LIFE HISTORY STRATEGIES OF MALE ALPINE CHAMOIS

–New insights on survival and mating behaviour–

Ph.D. Candidate: Luca Corlatti

Director of the School: Prof. Pietro Lupetti
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This thesis is based on the following papers:

I Unbiased sex-specific survival in Alpine chamois. Published in Mammalian Biology 77 (2012), 135-139 27

II Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage? Published in Behavioural Processes 92 (2013), 118-124 33

III Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs. Published in Animal Behaviour 84 (2012), 161-170 41
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PROLOGUE AND ACKNOWLEDGMENTS

Months ago I came across a comic strip by Jorge Cham (www.phdcomics.com) that describes quite well the excitement, the doubts and uncertainties that many grad students experience in the course of their PhD. Or that –at least– I did.

Lots of my non-specialist friends probably never had a clue as to what I was actually doing over the past three years. Quite often, when meeting other people, they ended up introducing me as “the one who counts chamois”… I’ve never had the guts to contradict, me myself feeling sometime uncertain of where my research would have led. Luckily enough, time was of great help clarifying most of my foggy thoughts.

My work experience with chamois traces back to quite some years ago. It was 2002 when, fellow student at the University of Padua, I started being fascinated by this species. At that time I was mainly interested in the demography of populations, but soon I realized the lack of information on the reproductive biology of chamois. It is my view that, to better understand a species, and to provide useful information for its conservation, we’re still often desperately in need of basic information on its biology.

This thesis is the attempt to shed a bit of light on some issues concerning the reproductive etho-ecology of chamois.

I spent the very first part of my PhD analysing pre-existing data collected in the Swiss National Park. Most of my time as a PhD student, however, was dedicated to fieldwork in the Gran Paradiso National Park (Italy). This, required very many hours spent in the field, staying grounded and modestly observing animals during their year-round activities. Indeed, capturing chamois, collecting behavioural and physiological data over several years in the Alpine environment, coordinating students and writing papers has not always been an easy task…

I must admit, however, I had many fortunes during my years as a PhD fellow. I remember, in my first year, reading Stephen C. Stearns’ “Modest advices to graduate students”, where he invites students to plan for alternatives, assuming that the proposed research might not work,
and that faculty advisers might become unsupportive—or even hostile.

I was lucky enough to have Prof. Sandro Lovari as my principal advisor. He’s always been supportive, ready to give me good advices, and eager to help me out with my papers. Yet he gave me lots of freedom. I guess no one could have hoped for a better advisor.

Likewise, I consider a privilege to have worked with Dr. Bruno Bassano, one of the most competent, profound and careful persons I’ve ever met. I owe him a lot.

The Gran Paradiso National Park Agency offered a great logistic support, and the park wardens were of immense help during all stages of this work. I’d like to thank in particular Piero Chabod and Paolo Guglielmetti for their great professionalism during captures and for the pleasant moments shared in the study site.

Likewise, I thank the Swiss National Park Agency and Dr. Flurin Filli for providing data for the survival analysis.

I must thank Prof. Klaus Hackländer, who’s always believed in this project, even before it got started! He encouraged me to carry on with my ideas and offered me his support throughout these years.

Thanks also to all my co-authors, and to Prof. Marco Festa-Bianchet for his precious advices on early drafts of all manuscripts.

A work such as this one necessarily needs a good team, to work out properly. I am grateful to all the students and internships that helped me with the data collection and analysis and eased my days in the study site. Some of them are still on board. In chronological and alphabetical order: Martina Caroli, Venusta Pietrocini, Valentina Lupano, Stéphanie Béthaz, Cecilia Benedetto, Giamberto Picca-Garino, Noémie Castaing, Laura Vacondio, Barbara Zanucco, Chiara Lorenzetti, Manon Vallant, Patrick Ugonino, Michel Dostert, Lucia Verdicchio.

I don’t forget to thank Enio Pacher, superb neighbour, who really contributed to make my stay, and that of my collaborators, a great pleasure!

In these years I have been lucky to be able to do what in my view is the best job in the world, studying my favourite animal, in one of the few remnant natural environments of the Alps… All the people I thanked made this experience even more splendid.

Luca Corlatti

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STUDY OVERVIEW

Survival and reproduction are key issues in the evolution of life history strategies. In highly polygynous species, the link between survival and reproduction is exemplified by intense male-male competition during the rut, often associated with the development of marked sexual-size dimorphism and with greater male than female mortality. Polygynous species with limited dimorphism, on the other hand, may adopt more conservative survival strategies, leading to unbiased sex-specific survival, that may underlie relatively less risky mating systems such as weak polygyny. Whatever the level of polygyny, within a population not all males will reproduce. For males, there are multiple tactics to pursue reproductive success. How did these tactics evolve within populations, however, is far from being clear and several issues still need to be properly addressed. Are tactics irreversible or reversible phenotypes? Do tactics show different cost-benefit trade-offs? Is frequency-dependence the only mechanism driving their maintenance within populations? Is there a condition-dependent process underlying individual costs and benefits?...

This work is an attempt to provide insights on some of these issues, using the Alpine chamois as a model species. The study of phenotypic plasticity or frequency dependence of different tactics ideally requires long-term datasets, which I was unable to collect. I will thus focus on the survival pattern in relation to mating system and on the proximate mechanisms underlying the costs-benefit trade-offs of alternative mating types. Before I proceed, however, it is worth introducing some concepts that will be used throughout the thesis.

Introduction

Mating systems and survival strategies

Mating system may be defined as the organization of reproductive behaviour in terms of relationships between sexual partners. Different mating systems may occur: (1) monogamy, where individuals mate with the same partner in one or more reproductive events; (2) polygamy, where males mate with several females (polygyny) or females mate with several males (polyandry); (3) promiscuity, where males and females mate with any receptive partner and there is no continuing bond between individual males and females after mating has occurred. Despite the practical value of the simple framework proposed above, mating systems may intergrade (Clutton-Brock 1989). While over 90% of birds are socially monogamous, male monogamy is exceptional in mammals, which tend to be polygynous (Alcock 2005).

In polygynous species, the intense male-male competition during the rut is often associated with the development of sexual-size dimorphism (SSD) which, in turn, imposes energetic costs that usually lead to greater mortality of males than of females (Clutton-Brock & Isvaran 2007), particularly under harsh environmental conditions (Toïgo & Gaillard 2003). Some polygynous species, however, show limited dimorphism and nearly unbiased sex-specific survival, which may underlie the occurrence of a relatively less risky mating system such as weak polygyny.

Mating strategies and Alternative Mating Tactics

To achieve polygyny, mating behaviour may vary amongst males; such
a variation often takes distinct forms (discrete patterns), which generate the so-called "alternative mating tactics" (hereafter AMTs). AMTs are thought to be the outcome of a strategy, i.e. of a decision rule that results into a sequence of tactics (Gross 1996). The distinction between strategy and tactic, however, is still debated (Isvaran 2005) and according to Shuster (2008), there is no need to distinguish between them. Following Taborsky et al. (2008) I use the term AMTs to refer to alternative ways to obtain fertilization.

The main forms of mating tactics (Clutton-Brock 1989, Alcock 2005) are female-defence polygyny, where males fight to monopolise individual females during part or all of their period of oestrus (individual female defence polygyny), or defend groups of females either during the mating season or throughout the year without the defence of any fixed area (female group defence polygyny); resource-defence polygyny, where males defend territories containing food or other resources attractive for receptive females; lek-polygyny, where males defend dispersed or clustered mating territories within a portion of the female range. Behavioural variations include irreversible phenotypes (individuals adopt a single tactic over their lifetime) and reversible phenotypes (individuals adopt different tactics sequentially or switch between them). AMTs are often associated with differences in morphological traits (e.g. plumage variation in birds, Lank et al. 1995; colour or size polymorphisms in fish, Gross 1991 and Seda et al. 2012) but differences in features other than body or weapon size, such as agility or aggressiveness (Linklater 2000, Rughetti & Festa-Bianchet 2011) may also be found.

**Evolution and maintenance of AMTs**

Understanding the maintenance of different tactics within or between populations requires the study of pay-offs in terms of individual reproductive success, since the mating systems of animals are the outcome of the reproductive strategies of individuals, rather than evolved characteristics of species (Clutton-Brock 1989).

Game theory is concerned with the study of AMTs in terms of their costs and benefits to evolutionary fitness (Gross 1996). Specifically, when the fitness of alternative phenotypes depends on their frequencies in the population, we encounter frequency-dependent selection (Fig. 1). This process is thought to be the most likely to maintain stable frequencies of alternative tactics within populations (Isvaran 2005).

![Figure 1: example of frequency-dependent selection of AMTs. When phenotype Y is at low frequency its fitness is greater than phenotype X, and it increases its frequency in the population (after Gross 1996).](image)
Frequency-dependent selection, however, is not the only mechanism involved in the maintenance of alternative phenotypes. For example, proximate studies of the maintenance of AMTs address the underlying cost-benefit trade-offs of processes that involve the role of hormones (Gross 1996). Other internal factors such as health, energy reserves (Gross 1996), age or dominance status (Hogg & Forbes 1997) or external factors such as weather, predation (Isvaran 2005), local density (Thirgood et al. 1999, Kokko & Rankin 2006) and female distribution (Clutton-Brock 1989, Carranza et al. 1995, Lovari et al. 2006) may concur in maintaining alternative phenotypes, for example thorough condition-dependent selection (Isvaran 2005). In contrast with frequency-dependent selection, condition-dependent selection may maintain AMTs only as long as internal and external factors show sufficient variation to allow for changes in fitness difference between alternative phenotypes (Isvaran 2005).

There is increasing evidence that multiple mechanisms may maintain alternative phenotypes (Brockmann 2001) and the study of AMTs may benefit from models combining frequency- and condition-dependent selections and solving for their joint equilibrium (Gross 1996).

Although mating systems have been so far extensively studied in animal taxa as diverse as arthropods, fish, amphibians, reptiles, birds and mammals, still many relevant issues have not been adequately investigated. Ungulates are ideal to study mating systems, since they are often easy to observe, their populations are socially structured and show variability in mating tactics (e.g. red deer Cervus elaphus, Carranza et al. 1995; fallow deer Dama dama, Thirgood et al. 1999; blue sheep Pseudois nayaur, Lovari & Ale 2001; feral goat Capra hircus, Saunders et al. 2005; Alpine chamois Rupicapra rupicapra, von Hardenberg et al. 2000, Lovari et al. 2006).

Despite their abundance and their economical importance, however, studies on AMTs within ungulate populations are relatively rare, and the mechanisms through which the factors mentioned above influence the pay-offs of AMTs are not fully understood. Thus, «much work remains to be done on the factors maintaining alternative male mating tactics and, more generally, intraspecific variation in ungulates» (Isvaran 2005). To investigate the costs and benefits of AMTs, long-term studies of marked individuals – that take into account survival and reproductive success of AMTs– are needed.

Alpine chamois life history

Adapted to living in rugged, rocky terrain, the chamois is about 70-90 cm tall at the shoulder and weighs 25-50 kg (Fig. 2). Males and females show little morphological differences; both sexes possess hollow, vertical horns that hook sharply backward at the tips. In summer, the chamois’ fur has a light-brown colour, which turns to a dark-brown in winter. Distinct characteristics are a white face with pronounced black stripes below the eyes, a white backside and a black dorsal strip. Female chamois and their kids (born after a gestation period of ca. 165-185 days) live in herds; grown-up males tend to live solitary for most of the year, but clump together during the rut (November, in Europe) (Krämer 1969).
Rupicapra genus provides a number of “Darwinian puzzles” in evolutionary terms. Behavioural observations (Krämer 1969) suggested that chamois are polygynous. The intense intrasexual competition among polygynous males is usually associated with the development of sexual-size dimorphism, often leading to differential sex-specific survival.

However, chamois sexes are nearly monomorphic, with males weighing 30-40% more than females only at the start of the rut (Garel et al. 2009, Rughetti & Festa-Bianchet 2011), but sharing all other morphologic features, with only slight differences. Indeed, sexual-size dimorphism is highly seasonal, rapidly declining to about 6% from November to January (Garel et al. 2009) possibly suggesting a unique conservative strategy to accumulate fat resources in summer (Pérez-Barberia et al. 1998) to be used during the rut and possibly reduce mortality costs over the winter (Bruno & Lovari 1989). In fact, there is growing evidence for an equal mortality of the two sexes (e.g. Gonzalez & Crampe 2001, Bocci et al. 2010). These characteristics appear at odds with the assumed high level of polygyny.

Whatever the level of polygyny, information is still needed to understand the mechanisms underlying variability in male reproductive success. Behavioural observations suggest that, during the rut, 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 (Krämer 1969, von Hardenberg et al. 2000). These alternative behaviours may show different cost-benefit trade-offs, and their maintenance may be favoured by several internal and external factors (e.g. local environmental conditions, Lovari et al. 2006).

**Aims of the thesis**

In this study, I investigate the life-history strategies of Alpine chamois in terms of survival and male mating tactics. I first explore potential relationships between survival pattern and mating system. I then explore potential costs and benefits – and factors underlying their expression – associated with alternative mating tactics. The thesis consists of three papers, addressing the following topics:

**Paper I**: Few studies investigated the survivorship of male and female chamois, producing conflicting results: these works, based on the use of life tables, require confirmation from researches carried out on living populations. I investigate the sex- and age-specific survival pattern of a protected Alpine chamois population, in relation to the mating system and the SSD observed in this species.

**Paper II**: I provide a quantitative analysis of the behavioural repertoire of Alpine chamois during the rut, and analyse the
differences between AMTs (territorial and nonterritorial males) in terms of frequencies of aggressive and courtship behaviour, and of mating opportunities.

**Paper III:** I investigate the temporal variation in mating effort and related physiological traits between AMTs in rutting male chamois. I also investigate differences in levels of mating effort, hormone secretion and parasite counts between AMTs, and explore the physiological mechanism underlying the expression of mating effort and parasite susceptibility between AMTs.

**Materials and methods**

**Study sites and populations**

**Paper I:** The study was carried out at “Il Fuorn”, an area of ca. 5 km² within the Swiss National Park, Switzerland (hereafter SNP, 46°40′10″ N, 10°9′15″ E). The area has a dry continental climate characterised by low precipitations (mean values of 54 mm and 104 mm in January and July, respectively), low humidity (0-10%) and large variations in diurnal and seasonal temperature (between -30 °C and +30 °C) (Haller 2006). The vegetation consists primarily of mountain pine *Pinus mugo* woodlands, with small patches of larch *Larix decidua* and, at higher altitudes, nutrient-rich and nutrient-poor pastures (Zoller 1995, Haller 2006).

In the SNP, over 13 years (1996-2008), 116 chamois (40 males and 76 females) were captured using box traps and snares (Gauthier & Michallet 1993, Filli 2006) and marked individually with collars and/or ear tags without sedation.

**Fig. 3:** overview of the GPNP study site in November.

The age at capture (estimated by counting growth rings, Schröder & von Elsner-Schack 1984) was between 0 and 12 years for males (median = 1) and between 0 and 17 years for females (median = 7).

**Paper II, III:** The studies were carried out in 2011 in the upper Orco Valley, within the Gran Paradiso National Park (GPNP, Western Italian Alps, 45°26′30″ N, 7°08′30″ E), an area of ca. 10 km² between 1,800 and 3,000 m above the sea level (Fig. 3). The GPNP has been protected since 1922, and the chamois population in the study site shows densities of ca. 20 individuals / km² (Corlatti L., unpublished data; GPNP census data).

