality). CORLATTI et al. (2012) indicate the existence of nonterritorial but still residential males. This clearly speaks for a third way of behaviour: a more or less year-round occupation of a certain area without defending it from (or excluding) other intra-sexual individuals. Even another type has been noted: individuals (adult males) who do occupy a territory, but only in late summer so that they cannot be categorised as pure residents, despite being territorial during the rut (CORLATTI L., personal communication). In summary, 4 types of male behaviour can be distinguished: (a) resident territorial (b) resident nonterritorial (c) non-resident nonterritorial (d) non-resident territorial.

If, as suggested, territorial animals achieve greater fitness, the definition of KAUFMANN (1983) imposes the associated costs to this behaviour. CORLATTI et al. (2012) were able to show clear-cut differences between territorial and nonterritorial males during the rut, in terms of faecal hormone metabolites, faecal parasite counts and time spent rutting. If, as observed by VON HARDENBERG et al. (2000), males occupy their territories before the actual rut, similar information (i.e. the investigation of costs and benefits as targeted in CORLATTI et al. 2012) may be of interest for the months before the rut.

The aim of this study is to investigate potential costs related to differential use of space (and time) of male chamois adopting Alternative Mating Tactics (AMTs). To achieve this, several aspects should be considered. VON HARDENBERG et al. (2000) observed 5 adult males for two years analysing seasonal spatial behaviour patterns for territoriality. On the other hand, LOVARI et al. (2006) monitored twenty-one adult males for almost two years regarding their movement patterns from a residential and/or migrational point of view. None of the two studies combine the two concepts of territoriality and residentiality. The first object of interest is whether and which male Alpine chamois show a territorial or nonterritorial behaviour. This should confirm findings of previous studies but also allow for more detailed information of several behavioural strategies which are of interest in this study. A deeper analysis, allowing for differences between resident and non-resident animals ideally requires larger sample sizes and is therefore not the object of this work. The second topic of investigation is the use of time. This analysis is based on two principal assumptions: a) if an individual occupies a territory, it might spend more time defending it, interacting with other males and b) given that territories are usually at lower elevations, territorial males might spend more time feeding as the forage quality is assumed to be lower than at higher elevations, where mostly nonterritorial individuals are. In summer, the high elevation pastures provide better conditions in terms of thermo-regulation and food-quality (Van Soest 1994). If territorial males stay at lower elevations as suggested by LOVARI et al. (2006), they might expose themselves to a greater threat of parasitism. As a consequence, the 3rd analysis in this study focuses on the parasite burden (in eggs per gram of faeces) that territorial and nonterritorial males would be subjected to. The last topic of investigation of this study focuses on faecal androgen metabolites. DECRISTOPHORIS et al. (2007) were able to demonstrate a suppressive influence of androgens on the immune system of male ibex *Capra ibex*, which showed a positive relationship between testosterone levels and the number of parasite eggs. This study was based on the immunocompetence handicap hypothesis (FOLSTAD & KARTER 1992), which considers strong development of secondary sexual features as a way of increasing an animal's fitness. Although the Alpine chamois is nearly monomorphic, the concept can also be extended to stress caused by territory defence and exposition to unfavourable climate conditions (lower elevations), the possibly elevated androgen levels inducing a higher parasite burden through immunosuppression. An animal that shows the "handicap" of living in lower elevations and is capable of defending a territory can offer genetic material of high quality to females, contributing to their fitness. For this analysis the individual levels of faecal androgen and cortisol metabolites are essential.

2 Hypotheses

1. Territorial and nonterritorial males should show, in terms of elevation, different use of space.

2. Territorial males should show higher burden of parasite eggs than nonterritorial males, which move to higher elevations.

3. Due to more stress, as a result of their more intense mating behaviour, territorial males should show higher levels of cortisol and androgen metabolites than do nonterritorials.

4. Territorials should spend more time feeding, possibly because of lower forage quality.

5. Hormone metabolite levels, relative feeding activity and parasite levels should be influenced by elevation, mating behaviour, age and several inter-relationships, as these are the major external factors impacting on both territorial and nonterritorial males.

3 Material and Methods

3.1 Study area and animals

The study area is located in the Gran Paradiso National Park in the Province of Turin, Northern Italy. It ranges from approximately 1600 m a.s.l. in the east-west orientated "Orco" river valley in the south up north to some 2800 m a.s.l. including the plateau of "Colle del Nivolet". The majority of the study area is southern exposed and is covered in coloured fescue *Festuca varia* and other drought-tolerating vegetation but very little woody plant cover. A small part of the study area, which in total amounts to ca. 10 000 hectares, also covers north-facing slopes mainly stocked with light forests of European larch *Larix decidua* and thickets of green alder *Alnus viridis* resulting from avalanche depressions.

The 19 animals used for this study were sedated by the personnel of the Park and equipped with individually recognizable GSM-GPS Pro-Light collars (Vectronic Aerospace GmbH, Berlin, Germany), all under supervision of an official veterinarian. The methods used for capturing, are within the Italian law and for detailed information on the sedation process I refer the reader to CORLATTI et al. (2012).

3.2 Data collection

VON HARDENBERG et al. (2000) showed that territorial males have small and exclusive home ranges and show a high level of intrasexual aggressiveness. Based on home range estimation and observational data, CORLATTI et al. (2012) classified the 19 animals used in

this study according to their behaviour in the rutting period 2011. They put forward the following hypotheses: (1) territorial males would show a higher degree of site fidelity combined with smaller home ranges and (2) would also win more intrasexual interactions compared to nonterritorial males. I used this classification in the present study, assuming that animals choose the same mating behaviour in the summer of 2012 as they did during the rutting season of 2011.

The basic samples that I needed for my study were of three different kinds: (a) GPS positions to determine the elevation used by the animal, (b) activity budget data covering a more or less balanced period of time and (c) individually assignable fresh faecal samples for every animal. For a complete overview of the collected data of each animal see Appendix I.

The GPS data were retrieved in regular intervals via GSM, although several difficulties occurred for 3 animals ranging from missing data of individual days to the complete absence of one animal's data set due to battery expiration. For these 3 animals, estimated average heights were used based on the area where I usually observed the animal in. For all other animals I employed the average value of elevation, as home ranges were small, stable and similar results would be obtained if I used the elevation values of the home range centre coordinates. Of all the GPS positions, only records with 3 satellites (2D) and DOP values <5 or 4 satellites (3D) and DOP values <10 were retained (LEWIS et al. 2007).

To cover activity budgets, each animal was sampled twice (1h+1h) per month. I tried to maintain an equal distribution (see Fig. 1) for territorial and nonterritorial males over day light time, which was therefore divided in three time classes: (1) morning, from 8:00-11:00, (2) noon, from 11:00-14:00 and (3) afternoon, from 14:00 to 20:00. No animal was monitored twice in the same time period during the same month; within one month at least two weeks were set between subsequent observations of the same animal. The method I used is described by ALTMANN (1974) as "instantaneous scan sampling", where the activity of the animal every 5 minutes is noted as an event. I differentiated between foraging, lying down, ruminating (if visible), moving, standing and interacting with a male or a female (see also CORLATTI et al. 2012). For my thesis, I only used the information on the relative proportion of feeding events. Animals were observed from at least 70m distance to prevent human interference within the time budget observation. I used an 8x42 binocular and, if necessary, a 20-60x65 spotting scope.

