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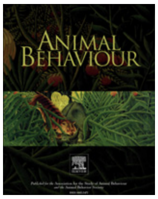

Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs

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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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In species with intense competition for mating, the pursuit of reproductive success may foster the development of alternative mating tactics (AMTs, Taborsky et al. 2008). Our understanding of the evolution and maintenance of AMTs may benefit from the comparison of the physiological and life history trade-offs underlying their expression (Garant et al. 2003; Oliveira et al. 2008).

From a life history perspective, individuals that invest a lot in current reproduction may have lower levels of survival or future reproduction (Stearns 1992). However, the proximate mechanisms underlying this trade-off are still poorly known (Cox et al. 2010). It is widely assumed that reproductive effort, defined as the allocation of energy resources to current reproduction, is traded off against the individual's ability to defend itself against pathogens (reviewed in Lochmiller & Deerenberg 2000; Zuk & Stoehr 2002; but see the study of Hõrak et al. 2006 on rats, *Rattus norvegicus*). Indeed, several studies have found a positive correlation between reproductive effort and parasitism in various taxa (e.g. zebra finches, *Taeniopygia guttata*: Deerenberg et al. 1997; collared flycatchers, *Ficedula albicollis*: Nordling et al. 1998; tree swallows, *Tachycineta bicolor*: Ardia et al. 2003; bighorn sheep, *Ovis canadensis*: Pelletier et al. 2005).

The physiological basis of this trade-off includes the role of the immune function. The steroid hormone testosterone may promote male reproductive effort (Knapp 2003; Hirschenhauser & Oliveira 2006) and enhance mating potential (Folstad & Karter 1992; Ezenwa et al. 2012; but see the recent study of Nie et al. 2012 on the giant panda, *Ailuropoda melanoleuca*) while simultaneously suppressing the immune function (e.g. in Alpine ibex, *Capra ibex*: Decristophoris et al. 2007). Immunosuppression may also be related to changes in secretion of glucocorticoids (Ezenwa et al.

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2012), 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 intrasexual 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 km^2 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/km^2 (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 CO$_2$ 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

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