In the GPNP, adult male chamois (*N* = 19) were sedated with a combination of xylazine and ketamine (Bassano et al. 2004), reversed with atipamezole (Dematteis et al. 2009). The age of each individual (relative to May 2011) was estimated by counting horn notches (Schröder & von Elsner-Schack 1984). Animals were equipped with individually recognizable GSM-GPS Pro-Light collars (Vectronic Aerospace GmbH, Berlin, Germany) (Fig. 4).
Data collection

To address the topics proposed in paper I, I used resighting data –collected by park wardens during their year-round activities– to develop capture-mark-resight (CMR) models.

To address the topics proposed in papers II and III, I adopted an integrated approach that includes behavioural and physiological studies, based on the collection of data on:

- space use, using GPS data sent by the collars;
- rutting behaviour, using a continuous focal animal sampling (Altmann 1974);
- activity budget, using an instantaneous focal animal sampling (Altmann 1974) (Fig. 5);
- parasite load, obtained through the analysis of fresh faecal samples using the McMaster counting procedure (Thienpont et al. 1979);
- hormone metabolite levels, obtained through the analysis of fresh faecal samples using specific enzyme immunoassays (Möstl et al. 2002, Palme & Möstl 1994).

I provide details on the collection and analysis of these data in each paper.

Results and discussion

Unbiased sex-specific survival in Alpine chamois (Paper I)

Sex- and age-specific survival patterns play a key role in the evolution of life history strategies (Stearns 1992). In polygynous ungulates, the intense male-male competition during the rut and the costs associated with the development of sexual-size dimorphism usually lead to higher mortality of males than of females (Clutton-Brock & Isvaran 2007), particularly under harsh environmental conditions (Toïgo & Gaillard 2003).

The Alpine chamois is often described as highly polygynous (Krämer 1969), but its SSD is highly seasonal (30-40% before the rut, rapidly declining to 4% in spring, Rughetti & Festa-Bianchet 2011) and the studies on sex-specific survival –based on life tables– are controversial (Schröder 1971, Bocci et al. 2010).
Fig. 6: yearly survival probability $[\Phi(sex + time) \ p(age \cdot sex)]$ for males (n=40) and females (n=76) chamois monitored over 13 years (1996-2008) within the Swiss National Park. The diagram shows estimate ± 95% CI.

The use of life tables, however, is based on assumptions that are often not met (see Ciucci et al. 2007), and cannot take into account between-years variability in survival (Loison et al. 1994). In paper I, by means of CMR models I investigate the sex- and age-specific survival pattern of 116 chamois, individually marked and monitored over 13 years, and discuss potential implications in relation to the mating system and the SSD observed in this species.

Resighting probabilities were sex-dependent, and survival rates were time-dependent. Females had higher resighting probabilities (0.84) than males (0.74). All over the time periods, sex had a weak influence on survival probability (males = 0.91; females = 0.92) and survival rates remained surprisingly high until advanced age (1 year = 0.90; 2-7 years = 0.91; 8+ years = 0.92) (Fig. 6).

Although large herbivores usually follow a Caughley-like mortality pattern with three stages (a low survival for the extreme classes and a higher survival for the intermediate classes, Caughley 1966, Gaillard et al. 2000, Festa-Bianchet et al. 2003), my study population did not show a significant effect of age on survival rates, which remained high from 1 year until late age. Furthermore, the non-negligible sample size and the model selection procedure based on AICc comparisons – supported by consistent effect sizes – clearly suggest that my data are consistent with a very weak sex effect on survival. The only two available studies on sex-specific survival of Alpine chamois (Schröder 1971, Bocci et al. 2010), based on life tables analysis, produced conflicting results: Bocci et al. (2010) did not detect high differences in the mortality rates of the two sexes, while Schröder (1971) reported a much higher male mortality. The study of Schröder (1971), however, likely suffered from a bias induced by trophy hunting through removal of mature males. My study population was protected and predation was negligible. The sex-and age-specific survival estimates confirm that chamois, unlike other prime-aged ungulates (e.g. red deer, Clutton-Brock et al. 1982, moose *Alces alces*, Boer 1988), with the exception of Alpine ibex *Capra ibex* (Toïgo et al. 2007), have very high survival and male and female survival rates are nearly identical.

The growing evidence for a weak differential mortality of the two sexes, together with a highly seasonal SSD might indicate the occurrence of a unique conservative strategy to accumulate fat resources in summer (Pérez-Barberia et al. 1998, Bruno & Lovari 1989) to be used during the rut and thus reduce mortality costs over the winter, contradicting the
commonly assumed high level of polygyny and suggesting the adoption of a less risky mating system.

**Rutting behaviour of territorial and nonterritorial male chamois (Paper II)**

Male mating effort can be expressed in a variety of ways. Polygynous mammals often show a positive relation between the degree of sexual dimorphism and mating effort and males using AMTs may show differences in physical features, such as body weight and size (e.g. in red deer, Clutton-Brock et al. 1982).

Some polygynous species, however, have limited dimorphism. Intrasexual competition and mating advantages, here, may depend on agility or aggressiveness (Linklater 2000, Rughetti & Festa-Bianchet 2011), rather than on size-related features.

In paper II, I provide a quantitative analysis of the behavioural repertoire of Alpine chamois during the rut, analyse the differences between territorial and nonterritorial males in terms of frequencies of courtship and indirect/direct aggressive behaviours over the rut, and in terms of mating opportunities.

The chamois showed a rich behavioural repertoire (31 behavioural patterns), with a sharp prevalence of aggressive behaviours that do not rely on size-related traits (e.g. horn size). Courtship behaviours increased in the mid-rut, possibly because of the timing of female oestrus, which in chamois is highly synchronised and occurs in the second half of November (Krämer 1969). The lack of variations in frequency of aggressive behaviours over the rut underlies behavioural differences between AMTs (Fig. 7). Territorial males had higher frequencies of aggressive and courtship behaviours than nonterritorial males over the early rut. This is not surprising, as male chamois in my study area start defending territories well before the rut (von Hardenberg et al. 2000) through a continuous active exclusion of competitors (Vehrencamp & Bradbury 1984).

Figure 7: hourly frequency of (a) courtship, (b) indirect and (c) direct aggressive behaviours displayed by territorial (T) and nonterritorial (NT) male chamois over three periods during the 2011 rut in the GPNP. Values are medians ± interquartile ranges.
Nonterritorial males, on the other hand, increased their mating effort later in the rut. It seems likely that the intensity of aggressiveness displayed by territorial males in the first two periods may force nonterritorials to allocate their mating effort late in the rut, when competition with dominant males is reduced.

The greater frequency of aggressive and courtship behaviours in territorial males suggests potentially greater mating advantages. Indeed, the number of females per hour near males was higher for territorials than for nonterritorials up to the 25th of November. All mating events occurred between the 16th and 25th of November and were monopolised by territorials. Nonterritorial males had a greater number of females per hour at the end of the rut, when the activity of territorial males was less intense. Such an increase in number of females, however, did not result into increased mating.

My results support the hypothesis that chamois may assert dominance mainly through intense aggressiveness rather than through size-related traits as found in other polygynous ungulates (e.g., Alpine ibex, Willisch & Neuhaus 2010). This hypothesis is in line with the weak sexual size dimorphism observed in this species (Rughetti & Festa-Bianchet 2011) and the absence of age and morphological differences between territorial and nonterritorial males (see Paper III). This evidence is consistent with the findings of Rughetti and Festa-Bianchet (2010) and does not support the suggestion by Chirichella et al. (2013) of a possible selective advantage of longer horns, in reproductive terms. Indeed, male reproductive success in Rupicaprinus does not seem to be related to horn size (Mainguy et al. 2009).

Most important, my results show how differences in mating effort mediated by AMTs resulted in different mating opportunities. The benefits that territorial males have, however, are traded off against greater costs, due to higher levels of hormone metabolites and greater parasitism (see paper III).

Hormone, parasites and male mating tactics in Alpine chamois (Paper III)

The life history theory predicts that individuals may invest more in a given trait (e.g. reproduction) to the detriment of other traits (e.g. survival) (Stearns 1992). However, the mechanisms underlying such trade-offs remain poorly known. It is widely assumed that reproductive effort is traded off against the individual’s ability to defend itself against pathogens: this pattern may be mediated by hormone secretion (e.g. testosterone, Folstad & Karter 1992).

In paper III, I investigate if variations in mating effort between the pre- and postrut are positively associated with variations in physiological costs, if AMTs show different values of mating effort and related physiological traits, and the mechanism underlying the expression of mating effort and parasite burden.

Territorial males sharply increased mating effort, faecal androgen and cortisol metabolites, and parasite levels during the rut, whereas nonterritorial ones displayed a similar pattern only for androgen metabolites (Fig. 8). The temporal distribution of the oestruses influences the intensity of rutting activity (Emlen & Oring 1977, Ims 1989).
Territorial males invested in mating activities almost exclusively during the rut, whereas nonterritorial males interacted more often in the postrut. This pattern is likely due to the synchronisation of oestruces over a few days in the second half of November (Krämer 1969) that led territorial males to increase the intensity of rutting behaviours to ensure access to females. This may have precluded access to females by nonterritorial males, which, in turn, may have concentrated their reproductive effort afterwards.

The increase in androgen metabolite levels is in line with the sexual cycle of chamois and other artiodactyls (Mooring et al. 2004, Hoby et al. 2006), while the pattern of cortisol metabolite levels underlies differences between AMTs.

Variations in parasite burden suggest the presence of an immunosuppressive effect (Folstad & Karter 1992) in territorial males, whereas the trend in nonterritorial males may be largely influenced by the lungworm seasonal cycle (Štefančíková et al. 2011). During the rut, territorial males invested more in rutting activities, while having higher levels of hormone metabolites and greater faecal counts of parasites than nonterritorial males. Before and after the rut, differences between male types (territorial and nonterritorial males) were smaller. The greater mating effort of territorial males during the rut suggests potentially higher mating benefits (i.e. greater access to females). My data on
mating success (see Paper II) support this hypothesis.

Territorial males have higher levels of FAM and FCM during the rut. There is increasing evidence that dominant individuals have high androgen and glucocorticoid levels more often than do subordinates (Creel 2001, Mooring et al. 2006, Oliveira et al. 2008). My results are consistent with the ‘stress of domination’ hypothesis: individuals engaged in energetically expensive behaviours are more stressed than subordinate individuals (Mooring et al. 2006).

The greater parasite susceptibility observed during the rut in territorial males, compared to nonterritorial males, may be an important cost in terms of overwinter survival, also considering the high mass loss that occurs during the rut (Rughetti & Festa-Bianchet 2011).

Although several studies found a positive correlation between reproductive effort and parasitism in various taxa (Deereenberg et al. 1997, Nordling et al. 1998, Pelletier et al. 2005), the causal relationships among behavioural, endocrine and health variables remain unclear. My analysis confirmed the existence of a life history trade-off among reproductive opportunities on one side and metabolic stress and increased level of parasites on the other; moreover, I showed how the mechanism underlying such a trade-off is mediated by androgens.

In conclusion, my results suggest that a trade-off between mating effort and parasitism exists, and that the proximate mechanism underlying this pattern may be found in the secretion of androgen metabolites. The greater investment in rutting activities, which territorial males make, suggests potentially high mating benefits. However, mating benefits could be countered by greater risk of injuries, consumption of fat reserves and higher hormone levels, which might favour the suppression of immunological defence and the subsequent decrease in parasite resistance.

Conclusions

The evidence for a highly seasonal SSD, together with the weak differential mortality of the two sexes in Alpine chamois, might indicate the occurrence of a conservative strategy unique among ungulate species. On the one hand, the pressure of sexual selection might not have been strong enough to fix more conspicuous physical features in males, as compared to females. On the other hand, the fat and muscles resources accumulated by males over summer can be used during the rut and possibly reduce mortality costs over the winter. These characteristics, together with the compensatory body growth observed for young males, the surprisingly long lifespan and the absence of differences in age and size-related traits between territorial and nonterritorial males, seem to contradict the commonly assumed high level of polygyny and suggest the adoption of a less risky mating system (e.g. weak polygyny).

Whatever is the level of polygyny that occurs within chamois populations, male mating success seems to depend on the tactic adopted by individuals. During this study, territorial males had greater success than nonterritorial males. Such mating benefits, however, could be counter-balanced by greater risks of injuries, consumptions of fat reserves and higher hormone levels, which favour the suppression of immunological defence and
the subsequent decrease in parasite resistance, possibly increasing mortality rates. This condition-dependent mechanism may partially explain the maintenance of AMTs within Alpine chamois populations.

I acknowledge the limitations of only one year of data: it remains unclear, for example, whether individuals consistently adopt a given tactic over a lifetime or show some flexibility. Moreover, even if the two tactics were fixed characteristics of individuals, the differential use of space between territorial and nonterritorial males may lead to different mating opportunities, depending on the distribution of female groups during the rut which, in turn, are influenced by the local meteorological conditions.

Long-term studies of marked individuals are necessary to understand whether the life history trade-offs found in this study may result in different lifetime fitness trade-offs. Genetic estimates of reproductive success coupled with reliable estimates of mortality rates for each male type, would help to investigate the lifetime fitness trade-offs between alternative tactics, hence understanding their maintenance within chamois populations.

Nonetheless, some hypotheses on the stability of AMTs may be put forward. Traditional studies of reproductive behaviour often assume that the stability of AMTs relies on equal mean fitness. If territorial males are advantaged only in years when heavy snowfalls force females to lower altitudes, where the territories are, the trade-offs between interaction rates, FAM and FCM levels and parasite burdens should therefore change from year to year, between male types, but may remain similar over their lifetimes. Eventually, territorial and nonterritorial males could have unequal yearly fitness, equal mean fitness, and similar opportunities of survival. Fitness variance would depend on the relative occurrence of advantageous years for one or the other tactic.

However, AMTs may also lead to unequal mean fitness. Territorial males might have greater reproductive success, but experience a trade-off between reproduction and survival. Male types would have unequal yearly fitness, unequal mean fitness and different survival.

The above strategies may obviously intergrade. For instance, territorial males may be more successful in reproduction than nonterritorials, but maintain the same survival rate if the costs of reproductive effort were reduced by a more efficient alternative strategy of energy intake before the mating season. If so, adopting a less successful tactic might be better than not mating at all.

**Literature cited**


**Mainguy, J., Côte, S., Festa-Bianchet, M. & Coltman, D.** 2009. Father–offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-


RIASSUNTO

**Strategie di life history nei maschi di camoscio alpino**
– Nuove conoscenze su sopravvivenza e tattiche di accoppiamento–

La teoria della *life history* si occupa delle strategie decisionali adottate da un individuo – in termini, per es., di sopravvivenza e riproduzione – plasmate dalla selezione naturale allo scopo di massimizzare la *fitness* dell’individuo stesso.