I collected faecal samples after direct and observed deposition by the animal. In case this did not occur during the monitoring of the activity budgets, the animal was forced to light

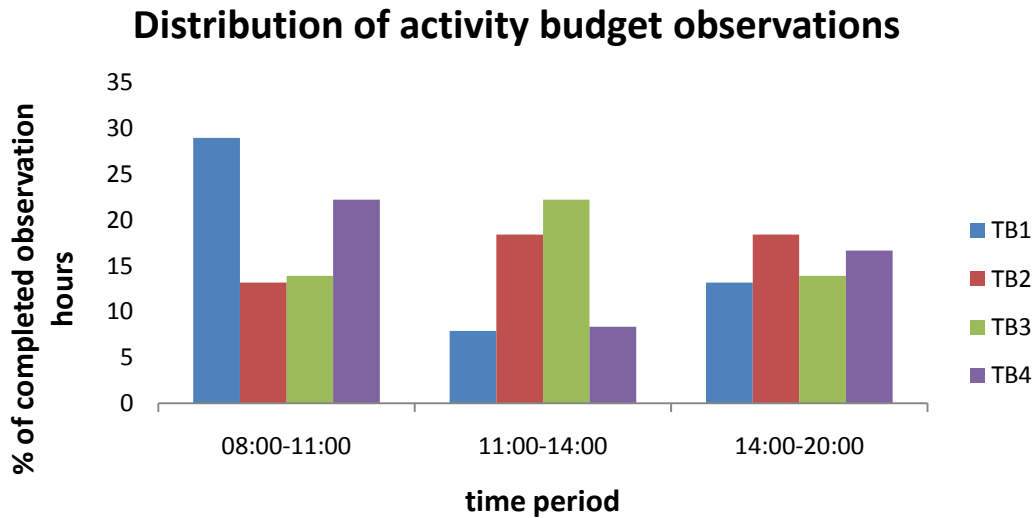## Distribution of activity budget observations

Fig. 1: TB1 = first time budget in July, TB2= second time budget in July, TB3= first time budget in August, TB4= second time budget in August

movement by a slow and visible approach from me or another observer. In most of the cases this light stress situation induced a release of faeces within a very short period of time (3-15 minutes approximately). Faecal samples of ca. 20g were recovered from the field within an hour and stored in plastic bags for transport. One half of the sample was then stored at 4°C for parasite analysis while the other half was stored at -20°C for hormone immunoassays.

3.3   Analysis of faeces

The faecal samples were analysed (1) to estimate the parasite burden carried by the animal, expressed in eggs per gram of faeces, and (2) to measure hormone metabolite levels.

The method used to determine the eggs per gram (epg) of faeces is described by THIENPONT et al. (1979). Two approaches are combined, the zinc flotation method and the McMaster counting procedure. To reach a density of 1.2 g/cm^3, Zinc sulphate solution was diluted at 33%. This allows the floating of parasite eggs, as they are lighter than the solution. Two grams of faeces were homogenized in 28ml of the solution and poured through a sift to remove undigested grass debris. After the solution had been well stirred, the McMaster chambers were filled using a Pasteur pipette. After at least 5 minutes the counting started, the final result being multiplied by 50 to obtain the number of eggs per gram of faeces. Targeted species were of the class Nematoda, order Strongylida, without differentiating between species, as this is not possible at the egg stage.

The hormone metabolite analysis was performed under the supervision of Dr. Rupert Palme, at the University of Veterinary Medicine Vienna, using specific enzyme immunoassays. For detailed information on the procedure see MÖSTL et al. (2002) and PALME and MÖSTL (1994).

3.4   Statistical analysis

For the statistical analysis, I used two different approaches on the gathered information. In a first step I checked for differences in the data of territorial and nonterritorial considering relative feeding time, parasite burden, faecal cortisol metabolites (FCM) and faecal androgen metabolites (FAM) and elevation. For these first evaluations, I used a Shapiro-Wilk test to check for normal distribution of the data. When this was the case, I employed the Student's t-test to check for differences between groups; alternatively, I used the Wilcoxon-Mann-Whitney test when data were not normally distributed. Values of relative feeding time were arcsine transformed (MCDONALD 2009) to meet the normality assumption. All statistics were calculated in R 2.15 (R CORE TEAM 2012) and referenced to a significance level P of 0.05. As the sample size in this study is rather limited, differences might not reach a statistically significant level, especially if the differences are small and variance is big (type II error). Therefore, to provide more detailed information I also used the Cohen's d calculator elaborated by DEFIFE (2009), to show the effect size for every comparison made.

In a second step, I explored the influence of several variables on relative feeding time, FAM levels, FCM levels and parasite burden (gutworms only, as lung helminths seemed to be almost completely absent in summer). In the first place, a test for multicollinearity was performed using the Variance Inflation Factor (VIF) for the regression of each independant variable on all other variables. According to WILLIAMS (2011), VIF values under 2.5 are tolerable. All the tests for multicollinearity turned out to be negative when this criterion was used. Therefore, all the variables could be retained in the global models. As the variables distribution is overdispersed, some data were discrete and not normally distributed and I needed to introduce a random effect (to account for autocorrelation caused by the identity of the animal), I chose a generalised linear mixed approach, using the glmm.admb package for R (FOURNIER et al. 2012). After defining a set of a priori models, I ran a model selection based on the AICc (AKAIKE 1974), and tried to obtain the best approximating model by ranking the competing models (with ΔAICc less than 2) and performing a model averaging of the competing models. The AICc can be used to compare multiple competing models and allows the model selection uncertainty to be quantified, describing the relative goodness of fit of a certain model within a set of multiple models (SYMONDS and MOUSSALI 2011).

4 Results

4.1 Differences between territorial and nonterritorial male chamois

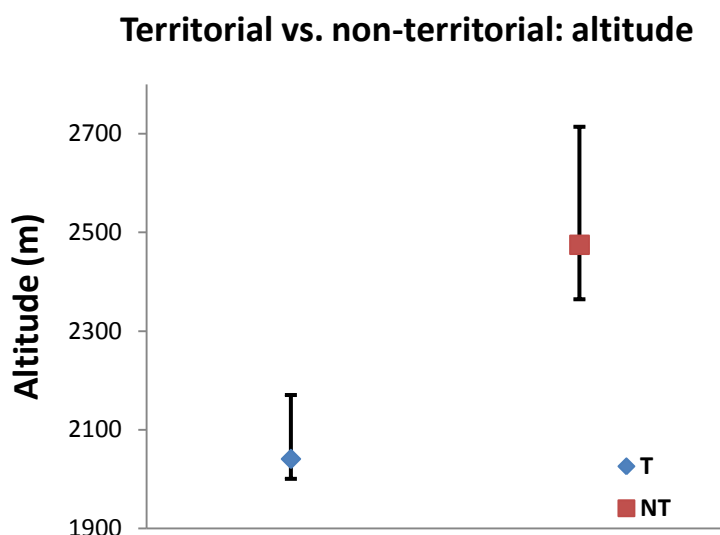### Territorial vs. non-territorial: altitude

Fig. 2: Comparison   of mean elevations in July and August 2012 between territorial (T) and nonterritorial (NT) males, Gran Paradiso National Park. Values are median and interquartiles

