University of Sassari
Ph.D. School in Natural Sciences
Via Muroni 25, I-07100 Sassari, Italy

Dissertation for the Degree of Doctor of Philosophy in Environmental Biology
presented at Sassari University in 2010

XXIII cycle

ECOLOGICAL FACTORS AFFECTING INVESTMENT IN BODY MASS, AND HORNS IN THE ALPINE CHAMOIS (*Rupicapra rupicapra*)

PH.D. CANDIDATE: ***Dr. Roberta Chirichella***
Roberta Chirichella

DIRECTOR OF THE SCHOOL: ***Prof. Marco Apollonio***
Marco Apollonio

SUPERVISOR: ***Prof. Marco Apollonio***
Marco Apollonio

CO-SUPERVISOR: ***Dr. Simone Ciuti***

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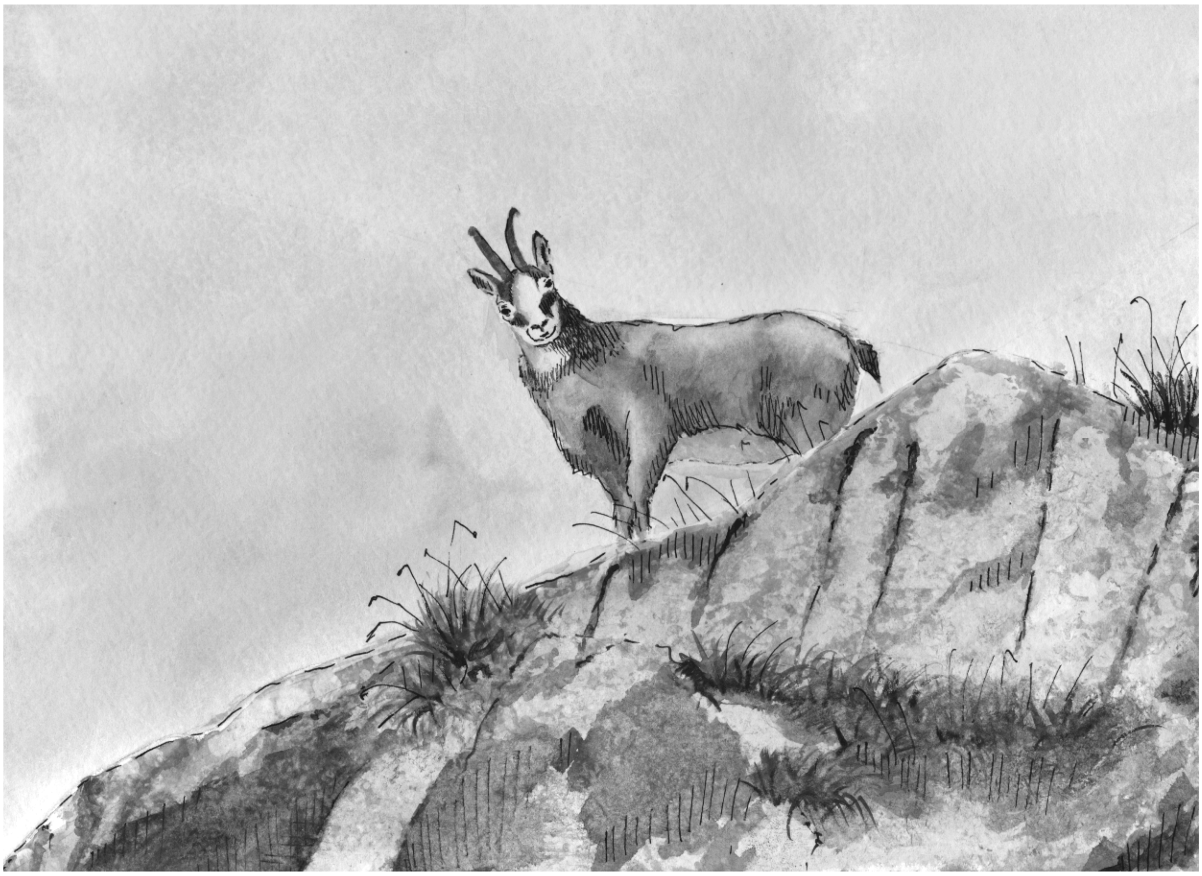

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SUMMARY

[ENGLISH] Fitness in herbivorous polygynous species is related both to body conditions and to secondary sexual traits. Ungulates therefore must balance resources between body size and antlers/horns growth.

Here I described how some ecological factors affected the investment in body mass and horn length in Alpine chamois (*Rupicapra rupicapra*). Chamois horns grow mainly in the first years of life and their size can be deciding for future individual success. Therefore I analyzed the horn size variation in yearlings according to a large set of ecological variables, including for the first time also soil type (calcareous or siliceous). I found that there are many environmental and climatic factors able to modify horn length. Both sexes showed a high investment in horn grow in good conditions but females on siliceous soil and after a harsh winter reduced this investment.

Moreover I analyzed the reproductive strategy over time in male Alpine chamois and I showed that the reproductive investment increased with age by continuing to invest more energy after prime age. This strategy is in agreement with the ‘terminal investment’ hypothesis.

Finally I investigated which factors negatively affected the free access to resources for this species. I demonstrated for the first time how livestock and a wild non native ungulate (*Ovis orientalis musimon*) may force chamois to use sub-optimal meadows, negatively affecting the gain of a proper body size during summer due to reduction of feed intake.