Nelle specie fortemente poliginiche, il legame fra sopravvivenza e riproduzione è esemplificato dall’intensa competizione fra maschi in periodo riproduttivo, spesso accompagnata da un marcato dimorfismo sessuale e una maggiore mortalità a carico dei maschi stessi. Specie poliginiche con dimorfismo sessuale limitato potrebbero tuttavia adottare strategie di sopravvivenza più conservative, potenzialmente legate a sistemi di accoppiamento meno rischiosi (per es. debole poliginia, oligoginia). Qualunque sia il livello di poliginia adottato, appare chiaro come – all’interno di una popolazione – non tutti i maschi saranno in grado di accoppiarsi. Per raggiungere il successo riproduttivo, maschi diversi possono adottare tattiche di accoppiamento alternative. Non è chiaro, tuttavia, come queste tattiche si siano evolute all’interno delle popolazioni, e molte sono le domande alle quali non è ancora stata data adeguata risposta. Le tattiche sono caratteristiche individuali reversibili o irreversibili? Tattiche diverse mostrano bilanci diversi fra costi e benefici? Quali sono i meccanismi in grado di mantenere tattiche differenti all’interno della stessa popolazione?

Questo lavoro si propone di offrire nuove conoscenze su alcuni dei temi sopra esposti, attraverso lo studio di due popolazioni protette di camoscio alpino (Parco Nazionale Svizzero, articolo I, Parco Nazionale Gran Paradiso, articoli II e III) con un approccio metodologico integrato che ha previsto l’utilizzo di diversi strumenti d’indagine (modelli di sopravvivenza, osservazioni comportamentali, analisi di laboratorio). Il lavoro si focalizza sullo studio del *pattern* di sopravvivenza in relazione al sistema di accoppiamento e sull’analisi dei meccanismi prossimi che sottendono il bilancio costi-benefici di fenotipi comportamentali alternativi.

**Introduzione**

**Sistemi di accoppiamento e sopravvivenza sesso-specifica**

Il sistema di accoppiamento può essere definito come l’organizzazione del comportamento riproduttivo fra *partner* sessuali. Oltre il 90% delle specie di uccelli è socialmente monogama, mentre la monogamia è raramente adottata dai mammiferi, che tendono invece a essere poliginici. Nelle specie poliginiche, l’intensa competizione fra maschi in periodo riproduttivo è spesso accompagnata dallo sviluppo di un marcato dimorfismo sessuale, che impone ai maschi costi energetici notevoli. Questi –normalmente– portano a una maggiore mortalità a carico dei maschi stessi, soprattutto in aree caratterizzate da condizioni climatiche severe. Alcune specie poliginiche, tuttavia, mostrano dimorfismo limitato (per es. equidi) e una sopravvivenza dei sessi simile: queste caratteristiche potrebbero sottendere l’adozione di un sistema di accoppiamento relativamente meno rischioso, come ad esempio una poliginia debole.
Strategie e tattiche alternative di accoppiamento

All’interno di un sistema poliginico, il tentativo di ottenere successo nell’accoppiamento può essere accompagnato da una notevole variabilità nel comportamento dei singoli maschi. Queste variazioni possono assumere diverse forme, che prendono il nome di “tattiche alternative di accoppiamento” (TAA).

Le principali forme di TAA sono: la difesa di femmine (singole o in gruppo), la difesa di risorse, il lek. Queste variazioni comportamentali possono rappresentare fenotipi irreversibili (gli individui adottano una singola tattica nel corso della loro vita) o reversibili (tattiche diverse adottate in sequenza, oppure in alternativa). Le TAA sono spesso associate a differenze morfologiche, quali ad esempio variazioni cromatiche nel piumaggio degli uccelli, o polimorfismo cromatico o dimensionale nei pesci. Tuttavia, le TAA possono anche essere associate a variazioni in tratti differenti (per es. comportamentali), come l’agilità o l’aggressività.

Evoluzione e mantenimento di TAA

Nell’ambito della teoria dei giochi, le TAA sono indagate in termini di costi e benefici per la fitness dell’individuo. In particolare, quando la fitness di un fenotipo alternativo dipende dalla sua frequenza nella popolazione, ci si trova di fronte ad un meccanismo di “selezione frequenza-dipendente”. Nell’ambito della biologia evolutiva, si ritiene che la frequenza-dipendenza sia il principale processo in grado di mantenere la stabilità nelle frequenze di tattiche alternative. Questo meccanismo, tuttavia, non è l’unico coinvolto nel mantenimento di fenotipi alternativi all’interno delle popolazioni. Gli studi sulle cause prossime del mantenimento di TAA s’interessano alla misurazione dei bilanci costi-benefici non in relazione alle frequenze delle tattiche, quanto in relazione a processi legati alle tattiche stesse, che includono sia fattori interni (livelli ormonali, stato di salute, riserve energetiche, età e status di dominanza) sia fattori esterni (condizioni meteorologiche, predazione, densità e distribuzione delle femmine). Questo meccanismo, detto “selezione condizione-dipendente”, permette il mantenimento di TAA nella misura in cui fattori interni ed esterni mostrano sufficiente variazione per permettere differenze di fitness fra fenotipi alternativi.

Il mantenimento delle tattiche alternative è, tuttavia, probabilmente legato a meccanismi multipli, e lo studio delle TAA potrebbe beneficiare di un approccio integrato che combini le selezioni frequenza- e condizione-dipendenti, alla ricerca di un punto di equilibrio congiunto.

Scopo della tesi

In questo studio, che consiste di tre articoli, sono state indagate le strategie di life history dei maschi di camoscio alpino in termini di sopravvivenza e tattiche di accoppiamento. In primo luogo sono state esplorate le relazioni fra sopravvivenza e sistema di accoppiamento (articolo I). Sono stati quindi indagati i benefici (articolo II) e i costi –e i fattori che sottendono alla loro espressione– (articolo III) legati a tattiche alternative di accoppiamento (territorialità vs. non territorialità).
**Risultati**

**Articolo I**: Ad oggi, solo due studi hanno indagato il pattern di sopravvivenza del camoscio alpino, producendo risultati contrastanti. Questi lavori, basati sull’utilizzo di tavole di vita, richiedono conferme da studi condotti su popolazioni vive. In questo lavoro sono stati indagati i tassi di sopravvivenza di una popolazione protetta di camoscio alpino all’interno del Parco Nazionale Svizzero, dove 116 individui sono stati marcati e monitorati per 13 anni (1996-2008). Attraverso l’utilizzo di modelli di cattura-markatura-ricattura è stata testata la dipendenza della sopravvivenza da parametri quali sesso, età e tempo. Le probabilità di ricattura sono risultate dipendenti dal sesso, mentre i tassi di sopravvivenza dipendenti dal tempo. Le femmine hanno mostrato probabilità di ricattura maggiori (0,84) rispetto ai maschi (0,74). Lungo l’intero arco temporale, il sesso ha avuto una debole influenza sulle probabilità di sopravvivenza (maschi = 0,91; femmine = 0,92) e la sopravvivenza è rimasta molto elevata fino a età avanzata (1 anno = 0,90; 2-7 anni = 0,91; 8+ anni = 0,92). La crescente evidenza di un’elevata sopravvivenza in età adulta e di una debole differenza di mortalità sesso-specifica, e il dimorfismo sessuale altamente stagionale, suggeriscono, per il camoscio alpino, l’adozione di una strategia di sopravvivenza conservativa in entrambi i sessi e un sistema riproduttivo maschile relativamente poco rischioso (es. poliginic con dimorfismo sessuale limitato, le possibilità di accoppiamento potrebbero, ad esempio, essere influenzate da differenze in termini di aggressività. In questo studio è stato registrato il comportamento sessuale di 8 maschi territoriali e 7 maschi non territoriali di camoscio alpino all’interno del Parco Nazionale Gran Paradiso, con lo scopo di indagare le differenze in sforzo di accoppiamento e opportunità di accoppiamento fra TAA. I maschi di camoscio hanno mostrato un repertorio comportamentale molto ricco (31 moduli), con prevalenza di forme di aggressività indiretta. I maschi territoriali hanno esibito una maggiore frequenza di comportamenti aggressivi e di corteggiamento rispetto ai non territoriali nella prima parte del periodo riproduttivo, mentre nella parte finale i maschi non territoriali hanno incrementato lo sforzo di accoppiamento, probabilmente in seguito alla diminuita competizione con i maschi dominanti. Gli individui territoriali hanno monopolizzato tutti gli accoppiamenti osservati. Questi risultati supportano l’ipotesi secondo la quale i maschi di camoscio esibiscano la loro dominanza principalmente attraverso un’intensa aggressività, piuttosto che attraverso caratteristiche fisiche (per es. la dimensione delle corna), come osservato in altri ungulati. Inoltre, le differenze in termini di sforzo di accoppiamento legate a TAA hanno portato a differenti opportunità di accoppiamento.

**Articolo III**: TAA possono avere bilanci differenti fra riproduzione e sopravvivenza; tuttavia, il meccanismo prossimo alla base di questo pattern rimane poco conosciuto. Fra gli altri, la
relazione fra sforzo di accoppiamento e resistenza ai parassiti mediata dalla secrezione ormonale sta ricevendo crescente attenzione. In questo studio sono stati monitorati 19 maschi adulti di camosci alpino nel Parco Nazionale Gran Paradiso prima, durante e dopo il periodo riproduttivo 2011 allo scopo di indagare, per ciascuna TAA, il bilancio fra sforzo di accoppiamento e suscettibilità ai parassiti, nonché il meccanismo fisiologico che sottende questo potenziale trade-off. I maschi territoriali hanno marcatamente incrementato lo sforzo di accoppiamento, i livelli di metaboliti ormonali (androgeni e cortisolo) e la suscettibilità ai parassiti durante il periodo riproduttivo, mentre i non territoriali hanno mostrato un andamento simile solo per gli androgeni. Durante il periodo riproduttivo, i maschi territoriali hanno investito maggiormente rispetto ai non territoriali, nello sforzo di accoppiamento mostrando al contempo maggiori livelli di metaboliti ormonali e maggiore suscettibilità ai parassiti. Prima e dopo il periodo riproduttivo, le differenze fra i due fenotipi comportamentali sono risultate non significative. L’analisi conferma l’esistenza di un trade-off fra sforzo di accoppiamento e suscettibilità ai parassiti, e suggerisce come il meccanismo alla base di questo pattern possa essere legato alla secrezione di androgeni, che contemporaneamente aumentano l’aggressività e abbattono le difese immunitarie.

Conclusioni

Il dimorfismo sessuale stagionale, la sopravvivenza simile dei due sessi e la longevità della specie suggeriscono, per i maschi di camosci alpino, l’adozione una strategia conservativa unica fra le specie ungulate. Da un lato, la pressione di selezione sessuale potrebbe non essere stata sufficientemente elevata da fissare nei maschi caratteristiche fisiche profondamente differenti da quelle femminili. Dall’altro lato, le risorse energetiche (massa grassa e muscolare) accumulate dai maschi in estate e utilizzate in periodo riproduttivo potrebbero ridurre i costi di mortalità durante l’inverno successivo. Queste caratteristiche, unitamente alla crescita corporea compensativa e all’assenza di differenze di età e morfologiche fra maschi territoriali e non territoriali, sembrerebbero contraddire l’assunto di elevata poliginia e suggerire l’adozione di un sistema riproduttivo meno rischioso (per es. poliginia debole, oligoginia).

Qualunque sia il livello di poliginia osservato nelle popolazioni di camosci, il successo di accoppiamento nei maschi sembra dipendere dalla tattica adottata. In questo studio, i maschi territoriali hanno registrato un maggiore successo di accoppiamento rispetto ai maschi non territoriali. Questi benefici, tuttavia, potrebbero essere controbilanciati da maggiori rischi durante gli scontri fisici, maggiore consumo di riserve energetiche e più elevati livelli ormonali, i quali potrebbero favorire l’abbattimento delle difese immunitarie e una maggiore suscettibilità ai parassiti, aumentando potenzialmente i tassi di mortalità.

Studi a medio-lungo termine che includano stime genetiche del successo riproduttivo e stime dei tassi di mortalità per ciascuna tattica adottata aiuterebbero a indagare questi aspetti, permettendo una maggiore comprensione del meccanismo di mantenimento di TAA nelle popolazioni di camosci alpino.
PAPER I

Unbiased sex-specific survival in Alpine chamois

Petroglyph of a chamois hunting scene (Valcamonica, Italy, ca. 5000 b.C.)

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Unbiased sex-specific survival in Alpine chamois

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Original Investigation

Unbiased sex-specific survival in Alpine chamois

Many polygynous ungulates show higher mortality of males than of females, because of the intense male–male competition during the rut and the costs associated with the development of sexual-size dimorphism. In the weakly dimorphic Alpine chamois Rupicapra rupicapra the occurrence of differential sex-specific survival strategies is controversial. To date, only two studies investigated the survivorship of males and females in this species, producing conflicting results: these works, based on the use of life tables, require confirmation from researches carried out on living populations. We assessed the survival pattern of a protected Alpine chamois population in the Swiss National Park, where 116 individuals were marked and monitored over 13 years (1996–2008). We tested for sex-, age- and year-dependence of survival by means of capture-mark-resight models. Resighting probabilities were sex-dependent, and survival rates were time-dependent. Females had higher resighting probabilities (0.84) than males (0.74). All over the time periods, sex had a weak influence on survival probability (males = 0.91; females = 0.92) and survival rates remained surprisingly high until late age (1 year = 0.90; 2–7 years = 0.91; 8+ years = 0.92). The growing evidence for a high adult survival and a weak differential mortality of the two sexes, together with the highly seasonal sexual-size dimorphism observed for Alpine chamois, might indicate the occurrence of a unique conservative survival strategy in both sexes and a low-risk mating strategy by males.

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Introduction

Sex- and age-specific survival patterns play a key role in the evolution of life-history strategies (Stearns 1992). Mammals commonly have three-age specific stages (juvenile, prime-aged adult, senescent) with differential survival rates (Caughley 1966). Furthermore, in polygynous ungulates, intense male–male competition during the rut and the costs associated with the development of sexual-size dimorphism (SSD) usually lead to higher mortality of males than of females (Clutton-Brock and Isvaran 2007), particularly under harsh environmental conditions (Toigo and Gaillard 2003).

From this evolutionary viewpoint, the Alpine chamois Rupicapra rupicapra, is puzzling. Behavioural observations suggest that the chamois is polygynous (Krämer 1969), though no genetic measures of siring success are available. Accordingly, the SSD during the rut is rather strong (31–32%, Bassano et al. 2003) but it rapidly declines over time (ca. 6% in January, Garel et al. 2009; 4% in spring, Rughetti and Festa-Bianchet 2011). To date only two studies, based on life tables analysis, investigated the sex-specific survival of Alpine chamois (Schröder 1971; Bocci et al. 2010), producing conflicting results.

The use of life tables, however, is based on assumptions that are often not met (see Ciucci et al. 2007), and cannot take into account between-years variations (Loison et al. 1994). To investigate the survival pattern and test for time and age dependent effects on survivorship, capture-mark-resight (CMR) models may be used, long-term monitoring of marked known-age individuals. Loison et al. (1999) used CMR models to investigate sex- and age-specific survival in a protected population of the closely related Pyrenean chamois Rupicapra pyrenaica and found no significant mortality difference between sexes, supporting the conclusions of Gonzalez and Crampé (2001). Loison et al. (1994) employed the CMR methodology to investigate solely the survivorship of female Alpine chamois; to date, however, no information is available on the survivorship of both sexes in Alpine chamois using CMR models.
Here, we describe the survival pattern of a protected population of Alpine chamois in which 116 animals were individually marked and monitored over 13 years. We investigate sex-, age- and year-dependence of survival rates by means of CMR models. We focus our attention on sex- and age-specific survival and discuss potential implications in relation to the mating strategy and the SSD observed in this species.