When comparing the differences in individual mean elevations in July and August, an obvious gap occurred between territorial and nonterritorial males, the former's median being ca. 450m lower than the one for males not occupying a territory (Fig 2). The statistical analysis, detected significant differences for single months as well as for the combined evaluation (w=53, n_t=20, n_{nt}=18, p=0.00021), as shown in Table 1. Cohen's d confirmed the strong difference between the groups with a strong preference for higher elevations for nonterritorial animals

Table 1: Differences between mean individual elevations used during July and August 2012, Gran Paradiso National Park (p-values and Cohen's d)

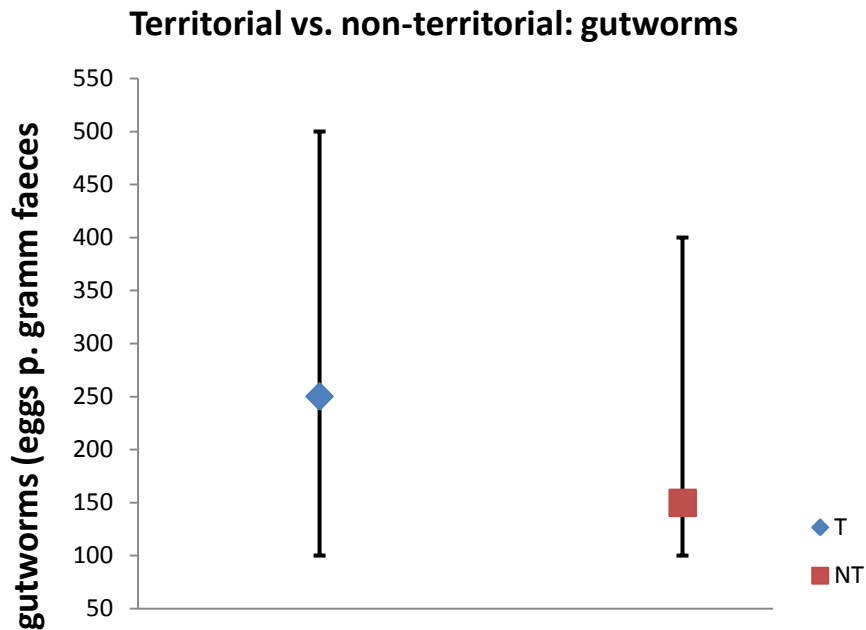|	p	Cohen's d
T ≠ NT Juli	0.00762	-1.397
T ≠ NT August	0.01013	-1.310
T ≠ NT combined	0.00021	-1.336

Fig. 3: Comparison of gutworms (epg, eggs per gram of faeces) between territorial and nonterritorial male alpine chamois during July and August 2012, Gran Paradiso National Park (values are median and interquartiles)

As far as the parasite burden carried by territorial and nonterritorial males is concerned, only a slight difference could be found (Fig. 3). Although the bimonthly median was about 150 eggs per gram of faeces less for nonterritorial animals, no significant difference could be detected (w=152, n_t=17, n_{nt}=18, p=0.987), as shown in Table 2.

Table 2: Differences between territorial and nonterritorial males in parasite burden, data from July and August 2012, Gran Paradiso National Park

	P	Cohen's d
T ≠ NT July	1	0.486
T ≠ NT August	0.9612	0.054
T ≠ NT combined	0.9867	0.346

The effect size did show a rather strong difference for the month of July, an almost equal value for August and a medium difference for the two months combined. None of the statistical tests showed a significant difference.
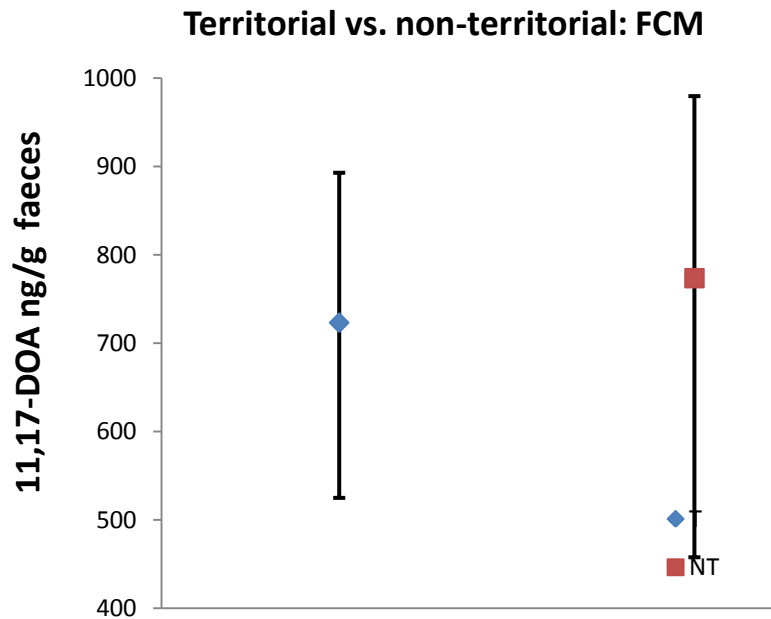
Fig. 4: Comparison of faecal cortisol metabolites (FCM) between territorial and nonterritorial male Alpine chamois during July and August 2012, Gran Paradiso National Park (values are median an interquartiles)

Considering faecal cortisol metabolites, measured as 11.17-dioxoandrostanes (11.17-DOA) resulting from the immunoassay, median values were very close but the interquartiles showed great variation (Fig 4.). Table 3 shows the controversial results found, although no difference appeared to be statistically significant.

Table 3 Differences between territorial and nonterritorial males regarding their faecal androgen metabolite levels, data from July and August 2012, Gran Paradiso National Park

	p	Cohen's d
T ≠ NT July	0.4363	-0.598
T ≠ NT August	0.3213	0.238
T ≠ NT combined	0.8578	-0.232

While territorial animals showed higher FCM levels for August, in July territorial and nonterritorial males did not show significant differences, but considering the effect size there emerged relatively strong differences of FCM levels. Altogether, there seems to be slightly higher values for nonterritorial animals (W = 147, n_t=17, n_{nt}= 18, p = 0.858).
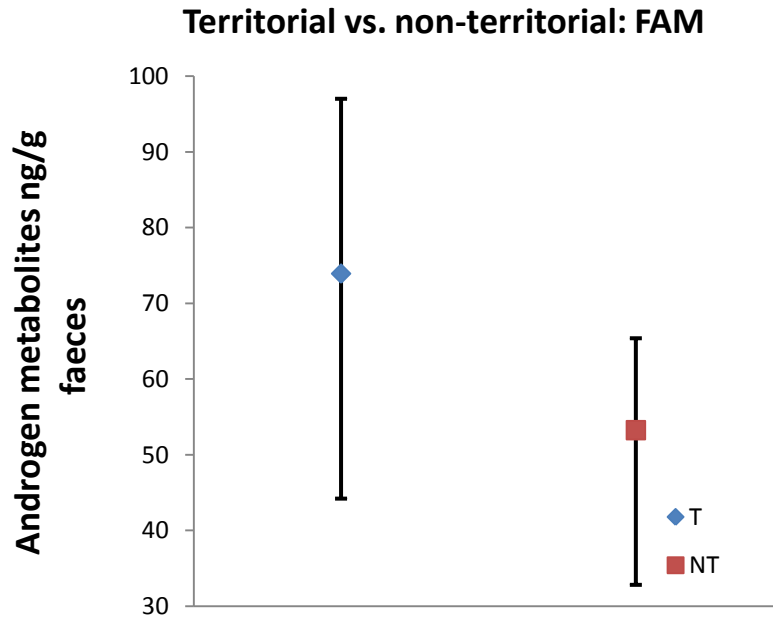
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Fig. 5: Comparison of faecal androgen metabolites (FAM) between territorial and nonterritorial male Alpine chamois during July and August 2012, Gran Paradiso National Park (median an interquartiles)

As for faecal androgen metabolites (FAM), a clear difference of medians was detected when comparing territorial to nonterritorial animals (Fig. 5), although the interquartiles showed great amount of variation within the two groups.