KEY WORDS: *Rupicapra rupicapra*, body condition, horn size, reproductive strategy, competition.

RIASSUNTO

[ITALIAN] La *fitness* delle specie erbivore poliginiche è legata sia alle condizioni fisiche sia allo sviluppo dei caratteri sessuali secondari. Gli ungulati pertanto devono bilanciare le risorse acquisite tra l'accrescimento delle dimensioni corporee e lo sviluppo di palchi/corna.

Qui ho descritto come alcuni fattori ecologici influenzano la crescita della massa corporea e la lunghezza del corno nel camoscio alpino (*Rupicapra rupicapra*). Dato che le corna in questa specie crescono soprattutto nei primi anni di vita, ho analizzato la variazione della lunghezza delle corna negli *yearling* rispetto ad un ampio insieme di variabili ecologiche, considerando per la prima volta anche il tipo di suolo (calcareo o siliceo). Ho dimostrato che ci sono molti fattori ambientali e climatici in grado di modificarne la lunghezza. Entrambi i sessi hanno mostrato di investire molto nella crescita delle corna in buone condizioni ma le femmine che vivono su substrato siliceo e che affrontano un duro inverno riducono questo investimento.

Ho inoltre analizzato la strategia riproduttiva dei maschi, dimostrando che l'investimento energetico aumenta negli anni a partire dalla prima riproduzione. Questa strategia è in accordo con l'ipotesi dell' 'investimento terminale'.

Infine ho studiato i fattori che influenzano il libero accesso alle risorse trofiche per questa specie. Ho dimostrato che ungulati domestici e selvatici alloctoni (*Ovis orientalis musimon*) possono forzare i camosci in pascoli sub-ottimali durante l'estate, influendo negativamente sulle condizioni fisiche per una riduzione della quantità di cibo ingerita.

PAROLE CHIAVE: *Rupicapra rupicapra*, condizioni fisiche, dimensione corna, strategia riproduttiva, competizione.

INTRODUCTION

This thesis consists of three main parts dealing with some crucial ecological factors able to affect investment in body size and secondary sexual traits in Alpine chamois (*Rupicapra rupicapra*). In the **First Part** I evaluate the factors which may either promote or restrain an early investment in body mass and horns for juveniles and yearlings. In the **Second Part** I analyze a fundamental life history question: how males allocate reproductive investment optimally over time. Finally, in the **Third Part**, I describe some factors negatively affecting the free access to resources for this species, therefore reducing the gain of a proper body size of chamois during summer.

The importance of body mass and secondary sexual traits in ecology and life history evolution cannot be understated (Peters 1983, von Hardenberg et al. 2004), especially in herbivores polygynous species.

Among ungulates, it is often crucial for juveniles and yearlings to quickly gain body size and, at the same time, to allocate resources to antlers or horns growth (e.g. Pérez-Barberia et al. 1996). This is especially valid for those bovid species where horns grow mainly in the first years of life and their size can be deciding for future individual success. As shown for species living in temperate areas, large and heavy juveniles of both sexes enjoy higher survival rates over their first winter than lighter and smaller ones (Loison et al. 1999b, Côté and Festa-Bianchet 2001). Moreover, unlike cervids' antlers, which are renewed year after year, the early development of permanent horns is a critical life-step for bovids. Given that the development of horns and body size is massive during the first years of life (Festa-Bianchet and Côté 2008), it is crucial analysing the factors affecting the choise to invest more resources in body mass or horn size.

Fecundity of females is strongly influenced by body mass so that fast-growing females reproduce earlier in life than slow-growing females (Sadleir 1969, Albon et al. 1983, Reimers 1983, Sæther and Haagenrud 1983, Gaillard et al. 1992, Garel et al. 2005,). For males of polygynous species, access to females depends on intrasexual competition and body size positively influences male reproductive success (Clutton-Brock et al. 1988, Skogland 1989, McElligott et al. 2001). Moreover, males with large horns usually dominate other males and have a greater chance to reproduce (Coltman et al. 2002, Bergeron et al. 2010). Consequently, large-horned males enjoy a substantial reproductive advantage.

Because they are energetically costly and are a major source of heat loss during winter (Picard et al. 1996), horns may be an honest signal of individual quality, as has been suggested for the antlers of some deer species (Folstad and Karter 1992, Ditchkoff et al. 2001).

In mountain goats (*Oreamnos americanus*; Festa-Bianchet and Côté 2008) for both sexes, horn length of yearlings is positively correlated with body mass, but even when effects of sex and mass were considered, horn length increased with early-June fecal crude protein. That may suggest that yearlings allocated more resources to body rather than to horn growth when resource were scarce, as reported for bighorn rams (*Ovis canadensis*; Festa-Bianchet et al. 2004).

Among *Rupicaprinae*, the horns of males are usually only 10 to 20% longer and thicker than those of females, and sexual dimorphism is mostly due to the greater horn growth reported in males during the first few years of life (Pérez-Barberia et al. 1996). In this context, Alpine chamois is an ideal case study for investigating the ecological factors able to affect horn growth and if there is a trade off between body mass and secondary sexual traits investment under particular conditions. The final size of horns and body mass provides key information for the study of individual life histories (von Hardenberg et al. 2004), and for a deeper understanding of population dynamics of large herbivores (Toïgo et al. 2006, Bergeron et al. 2008).