Material and methods

Alpine chamois sex- and age-specific survival was monitored over 13 years (1996–2008) at “Il Fuorn” (5026 ha within the Swiss National Park, Switzerland, hereafter SNP; 46° 40’ 10.74” N, 10° 9’ 15.15” E). The area has a dry continental climate characterized by low precipitations (mean values of 54 mm and 104 mm in January and July, respectively), low humidity (0–10%) and large variations in diurnal and seasonal temperature (between –30° C and 30° C) (Haller 2006). The vegetation consists primarily of mountain pine Pinus mugo woodlands, with small patches of larch Larix decidua and, at higher altitudes, nutrient-rich and nutrient-poor pastures (Zoller 1995; Haller 2006). At the study site hunting is not allowed and the only predator is the Golden eagle Aquila chrysaetos that can only take very small kids, and likely take very few (Bertolino 2003). Over the 13-year study, 116 chamois (40 males and 76 females) were captured using box traps and snares (Gauthier and Michallet 1993; Filli 2006) and marked individually with collars and/or ear tags without sedation. The age at capture (estimated by counting growth rings, Schröder and Elsner-Schack 1985) was between 0 and 12 years for males (median = 1), and between 0 and 17 years for females (median = 7) (Table 1). Most animals were captured between May and October; individuals of age x captured between November and April were considered for analysis only from age x + 1, as if they were captured in the following May. Kids (individuals younger than 1 year) were excluded from the analysis because of small sample size (n = 7). Every year park rangers recorded all sightings of marked individuals (ID, date, time, geographical coordinates), providing more than 7000 resightings.

To analyze yearly survival (Φ, the combined effect of mortality and emigration) and re-sighting probabilities (p) we used Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992). CJS models make the following assumptions: (1) every marked animal present in the population at the sampling period has the same probability p of recapture or resighting; (2) every marked animal present in the population immediately after period i has the same probability Φ of survival from i to i + 1; (3) marks are neither lost nor overlooked, and they are read correctly; (4) sampling periods are instantaneous, and animals are released immediately after sampling.

We first tested whether our data fitted assumptions (1) and (2) by using goodness of fit tests implemented in R (R Development Core Team 2011). The full time dependent CJS model [Φ(age · sex · time) p(age · sex · time)] could not be used, because recapture probabilities for “time” were not estimable. We therefore reduced our global model to [Φ(age · sex · time) p(age · sex)]. This model fitted the assumptions of equal survival and re-sighting probabilities across individuals (bootstrap goodness of fit test, 1000 simulations, p = 0.074). We then used package RMark (Laake and Rexstad 2008) to build simpler models for program MARK 5.1 (White and Burnham 1999). To assess sex- and age-dependence in survival and re-sighting probability, we tested for effects of age (3 groups: animals aged 1, 2–7 years or 8 years and older; Gaillard et al. 2000) as additive (“+”) as well as in interaction (“·”) with sex. To determine which model fitted the data best we selected the model with the lowest AICc (Akaike Information Criterion corrected for small sample size) (Akaike 1973; Burnham and Anderson 2002). All models within a difference of a ΔAICc ≤ 2 from the best model were considered, as they have a substantial level of empirical support (Burnham and Anderson 2002). We computed mean sex- and age-specific survival rates over all time periods, and calculated their confidence intervals using the delta method as described in Oehlert (2010).

Results

All five models within the ΔAICc ≤ 2 included the factor “time” for the survival probability. The estimated rates suggest a decrease in the survival probability in recent years, although this effect was not significant (Figs. 1 and 2). We found no evidence for age dependence, as models without any age classification were superior to models including age effects (Fig. 1 and Table 2). We found little evidence of sex effect either: although the “sex” factor was included in models #4 and #5, there was very small difference between

Fig. 1. Yearly survival probability [Φ(time)p(age · sex)] of 116 Alpine chamois monitored over 13 years (1996–2008) within the Swiss National Park. The diagram shows estimate ± 95% CI.

Fig. 2. Yearly survival probability [Φ(sex · time)p(age · sex)] for males (n = 40) and females (n = 76) chamois monitored over 13 years (1996–2008) within the Swiss National Park. The diagram shows estimate ± 95% CI.
Table 1
Age-specific number of male and female chamois captured and marked between 1996 and 2008 within the Swiss National Park.

<table>
<thead>
<tr>
<th>Age at capture</th>
<th>No. of males</th>
<th>No. of females</th>
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</tr>
<tr>
<td>1</td>
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<tr>
<td>17</td>
<td>1</td>
<td>1</td>
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</table>

Table 2
Number of parameters, AICc values, differences in AICc values (ΔAICc) and Akaike’s weights for the best ten models used to investigate survival and resighting probabilities of 116 Alpine chamois monitored over 13 years (1996–2008) within the Swiss National Park (competitive models highlighted in bold).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Model</th>
<th>Number of parameters</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Alkaike’s weights</th>
</tr>
</thead>
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<td>1</td>
<td>(\Phi(t)) (age · sex)</td>
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<td>1043.01</td>
<td>0.00</td>
<td>0.25</td>
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<td>2</td>
<td>(\Phi(t)) (sex)</td>
<td>15</td>
<td>1043.39</td>
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<td>0.20</td>
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<td>1044.66</td>
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<td>0.11</td>
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<td>(\Phi(sex + time)) (age · sex)</td>
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<td>1044.71</td>
<td>1.70</td>
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<td>16</td>
<td>1044.89</td>
<td>1.88</td>
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<td>18</td>
<td>1046.17</td>
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<td>7</td>
<td>(\Phi(age + time)) (age · sex)</td>
<td>21</td>
<td>1046.74</td>
<td>3.73</td>
<td>0.04</td>
</tr>
<tr>
<td>8</td>
<td>(\Phi(age + time)) (sex)</td>
<td>17</td>
<td>1047.23</td>
<td>4.22</td>
<td>0.03</td>
</tr>
<tr>
<td>9</td>
<td>(\Phi(age + time)) (age · sex)</td>
<td>19</td>
<td>1048.37</td>
<td>5.36</td>
<td>0.02</td>
</tr>
<tr>
<td>10</td>
<td>(\Phi(age + sex + time)) (age · sex)</td>
<td>22</td>
<td>1048.64</td>
<td>5.63</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Males and females (confidence intervals of beta estimate for \(\Phi\) factor “sex” of model #4 include 0) (Fig. 2 and Table 3). Mean sex- and age-specific survival rates (calculated from models #4 and #7, respectively) are reported in Table 4.

For resighting probability, all five models included the factor “sex”; sex was significant in \(\Phi(sex)\) and \(\Phi(sex + age)\) models, but not in \(\Phi(age + sex)\) models and indicated that females had higher recapture probabilities (0.84 ± 0.02 SE) than males (0.74 ± 0.03 SE) (Table 3). Age was not a significant factor.

Table 3
Beta estimates of model #1 [\(\Phi(time)\) (age · sex)] and model #4 [\(\Phi(sex + time)\) (age · sex)], used to investigate survival and resighting probabilities of 116 Alpine chamois monitored over 13 years (1996–2008) within the Swiss National Park.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Lower level</th>
<th>Upper level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\Phi): (intercept)</td>
<td>2.331</td>
<td>0.762</td>
<td>0.838</td>
<td>3.824</td>
</tr>
<tr>
<td>(\Phi): sex male</td>
<td>-0.197</td>
<td>0.300</td>
<td>-0.784</td>
<td>0.390</td>
</tr>
<tr>
<td>(\Phi): year 2</td>
<td>16.821</td>
<td>2629.093</td>
<td>-5136.201</td>
<td>5169.843</td>
</tr>
<tr>
<td>(\Phi): year 3</td>
<td>-0.237</td>
<td>0.917</td>
<td>-2.035</td>
<td>1.560</td>
</tr>
<tr>
<td>(\Phi): year 4</td>
<td>1.722</td>
<td>1.609</td>
<td>-1.432</td>
<td>4.876</td>
</tr>
<tr>
<td>(\Phi): year 5</td>
<td>0.924</td>
<td>1.080</td>
<td>-1.193</td>
<td>3.041</td>
</tr>
<tr>
<td>(\Phi): year 6</td>
<td>1.178</td>
<td>1.296</td>
<td>-1.363</td>
<td>3.719</td>
</tr>
<tr>
<td>(\Phi): year 7</td>
<td>0.464</td>
<td>1.975</td>
<td>-1.447</td>
<td>2.375</td>
</tr>
<tr>
<td>(\Phi): year 8</td>
<td>0.784</td>
<td>1.119</td>
<td>-1.409</td>
<td>2.978</td>
</tr>
<tr>
<td>(\Phi): year 9</td>
<td>-0.488</td>
<td>0.857</td>
<td>2.168</td>
<td>1.192</td>
</tr>
<tr>
<td>(\Phi): year 10</td>
<td>-0.037</td>
<td>0.962</td>
<td>-1.848</td>
<td>1.923</td>
</tr>
<tr>
<td>(\Phi): year 11</td>
<td>-0.759</td>
<td>0.868</td>
<td>-2.460</td>
<td>0.943</td>
</tr>
<tr>
<td>(\Phi): year 12</td>
<td>-1.280</td>
<td>0.838</td>
<td>-2.923</td>
<td>0.362</td>
</tr>
<tr>
<td>(\Phi): year 13</td>
<td>1.420</td>
<td>3.499</td>
<td>-5.437</td>
<td>8.277</td>
</tr>
<tr>
<td>(\Phi): (intercept)</td>
<td>2.079</td>
<td>1.061</td>
<td>0.001</td>
<td>4.158</td>
</tr>
<tr>
<td>(\Phi): age 2–7</td>
<td>0.254</td>
<td>1.362</td>
<td>-2.415</td>
<td>2.922</td>
</tr>
<tr>
<td>(\Phi): age 8+</td>
<td>-0.895</td>
<td>1.329</td>
<td>-3.500</td>
<td>1.710</td>
</tr>
<tr>
<td>Model 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\Phi): (intercept)</td>
<td>2.407</td>
<td>0.771</td>
<td>0.896</td>
<td>3.919</td>
</tr>
<tr>
<td>(\Phi): sex male</td>
<td>-0.197</td>
<td>0.300</td>
<td>-0.784</td>
<td>0.390</td>
</tr>
<tr>
<td>(\Phi): year 2</td>
<td>16.243</td>
<td>1962.297</td>
<td>-2829.859</td>
<td>3862.344</td>
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<tr>
<td>(\Phi): year 3</td>
<td>-0.262</td>
<td>0.918</td>
<td>-2.060</td>
<td>1.537</td>
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<tr>
<td>(\Phi): year 4</td>
<td>1.718</td>
<td>1.618</td>
<td>-1.453</td>
<td>4.890</td>
</tr>
<tr>
<td>(\Phi): year 5</td>
<td>0.912</td>
<td>1.081</td>
<td>-1.206</td>
<td>3.030</td>
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<tr>
<td>(\Phi): year 6</td>
<td>1.153</td>
<td>1.285</td>
<td>-1.366</td>
<td>3.673</td>
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<tr>
<td>(\Phi): year 7</td>
<td>0.461</td>
<td>1.976</td>
<td>-1.453</td>
<td>2.375</td>
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<td>(\Phi): year 8</td>
<td>0.781</td>
<td>1.120</td>
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<tr>
<td>(\Phi): year 9</td>
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<td>0.857</td>
<td>-2.174</td>
<td>1.187</td>
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<tr>
<td>(\Phi): year 10</td>
<td>0.019</td>
<td>0.961</td>
<td>-1.864</td>
<td>1.903</td>
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<tr>
<td>(\Phi): year 11</td>
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<td>0.868</td>
<td>-2.473</td>
<td>0.931</td>
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<tr>
<td>(\Phi): year 12</td>
<td>-1.298</td>
<td>0.838</td>
<td>-2.940</td>
<td>0.344</td>
</tr>
<tr>
<td>(\Phi): year 13</td>
<td>2.163</td>
<td>7.506</td>
<td>-12.549</td>
<td>16.674</td>
</tr>
</tbody>
</table>

Discussion

Our results indicate that survival rates for the chamois population of Il Fuorn are time-dependent, with an apparent – though not significant – decrease over the last 4–5 years of the study. Because presumably our sample of marked chamois is getting older as time goes on, an effect of correlation between age and time might partly explain this pattern; however, the models including age alone (\(\Phi(age)\)) were not adequate to interpret our dataset (they rank 10, hence they are not included in Table 2) suggesting the need for additional explanations. We might hypothesize the occurrence of a density-dependent process, as the population density of our study site between 2004 and 2008 increased (Filli, pers com) and the chamois populations of the SNP appear to be regulated by a density-dependence mechanism (Lande et al. 2002).

Although large herbivores usually follow a Caughley-like mortality pattern with three stages (a low survival for the extreme classes and a higher survival for the intermediate classes; Caughley 1966; Gaillard et al. 2000; Fest-Aubigné et al. 2003), our study population did not show a significant effect of age on survival rates, which remained high from 1 year until late age (Table 4). We monitored 35 animals older than 15 years, and 20 animals older than 18 years, suggesting that chamois are an unusually long-lived ungulate. The high maximum longevity of individuals within our population (21 years for males, 22 years for females), compared to previously recorded figures of 17 years in both sexes (Bocci et al. 2010) seems unlikely to be due to methodological reasons, as in...
both cases age was estimated by counting growth rings. Likewise, Loison et al. (1994) found high survival in female chamois older than 3.5 years (0.95, 95% CI = 0.93–0.99), suggesting that survival senescence in chamois may be weaker than in other ungulates. However, other studies have clearly established the existence of survival senescence, in chamois and in other ungulates (Loison et al. 1999). The lack of statistical significance in our dataset should not be taken as evidence that survival does not decline with age: we hypothesize that the age effect in chamois is rather small and a higher number of marked animals might help to detect survival senescence; in addition, the sample of monitored chamois was increasingly female-biased with age (Table 1), further limiting the ability to detect senescence, as older age classes had a higher proportion of animals with the better-surviving sex (see below).

The non-negligible sample size and the model selection procedure based on AICc comparisons supported by consistent effect sizes clearly suggest that our data are consistent with a very weak sex effect on survival. Table 4 shows that sex-specific differences in survival rates are very small, though females survived slightly more than males. The only two available studies on sex-specific survival of Alpine chamois (Schröder 1971; Bocci et al. 2010), based on life tables analysis, produced conflicting results: Bocci et al. (2010) did not detect high differences in the mortality rates of the two sexes, while Schröder (1971) reported a much higher male mortality. The study of Schröder (1971), however, likely suffered from a bias induced by trophy hunting through removal of mature males. Our study population was protected and predation was negligible. Bocci et al. (2010) based their conclusions on carcasses found in the field, as well as on yearly counts, which showed a stable structure of the living population through over a decade. That methodology requires restrictive assumptions and is unreliable when differential mortality affects age or sex classes, bias cannot be controlled, or the sample size is not large enough to be representative of the local, stable, population structure (Ciucci et al. 2007). Estimating survival from mark-recapture data, on the other hand, can provide precise estimates under milder assumptions (Krebs 1999). Our analysis, based on the use of CJS models and monitoring marked individuals, supports the results found by Bocci et al. (2010). Our results also agree with studies on the closely related Pyrenean chamois, which found no significant differences in sex-specific survival (Loison et al. 1999; Gonzalez and Crampé 2001). The sex-and age-specific survival estimates (Table 4) confirm that chamois, unlike other prime-aged ungulates (e.g., red deer Cervus elaphus, Clutton-Brock et al. 1982; moose Alces alces, Boer 1988; roe deer Capreolus capreolus and bighorn sheep Ovis canadensis, Loison et al. 1999), with the exception of Alpine ibex Capra ibex (Toigo et al. 2007), have very high survival and male and female survival rates are nearly identical.