Table 4: Differences between territorial and nonterritorial males in faecal androgen metabolite levels, data from July and August 2012, Gran Paradiso National Park

	p	Cohen's d
T ≠ NT July	0.1298	0.799
T ≠ NT August	0.4511	0.417
T ≠ NT combined	0.0937	0.607

Whereas for the separate months, as shown in Table 4, relatively strong differences occurred, yet not significant, the analysis over the two months combined showed a marginally significantly higher testosterone level for territorial males ($t = 1.7302$, $df = 30,66$, $p = 0.094$).

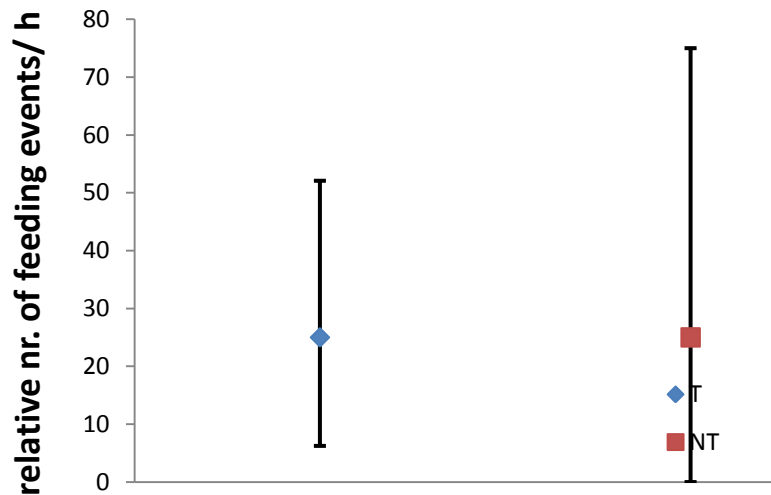## Territorial vs. non-territorial: relative feeding

Fig. 6: Comparison of relative feeding events between territorial and nonterritorial male alpine Chamois during July and August 2012, Gran Paradiso National Park (median and interquartiles)

When relative feeding events, used as activity budget, were considered, only slight differences of medians occurred. The lower quartile of nonterritorial males was 0, but the upper quartile of the same male type was rather high (Fig 6). Both groups showed large variation.

Table 5: Differences between territorial and nonterritorial males regarding their relative feeding time, data from July and August 2012, Gran Paradiso National Park

	p	Cohen's d
T ≠ NT Juli	0.6747	0.146
T ≠ NT August	0.8773	-0.086
T ≠ NT kombiniert	0.6731	0.02

All the tests, as shown in Table 5, showed nonsignificant differences for the relative feeding time of territorial and nonterritorial male chamois. For the two months combined, the differences were not significant (t=0,4257, df = 33,282, p=0.673) and the effect size was very

small whereas for July a slightly higher relative feeding time could be detected for territorial males.

4.2 Model selection

4.2.1 Relative feeding activity

To determine the influence of several variables on relative feeding activity, I created a set of apriori models, starting from the most complicated one (global model):

Relative feeding activity ~ mating behaviour + elevation + FAM levels + FCM levels + gutworms

Table 6: list of retained models, which were averaged to explain the relationship between relative feeding activity and other variables. Observation samples (n=73) of Alpine chamois recorded during July and August 2012 in the Gran Paradiso National Park. The table contains differences of Akaike's information corrected for small sample size (ΔAICc); only models with a ΔAICc < 2 were retained. An x indicates that the parameter is used in the model

gutworms	elevation	FAM	mat_beT	ΔAICc
x				0
x	x			0.5924
	x			1.43
x		x		1.8724
x			x	1.8944

Rather simple relationships formed the base for the averaged model on relative feeding activity (Table 6). No more than two independent variables were part of a competing model.

Table 7: Average parameter estimates from the models with an AICc under 2 for the relative feeding activity of alpine chamois (R.r. rupicapra) during July and August in the Gran Paradiso National Park, Italy. eggs/gram of faeces (epg), elevation in m, faecal androgen metabolites (FAM), , mating behaviour (mat_be, T = territorial). SE = standard error

	Estimate	SE	CI$_{0.025}$	CI$_{0.0975}$
Intercept	1.982939	0.9553642	0.11043	3.85545
epg	-0.0002474	0.0001411	-0.00052	0.00003
elevation	-0.0005558	0.0004527	-0.00144	0.00033
FAM	0.0027529	0.0040421	-0.00517	0.01068
mat_beT	0.1817007	0.27238	-0.35216	0.71557

The averaged model explaining relative feeding activity shows no significant influence of any of the independant variables (Table 7). A positive relationship on feeding activity was detected for FAM levels and territorial mating behaviour, a negative one for the parasite burden (gutworms) and the mean elevation used by the animal.

4.2.2 Parasite burden

To determine the influence of several variables on the parasite burden (epg of faeces), I created a set of apriori defined models starting from the most complicated one (global model):

Gutworms ~mating behaviour + age + elevation +FCM levels+FAM levels + FCM:age + mating behaviour:age + FAM:age

Table 8: Model selection for the influence of mating behaviour (mat_be), age class (Age, A=5-7 years, B=8+years), faecal androgen metabolites (FAM), faecal cortisol metabolites (FCM) on faecal egg counts (epg, eggs per gram). Samples (n=35) of Alpine chamois collected during July and August 2012 in the Gran Paradiso National Park. The table contains differences of Akaike's information corrected for small sample size (ΔAICc), only models with a ΔAICc < 2 were retained. An x indicates that the parameter is used in the model.

mat_be	age	FAM	FCM	elevation	ΔAICc
			x		0
		x			0.474
	x				0.61
				x	0.65
	x		x		1.1657
	x			x	1.5437
	x	x			1.6157
x	x				1.6317
		x	x		1.9977

Although the a priori defined set of models did also contain interactions between mating behaviour and age, FCM and age as well as FAM and age, none of the latter interactions were retained for the final averaged model (Table 8). No significant relationships could be found for the model of the parasite burden (Table 9). There was a negative tendency for FCM, elevation and older animals, a positive one for FAM levels and territorial mating behaviour

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Table 9: Average parameter estimates from the models with an AICc under 2 for the eggs per gram of faeces of alpine chamois (R.r. rupicapra) during July and August in the Gran Paradiso National Park, Italy (n=35). 5-7 year olds (ageA), 8+year olds (ageB), faecal androgen metabolites (FAM), faecal cortisol metabolites (FCM), mating behaviour (mat_be, T = territorial)

	Estimate	SE	$CI_{0.025}$	$CI_{0.0975}$
Intercept	6.8687641	1.8506143	3.24156	10.49597
FCM	-0.0007733	0.0005536	-0.00186	0.00031
FAM	0.0102401	0.0093028	-0.00799	0.02847
ageB	-0.7248221	0.5585704	-1.81962	0.36998
elevation	-0.0012471	0.0010741	-0.00335	0.00086
mat_beT	0.7956122	0.49345	-0.17155	1.76277