In this study, for the first time, I describe the importance of living on different environmental conditions (i.e. calcareous *vs* siliceous substrate) in allocating resources in body mass and horn development.

Beside the heritable and genetic component, it was proved that secondary sexual traits are affected by a number of non-genetic factors such as age, habitat, winter harshness, and, more in general, environmental conditions (Jorgenson et al. 1998, Festa-Bianchet et al. 2000, 2004, Mysterud et al. 2005a). Previous studies showed that horn and antler growth was greatly affected by climatic factors such as rainfall (Pérez-Barberia et al. 1996, Côté et al. 1998), temperatures (Schmidt et al. 2001, Giacometti et al. 2002), and winter conditions (Mysterud et al. 2005a), which, in turn, are responsible in affecting food quality and quantity. However among factors supposed to affect growth and size of sexual secondary traits, researchers have not yet deeply investigated the relation between soil quality and horn/antler size. Characteristics of soil, though, are important features that could affect vegetation communities and forage qualities, and, consequently, growth rate and size of secondary sexual traits of ungulates. Pastures on calcareous soils have a higher grazing value than pastures on siliceous soils due to nitrogen-richness (Rameau et al. 1993), best quality of grassland communities (Cavallero et al. 2007) and high species richness (Michalet et al. 2002). Other factors responsible of a decrease of food availability such as population density due to intra-specific competition may have profound indirect effects on secondary sexual traits, as showed for bighorn ewes (Jorgenson et al. 1998) and red deer stags (Schmidt et al. 2001, Mysterud et al. 2005a).

Studies on the influence of phenotypic quality on life history traits should not be limited to adult individuals or to one sex only: for instance horns in Alpine chamois have an importance in intrasexual and intersexual social relationship for both sexes (Krämer 1969). Horns can give information about the life history of an individual and predict the onset of senescence (von Hardenberg et al. 2004). Given that the development of horns is massive during the first years of life (Festa-Bianchet and Côté 2008), it is crucial analysing the factors affecting such an early investment.

Consequently, in this First Part I analize the variation of horn size in yearling Alpine chamois according to a large set of ecological variables. Yearlings were legally shot in autumn-winter (when about 1.5 y.o.) during 5 consecutive years (from 2005 to 2009) in the central-eastern Italian Alps. Thus, by controlling the effect of the age (the same for the whole sample), I model the variation of horn size according to single and combined factors such as sex, soil types (calcareous or siliceous substrate), elevation and exposure of autumn-winter ranges, climatic factors (rainfalls, snow cover, temperatures, winter harshness) recorded from the birth period to the shooting day, and local chamois density (**Chapter 1**). Moreover, I describe if this bovid decide to allocate resources more in body mass or in horn development in relation to the different environmental conditions (i.e. calcareous *vs* siliceous substrate, aspect and altitude), climatic factors and density rate experienced. Thus, by controlling the effect of the age (the same for the whole sample) and by comparing populations living in different conditions, I investigate if males and females invest resources to body and horn growth in the same way (i.e. greater investment in horn growth for a given body mass in the same conditions). This aspect is crucial to be considered in population dynamic because the trade off between body and horn size investment might increase the yearling survival probability, possibly to the detriment of their short-term reproductive success, shaping demographic parameters of chamois populations (**Chapter 2**).

According to the Second Part of this thesis, I discuss how males allocate reproductive investment optimally over time. The question of how long-lived iteroparous animals should allocate resources to reproduction over their lives is of great ecological importance (Williams 1966, Stearns 1992). Trade-offs exist not only between survival and reproduction, but also between current and future reproduction (Williams 1966, Clutton-Brock 1984, Stearns 1992). For instance, in order to maximise lifetime reproductive success, an individual may forego mating in the present if conditions are unfavourable and there is a good chance of breeding in the future. Prime-aged individuals generally have the highest competitive ability and, thus, might be expected to benefit most from investing energy in reproduction (Yoccoz et al. 2002). Indeed, the 'mating strategy-effort' hypothesis (Yoccoz et al. 2002), which predicts that reproductive investment (the investment of energy in current reproduction rather than in future reproduction, growth or survival) peaks in prime-aged adults before decreasing in older individuals, has received support from studies on a range of taxa (Cameron et al. 2000, Billing et al. 2007, Mainguy and Côté 2008). A contrasting hypothesis, the theory of 'terminal investment', predicts that reproductive investment should continue to increase after prime age due to a diminishing residual reproductive value (RRV) (Williams 1966). Despite the theoretical appeal of the terminal investment hypothesis, it has rarely been empirically proven.

Ungulate species provide good model systems in which to study the allocation of reproductive investment over time. Male reproductive success depends on competing for access to females during a short rutting season (Clutton-Brock et al. 1988). Specifically, male reproductive behaviour consists of competing with other males for access to oestrus females and performing courtship behaviours to attract females (McElligott et al. 2001, Yoccoz et al. 2002, Forsyth et al. 2005). Male reproductive investment can be relatively easily studied over the rut by measuring the somatic costs of reproductive behaviour. Male ungulates often adopt a strategy of 'appetite suppression' during the rut, meaning that they are 'capital breeders' (or rather, towards the capital end of the capital-income breeder continuum) and are reliant on stored energy to breed (Stearns 1992, Jonsson 1997, Willisch and Ingold 2007, Stephens et al. 2009). As such, the proportion of mass lost by a male during the rut can be used as an estimate of the energy invested in reproductive behaviour (Doughty and Shine 1997). As such, rutting males that lose more body mass may be less likely to breed the following season, highlighting the important life history trade-off between current and future reproduction.