The growing evidence for almost equal survival rates of the two sexes, together with the surprisingly long lifespan observed for Rupicapra sp., appear at odds with the highly seasonal SSD and the suggested high polygyny of these species. Polygyny leads to intrasexual competition, often accompanied by sexual size dimorphism (Isaac 2005). This imposes an energetic cost, as well as risk of injury, on males, possibly reducing male survival (Clutton-Brock et al. 1982; Clutton-Brock et al. 1985; Promislow 1992). Loison et al. (1999) question the assumption that adult survival of a sexually dimorphic species is actually related to the cost of polygyny in males, suggesting that mating tactics may affect survival more than the level of polygyny: reproductive costs in males could be higher for territorial than for nonterritorial species. However, von Hardenberg et al. (2000) reported a territorial strategy also in Alpine chamois.

We acknowledge that several ecological and evolutionary variables can affect survival patterns. However, the growing evidence for a weak differential mortality of the two sexes, together with a highly seasonal SSD might indicate the occurrence of a unique conservative strategy to accumulate fat resources in summer (Pérez-Barbería et al. 1998; Bruno and Lovari 1989) to be used during the rut and thus reduce mortality costs over the winter, contradicting the commonly assumed high level of polygyny and suggesting the adoption of a less risky mating strategy. The compensatory body growth observed for young males (Rughetti and Festa-Bianchet 2010) and the surprisingly long lifespan observed in our study site, as well as in other studies (e.g., Gonzalez and Crampé 2001) support this hypothesis.

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We thank all the people who helped to capture and mark chamois as well as all those who helped carrying out chamois sightings. We are grateful to Seraina Campbell (Swiss National Park) for her help during the data collection and to Rebecca Drury for correcting the English language. We thank Marco Festa-Bianchet and Sandro Lovari for helpful comments on earlier drafts of the manuscript.

References


Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage?

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Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage?

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\section*{A B S T R A C T}

Males using alternative male mating tactics (AMTs) may express their mating effort in a variety of ways. In polygynous species with limited sexual dimorphism, differences in male aggressiveness may affect mating opportunities. We recorded the behaviour of 8 territorial and 7 nonterritorial male Alpine chamois Rupicapra rupicapra, a nearly monomorphic ungulate, during the 2011 rut in the Gran Paradiso National Park (Italy), to analyse differences in mating effort and mating opportunities between AMTs. The chamois showed a rich behavioural repertoire (31 behavioural patterns), with a prevalence of indirect aggression. Territorial males had higher frequency of aggressive and courtship behaviour than nonterritorial males over the early rut. Later, nonterritoriais increased their mating effort, possibly because of reduced competition with dominant males. Territorial males monopolised all observed mating events. Our results support the hypothesis that chamois may assert dominance through intense aggressiveness rather than through horn size or body mass as found in other polygynous ungulates. Most important, differences in mating effort mediated by AMTs resulted in different mating opportunities; these benefits, however, are traded off against greater costs, due to higher levels of hormone metabolites and parasitism. Data on AMTs flexibility, lifetime reproductive success and survival are needed to clarify the mechanisms underlying the evolution and maintenance of AMTs within chamois populations.

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1. Introduction

Males usually expend much energy in searching, defending or attracting females. The way males attempt to obtain matings can take distinct forms (i.e. alternative mating tactics – AMTs – Taborsky et al., 2008), and male mating effort can be expressed in a variety of ways (Engqvist and Sauer, 2002).

For example, AMTs may be associated with differences in morphological traits (e.g. plumage variation in birds, Lank et al., 1995; colour or size polymorphisms in fish, Gross, 1991; Seda et al., 2012). In polygynous mammals, where access to females depends mainly on male–male combat, the degree of sexual dimorphism is often positively related to mating effort and AMTs may show differences in physical features, such as body weight and size (e.g. in red deer Cervus elaphus, Clutton-Brock et al., 1982 and in fur seal Arctocephalus forsteri, Negro et al., 2010).

Some polygynous species, however, show limited dimorphism (e.g. equids, camelids), and intrasexual competition may depend on features other than body or weapon size, such as agility or aggressiveness (Linklater, 2000; Rughetti and Festa-Bianchet, 2011). Males, in these groups, may therefore express their mating effort primarily through the development of behavioural polymorphism, such as different levels of aggressiveness.

Although many studies investigated the rutting behaviour of different Caprinae (e.g. Spanish ibex Capra pyrenaica, Alados, 1986; Barbary sheep Ammotragus lervia, Habibi, 1987; Nilgiri tahr Hemitragus hyloryctis, Rice, 1988; Bighorn sheep Ovis canadensis, Pelletier et al., 2006), information on the rutting behaviour of Rupicaprina remains limited and largely descriptive (e.g. Alpine chamois Rupicapra rupicapra Krämer, 1969), with few exceptions (e.g. mountain goat Oreamnos americanus Mainguy et al., 2008; Apennine chamois Rupicapra pyrenaica ornata Locati and Lovari, 1990; Lovari and Locati, 1991). Moreover, no quantitative information is available on the behaviour of individuals adopting AMTs. Because greater investments in mating effort may increase current reproduction, to the detriment of future reproduction or survival (Stearns, 1992), variations in the expression of behaviours may help to understand the variations in AMTs outcome, hence on their maintenance within and between populations.

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The Alpine chamois is a nearly monomorphic ungulate (Bocci et al., 2010), whose mating system is poorly known, though recent studies suggest weak polygyny (Bocci et al., 2010; Rughetti and Festa-Bianchet, 2011; Corlatti et al., 2012a). Two tactics occur among male chamois: territorial and nonterritorial (Krämer, 1969; Corlatti et al., 2012b). Chirichella et al. (in press) hint at a possible fitness advantage for male chamois with longer horns. In Rupicaprina, however, horn size does not seem to be related to reproductive success (as shown, e.g. in mountain goats by Mainguy et al., 2009). Moreover, Corlatti et al. (2012b) showed that territorial and nonterritorial male chamois do not differ in age, body weight or horn size. Ungulates may use direct and indirect aggression (Schaller, 1977) to establish social dominance which, in turn, facilitates access to oestrous females (McElligott et al., 2001; Pelletier et al., 2003). The limited sexual dimorphism and the rich behavioural repertoire of chamois (Lovari, 1985) suggest that mating advantages may be associated with aggressiveness, rather than with specific physical features as reported in other polygamous ungulates (e.g. Alpine ibex Capra ibex, Willisch and Neuhaus, 2010).

In this study, we aim to (1) provide the first quantitative analysis of the behavioural repertoire of Alpine chamois during the rut, (2) analyse the differences between territorial and nonterritorial males in terms of frequencies of courtship and indirect/direct aggressive behaviours over the rut, and (3) analyse differences between territorial and nonterritorial males in mating opportunities. We predicted that:

(1) the frequency of courtship behaviour would peak in mid-rut, when most female oestruses occur (Krämer, 1969), whereas the level of aggressiveness should remain similar across the rut, because of the active competition with other males by territorial ones; given the limited sexual-size dimorphism, we hypothesise that male chamois will make large use of behaviour patterns that do not rely on size-related traits;

(2) territorial males would show greater frequencies of both courtship and aggressive behaviours, because defending a territory may imply not only an increased encounter rate with receptive females but also active exclusion of other males (Vehrencamp and Bradbury, 1984). Subordinate males may show late breeding (Preston et al., 2001): towards the end of the rut, territorial males should reduce their mating effort, allowing nonterritorial males to invest more in intra- and intersexual interactions;

(3) greater mating effort in the early-mid rut, up to the occurrence of most female oestruses, would give territorial males an advantage over nonterritorial males in terms of mating opportunities.

2. Methods

2.1. Study site and population

The study site extended over ca. 10 km² between 1800 and 3000 m asl in the upper Orco Valley, Gran Paradiso National Park (hereafter GPNP), Western Italian Alps, 45°26’N, 7°08’E. The valley is oriented East–West and characterised by relatively low precipitation (daily mean: 5.4 mm in spring, 7.1 mm in autumn) and average temperatures between –4.2 °C in winter and +9.5 °C in summer (Brambilla et al., 2006). The south-facing slope is dominated by meadows of coloured fusee Festuca varia, whereas woods of larch Larix decidua and patches of alder shrubs Alnus viridis are prevalent on the north-facing slope. The chamois population in the study site has been protected since 1922 and shows densities of ca. 20 individuals/km² (Corlatti, unpublished data). Chamois survival in the Park is limited mainly by winter starvation (Rughetti et al., 2011).

Adult male chamois (N = 15) were sedated with a combination of xylazine and ketamine (Bassano et al., 2004), reversed by an injection of atipamezole (Dematteis et al., 2009). The procedure was always performed with a veterinarian present. The age of each individual (relative to May 2011) was estimated by counting horn notches (Schröder and von Elsner-Schack, 1984). Animals were equipped with individually recognisable GSM-GPS Pro-Light collars (Vectronic Aerospace GmbH, Berlin, Germany). These methods are in line with Italian law. We did not record any changes in the social behaviour of Alpine chamois following capture, and we assumed that behaviour was not affected by radio-collars (Nussberger and Ingold, 2006).

2.2. Territorials versus nonterritorials

To distinguish between territorial and nonterritorial males, we assumed that during the rutting season, territorial males would (1) show higher site fidelity and (2) win more intra-sexual interactions than nonterritorial males. For the 2011 rut (early November–early December), for 15 males, we therefore calculated (1) individual home ranges (90% Fixed Kernel), using high-quality GPS locations (with at least 4 satellites and Dilution of Precision values <10, Lewis et al., 2007) and (2) the proportion of intra-sexual interactions won. We then combined these two parameters in a matrix and used the Mahalanobis distance (Mahalanobis, 1936) as a metric to perform multivariate hierarchical clustering (Everitt et al., 2011) in R 2.14.1 (R Development Core Team, 2011).

The cluster analysis grouped eight males with very small home ranges and very high values of intra-sexual interactions won. The territoriality hypothesis for these individuals is therefore strongly supported from both spatial and behavioural viewpoints. For a detailed description of the methods used to distinguish territorial and nonterritorial males, see Corlatti et al. (2012b).

2.3. Behavioural observations

Data collection occurred during the rutting season 2011, between the 6th of November and the 5th of December (Lovari and Locati, 1991; Pérez-Barbería et al., 1998; Martinez-Pastor et al., 2005). To analyse the temporal variation of behaviour over the rut, we divided the season in 3 periods of 10 days (hereafter period I, II and III). We observed 8 territorial and 7 nonterritorial marked males throughout the rut. Behavioural data were recorded by focal animal sampling (Altman, 1974) noting all-occurrences of behaviour patterns a focal animal performed in 1 h. For each individual, we collected at least 3 h of observations (morning, midday, afternoon) per period, so that each male was observed for at least 9 h during the rut, for a total of 140 h of observations. The behaviour patterns recorded are described in Lovari (1985) and Krämer (1969). One behaviour, the “rut call”, was often observed but not included in the analysis because quantitative measures were biased by variable distances and weather during observations. According to Schaller (1977), behaviour patterns were subsequently grouped in three categories: courtship, indirect aggression and direct aggression. Some behaviours are present both in courtship and aggressive displays, because the same pattern may assume different meanings in different contexts. All observers (L.C., M.C., V.P. and S.L.) had previous experience in observing and recording the Alpine chamois behavioural repertoire. Every 20 min, during each sampling hour, we recorded the number of females within 50 m of the focal male, as a proxy of mating opportunities.

2.4. Population-level behavioural repertoire (hypothesis 1)

Prior to analyses, the absolute frequencies of behaviour types within each period were transformed to hourly frequencies. To
investigate variation in courtship, indirect and direct aggressive behaviour over periods for the entire population we used Wilcoxon tests for repeated measurements. This analysis required multiple comparisons (N=3); we therefore applied a Bonferroni correction and considered 0.016 as the critical p-value (Sokal and Rohlf, 1981).

2.5. Behavioural repertoire of territorial and nonterritorial males (hypothesis 2)

To investigate the variation in courtship, indirect and direct aggressive behaviour over periods for territorial and nonterritorial males we used Wilcoxon tests for repeated measurements and applied the Bonferroni correction (see above).

To compare the frequencies of courtship, indirect and direct aggressive behaviour between territorial and nonterritorial males, within each period we used the Wilcoxon–Mann–Whitney test for independent samples and considered 0.05 as the critical p-value.

2.6. Mating opportunities of territorial and nonterritorial males (hypothesis 3)

Within each period, we calculated the mean number of females per hour near each male. To compare the mean number of females per hour and the frequencies of mating events between territorial and nonterritorial males, within each period we used Wilcoxon–Mann–Whitney tests for independent samples and considered 0.05 as the critical p-value.

If not specified, all tests are two-tailed. All statistical analyses were performed using R 2.14.1 (R Development Core Team, 2011).

3. Results

3.1. Population-level behavioural repertoire (hypothesis 1)

We observed 27 different behaviour patterns (Table 1). Among the most frequent were two courtship behaviours (“head up”: N=425; % =18.9 and “head down”: N=188; % =8.4) and two indirect forms of aggression (“marking”: N=511; % =22.8 and “neck up”: N=208; % =9.3).

The chamois increased the frequency of courtship behaviours between period I and period II (1 tailed: V=1; N1 =15; N2 =15; P=0.002), whereas no significant difference emerged between period I–III (V=32.5; N1 =15; N2 =15; P=0.638) and period II–III (1 tailed: V=72; N3 =15; N4 =15; P=0.117) (Fig. 1).

The indirect forms of aggression did not vary across periods (I–II: V=26.5; N5 =15; N6 =15; P=0.061. I–III: V=39; N7 =15; N8 =15; P=0.252. II–III: V=57; N9 =15; N10 =15; P=0.890) (Fig. 1). Similarly, direct aggression did not vary across periods (I–II: V=41.5; N5 =15; N6 =15; P=0.807. I–III: V=40.5; N7 =15; N8 =15; P=0.937. II–III: V=56; N9 =15; N10 =15; P=0.851) (Fig. 1).

During the rut, the frequency of indirect forms of aggression was constantly higher than that of direct forms of aggression (1-tailed tests; period I: V=91; N1 =15; N0 =15; P=0.001. Period II: V=120; N3 =15; N0 =15; P<0.001. Period III: V=77; N4 =15; N0 =15; P=0.002) (Fig. 1).
3.2. Behavioural repertoire of territorial and nonterritorial males (hypothesis 2)

Territorial males showed a peak in courtship behaviours between November 16 and 25 (1-tailed tests; I–II: \( V = 1; N_1 = 8; N_2 = 8; P = 0.008 \). II–III: \( V = 33; N_2 = 8; N_3 = 8; P = 0.019 \)). No differences occurred between periods I and III (\( V = 20.5; N_1 = 8; N_2 = 8; P = 0.779 \)) (Fig. 2a). Nonterritorial males did not show significant variations in the frequency of courtship behaviours across the rut (I–II: \( V = 0; N_1 = 7; N_2 = 7; P = 0.098 \). I–III: \( V = 0; N_1 = 7; N_2 = 7; P = 0.100 \). II–III: \( V = 6; N_2 = 7; N_3 = 7; P = 0.402 \)) (Fig. 2a). The frequency of courtship behaviours was higher for territorial than nonterritorial males in the early rut (1-tailed tests; period I: \( W = 56; N_T = 8; N_{NT} = 7; P < 0.001 \). Period II: \( W = 56; N_T = 8; N_{NT} = 7; P < 0.001 \)), whereas in late rut no difference was detected between male types (1-tailed test; period III: \( W = 27.5; N_T = 8; N_{NT} = 7; P = 0.549 \)) (Fig. 2a).