The different relationships between age, FAM levels and parasite burden are also shown in figure 7, where younger animals (5-7 year olds) seemed to suffer a higher parasite burden than animals older than 8 years.
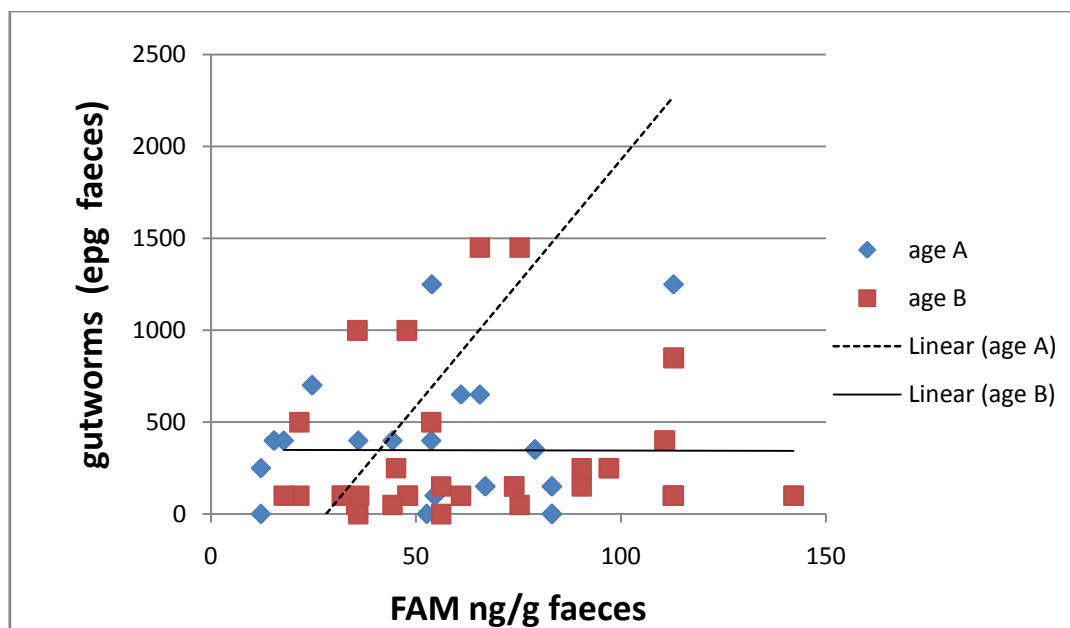
Fig. 7: Different age groups (A = 5-7 years, B = 8+ years) and the influence of faecal androgen levels (FAM) and parasite burden (epg)

4.2.3 Faecal androgen metabolites

To determine the influence of several variables on faecal androgen metabolites, I created a set of apriori defined models starting from the most complicated one (global model):

FAM levels ~ mating behaviour + age + mating behaviour:age

Table 10: Model selection for the influence of age class (Age, A=5-7 years, B=8+years) and mating behaviour (mat_be, T = territorial) on faecal androgen levels of alpine chamois (*R.r.rupicapra*) during July and August 2012 in the Gran Paradiso National Park.

mat_beT	ageB	ΔAICc
x		0
	x	0.978
x	x	1.8157

Regarding faecal androgen metabolite levels, 3 a priori defined models were retained (Table 10), the best fitting model (with the lowest AICc value) was the regression with mating behaviour. In the averaged final model (see Table 11), no variables had a significant influence, although there seemed to be a negative relationship between them. If this was true, older territorial males would show lower FAM levels. This assumption may be confirmed by figure 7.

Table 11: Average parameter estimates from the models with an AICc under 2 for faecal androgen levels of Alpine chamois during July and August in the Gran Paradiso National Park, Italy. mating behaviour (mat_be, T = territorial), age class (age, B= older than 8 years).

	Estimate	SE	$CI_{0.025}$	$CI_{0.0975}$
Intercept	3.949	0.1502	3.65461	4.24339
mat_beT	0.2986	0.194	-0.08164	0.67884
ageB	0.2267	0.1962	-0.15785	0.61125

4.2.4 Faecal cortisol metabolites

To determine the influence of several variables on faecal cortisol metabolites I created a set of apriori defined models starting from the most complicated one (global model):

FCM levels ~ mating behaviour + age + elevation + mating behaviour:age

Table 12: Model selection for the influence of elevation (in m a.s.l.) and mating behaviour (mat_be, T = territorial) on faecal cortisol metabolite levels of Alpine chamois during July and August 2012 in the Gran Paradiso National Park.

elevation	mat_beT	ΔAICc
x		0
x	x	1.8657

For faecal cortisol metabolites, as for FAM levels, mating behaviour was retained in the final model (Table 12). Interactions showed a significant influence of elevation (Table 13) which is, in the final averaged model, positively related to FCM levels. This relationship is the only significant one of all the models retained after analysis (Fig. 8).
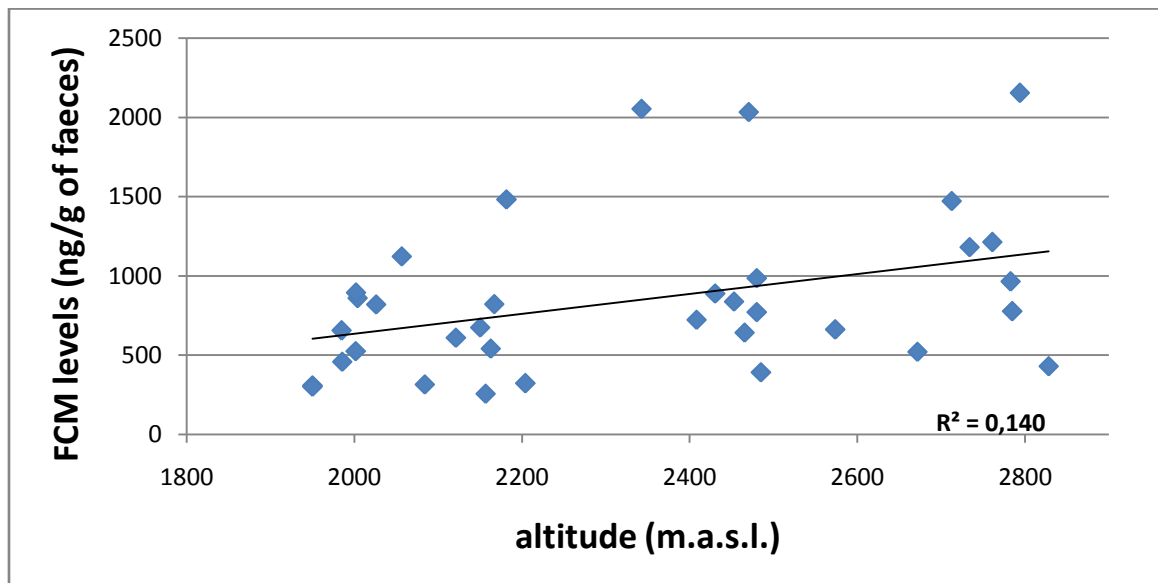
Fig. 8: Relationship between faecal cortisol metabolite levels and the mean elevation of Alpine chamois during July and August 2012 in the Gran Paradiso National Park.

Table 13 Average parameter estimates from the models with an AICc under 2 for faecal cortisol levels of Alpine chamois during July and August in the Gran Paradiso National Park, Italy. Mating behaviour (mat_be, T = territorial), age class (age, B= older than 8 years).