The allocation of reproductive investment has been studied in a number of male ungulates. Findings have tended to support the ‘mating strategy-effort’ hypothesis (e.g. *Cervus elaphus* [Clutton-Brock et al. 1985, Yoccoz et al. 2002], *Bison bison* [Maher and Byers 1987], *Oreamnos americanus* [Mainguy and Côté 2008]). It is thought that, because males often adopt alternative mating strategies as they senesce and become less competitive, an increase in reproductive investment is unlikely to be observed after prime age (Yoccoz et al. 2002, Mainguy and Côté 2008). To date, there is a lack of strong evidence supporting terminal investment in a male ungulate. Intriguingly, Mysterud et al. (2005b) put forward evidence of increasing reproductive investment with age in male moose *Alces alces*; however, they found that the investment of the oldest males actually tended to stabilise or decrease (Mysterud et al. 2005b).

Given such scenario, the aim of the Second Part is to analyse the relationship between age and reproductive investment among male Alpine chamois, using hunting data (28,011 Alpine chamois, 14,627 males and 13,384 females, culled over 37 consecutive hunting seasons between 1973 and 2009). Chamois are a polygynous (Loison et al. 1999a, von Hardenberg et al. 2000) yet relatively sexually monomorphic mountain-dwelling ungulate (only modest sexual dimorphism exists with respect to body mass and horn size (Couturier 1938, Kramer 1969, Knaus and Schröder 1983). Breeding male chamois defend small clustered territories during the rut, excluding rival males and defending oestrus females (Kramer 1969, von Hardenberg et al. 2000). Male rutting behaviour consists of agonistic interactions with rival males such as chasing and posturing, and interactions with sexually mature females, including herding and copulation (Kramer 1969). During the rut, males allocate much of their non-rutting time to rest rather than foraging; they are thus capital breeders (Willisch and Ingold 2007). The goal of **Chapter 3** is to test variation in male reproductive investment across age classes using relative body mass change as an estimate of investment.

Finally in the Third Part of this thesis I investigate on factors negatively affecting the free access to resources (i.e. meadows with higher quality) for this species, and able to reduce the gain of a proper body size of chamois during summer.

Among ungulates, interaction between different species has been the object of several studies (Gordon and Illius 1989, Homolka 1996, Putman 1996, Bartos et al. 2002). Moreover, competition can be strongly enhanced when we consider ecosystems where wild ungulates coexist and likely compete with non-native ungulate species and/or domestic livestock (Chapman et al. 1993, Vázquez 2002, La Morgia and Bassano 2009). Indeed, while native sympatric species commonly show low negative interactions as a consequence of niche separation and resource partitioning (Hartnett et al. 1997), the introduction of non native species can dramatically change previous set up in the herbivore community. This kind of phenomena can interfere with mechanisms of competitive equilibrium and could lead to competition with one or more native species (Chapman et al. 1993, Vázquez 2002). At the same time, livestock grazing impact on native herbivores is an important conservation concern on a global scale (Prins 1992, Fleischner 1994, Noss 1994, Voeten 1999) and the compatibility among wild and domestic ungulates has been studied both to gain insight into coexistence processes in general and to solve practical management problems, such as the compatibility between wild and domestic ungulates (Mishra et al. 2004, La Morgia and Bassano 2009, Brown et al. 2010).

Moreover, the wildlife-livestock compatibility issue recently increased because of the rise in distribution and population size of many ungulate species in Europe (Apollonio et al. 2010). As interactions between wildlife and human activities become more relevant, the use of mountain ranges for grazing of domestic ungulates (cattle, sheep and goats) get to be a potential source of conflict of interests. In fact, the presence of domestic livestock can adversely affect the spatial distribution, activity budgets and/or the diets of wild ungulates (Kie et al. 1991, Loft et al. 1991, Kie 1996, Putman 1996, Mattiello et al. 2002, Brown et al. 2010). Domestic animals are often abundant and potentially competitors of wild ungulates and, likely, domestic animals prevail in such a competition (Latham 1999). This contest for space and food may also have negative consequences for reproductive success and long-term population dynamics of wildlife species (Forsyth and Hickling 1998, Forsyth 2000, Madhusudan 2004, Mishra et al. 2004). In this context it is therefore arguable that the simultaneous presence of livestock and alien species can be a critical issue for native ungulates. However, little is known about the competitive interactions among ungulates, especially between native and exotic species, with the possible co-presence of domestic ungulates as a further additive factor.

The issue about the possible negative effect of non-native species and/or livestock on wild ungulates remains unsolved. This problem seems to be pronounced in rural and mountainous areas, where the conditions for this competition occur (Apollonio et al. 2010). In the Alps, for instance, the question of if Alpine chamois, a native species, interacts negatively for the same meadows with mouflon (*Ovis orientalis musimon*) and domestic species are important issues to improve the management of current natural ungulate populations. Indeed, the introduction of the mouflon in the Alps begun in 1962 and the alpine population in Italy has grown to over 5000 animals (Bertolino et al. 1998, Apollonio et al. 2010). The effects of these introductions have been poorly assessed, and some insights were given in the Pyrenees, where *Rupicapra pyrenaica* have apparently been displaced by the presence of introduced mouflons (Gonzales 1984, 1986). Moreover, preliminary researches performed in the Alpine meadows showed a marked spatial segregation between Alpine chamois and livestock, suggesting a direct negative interaction between the two species (Berdoucou 1986, Garcia-Gonzales et al. 1990), as well as chamois avoided sheep ranges when occurring in the same areas (Rebollo et al. 1993).