The frequency of indirect aggressive behaviours of territorial males did not vary across the rut (I–II: \( V = 15; N_1 = 8; N_2 = 8; N_3 = 8; P = 0.742 \). I–III: \( V = 21; N_1 = 8; N_2 = 8; N_3 = 8; P = 0.742 \). II–III: \( V = 24; N_2 = 8; N_3 = 8; P = 0.461 \)) (Fig. 2b). Nonterritorial males, on the other hand, increased the frequency of indirect aggressiveness over the rut (I–II: \( V = 0; N_1 = 7; N_2 = 7; P = 0.015 \). I–III: \( V = 1; N_1 = 7; N_2 = 7; P = 0.015 \). II–III: \( V = 7; N_2 = 7; N_3 = 7; P = 0.270 \)) (Fig. 2b). The frequency of indirect aggression was higher for territorial males in early rut (1-tailed tests; period I: \( W = 56; N_T = 8; N_{NT} = 7; P < 0.001 \). Period II: \( W = 46; N_T = 8; N_{NT} = 7; P = 0.021 \)), whereas in late rut no difference was detected between male types (1-tailed test; period III: \( W = 21.5; N_T = 8; N_{NT} = 7; P = 0.793 \)) (Fig. 2b).

The frequency of direct aggressive behaviour in territorial males did not vary across the rut (I–II: \( V = 24; N_1 = 8; N_2 = 8; P = 0.461 \). I–III: \( V = 22.5; N_1 = 8; N_2 = 8; P = 0.176 \). II–III: \( V = 25.5; N_2 = 8; N_3 = 8; P = 0.326 \)) (Fig. 2c). Although Fig. 2c suggests an increase in the frequency of direct form of aggression in nonterritorial males, no significant differences could be detected (I–II: \( V = 0; N_1 = 7; N_2 = 7; P = 0.058 \). I–III: \( V = 2; N_1 = 7; N_2 = 7; P = 0.178 \). II–III: \( V = 7; N_2 = 7; N_3 = 7; P = 0.529 \)), possibly because of the small sample size. Territorial males showed a higher frequency of direct aggressive behaviours only in the early rut (1-tailed tests; period I: \( W = 47.5; N_T = 8; N_{NT} = 7; P = 0.008 \). Period II: \( W = 34.5; N_T = 8; N_{NT} = 7; P = 0.242 \). Period III: \( W = 25; N_T = 8; N_{NT} = 7; P = 0.662 \)) (Fig. 2c).

3.3. Mating opportunities of territorial and nonterritorial males (hypothesis 3)

The mean number of females per hour near males was greater for territorials in the first two periods of the rut (1-tailed tests; period I: \( W = 50; N_T = 8; N_{NT} = 7; P = 0.006 \). Period II: \( W = 55; N_T = 8; N_{NT} = 7; P = 0.001 \)) (Fig. 3a), whereas at the end of the rut we found no differences between male types (period III: \( W = 29; N_T = 8; N_{NT} = 7; P = 0.477 \)) (Fig. 3a). All mating events occurred by the 25th of November, and were monopolised by territorial males (Fig. 3b).
4. Discussion

4.1. Population-level behavioural repertoire

Krämer (1969) described 25 behavioural patterns for male Alpine chamois. We observed 27 behaviours, 4 of which had not been described in this species (“stare”, “croup touch”, “flank stroke” and “dynamic head down”). Preliminary observations carried out in the same populations in 1996, 2002 and 2010 confirmed the presence of such behaviours. The “mild low stretch”, “extreme low stretch” (Krämer, 1969), “kick” and “urinating in female posture” (described in Lovari, 1985), were not observed in this study. Therefore, to date, 31 behavioural patterns have been described and constitute the behavioural repertoire of the Alpine chamois.

When females are aggregated, the temporal distribution of oestruses is likely to influence the intensity of rutting activity (Emlen and Oring, 1977; Ims, 1989). On the one hand, the increase of courtship behaviours in the mid-rut may depend on the timing of female oestrus, which in chamois is highly synchronised and occurs the second half of November; individual oestrous lasts about 1–2 days (Krämer, 1969). On the other hand, the lack of variations in frequency of aggressive behaviours over the rut, underlies behavioural differences between AMTs (see below).

Males made greater use of indirect forms of aggression (indirect aggression = 50%; direct aggression = 9%), in line with preliminary observations carried out on the same population in 2002 (indirect forms of aggression = 71%; direct forms of aggression = 20%) and in

2010 (indirect forms of aggression = 70%; direct forms of aggression = 9%) (Lovari et al., unpublished). Locati and Lovari (1990) observed the same pattern in the behavioural repertoire of the Apennine chamois and hypothesised this may be due to the weak degree of sociality of males outside the rut. The rather solitary life of males would bring them to ignore an opponent’s fighting ability, therefore imposing some caution in aggressive contests during the rut.

The rich behavioural repertoire and the sharp prevalence of aggressive behaviour patterns – mainly indirect – that do not rely upon size-related traits, support the hypothesis that chamois may assert dominance through intense levels of aggressiveness, rather than through physical features. Our hypothesis is in line with the weak sexual size dimorphism observed in this species (Rughetti and Festa-Bianchet, 2011) and the absence of age and morphological differences between territorial and nonterritorial males (Corlatti et al., 2012b). Such evidences does not support the suggestion by Chirichella et al. (in press) of a possible selective advantage, in reproductive terms, for male chamois possessing longer horns. On the other hand, male reproductive success in Rupicaprina does not seem to be related to horn size, but it may be related to body mass, at least in mountain goats (see Mainguy et al., 2009).

4.2. Behavioural repertoire of territorial and nonterritorial males

Territorial males showed higher levels of aggressiveness than nonterritorial ones from the start of the rut. This is not surprising, as male chamois in our study area start defending territories well before the rut (von Hardenberg et al., 2000) through a continuous active exclusion of competitors (Vehrencamp and Bradbury, 1984). Territorial males defend their ground until the end of the season; however, Fig. 2b suggests a great variability in individual behaviour, as some males stopped rutting, others did not, possibly due to the defence of a small number of receptive females still present within some territories. This hypothesis is supported by the sharp decrease in courtship frequency towards the end of the rut. Courtship behaviour peaked between the 16th and 25th of November, in line with the timing of the female oestrus suggested by Krämer (1969).

Nonterritorial males showed a lower frequency of aggressive and courtship behaviour during the first two periods of the rut, compared to territorial ones. Nonterritorials, on the other hand, tended to increase the frequency of aggressive behaviours towards the end of the season. The intensity of aggressiveness displayed by territorial males in the first two periods may force nonterritorials to allocate their mating effort late in the rut, when competition with dominant males is reduced. This pattern is in line with the frequency of courtship behaviour, which, for nonterritorial males, is restricted to the last part of the mating season. Late breeding in subordinate males has been observed in Soay sheep Ovis aries (Preston et al., 2001).

Androgens normally promotes aggressive and courtship behaviours (Folstad and Karter, 1992; Knapp, 2003; Hirschenhauser and Oliveira, 2006). On the other hand, androgens may suppress the immune function (Folstad and Karter, 1992; Decristophoris et al., 2007), increasing susceptibility to parasite infections (Hau, 2007). Indeed, Corlatti et al. (2012b), for the same individuals and mating season, showed that mating effort of territorial males is traded off against their ability to defend themselves against pathogens (Lochmiller and Deerenberg, 2000; Zuk and Stoehr, 2002) and that such a trade-off is mediated by androgens.
4.3. Mating opportunities of territorial and nonterritorial males

The greater frequency of aggressive and courtship behaviours observed in territorial males, compared to nonterritorial ones, suggests potentially greater mating advantages. von Hardenberg et al. (2000), for the same population, suggest that territorial males may have mating advantages because of the strong correlation between the mean number of females per hour in each territory during the rut and the date of territory occupancy. Indeed, the number of females per hour around males is higher for territories than for nonterritoriauls up to the 25th of November. Mating events occurred between the 16th and 25th of November and were monopolised by territorials.

Nonterritorial males, on the other hand, had a greater number of females per hour at the end of the rut, when the activity of territorial males was less intense. It is worth noting that such an increase in mating opportunities did not result into increased mating: no copulations and no mounts were observed after the 25th of November, and no nonterritorial male was observed mating. It seems likely that the low number of fertile females remaining at the end of the season mitigated against the increased mating effort by nonterritorial males.

5. Conclusions

Our results emphasise the importance of bearing in mind the presence of AMTs within populations, when studying reproductive behaviour. Alpine chamois, show different mating benefits between tactics. The greater levels of aggressiveness, that territorial males displayed, led to higher frequencies of courtship behaviours and, in turn, to greater mating opportunities. On the other hand, territorial males may encounter greater costs, following higher levels of hormone metabolites and greater parasitism.

We acknowledge the limitations of only one year of data: it remains unclear, for example, whether individuals consistently adopt a given tactic over a lifetime or show some flexibility. Moreover, even if the two tactics were fixed characteristics of individuals, the differential use of space between territorial and nonterritorial males may lead to different mating opportunities, depending on the distribution of female groups during the rut which, in turn, are influenced by the local meteorological conditions (Lovari et al., 2006).

Long-term studies of marked individuals are necessary to understand whether the different trade-offs between mating opportunities and mating costs in AMTs are consistent over an individual’s lifetime. Genetic estimates of reproductive success coupled with reliable estimates of mortality rates would help to investigate the lifetime fitness trade-offs between AMTs, hence understanding the maintenance of AMTs within chamois populations.

Conflict of interests

We declare no conflict of interests.

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Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs.
Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs

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Alternative mating tactics (AMTs) may show different trade-offs between current reproduction and survival; however, the proximate mechanisms underlying this pattern remain unclear. Among them, the relationship between reproductive effort and parasite resistance mediated by hormonal secretion has received increasing attention. We monitored 19 marked adult male chamois, Rupicapra rupicapra, within the Gran Paradiso National Park (Italy) between the pre- and postrut 2011, to investigate the trade-off between mating effort and parasites associated with AMTs, and the underlying physiological mechanism.

Territorial males sharply increased mating effort, faecal androgen and cortisol metabolites, and parasite levels during the rut, whereas nonterritorial ones displayed a similar pattern only for androgen metabolite levels. During the rut, territorial males invested more in rutting activities, while having higher levels of hormone metabolites and greater faecal counts of parasites than nonterritorial males. Before and after the rut, differences between male types (territorial and nonterritorial males) were smaller. Our analysis suggests that a trade-off between mating effort and parasitism exists, and that the proximate mechanism underlying this pattern may be found in the secretion of androgen metabolites. The greater investment in rutting activities, which territorial males make, suggests potentially high mating benefits. However, mating benefits could be counterbalanced by greater risk of injuries, consumption of fat reserves and higher hormone levels, which might favour the suppression of immunological defence and the subsequent decrease in parasite resistance.

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which share several enzymatic pathways in common with androgens (Knapp 2003). The increase in parasite infection (Folstad & Karter 1992; Decristophoris et al. 2007; Hau 2007), in turn, draws resources that may be used for other activities such as reproduction and survival, reducing the host’s fitness (Lehmann 1993).

The expression of AMTs normally involves hormonal regulation: for example, dominant males usually have higher levels of testosterone than subordinates (Taborsky et al. 2008), as shown in bison bulls, Bison bison, by Mooring et al. (2004). This may lead to different mating potential and parasite susceptibility between AMTs. Therefore, the interplay among hormone levels, mating effort and parasite susceptibility may help us to understand the maintenance of alternative tactics, as it may ultimately contribute to shaping the differential trade-off between individual reproductive success and individual opportunities of survival (see, e.g. in fur seal, Arctocephalus forsteri: Negro et al. 2010; Grant’s gazelle, Nanger granti: Ezenwa et al. 2012).

The Alpine chamois, Rupicapra rupicapra, is a nearly monomorphic ungulate, with males weighing 30–40% more than females only at the start of the rut (Garel et al. 2009; Rughetti & Festa-Bianchet 2011), but sharing all other morphological features, with only slight differences. Its mating system is still scarcely understood, although recent studies suggest the adoption of a low-risk strategy by males (Bocci et al. 2010; Rughetti & Festa-Bianchet 2011; Corlatti et al. 2012). Behavioural observations suggest that, during the rut, territorial males patrol a relatively small area in which they try to keep females and chase away intruders, whereas nonterritorial males display following behaviour and territory intrusions (Krämer 1969; von Hardenberg et al. 2000). Given the limited sexual size dimorphism and the rich behavioural repertoire of chamois (Lovari 1985), we suggest that mating effort of territorial and nonterritorial males may be related to different investment in rutting activity, rather than to the differential body and weapon size found in other polygynous ungulates (e.g. Alpine ibex: Willisch & Neuhaus 2010).

In this study we aimed to (1) investigate the temporal variation in mating effort and related physiological traits between AMTs in rutting male chamois, (2) investigate differences in levels of mating effort, hormone secretion and parasite counts between AMTs, and (3) explore the physiological mechanism underlying the expression of mating effort and parasite susceptibility between AMTs. Specifically, we had three hypotheses. (1) The levels of inter- and intra-sexual interactions (i.e. mating effort), hormone metabolites and parasites would peak during the rut in both AMTs. (2) Territorial males would show a greater number of interactions (with both males and females) and higher hormone and parasite levels than nonterritorial males during the rut. Before and after the mating period, AMTs should show smaller differences for each of these variables. (3) The increase in parasite susceptibility, following greater mating effort, would be mediated by testosterone, in accordance with the immunocompetence handicap hypothesis (Folstad & Karter 1992).

METHODS

Study Site and Population

The study site was located in the upper Orco Valley, within the Gran Paradiso National Park (hereafter GPNP, Western Italian Alps, 45°26’30” N, 7°08’30” E) and covered an area of ca. 10 km² between 1800 and 3000 m above sea level. The valley, east to west oriented, is characterized by low precipitation rates (daily mean: 5.4 mm in spring, 7.1 mm in autumn) and average temperatures between −4.2 °C in winter and −9.5 °C in summer (Brambilla et al. 2006). Meadows of coloured fescue, Festuca varia, dominate the south-facing slope, whereas woods of larch, Larix decidua, and patches of alder shrubs, Alnus viridis, are prevalent on the north-facing slope. The GPNP has been protected since 1922, and the chamois population in the study site shows densities of ca. 20 individuals/km² (L. Corlatti, unpublished data; GPNP census data). Chamois survival in the Park is limited mainly by winter starvation (Peracino & Bassano 1987; Rughetti et al. 2011).