	Estimate	SE	$CI_{0.025}$	$CI_{0.0975}$
Intercept	4.6328843	0.8449604	2.97676	6.28901
Elevation	0.0008701	0.0003439	0.00020	0.00154
mat_beT	0.2037851	0.21919	-0.22583	0.63340

5 Discussion

Territorial males used significantly lower elevations, while effect sizes suggest a higher parasite burden and slightly higher FAM levels. Nonterritorial males on the other hand show a marginally higher FCM output, although this was not significant. No significant difference was found when comparing relative feeding activity. Among the apriori defined models, elevation showed a significant effect on FCM levels, whereas no other relationship was found for FAM levels, parasite burden or relative feeding activity.

5.1 Differences between territorial and nonterritorial males

5.1.1 Elevation

Nonterritorial males used a higher mean elevation than territorial males. These findings go hand in hand with the results of von HARDENBERG et al. (2000), who showed a differentiation between males occupying territories in early summer and some that didn't occupy a territory at all. Those territorial males appeared to be at preferred winter feeding sites for females, thus attractive for them during the rut. A higher mating success of territorial males has been observed (CORLATTI et al. 2013). LOVARI et al. (2006) observed that all males moved to higher elevations in summer, but showed that 76.2% had overlapping winter and summer home ranges. This suggests the existence of territoriality, although this mating behaviour is not applied in their study, which only differentiates between residents and migrants. NESTI et al. (2010) confirmed these results and showed a strong preference of

territorial males for pastures and meadows. They also found that females spend their summer in higher elevations than territorial males and that they preferred to reside in areas of higher quality.

5.1.2 Relative feeding time

While I was not able to find a significant difference for relative feeding time comparing territorial and nonterritorial males during summer, there is evidence that such a differentiation may take place during the rut. In the main rutting period, males seem to reduce their feeding activity (WILLISCH and INGOLD 2007), while they increase their mating effort (CORLATTI et al. 2012). However my study aimed to address this from a different perspective: a) defence of territories may consume time otherwise spend feeding and b) lower forage quality may result in longer feeding time. Although many hours were spent in the field during the sample collection for this study, no major defence activity pattern was observed. The first announced reason seems unlikely to affect animals, as they were not obliged to defend their territories. This can be explained, as nonterritorial animals inhabited higher elevations, and establishment of territories occurs in early summer (KRAEMER 1969) before my sampling took place. In this context, von HARDENBERG et al. (2000) found that aggressiveness was higher in summer than in spring. Regarding the second argument for elevated feeding time, a noteworthy explanation might be the fact that a big part (an estimated 60%) of the study area were regularly grazed by sheep, thereby allowing young shoots to grow back in their absence. RÜTTIMANN (2008) found no influence of sheep grazing on chamois behaviour or distribution, so that an overall negative influence is likely to be excluded, although CORLATTI (personal communication) suggests that territorial males might well be influenced by livestock. MOORE (2002) considers foraging itself as an exposure to parasites. Considering my hypothesis for the relative feeding time where no difference seems to occur, the following chapter on gastro-intestinal nematodes may be able to offer an explanation.

5.1.3 Gutworms

Comparing the parasite burden carried by territorial and nonterritorial males, no significant difference can be found, although a strong effect size in July suggests that a difference occurs. In August, the effect size is small. Lung helminths were only found in 6 animals during July and a single animal in August and are therefore not considered in this study. ŠTEFANČÍKOVÁ et al. (2011) found significantly lower prevalence levels of lung parasites

during summer for Alpine chamois in Slovakia, thus confirming my results. CORLATTI et al. (2012) found a greater parasite output for territorial males during the rut, while differences before and after the rutting period were smaller. Although RÜTTIMAN (2008) did not observe behavioural changes when sheep grazed on chamois feeding sites, the results of FRANKHAUSER et al. (2008) suggest that a strong feeding site contamination by sheep faeces prevents chamois from using it, as they might try to minimize parasite uptake by feeding. As this was only observed for strong contamination, low frequency grazing might still increase the parasite burden on feeding sites themselves. If territorial males prefer to stay at lower elevations as observed in this study, they might expose themselves to this higher prevalence of parasites on the ground they feed on. FLEURANCE et al. (2005) showed for horses that they were primarily driven by nutritional aspects and put a higher priority on these than on parasite prevention by not using contaminated feed. This might be the case as well for the territorial male chamois analysed in this study, especially if their mating strategy also influences spatial behaviour patterns. As home ranges of territorial animals are likely to be smaller (CORLATTI et al. 2012, von HARDENBERG et al. 2000), density might affect parasitism in these animals. In their study, STANCAMPIANA and GUBERTI (2006) did not find a density effect on the intensity of infection; however, host density seems to affect parasite species composition. Generally speaking, one might suggest that because of the time span of my study, and the animals sampled may being in prime condition - also favoured by the availability of food, and the latter having a positive effect on their immune system, that the analysed form of parasitism does not play a major role during summer.

5.1.4 Faecal androgen metabolites

Although the differences of faecal androgen metabolites that I found were only significant at the 10% significance level, the strong effect size advocates for higher FAM values for territorial males. This result is in line with the findings of CORLATTI et al. (2012), although their study focussed on the rutting period. HOBY et al. (2006) found strong evidence for a relationship between lungworms and FAMs, but not for gastro-intestinal nematodes. Nevertheless they found a generally higher level of internal parasites for male chamois when comparing them to females. This still proposes a likely influence of faecal androgen metabolites and parasitism, thus relating to the immunocompetence handicap hypothesis (FOLSTAD & KARTER 1992). On the other hand, as pointed out in the chapter above, favourable conditions might prevent the establishment of parasites to a certain level. HOBY et al. (2006) found the lowest values of FAM levels during summer. This might also be caused by the prior establishment of territories (KRÄMER 1969, von HARDENBERG 2000), thus enabling the animals to grow stronger for

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the upcoming rut. MARTINEZ-PASTOR et al. (2005) found lower testis weight and sperm quality outside the breeding season. Lower levels of FAMs for that period were able to explain similar results for red deer (MALO et al. 2009). Very little literature seems to exist on this topic, and further studies might be able to show stronger evidence for such effects.

5.1.5   Faecal cortisol metabolites

Considering both months combined, nonterritorial males showed higher 11,17-DOA levels than territorial ones, although the latter had higher values for August. The hypothesis behind this analysis was to determine whether territorial males were exposed to higher level of stress as they had to maintain territories and were subject to higher temperatures and possibly lower forage quality, indicated by FCM values. Clearly the results are controversial and do not show a clear trend. This is possibly due to the limited sample size and high variation between animals, but may also be a result of different reasons for high faecal cortisol levels. For both males and females, HOBY et al. (2006) and DALMAU et al. (2007) found the lowest values of FCM during summer. While glucocorticoids are usually associated with stress (AXELROD and REISINE 1984), other factors might influence cortisol secretion. It can also be the result of limited caloric intake and thereby induce the transformation of muscle protein to energy, a process called gluconeogenesis (FOSTER and MCGARRY 1988). This is usually associated with limited food availability or lower fodder quality, which can be excluded for my study since the animals were sampled during the main vegetation period. Also no significant difference in faecal nitrogen content was observed (CORLATTI, unpublished data). Possibly, extreme temperatures might be a reason for the stress that nonterritorial males in higher elevations are exposed to (CORLATTI et al. 2011b). While territorial males do not seem to need to defend their territories (see above), they are probably not subjected to stress. If the assumed hypothesis was to be supported, territorial animals would have been the ones to show a generally higher output of FCM. This shows that individual variation and possibly unconsidered factors might also be responsible for the results.