Under these circumstances, in this Third Part I evaluate the possible effect of non-native wild and domestic ungulates on the Alpine chamois. The main goal of **Chapter 4** is to investigate if the free access by Alpine chamois to high-quality meadows during summer is negatively affected by the presence of mouflon and/or livestock. This, in turn, may negatively affect the gain of a proper body size of chamois during summer due to reduction of feed intake, and it could have strong impacts on the productivity of females, on the winter survival of both sexes, and, more in general, on its population dynamic parameters.

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FIRST PART

The role of ecological processes in the early stages of individual life histories

Chapter 1

Horn length in yearling Alpine chamois (*Rupicapra rupicapra*): ecological factors affecting an early investment

Horn length in yearling Alpine chamois (*Rupicapra rupicapra*): ecological factors affecting an early investment

Roberta Chirichella[1,2], Simone Ciuti[1], Michele Rocca[3], Stefano Grignolio[1] and Marco Apollonio[1]

1 - Department of Zoology and Evolutionary Genetics, University of Sassari,
via Muroni 25, I-07100, Sassari, Italy

2 - Adamello Brenta Nature Park,
via Nazionale 24, I-38080, Strembo (TN), Italy

3 - Hunting association of the Trento province (Associazione Cacciatori Trentini),
via Guardini 41, I-38121, Trento, Italy

ABSTRACT

The role of ecological processes in the early stages of individual life histories in mammals is particularly interesting. If we take into account ungulates, and among them bovids for instance, it is often crucial for juveniles and yearlings to gain body size and horns quickly, as both grow primarily during the first years of life. Consequently, it is important to disentangle the factors which may either promote or restrain such an early investment. We modelled a comprehensive set of ecological factors accounting for the variation of horn size in 1,330 yearling Alpine chamois (*Rupicapra rupicapra*) which were legally shot during 4 consecutive years in central-eastern Italian Alps. For the first time in bovids, horns were found to be shorter in chamois of both sexes shot on siliceous soils, when compared to those shot on calcareous soils. Adverse environmental and climatic conditions (e.g. elevation, snow cover, northerly aspects) negatively affected horn length in yearling chamois of both sexes. We found significant interactions between substrate type and both snow cover and aspect, with significantly longer horn length on calcareous substrates with low snow cover and northerly exposure. This was likely due to the high-quality grasslands growing over calcareous soils in wet conditions and to the more negative impact of high snow cover in calcareous environments. Moreover, we found that rainfall positively affected horn growth not only in kids, but also later, when 1 y.o. individuals directly benefited from high quality meadows, confirming that horn growth is a cumulative process which reflects environmental conditions. In general, ecological factors such as temperature and precipitation positively affected horn size during the first year of life more than during the second, confirming that the early stage of development is crucial in the individual life history of ungulates.

INTRODUCTION

The analysis of ecological factors able to affect horn and antler growth and their final size provides key information for the study of individual life histories (von Hardenberg et al. 2004), and for a deeper understanding of population dynamics of large herbivores (Toïgo et al. 2006, Bergeron et al. 2008). Body mass and condition are strongly related with antler and horn size in many ungulate species (*Rupicapra pyrenaica parva*, Pérez-Barberia et al. 1996; *Rupicapra rupicapra rupicapra*, Bassano et al. 2003; *Oreamnus americanus*, Côté et al. 1998; *Capra ibex*, von Hardenberg et al. 2004; *Ovis canadensis*, Festa-Bianchet et al. 2000, 2004; *Cervus elaphus hispanicus*, Gaspar-López et al. 2008). In bighorn sheep (*Ovis canadensis*), for instance, there are positive genetic and phenotypic correlations between horn length and body mass (Coltman et al. 2002). These two heritable traits are correlated with male reproductive success (Coltman et al. 2002). Beside the heritable and genetic component, which is only partly responsible for variance in the size of cervids' antlers (Kruuk et al. 2002) and bovids' horns, it was proved that secondary sexual traits are affected by a number of non-genetic factors such as age, habitat, winter harshness, and, more in general, environmental conditions (Jorgenson et al. 1998, Festa-Bianchet et al. 2000, 2004, Mysterud et al. 2005a). Previous studies showed that horn and antler growth was greatly affected by climatic factors such as rainfall (Pérez-Barberia et al. 1996, Côté et al. 1998), temperatures (Schmidt et al. 2001, Giacometti et al. 2002), and winter conditions (Mysterud et al. 2005a), which, in turn, are responsible in affecting food quality and quantity. This was for the first time predicted by Nievergelt (1966) who showed remarkable differences in the horn growth of Alpine ibex males living in different ecological contexts. However among factors supposed to affect growth and size of sexual secondary traits, researchers have not yet deeply investigated the relation between soil quality and horn/antler size. Characteristics of soil, though, are important features that could affect vegetation communities and forage qualities, and, consequently, growth rate and size of secondary sexual traits of ungulates. Pastures on calcareous soils have a higher grazing value than pastures on siliceous soils due to nitrogen-richness (Rameau et al. 1993), best quality of grassland communities (Cavallero et al. 2007) and high species richness (Michalet et al. 2002). Thus, we may expect herbivores grazing on calcareous soil may be in a comparatively better body condition and consequently exhibit larger secondary sexual traits. In this respect, regional differences in white-tailed deer antler size (*Odocoileus virginianus*) were found to be likely due to differences in soil fertility (Strickland and Demarais 2000). Analysis on small areas with similar climatic characteristics and different soil types could help to understand the relation between different soil types and growth rate and size of secondary sexual traits of ungulates. Other factors responsible for decreased food availability, such as population density due to intra-specific competition, may have profound indirect effects on secondary sexual traits, as shown for bighorn ewes (Jorgenson et al. 1998) and red deer stags (Schmidt et al. 2001, Mysterud et al. 2005a).