For this study, 19 adult male chamois were darted by the personnel of the GPNP, with a CO₂ injection rifle (DAN-INJECT, model JM Standard) from a mean distance ±SD of 41.5 ± 6.1 m. Chamois were darted by surprise (i.e. park wardens used hiding places, mainly rocks, prior to darting). No chase occurred, as this method is not suitable for mountainous, rocky habitats. Whenever the chamois climbed on rocks, the approach immediately stopped, to prevent any potentially harmful situation. The syringes were filled with a combination of xylazine (40 mg/animal) and ketamine (20 mg/animal), with the aim to reduce any negative effects of alpha-agonist on the rumen, heart and breathing activity (Bassano et al. 2004). The mean induction time was 16.9 ± 12.4 min. The chemical immobilization of chamois allows handling with minimum levels of stress, as opposed to mechanical capture (i.e. using traps and nets), which may have a strong impact on animals. After sedation had occurred, it took on average 10.0 ± 6.4 min to reach the animal. We estimated the age of each individual (relative to May 2011) by counting horn notches (Schröder & von Elsner-Schack 1984), collected biometric measurements (e.g. weight, horn length) and monitored physiological parameters (i.e. temperature, heart and breathing activity). Finally, we equipped all chamois with individually recognizable GSM-GPS Pro-Light collars (Vectronic Aerospace GmbH, Berlin, Germany). Ten animals were equipped with 2D collars (630 g, 1.9% of the mean weight, 2.4% of the minimum weight) and nine animals were equipped with 1D collars (450 g, 1.5% of the mean weight, 1.8% of the minimum weight). The mean handling time was 32.2 ± 16.2 min.

The sedative effect was reversed by an injection of atipamezole (5 mg/animal; Dematteis et al. 2009). The mean recovery time, recorded from the moment of the administration of the antagonist, was 5.4 ± 2.7 min. During this time, a veterinarian kept the animals under direct observation. The entire procedure, from darting to release, took on average 63.1 ± 20.0 min, and was always performed with the assistance of a veterinarian.

The behavioural changes following the use of xylazine and ketamine are related to the dose administered to the animal: with the use of 40 mg of xylazine, rapidly antagonized by antagonists (atipamezole), we did not record any changes in social behaviour of Alpine chamois. Similarly, following captures we did not observe alterations in the behaviour of chamois equipped with radiocollars, and to date we have no evidence for long-term effects, as already shown by Nussberger & Ingold (2006).

These methods are in line with the Italian law, as the capture of any wild animal within the GPNP can be made only after receiving authorization from the Italian Ministry of Environment, with the permission of ISPRA (The Institute for Environmental Protection and Research).

Territorial Males Versus Nonterritorial Males

The existing literature lacks unambiguous definitions of territoriality. Maher & Lott (1995, page 1589) reviewed 48 definitions of territoriality in vertebrate species, and suggested that territory could be defined as a ‘fixed space from which an individual, or group of mutually tolerant individuals, actively excludes competitors for a specific resource or resources’. This definition includes both spatial and behavioural elements, and was previously used in the same population by von Hardenberg et al. (2000). They showed
that territorial male chamois have small and exclusive home ranges, and a high degree of intrasexual aggressiveness; in addition, territorial males tend to win almost all male–male interactions within their territory. To distinguish between territorial and nonterritorial males, we assumed that during the rutting season: (1) territorial males would show a higher degree of site fidelity and hence they should have smaller home ranges than nonterritorial males; and (2) territorial males would win more intrasexual interactions (i.e. they exhibit land ownership) compared to nonterritorial males.

In the rutting season 2011 (early November–early December), for 19 males, we therefore calculated the following:

(1) Individual home ranges were calculated using high-quality GPS locations (i.e. with at least four satellites and dilution of precision values lower than 10; Lewis et al. 2007), collected every hour (mean number of fixes ± SD = 437 ± 127). Violation of data independence is unlikely to affect home range estimation when fixed kernel density (KD) is used (De Solla et al. 1999). With large sample sizes the 90% density threshold is recommended (Börger et al. 2006), provided an appropriate bandwidth (i.e. smoothing parameter) is chosen (Wand & Jones 1995; Kie et al. 2010). To account for this, we calculated the 90% KD in R 2.14.1 (R Development Core Team 2011) as follows: we first represented our study area as a grid and set the resolution of grid cells to 25 m × 25 m. Using the ‘ks’ library (Duong 2007) we kernel-smoothed the data for each individual track with the plug-in bandwidth selector (‘hpi’) developed by Duong & Jones (1995). As a result, each cell was assigned a density of usage (between 0 and 1). Finally, we calculated the number of grid cells within the 0.90 (i.e. 90%) density threshold using the ‘GenKern’ library to fuzzy match the nearest value to the given threshold, and calculated the home range by multiplying the number of grid cells obtained by the resolution specified (625 m²). The main advantage of this procedure lies in the better performance of plug-in bandwidth selectors over cross-validation selectors (Duong 2007; Chacon & Duong 2010), which might over- or undersmooth data (Kie et al. 2010).

(2) We also calculated the ratio of intrasexual interactions won (IW) as the number of interactions won divided by the total number of interactions. Behavioural data were recorded throughout the mating season, during independent (i.e. not aimed at recording activity budget, see below) hourly sessions of ad libitum observation (Altman 1974). Each individual was observed for at least 7 h during the rut, with the exception of four animals, which were only observed for 2 h. We considered the focal animal as involved in intrasexual interactions if he displayed direct or indirect forms of aggressiveness (Lovari 1985) towards one or more males. We counted the aggressive interactions displayed by the focal male and if the animal interacted with more males at the same time (e.g. three males) we counted more interactions (i.e. three interactions). We considered the focal male as winner if the antagonist male(s) was chased away or displayed submissive behaviour patterns (Lovari 1985); vice versa, when the focal male was chased away after an interaction, or showed submissive behaviours, he was considered a loser. If none of the rival males displayed submissive behaviours or moved away after interactions had occurred, we considered the interaction had ended in a tie.

To distinguish between territorial and nonterritorial males, in R 2.14.1 we combined individual KD home ranges and IW values (Table 1) in a data matrix and used the Mahalanobis distance (a measure based on correlations between variables, Mahalanobis 1936) as a distance metric to perform multivariate hierarchical clustering (Everitt et al. 2011) using the function `hclust` from the ‘stats’ library. The main advantage of Mahalanobis distance over Euclidean distance is the possibility to account for correlations in the data set and for objects at different scales (i.e. with unequal variances) returning a standardized, uncorrelated data matrix (Everitt et al. 2011). According to the definition of territoriality given above, territorial males should be clustered as the group with smaller KD home ranges and higher IW values.

We investigated differences in age during the rut, body weight and maximum horn length at capture (Table 2) between territorial and nonterritorial males. Age was compared using the Wilcoxon rank sum test for independent samples. Body weight was analysed by fitting a linear model (LM), using body weight as a response variable, mating behaviour as a predictor, age (in months) and date of capture (in months, assuming 1 May as date of birth) as predictors, as well as the GPNP during the 2011 rut (Everitt et al. 2011) as a result, each cell was assigned a density of usage (between 0 and 1). Finally, we calculated the number of grid cells within the 0.90 (i.e. 90%) density threshold using the ‘GenKern’ library to fuzzy match the nearest value to the given threshold, and calculated the home range by multiplying the number of grid cells obtained by the resolution specified (625 m²). The main advantage of this procedure lies in the better performance of plug-in bandwidth selectors over cross-validation selectors (Duong 2007; Chacon & Duong 2010), which might over- or undersmooth data (Kie et al. 2010).

<table>
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<tr>
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The results of the comparisons of body weights and horn lengths between territorial males and nonterritorial males (estimated through linear models and generalized linear models, respectively) are given in the text.

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<th>Mating behaviour</th>
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<th>Age at capture (months)</th>
<th>Body weight at capture (kg)</th>
<th>Maximum horn length at capture (cm)</th>
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<td>Mean = 29.5</td>
<td>Median = 22.4</td>
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</table>
of capture (transformed in Julian date) as covariates. Horn length was analysed by fitting a generalized linear model (GLM), using horn length as a response variable, mating behaviour as a predictor and age (in months) as a covariate.

*Activity Budget, Hormone Metabolites and Faecal Parasite Counts*

We carried out data collection over three periods in 2011: prerut (1 October—3 November), rut (4 November—3 December) and postrut (3 December—31 December). In chamois, the first signs of rutting behaviour usually occur in early November (see Lovari & Locati 1991; Pérez-Barberia et al. 1998; Willisch & Ingold 2007). This timing appears rather stable, also in captive chamois (Forthman Quick & Pappas 1986). Moreover, there are physiological indications that the rut occurs in November, that is, when spermatogenesis and the weights of the testis and epididymis reach their maximum levels (Martinez-Pastor et al. 2005).

Activity budget data were collected using scan sampling at 5 min intervals (Altman 1974) for 2 h (1 h + 1 h) within each period, for each individual. Behavioural categories included foraging, lying down (which typically includes rumination), moving, standing, interactions with males or females (cf. Lovari 1985). In this study, we used only the sum of inter- and intra-sexual interactions (hereafter called ‘number of interactions’), as a proxy of mating effort. Between the pre- and postrut 2011 we observed 17–19 marked animals (overall observations of 100 h) with 15–60 binoculars and 20–60 × 65 spotting scopes from at least 50 m distance to avoid disturbance. Observations were evenly distributed throughout daylight hours.

We collected faecal samples to measure the concentrations of faecal cortisol (FCM) and androgen (FAM) metabolites, as well as faecal counts of larvae of bronchopulmonary parasites. For each observed individual, we collected one fresh faecal sample per period, for an overall 51 scats. Faecal sampling was evenly distributed throughout each period for both territorial and non-territorial males. Within 10 h from sampling, each scat was divided into two fractions and put in separate plastic bags: the one for FCM and FAM analyses was frozen at -20 °C, and the one for the analysis of faecal counts of parasite larvae was kept refrigerated at -4 °C.

A total of 0.5 g of each well-homogenized faecal sample was extracted with 5 ml aqueous methanol (80%; Palme & Möstl 1997). All samples were analysed in duplicate. FCM and FAM levels were measured with an 11-oxoaoctaholanolone enzyme immunnoassay (EIA) and a testosterone EIA, respectively. Details of the two EIAs, including cross-reactions of the antibodies, are given by Möstl et al. (2002) and Palme & Möstl (1994), respectively. The sensitivity of these methods was 3 and 0.3 pg/well. The intra- and interassay coefficients of variation were 9.7 and 12.5% and 7.9 and 12.9%, for the two assays, respectively. These methods proved suitable for a number of ruminant species (e.g. Möstl et al. 2002; Huber et al. 2003; Hoby et al. 2006; Kleinasser et al. 2010).

To identify and quantify bronchopulmonary larvae, we used the zinc sulphate flotation method and the McMaster counting procedure (Thienpont et al. 1979). Zinc sulphate solution was diluted at 33% to obtain a specific density of 1200 kg/m³. Two grams of faeces were mixed with the solution and subsequently filtered with a strainer. The two chambers of the McMaster slide were then filled using a Pasteur pipette. Counting, performed using a light-optical microscope at 100 x magnification, started 5 min after loading the slide. We summed all the counted larvae, and the sum was multiplied by 50 to obtain the number of larvae per gram of faeces. The multiplication factor depends on the dilution of the faecal sample and on the area of the McMaster slide.

Mating Effort, FAM, FCM Levels and Faecal Parasite Counts (Hypothesis 1)

To investigate the variation in the number of interactions and in the faecal counts of parasite larvae over the three periods, we fitted generalized linear mixed models using the function `glmmPQL` (‘MASS’ library) separately for territorial and nonterritorial males, assuming a Poisson distribution corrected for overdispersion (as the residual deviance of each model was greater than its residual degrees of freedom). The number of interactions and the faecal counts of parasite larvae were separately set as response variables, the time period was used as a categorical predictor and the age as a covariate (i.e. the models fitted for territorial and nonterritorial males were: number of interactions ~ time period + age; faecal counts of parasite larvae ~ time period + age). We accounted for autocorrelation over different periods by setting animal identity as a random factor.

To investigate the variation in FAM and FCM levels over the three periods, for territorial and nonterritorial males we fitted linear mixed-effect models (LME) using the function `lmer` (‘lme4’ library) using FAM and FCM levels, separately, as response variables. The time period was set as a categorical predictor and we used age as a covariate (i.e. the models fitted for territorial and non-territorial males were: FAM ~ time period + age; FCM ~ time period + age). We accounted for autocorrelation over different periods by setting animal identity as a random factor. Prior to analysis, FAM and FCM were log transformed and the assumption of normality was tested using the Shapiro–Wilk test (FAM levels: territorial males: W = 0.962, P = 0.404; nonterritorial males: W = 0.946, P = 0.168. FCM levels: territorial males: W = 0.979, P = 0.842; nonterritorial males: W = 0.949, P = 0.199).

Finally, for each of the eight fitted models, we ran a post hoc test, using the `glht` function (with user-defined contrasts) from the ‘multcomp’ library, to compare each period with every other period 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).

Territorial Versus Nonterritorial Males Within Periods (Hypothesis 2)

To test for differences between territorial and nonterritorial males, within each period we used the Wilcoxon rank sum test for independent samples for the number of interactions and the faecal counts of parasite larvae, and the Student’s t test for FAM and FCM levels. Following the design of hypothesis 2, for the pre- and postrut we used two-tailed tests, whereas for the rut we used one-tailed tests.

Effect of FAM on Mating Effort and Faecal Parasite Counts (Hypothesis 3)

We used confirmatory path analysis (Shipley 2000a) to test prespecified hypotheses for the causal relationships among our variables. Specifically we wished to test the hypothesis that FAM directly influences the number of interactions and faecal counts of lungworm larvae, thus mediating the effect of AMTs. Standard path analysis methods, such as those implemented in structural equation models (SEM), compare the observed covariance matrix with the covariance matrix predicted by the tested causal model. SEM, however, cannot deal with data having a hierarchical structure, such as the data in the present study, owing to the repeated measurements conducted on the same individuals. We therefore used the d-sep test, developed by Shipley (2000b), which tests the
conditional probabilistic independences implied in the directed acyclic graph of the hypothesized causal model and which can be easily generalized to deal with data having an underlying hierarchical or multilevel structure (Shipley 2009). To perform the d-sep test using R 2.14.1 (R Development Core Team 2011) we followed the instructions provided by Shipley (2009) to which we refer readers for more details. To test in R the single conditional independencies implied by the models, we used linear mixed models using the function lme (‘nlme’ library) and generalized linear mixed models using the function glmPQL (‘MASS’ library) according to the nature of the dependent variable in the test. An overall test of the fit of the causal model is provided by the Fisher C statistic, which combines the probabilities of all independence claims implied by the model and which follows a chi-square distribution with $2k$ degrees of freedom (where $k$ is the number of independence tests in the model). The path model is thus considered to fit the data when the $C$ value is not significant ($P > 0.05$; Shipley 2000a, 2004).

All statistical analyses were performed using R 2.14.1. The significance level $P$ was set at 0.05. All graphs refer to untransformed data, except for the number of interactions, which was transformed to percentage to facilitate interpretation.