5.2   Relationships between bio-ecological variables

Of all the predefined models, only the averaged model relating faecal cortisol metabolite values to the average elevation used by the animal showed a significant relationship. While in the same model the territorial mating behaviour was retained for the averaging, it did not seem to have a significant influence on FCM values. Figure 8 also clearly indicates a positive

relation between elevation and FCM values. As discussed in chapter 6.1.5. it remains unclear why nonterritorial males, which my hypothesis subjected to lower stress exposure, show higher FCM levels. Fig. 7 differentiates faecal androgen metabolite values to two different age classes. Clearly younger animals seem exposed to higher testosterone secretion and carried, following the immunocompetence handicap hypothesis (FOLSTAD & KARTER 1992), a higher parasite load. MILLER and CORLATTI (2009) classify 4 year old animals as adults, so that an age related, physiological explanation cannot be given to this. On the other hand, male Alpine chamois are able to maintain territories up to a high age (CORLATTI and DOSTERT 2013), and younger males might not be able to establish and maintain territories as these are occupied by competitors. The limited sample size of this study and the non-random selection of animals for sampling do not allow assumptions to be made if the relation of territoriality and age is concerned. It seems unlikely that only older animals opt for territoriality, as the youngest animal of CORLATTI et al. (2012) successfully occupied a territory already at 5 1/2 years of age, while other animals managed to sire kids at that age (CORLATTI, personal communication).

6 Conclusion

The consequences of opting for one or the other alternative mating tactic do not appear at their strongest level during the summer months. Still, territoriality seems to cause costs but appears to be beneficial for mating success (CORLATTI et al. 2013). CORLATTI et al. (2012) were able to show much clearer differences during the rut. In my study, territorial males occupied territories at lower elevations than nonterritorial males. I assume that their nonsignificantly elevated FAM levels might lead to a higher parasite load, although strong variation seems to occur. Nevertheless the combination of FAM values and its importance for the immunocompetence theory, as well as parasite output by grazing sheep in combination with possibly better conditions for larvae development on the ground might explain higher parasitism of gutworms in territorial male Alpine chamois. Also, these costs might play a greater role after summer when the stress of the rut and the lower abundance of fodder in combination with higher parasite prevalence increase the animals' vulnerability. Why nonterritorial males indicate elevated stress exposure remains unclear, especially when considering that almost no aggression on behalf of territorial males took place, and that nonterritorial males spent their summer in better climatic conditions in an environment that provides fodder of higher quality. However, a permanent surveillance by territorial males might still affect nonterritorials, as they have to submit themselves to a constant dominance

by others. For future investigations I recommend to increase the sample size if available resources allow it, and to consider study sites which offer a broader elevation range (e.g. from 700 – 2500 m a.s.l.).

7 References

AKAIKE H. (1974). A new look at the statistical model identification", IEEE Transactions on Automatic Control 19 (6) p. 716–723

ALTMANN J. (1974). Observational study of behaviour: sampling methods. Behaviour, 49, p. 227-267AULAGNIER S., GIANNATOS G., HERRERO J.(2008). *Rupicapra rupicapra*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. www.iucnredlist.org. Downloaded on 22 August 2012.

CATCHPOLE E. A., FAN Y., MORGAN B. J. T., CLUTTON-BROCK T. H., COULSON T. N. (2004). Sexual dimorphism, survival and dispersal in red deer. Journal of Agricultural, Biological, and Environmental Statistics Vol. 9 pp.1-26

CORLATTI L., LORENZINI R., LOVARI S. (2011). The conservation of the chamois *Rupicapra* spp. Mammal Review, Volume 41, No. 2, pp. 163–174

CORLATTI L., PALME R., FREY-ROOS F., HACKLÄNDER K.(2011b). Climatic cues and glucocorticoids in a free-ranging riparian population of red deer (*Cervus elaphus*). Folia Zoologica 60 (2), pp. 176-180

CORLATTI L., BÉTHAZ S., VON HARDENBERG A., BASSANO B.,PALME R., LOVARI S. (2012). Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs. Animal Behaviour, Available online 23 August 2012

CORLATTI L., CAROLI M., PIETROCINI V., LOVARI S.(2013). Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage? Behavioural Processes 92, pp. 118–124

CORLATTI L., DOSTERT M .(2013). Gamswild : Altersklassen überdenken ? Der Anblick 2, pp. 18-21

COUTURIER M. (1938) Le Chamois. Arthaud, Grenoble.

COUTURIER M. (1964). Le gibier des montanges françaises. Collection SEMPERVIVUM, Editions Arthaud, France. 463 p.

DALMAU A., FERRET A., CHACON G., MANTECA X. (2007). Seasonal changes in faecal cortisol metabolites in Pyrenean Chamois. Journal of Wildlife Management, 71(1) pp. 190-194

DEFIFE J. (2009). Effect Size Calculator for Microsoft Excel. Unpublished, Emory University

FLEURANCE G., DUNCAN P., FRITZ H., CABARET J. GORDON I. J. (2005). Importance of nutritional and anti-parasite strategies in the foraging decisions of horses: an experimental test. OIKOS 110 pp. 602-612.

FOLSTAD I. AND KARTER A.J. (1992). Parasites, bright males, and the immunocompetence handicap. The American Naturalist Vol. 139 No 2: 603–622.

FOSTER D.W., MCGARRY J.D.(1988). Glucose, lipid, and protein metabolism. In: Griffin J.E., Ojeda S.R. (Eds.), Textbook of Endocrine Physiology. Oxford University Press, New York, pp. 349–374. Cited from HUBER S., PALME R., and ARNOLD W. (2003). Effects of season, sex, and sample collection on concentrations of fecal cortisol

metabolites in red deer (Cervus elaphus). General and Comparative Endocrinology 130, pp.48–54

FOURNIER D.A., SKAUG H.J., ANCHETA J., IANELLI J., MAGNUSSON A., MAUNDER M.N., NIELSEN A., AND SIBERT J.(2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software. 27 pp. 233-249.

FRANKHAUSER R.,CORDULA GALEFFI C., SUTER W. (2008). Dung avoidance as a possible mechanism in competition between wild and domestic ungulates: two experimentswith chamois Rupicapra rupicapra. European Journal for Wildlive Research 54, pp.88–94.

GAREL M., LOISON A., JULLIEN J.-M., DUBRAY D., MAILLARD D., GAILLARD J.-M. (2009). Sex-specific growth in Alpine chamois. Journal of Mammalogy, Volume 90, No.4 pp.954–960

GIACOMETTI M., HARTL G. B., VÖLK F. (1997). Regional summary: Europe. In: Wild Sheep and Goats and Their Relatives: Status Survey and Conservation Action Plan for Caprinae (Shackleton D.M., ed). IUCN, Gland, pp.143-147. After VON HADENBERG et al. 2000

KRÄMER A. (1969) Soziale Organisation und Sozialverhalten einer Gemspopulation *Rupicapra rupicapra* der Alpen. Zeitschrift für Tierpsychologie, Volume 26 pp. 889–964.