Studies on the influence of phenotypic quality on life history traits should not be limited to adult individuals or to one sex only: for instance horns in Alpine chamois have an importance in intrasexual and intersexual social relationships for both sexes (Krämer 1969). This is especially valid for those bovid species where horns grow mainly in the first years of life and horn size can be critical for future individual success. As shown for ungulate species living in temperate areas, large and heavy juveniles of both sexes enjoy higher survival rates over their first winter than lighter and smaller conspecifics (Loison et al. 1999, Côté and Festa-Bianchet 2001). Unlike cervids' antlers, which are renewed year after year, the early development of permanent horns is a critical life-step for bovids. Horns can give information about the life history of an individual and predict the onset of senescence (von Hardenberg et al. 2004). Given that the development of horns is massive during the first years of life (Festa-Bianchet and Côté 2008), it is crucial analysing the factors affecting such an early investment.

Alpine chamois (*Rupicapra rupicapra*) represent an ideal case study for investigating investment on secondary sexual traits. For instance, 60-70% of horn growth takes place in the first 2 years of life in both males and females (Schröder 1971, Bassano et al. 2003). Although the Alpine chamois is the most widespread and most hunted ungulate species in the Alps from France to Slovenia (Apollonio et al. 2010), little is known about the role of key ecological factors influencing body condition, horn growth and their final size in this bovid. In this study we analysed the variation of horn size in 1,330 yearling Alpine chamois (592 females and 738 males) according to a large set of ecological variables. Yearlings were legally shot in autumn-winter (when about 1.5 y.o.) during 4 consecutive years in the central-eastern Italian Alps. By controlling for the effect of age (the same for the whole sample), we modelled the variation of horn size according to single and combined factors such as sex, soil types (calcareous or siliceous substrate), elevation and aspect of autumn-winter ranges, climatic factors (rainfall, snow cover, temperature, winter harshness) recorded from the birth period to the shooting day, and local chamois density.

METHODS

Study area

This study was carried out in the central-eastern Italian Alps (Figure 1), in a 121,906 ha-wide area of the Trento Province (46°02'N; 10°38'E). This mountainous area (Figure 1) was subdivided into 2 main sectors: the Adamello-Presanella Massif (51,847 ha), characterized by siliceous substrate, and the Brenta and Cadria Altissimo Massif (70,059 ha), characterized by calcareous substrate with sedimentary rocks (mainly limestone and dolomite). This soil composition accounts for the natural development of botanic endemisms and peculiar plant associations, especially in the area above the tree line. Two vegetation patterns were detectable corresponding to the two soil compositions. Typical primary grassland covering the calcareous substrate was mainly composed by *Sesleria albicans* and *Carex firma*, whereas grassland covering the siliceous substrate was composed by *Festuca scabriculmis* and *Carex curvula* (Adamello Brenta Nature Park – digitized official data). Elevation ranged from 65 to 3,558 m a.s.l., with a mean of 1,630 m a.s.l.. The tree line was around 2,000 m a.s.l. (Figure 1).

The study area consisted of 5 hunting districts (Figure 1) where chamois hunting with rifles was allowed from mid-September to mid-December. In the Trento Province hunting was controlled through licenses issued by local wildlife boards, and shot chamois were checked in municipal reserves (n = 68) corresponding to further subdivisions of the 5 hunting districts.

As regards other ungulates, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) were abundant but rarely used the areas above the tree line, which were commonly populated by the Alpine chamois. In contrast, mouflon (*Ovis orientalis musimon*) and Alpine ibex, which potentially used chamois areas, were limited to small areas, having been respectively introduced and reintroduced in the recent past only. Finally, the wild boar (*Sus scrofa*) was occasionally seen in the southern portion of the study area.