RESULTS

Territorial Males Versus Nonterritorial Males

The cluster analysis confirmed the grouping of nine ($N = 9$) males with very small home ranges and very high values of IW (Fig. 1, Table 1). The territoriality hypothesis for these individuals is therefore strongly supported from both the spatial and behavioural viewpoints. Territorial males occupied exclusive (i.e. nonoverlapping) home ranges in the lower part of the study site; their median home range was 4.63 ha (quartiles range [QR]: 3.13–7.81), much smaller than nonterritorial males’ ($N = 10$) median home range, 20.34 ha (QR: 16.16–196.91). The IW value of territorial males (median = 1; QR: 0.93–1) was higher than that of nonterritorial males (median = 0.04; QR: 0–0.34). Territorial and nonterritorial males did not show substantial differences in median age: 7 years for both groups (QR territorial males (T): 7–8; QR nonterritorial males (NT): 6–8; Wilcoxon rank sum test: $W = 48.5, N_{NT} = 10, N_T = 9, P = 0.803$). Body weight did not differ between territorial and nonterritorial males (LM: $t_{15} = 0.707, P = 0.491$; Table 2). The length of the longest horn measured at capture also did not differ between territorial and nonterritorial males (GLM: $z_{15} = −0.281, P = 0.779$; Table 2).

Mating Effort, FAM, FCM Levels and Faecal Parasite Counts (Hypothesis 1)

In territorial males, the number of interactions drastically increased from the prerut to the rut, and subsequently dropped in the postrut (Fig. 2a, Table 3). FAM and FCM levels, as well as faecal counts of parasite larvae, followed the same pattern (Fig. 2b, c, d), albeit FAM levels and faecal counts of parasite larvae remained significantly higher in the postrut than in the prerut (Table 3).

Nonterritorial males constantly increased their investment in inter- and intrasexual interactions over the time periods, although the difference was nearly significant only between the pre- and the postrut (Fig. 2a, Table 3). FAM levels were significantly higher during the rut, but FCM levels did not differ between periods (Fig. 2b, c, Table 3). Faecal counts of parasite larvae were significantly lower in the prerut (Fig. 2d, Table 3).

Territorial Versus Nonterritorial Males Within Periods (Hypothesis 2)

Territorial and nonterritorial males did not show differences in the number of interactions before the rut (two-tailed Wilcoxon rank sum test: $W = 29, N_{NT} = 8, N_T = 9, P = 0.464$). During the

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**Figure 1.** Dendrogram of the hierarchical clustering of male chamois ($N = 19$) marked in the GPNP, based on Mahalanobis distance using home range size and proportion of intrasexual interactions won during the 2011 rut. The dashed rectangle includes individuals labelled as territorial males. One male (M23) is not represented in the dendrogram because its distance was well above 7; given its large, undefended home range (Table 1), it was labelled as nonterritorial.
rutting period, territorial males interacted significantly more often (one-tailed; $W = 2, N_{NT} = 9, N_T = 9, P < 0.001$) than nonterritorial males, whereas nonterritorial males interacted more often than territorial males in the postrut (two-tailed; $W = 61, N_{NT} = 9, N_T = 8, P = 0.014$; Fig. 2a). FAM levels were significantly higher in territorial males in the prerut (two-tailed Student’s $t$ test: $t_{14.334} = -3.647, P = 0.003$). The comparison between FAM levels did not show significant differences between AMTs during the rut (one-tailed; $t_{14.355} = 1.320, P = 0.104$), yet we found evidence for a medium-large effect size ($Cohen’s d = 0.7, 95\% CI = 0.4 – 0.9$; Nakagawa & Cuthill 2007). FAM levels were similar in both male types in the postrut (two-tailed; $t_{14.371} = 0.272, P = 0.789$). The level of FCM

![Diagram](image)

**Figure 2.** (a) Percentage of time spent interacting, (b) levels of faecal androgen metabolites (ng/g), (c) levels of faecal cortisol metabolites (ng/g), and (d) faecal counts of parasite larvae (number of lungworms/g) of territorial (T) and nonterritorial (NT) male chamois from the pre- to the postrut 2011 in the GPNP. Values are medians ± interquartile ranges.

<table>
<thead>
<tr>
<th>Mating tactic</th>
<th>Between-periods comparison</th>
<th>Interactions</th>
<th>FAM</th>
<th>FCM</th>
<th>Lungworms</th>
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Significant results are shown in bold.

Table 3 Post hoc multiple comparisons for models analysing temporal variations in number of interactions, faecal counts of lungworm larvae (estimated through generalized linear mixed models), faecal androgen (FAM) and cortisol (FCM) metabolites (estimated through linear mixed effect models) in territorial ($N = 9$) and nonterritorial ($N = 10$) male chamois, in the GPNP, in 2011.
(Fig. 2c) was significantly higher in territorial males during the rut (one-tailed; \( t_{14.981} = -2.135, P = 0.025 \)), whereas FCM levels did not differ before (two-tailed; \( t_{15.904} = -1.121, P = 0.279 \)) and after (two-tailed; \( t_{14.840} = 0.237, P = 0.816 \)) the rut. Similarly, lungworm burdens did not differ between male types in the prerut (two-tailed; \( W = 40.5, N_{NT} = 10, N_{T} = 9, P = 0.739 \)) and postrut (two-tailed; \( W = 31.5, N_{NT} = 9, N_{T} = 9, P = 0.448 \)), but were significantly greater for territorial males during the rut (one-tailed; \( W = 11.5, N_{NT} = 8, N_{T} = 9, P = 0.010 \); Fig. 2d).

**Effect of FAM on Mating Effort and Faecal Parasite Counts (Hypothesis 3)**

The best fitting path analysis model is represented as a directed acyclic graph in Fig. 3. In this model, time period is a causal parent of FAM, FCM, mating effort and faecal counts of parasite larvae. FAM is a causal parent of FEC, ME and FCM, while it depends directly on the alternative mating tactic (AMT). This model is not rejected by the data (\( C = 16.653, P = 0.275 \)) and thus it can be accepted as a plausible explanation of the cause—effect relationships among the variables. This model suggests that the effect of alternative mating tactics on mating effort and level of parasite infection is mediated through the effect of FAM. While territorial behaviour, through the mediation of FAM, increases the number of social interactions (a proxy of increased mating opportunities), FAM directly increases the level of parasite infection (measured as FEC) and the level of stress measured as FCM.

**DISCUSSION**

Territorial males sharply increased mating effort, faecal androgen and cortisol metabolites and parasite levels during the rut, whereas nonterritorial males displayed a similar pattern only for faecal hormone metabolites. During the rut, territorial males had higher reproductive effort, higher levels of faecal hormone metabolites and greater faecal counts of parasite larvae than nonterritorial males. Before and after the rut, differences between males were smaller. A path analysis model suggests that the increase in mating effort and faecal counts of larva of bronchopulmonary parasites were mediated by faecal androgen metabolite secretion.

**Territorial Males Versus Nonterritorial Males**

To date, it has been unclear whether the nonterritorial mating tactic would be limited exclusively to the extreme age classes. While it is likely that very young and very old males would be excluded from the competition for land ownership, for both social and physiological reasons (Bubenik & Schwab 1975), we showed that the nonterritorial tactic is also widespread in adult individuals. Territorial males can be as young as 5.5 years (M13) and they may hold a territory at least until the age of 9.5 (M14). This is not surprising, as male Alpine chamois are fully grown when they are 4.5 years old, and their decline in body weight begins after a further 5–6 years (Bassano et al. 2003; Garel et al. 2009). The early onset of territoriality may be indirectly supported by our preliminary results on individual reproductive success (M16 and M17 successfully sired kids when they were 5.5 years old; L. Corlatti, unpublished data). Territorial males’ median home range was in line with von Hardenberg et al. (2000; mean 95% MCP: 3.3 ha; SE ± 0.9) and the median IW value of territorial males, too, was similar to that found by von Hardenberg et al. (2000; 95.3% of interactions won). The lack of morphological differences (i.e. body weight and horn length) between AMTs may suggest a weak pressure of sexual selection, compared to other species (e.g. Alpine ibex), which in turn would support a weak level of polygyny in Alpine chamois, as already hypothesized by Boci et al. (2010), Rughetti & Festa-Bianchet (2011) and Corlatti et al. (2012).

**Mating Effort, FAM, FCM Levels and Faecal Parasite Counts**

When females are aggregated, the temporal distribution of the oestrous is likely to influence the intensity of rutting activity (Emlen & Oring 1977; Ims 1989). Territorial males invested in mating activities almost exclusively during the rut, whereas nonterritorial males interacted more often in the postrut. Most female chamois synchronize their oestrous over a few days in the second half of November (Krämer 1969). During this time, territorial male chamois therefore increased the intensity of rutting behaviours to ensure access to females. This may have precluded access to females by nonterritorial males, which, in turn, may have concentrated their reproductive effort afterwards, when territorial males stopped rutting and a small number of females might still be receptive.

FAM levels significantly increased during the rut for both AMTs. This pattern is in line with the sexual cycle of chamois and other artiodactyls (Mooring et al. 2004; Hoby et al. 2006), and it is unlikely to be the result of a dilution effect caused by seasonal variations in nutritional strategies (Klasing 2005), such as rut-induced hypophagia (Willisch & Ingold 2007). During the rut, territorial males’ feeding rate was similar to that registered in spring, whereas nonterritorial males’ feeding rate was similar to that registered in the prerut (L. Corlatti, personal observation); despite the similarities in feeding rates between the mating season and previous periods, FAM levels in the rut were clearly higher for both male types.

The relationship between FCM levels and the biological cycle of ungulates is somewhat controversial. Although some studies suggest that the onset of the rutting season may trigger the peak of glucocorticoid secretion (Creel 2001; Mooring et al. 2006), several ungulate species do not show this pattern (e.g. white-tailed deer, *Odocoileus virginianus*: Bubenik et al. 1983; chital deer, *Axis axis*: Chapple et al. 1991; red deer, *Cervus elaphus*: Huber et al. 2003; Pyrenean chamois, *Rupicapra pyrenaica*: Dalmay et al. 2007). These latter studies, however, did not take into account potential differences between alternative male tactics. In our population, the level of FCM increased during the rut only in territorial males: if all males were considered, the effect of the rutting season would be diluted, possibly leading to undetectable variations. The peak of FCM levels for territorial males is unlikely to be caused by reduced nutritional intake (for the same reasons seen above for FAM levels).
Parasite burden showed a peak during the rut only in territorial males. This trend is in line with the pattern of FAM and FCM, as already shown by Hoby et al. (2006), and suggests that, if variation in parasite burdens was due to immunosuppression (Folstad & Karter 1992), this effect may be marked in territorial males. Faecal counts of parasite larvae in nonterritorial males, on the other hand, may be largely influenced by the lungworm seasonal cycle, which shows a peak during the autumn months (Stefaničková 1994; Stefaničková et al. 2011).

**Territorial Versus Nonterritorial Males Within Periods**

The mating effort of territorial males was greater than that of nonterritorial males during the mating period. The territorial strategy entails the maintenance of a mating ground long before the rut (i.e. from May to June, von Hardenberg et al. 2000); such an investment of energy suggests potentially higher mating benefits (i.e. greater access to females) during the mating season. This hypothesis is supported by our results on mating success, as all observed matings occurred between 16 and 25 November, and were monopolized by territorial males (L. Corlatti, unpublished data).

Territorial males had higher levels of FAM in the prerut, possibly related to the early occupancy of territories (von Hardenberg et al. 2000). Dominant males usually have a higher level of androgen metabolites than subordinate males during the rut (Mooring et al. 2004; Oliveira et al. 2008). In our population, territorial and non-territorial chamois did not show significant differences, but a clear trend for higher levels of FAM in territorial males during the rut.

FCM levels during the rut were significantly higher in territorial males. Although it has been often argued that social subordinates would show elevated levels of cortisol metabolites, there is increasing evidence that dominant individuals have high glucocorticoid levels more often than do subordinates (Creel 2001; Mooring et al. 2006; Oliveira et al. 2008). Our results are consistent with the ‘stress of domination’ hypothesis: individuals engaged in energetically expensive behaviours are more stressed than subordinate individuals (Mooring et al. 2006). Our path analysis model, which highlights a direct causal link between FAM and FCM, supports this hypothesis. In the long term, several weeks of high FCM levels may lead to overall reduced survival (Sapolsky 1992; Möstl & Palme 2002).

The infections caused by protostrongylid species are among the most common diseases in wild chamois populations. Pulmonary nematodes may activate bacterial pneumonia, a common cause of mortality in Alpine chamois (Richomme et al. 2006). As such, the greater parasite infections observed during the rut in territorial males, compared to nonterritorial males, may be an important cost in terms of overwinter survival, also considering the high mass loss that occurs during the rut (Rughetti & Festa-Bianchet 2011).

**Effect of FAM on Mating Effort and Faecal Parasite Counts**

Androgens are widely known to be mediators of aggressive and courtship behaviours (Knapp 2003; Hirschenhauser & Oliveira 2006), while simultaneously suppressing the immune function (Folstad & Karter 1992). Several studies found a positive correlation between reproductive effort and parasitism in various taxa (Deerenberg et al. 1997; Nordin et al. 1998; Pelletier et al. 2005), but the causal relationships among behavioural, endocrine and health variables remain unclear.

Our analysis confirmed the existence of a life history trade-off among reproductive opportunities on one side and metabolic stress and increased level of parasite infection on the other; moreover, we showed how the mechanism underlying such a trade-off is mediated by androgens. As far as the expression of AMTs normally involves hormonal regulation, AMTs may entail different trade-offs between opportunities to invest in reproduction and in survival.

**Conclusions**

Our results suggest that, for the given mating season, variations in mating effort are positively associated with variations in physiological costs and that such a trade-off is mediated by androgens. They also suggest that AMTs, in rutting male chamois, may have different costs and benefits. Territorial males invest more in rutting activities, potentially gaining mating benefits, but may pay several costs, owing to greater energy consumption, higher levels of hormone metabolites and greater parasite susceptibility. On the other hand, nonterritorial males, which invest less in rutting, may benefit from saving energy, having lower levels of hormone metabolites and fewer lungworms.

Different strategies of energy allocation during the rut may eventually lead to different survival probabilities (Garel et al. 2011). The estimation of mortality rates, however, requires long-term studies and large sample sizes (see Corlatti et al. 2012), which we were unable to record. Furthermore, our results do not allow us to investigate whether a tactic is a short-term strategy or a fixed characteristic of a given individual. AMTs that diverge only in behavioural traits should be more flexible than AMTs that imply morphological variations (Taborsky et al. 2008). In that context, it may be possible that (owing to the high cost of territoriality) some males might breed in alternate years. Such year skipping is recognized in other species (e.g. water pythons, Liasis fuscus: Madsen & Shine 1999; Alpine ibex: Toigo et al. 2002). Moreover, Lovari et al. (2006) showed the occurrence of alternative strategies of space use in male chamois (i.e. resident and migrant), possibly associated with AMTs. In the study area, snowfalls tend to move females to lower altitudes at the peak of the rut, where resident, mostly territorial males would monopolize mating. When snowfalls are late, nonterritorial males would have an advantage. Yearly variations in individual status and meteorological conditions may therefore lead to different strategies of energy allocation in AMTs.

To understand whether such clues to life history trade-offs may result in different lifetime fitness trade-offs, long-term investigations of marked individuals are needed. Studies on survival, reproductive success, flexibility and frequency dependence may eventually help disclose the mechanisms underlying the maintenance of AMTs in Alpine chamois.

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collected data in the field, carried out the parasitological and (part of) the hormone analyses and participated in writing up this paper. A.V.H. did the confirmatory path analysis and participated in writing up this paper. B.B. participated in the capture of all animals and in writing up this paper. R.P. supervised the hormonal analyses and participated in writing up this paper. S.L. supervised all stages of this work, took part in the data collection, and participated in the preparation of all drafts of the manuscript.

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