LEWIS J. S., RACHLOW J. L., GARTON, E. O. VIERLING L. A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology, 44, pp. 663-671

MALO A.F., ROLDAN E.R., GARDE J.J., SOLER A.J., VICENTE J., GORTAZAR C., GOMENDIO M.(2009). What does testosterone do for red deer males? Proceedings of the Royal Society: Biological Sciences 276 (1658) pp. 971–980

FELIPE MARTINEZ-PASTOR F., GUERRA C.B., MOHAMMED KAABI M., GARCIA-MACIAS V DE PAZ P., ALVAREZ M., HERRAEZ P., LUIS ANEL L.(2005). Season effect on genitalia and epididymal sperm from Iberian red deer, roe deer and Cantabrian chamois. Theriogenology 63 pp. 1857–1875

MCDONALD J.H. 2009. Handbook of Biological Statistics, 2nd ed. Sparky House Publishing, Baltimore, Maryland, 239 p.

MOORE J. (2002). Parasites and the behaviour of animals. Oxford University Press, New York. 329 p.

MÖSTL E., MAGGS J. L., SCHRÖTTER G., BESENFELDER U., PALME, R. (2002). Measurement of cortisol metabolites in faeces of ruminants. Veterinary Research Communications, 26, pp. 127-139.

MILLER C. and CORLATTI L. (2009). Das Gamsbuch. Für Einsteiger und Profis. Neumann-Neudamm-Verlag, Melsungen. 207 p.

NESTI I., POSILLICO M. and LOVARI S.(2010) Ranging behaviour and habitat selection of Alpine chamois', Ethology Ecology & Evolution, 22 (3) pp. 215-231

PALME, R. and MÖSTL, E. (1994). Biotin-streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. In: Advances of Steroid Analysis '93 (Ed. by S. Görög), pp. 111-117. Budapest: Akadémiai Kiadó.

R CORE TEAM.(2012). R: A Language and Environment for Statistical Computing. Vienna, Austria. http://www.R-project.org

RUGHETTI M., FESTA-BIANCHET M. (2011). Seasonal changes in sexual size dimorphism in northern chamois. Journal of Zoology 248 (4), pp. 257–264

RÜTTIMANN S., GIACOMETTI M., MCELLIGOT A.G.(2008). Effect of domestic sheep on chamois activity, distribution and abundance on sub-alpine pastures. European Journal of Wildlife Research, Volume 54, (1), pp 110-116

STANCAMPIANO L., GUBERTI V. (2006). Models of parasite biocoenosis dynamic: host density and gastrointestinal parasites in alpine chamois. Parassitologia 48, pp 47-49

ŠTEFANČÍKOVÁ A., CHOVANCOVÁ B., HÁJEK B., DUDIŇÁK V, ŠNÁBEL V.(2011). Revision of chamois infection by lung nematodes under ecological conditions of national parks of Slovakia with respect to ongoing global climate changes. Helminthologia, 48 (3) pp. 145 – 154

SYMONDS R.E.M. and MOUSSALI A.(2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioural Ecologyand Sociobiology 65 pp.13–21

THIENPONT D., ROCHETTE F. , VANPARIJS O. F. J. (1979). Diagnostic de Verminose par Examen Coprologique. Beers: Janssen Research Foundation.

TRUTMANN C. (2009). Diet composition of alpine chamois (*Rupicapra rupicapra* L.): Is there evidence for forage competition to the alpine ibex (*Capra ibex* L.)? Master Thesis in Ecology at University of Zurich, 42 p.

VAN SOEST, P. J. (1994). Nutritional ecology of the ruminant. Comstock Publishing Associates, Ithaca, New York

VON HARDENBERG A., BASSANO B., PERACINO A., LOVARI S. (2000). Male Alpine Chamois Occupy Territories at Hotspots Before the Mating Season. Ethology Vol.106 pp.617-630

WILLIAMS R. (2011). Multicollinearity. http://www.nd.edu/~rwilliam/stats2/l11.pdf   Retrieved on 29.11.2012

WILLISCH C.S., INGOLD P. (2007). Feeding or Resting? The Strategy of Rutting Male Alpine Chamois. Ethology 113 p. 97–104

8 List of tables

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Appendix I
Data from July 2012, Gran Paradiso National Park

id	name	age	mating behaviour	mean elevation (m.a.s.l.)	lungworms (epg)	gutworms (epg)	relative feeding	FCM (ng/g)	FAM ng/g
M01	KLAUS	7	T	2150	50	6300	1,5	674	112,86
M04	PETER	9	T	1985	0	850	1,5	458	112,86
M05	VALERIO	8	T	2181	0	150	0,5	1482	73,92
M07	FUMETTO	8	NT	2465	0	1000	1,5	642	35,64
M08	PERTICO	7	NT	2204	0	150	3,5	322	83,16
M11	CAVALERO	9	T	2408	50	1000	1	723	47,74
M12	GIO	5	NT	2761	0	400	1,5	1212	15,378
M13	ICE	6	T	2026	50	350	7,5	820	78,98
M14	GERONIMO	10	T	2002	50	100	6,5	525	142,12
M15	CLINT	8	NT	2084	650	400	5,5	315	110,66
M16	FREDY	8	T	2671	0	250	1,5	520	97,02
M17	Luke	8	T	2002	n.a.	n.a.	5	n.a.	n.a.
M18	ASSO	9	NT	2342	0	100	7,5	2053	112,64
M19	Artu	9	T	2121	50	50	6	609	35,42
M21	VITTO	8	NT	2480	0	100	0	985	47,96
M22	ARICE	6	NT	2794	50	100	1,5	2153	54,56
M24	ULTIMO	7	NT	2485	50	700	4,5	392	24,64
M25	CRACK	7	T	1950	0	0	9,5	308	83,16
M26	BAX	6	NT	2453	0	150	6,5	837	66,88

Appendix I
Data from August 2012, Gran Paradiso National Park

id	name	age	nating behaviour	mean elevation (m.a.s.l.)	lungworms (epg)	gutworms (epg)	relative feeding	FCM (ng/g)	FAM (ng/g)
M01	KLAUS	7	T	2150	n.a.	n.a.	n.a.	n.a.	n.a.
M04	PETER	9	T	2002	0	100	6,5	893	112,86
M05	VALERIO	8	T	2167	0	500	7,5	821	53,68
M07	FUMETTO	8	NT	2785	0	150	5	776	56,1
M08	PERTICO	7	NT	2574	0	1250	0,5	661	53,9
M11	CAVALERO	9	T	1985	150	1450	4,5	655	65,56
M12	GIO	5	NT	2828	0	250	5	430	45,1
M13	ICE	6	T	2056	0	0	2,5	1122	12,144
M14	GERONIMO	10	T	2004	0	250	7	859	90,42
M15	CLINT	8	NT	2156	0	50	4,5	256	75,24
M16	FREDY	8	T	2734	0	0	6,5	1181	35,86
M17	Luke	8	T	1997	n.a.	n.a.	5	n.a.	n.a.
M18	ASSO	9	NT	2430	0	100	4,5	888	31,9
M19	Artu	9	T	2712	0	100	0	1471	36,08
M21	VITTO	8	NT	2480	0	100	5	771	21,516
M22	ARICE	6	NT	2782	0	0	6,5	964	52,58
M24	ULTIMO	7	NT	2470	0	400	6,5	2033	17,732
M25	CRACK	7	T	1950	0	400	1,5	300	44,22
M26	BAX	6	NT	2163	0	650	2,5	541	60,94