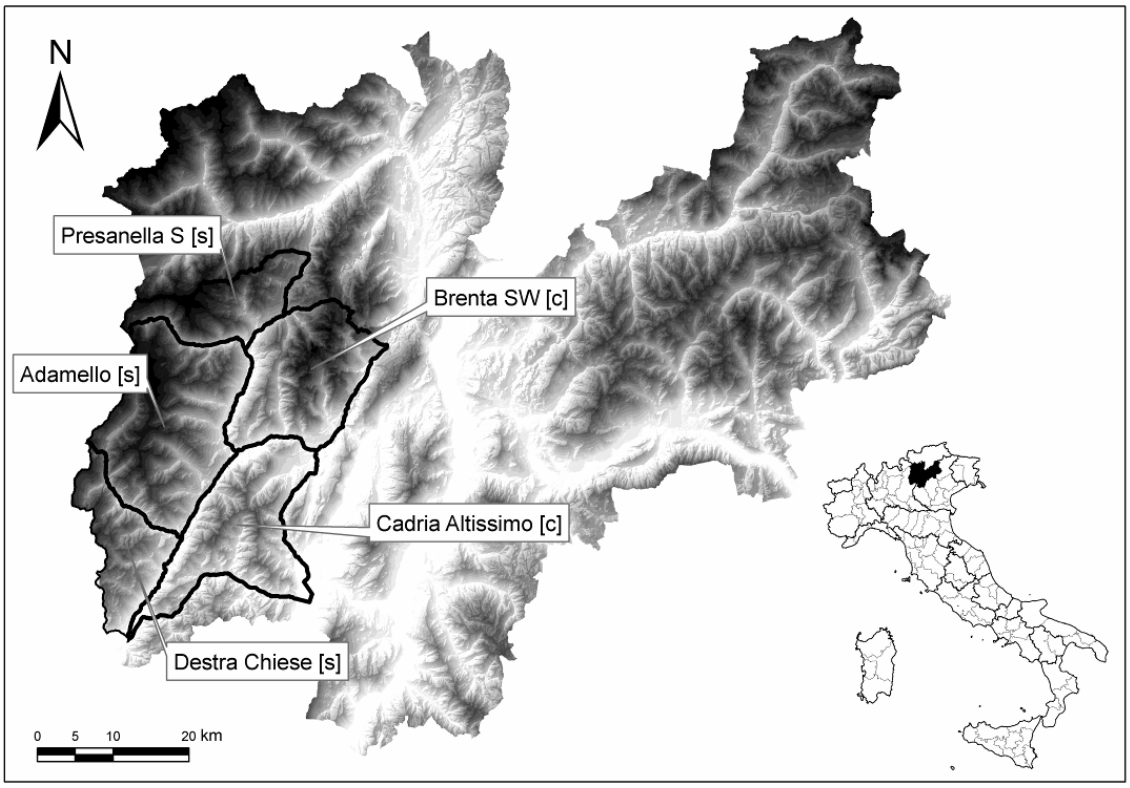

Figure 1 - Map of the Trento Province (Central-Eastern Alps, Italy).
The 5 hunting districts (and corresponding soil type, i.e. either [s] = siliceous substrate or [c] = calcareous substrate) where yearling chamois were legally shot (n = 1,330) during 4 consecutive years are indicated on the map. The darker the colour of the map surface, the higher the elevation (a.s.l.).

Potential terrestrial predators of chamois were represented by a small and yet stable population of brown bear (*Ursus arctos*) and a few lynx (*Lynx lynx*), even though cases of predation by the latter were never reported by game keepers or hunters. Among birds of prey, the golden eagle (*Aquila chrysäetos*) was the only one which may prey upon kids in their first weeks of life.

Data collection and analyses

From 2005 to 2008, we measured the left horn length of 1,330 yearling Alpine chamois shot during 4 consecutive hunting seasons (see Table 1 for sample size). The length of the left horn was measured to the nearest 0.5 millimetre along front side using a flexible ruler. For each shot chamois, we also collected empty body weight, recorded with a digital balance to the nearest 0.1 kilogram.

Kids of chamois were usually born in May (Schröder 1971), and, consequently, yearling Alpine chamois were about 16-19 months old when shot. In order to model the horn size variation in yearling chamois, as a first step a set of candidate independent variables was selected. Each yearling chamois (and its horn length) was assigned to a large data set according to the location in which it was shot. Such data were available on a broad scale (i.e. for the 5 hunting districts) or on a finer scale (i.e. for the 68 municipal reserves) depending on their accuracy. The following independent variables were initially included in the model:

- snow data: (i) monthly average snow cover in cm for each month from November to April, (ii) average snow cover in cm in November-April; (iii) number of days with snow cover of more than 10 cm from November to April (iv) number of days with snow cover of more than 10 cm in March-April (broad scale);

- precipitations: total precipitations (mm) in spring-summer grouped as follows: (i) April-May, (ii) June-July, and (iii) August-September (broad scale);

- spring temperatures: (i) average maximum, (ii) average minimum, and (iii) average temperatures (°C) in spring (March-May, broad scale);

- July temperatures (°C): (i) average maximum, (ii) average minimum, and (iii) average temperatures during the hottest month of the year (July) (broad scale);

- winter temperatures: (i) average maximum, (ii) average minimum, and (iii) average temperatures (°C) during the coldest months (December-February) of the year (broad scale);

- aspect of the shooting place: i.e. the expression of the average mountainside exposure with respect to the North. Originally expressed within the 0-360° range, it was cosine transformed, therefore assuming values from -1 (i.e. shooting place totally on the southern mountainside) to 1 (i.e. totally on the northern mountainside). These data were available on a fine scale, i.e. the average exposure was calculated for each of the 68 council municipal reserves;

- elevation (meters a.s.l.) of the shooting place: (i) maximum, (ii) minimum, and (iii) average elevation of the municipal reserve (n = 68) where chamois were shot in autumn-winter;

- main substrate type: either calcareous or siliceous;

- hunting day: calculated as the number of days following the beginning of the hunting season (7th September);

- chamois population density (number of heads per 100 ha); censuses were performed in each hunting district by both hunters and game keepers, using the block count census technique during the summer, i.e. after the birth period and prior to the hunting season.

		SAMPLE SIZE		
Year	**Hunting districts**	**Females**	**Males**	**Total**
2005	Adamello [s]	57	67	**124**
	Brenta SW [c]	40	48	**88**
	Cadria Altissimo [c]	10	18	**28**
	Destra Chiese [s]	10	9	**19**
	Presanella S [s]	25	32	**57**
2006	Adamello [s]	61	76	**137**
	Brenta SW [c]	39	45	**84**
	Cadria Altissimo [c]	14	17	**31**
	Destra Chiese [s]	6	11	**17**
	Presanella S [s]	26	33	**59**
2007	Adamello [s]	81	91	**172**
	Brenta SW [c]	36	45	**81**
	Cadria Altissimo [c]	14	19	**33**
	Destra Chiese [s]	8	13	**21**
	Presanella S [s]	20	24	**44**
2008	Adamello [s]	58	85	**143**
	Brenta SW [c]	34	45	**79**
	Cadria Altissimo [c]	15	16	**31**
	Destra Chiese [s]	12	11	**23**
	Presanella S [s]	26	33	**59**
	Total	**592**	**738**	**1330**

Table 1 - Sample size.
Yearling chamois (n = 1,330) shot in a south-western area of Trento province, Italy. The sample was split according to hunting season (4 consecutive years), hunting district (with corresponding soil type, i.e. either [s] = siliceous substrate or [c] = calcareous substrate) and sex.

The horn length, i.e. the dependent variable, was the result of lifetime growth. Given that sampled chamois were born in May, about 1 year and half years before they were shot, they only experienced two summers and one winter. As a consequence, we considered the independent variables relevant to the summer period, i.e. temperatures and precipitations, for both summers. However, also spring climatic conditions are potentially able to affect horn growth, by directly influencing the quality of summer pastures, and indirectly affecting the conditions of chamois mothers during late pregnancy, birth, and early lactation. Therefore, we also considered the data relative to the spring period, i.e. temperatures and precipitations, of the first and second year, i.e. during the birth period and when the kids were about 1 y.o., respectively.

Five weather stations and snow-gauges supplied data on temperatures, precipitations and depth of snow cover (Forecasts and Organization Office - Civil Protection and Infrastructures Department – Trento Province, official data). The independent variables were assigned to each chamois by means of ArcGIS 9.3 (ESRI inc. 1999-2008) (Trento Province geological maps, official data).

To avoid collinearity issues (Sokal and Rohlf 1995), we built a correlation matrix (Pearson correlation coefficient) of explanatory variables. For each group of correlated variables, we chose the one that was found to show the highest correlation with the dependent variable.

We modelled the variation of the left horn length by fitting a Linear Mixed Effect (LME) model with Restricted Maximum Likelihood (REML) method. Fixed factors in the model were sex (male, female) and substrate (calcareous, siliceous). The selected covariates were snow cover days (i.e. number of days between November and April with more than 10 cm of snow cover), maximum elevation of the shooting place, aspect (i.e. cos-mountainside), hunting day, total precipitations during the following bimonthly periods of the first (I) and second (II) year of life of shot individuals (rain Apr-May I, rain Jun-Jul I, rain Aug-Sep I, rain Apr-May II, rain Jun-Jul II, rain Aug-Sept II), chamois population density, average maximum temperatures in December-February, average maximum July temperatures during the first and second year of life (max temperature July I, max temperature July II), and average temperatures in March-May, again for both years (mean temperature Mar-May I, mean temperature Mar-May II) (see Table 2 for a complete list of variables). We considered the hunting districts repeated among different years as a random factor, in order to avoid pseudo-replication of data (Machlis et al. 1985). As a starting point, we included all the main effects and all two-way and three-way interactions in the LME model. Then, we modelled the dependent variable excluding not significant interaction terms and including a lower number of fixed factors (see Table 2). Akaike information criterion values (AIC; Burnham and Anderson 1998) were reported for each model. Following Mysterud et al. (2005b), we chose the model with the lowest AIC value as the best model, for which we calculated parameter estimates. All data were successfully checked for normality and homoscedasticity. All analyses were run using the SPSS 13.0 program (SPSS inc. 1989-2004), and all means were reported with standard errors.

RESULTS

The model with the lowest AIC value (Table 2) included substrate and sex as fixed factors. As regards to climatic covariates, the best model included the following: snow cover days (number of days between November and April with more than 10 cm of snow cover), the data relative to rainfalls in the 1st year of life of shot individuals (total precipitation in April-May I, June-July I, and August-September I) and in their 2nd year (only in April-May II), average maximum temperature recorded in December-February, average maximum temperatures recorded in July I and July II, and average mean temperatures in March-May I and II. The best model also included the following environmental covariates: maximum elevation of the municipal reserve, cos-mountainside, hunting day, and chamois population density (Table 2). Finally, the best model included four two-way interactions (Table 2). Parameter estimates (Table 3) showed that predictor variables included by the best model significantly affected horn size, with the exception of chamois population density, average maximum temperature in December-February, and mean temperature in March-May II. Only 2 two-way interactions significantly affected horn size: substrate * snow cover and substrate * cos-mountainside (Table 3).

As shown by parameter estimates (Table 3), males (n = 738) displayed longer horns (159.56 ± 0.66 mm) than females (n= 592, 131.28 ± 0.68 mm). Horns were recorded to be longer among chamois shot on calcareous soils than on siliceous ones, both for females and males (Figure 2). The higher the number of days between November and April with more than 10 cm of snow cover, the shorter the horn size of shot individuals (Table 3). The higher the maximum elevation of the municipal reserve where the chamois was shot, the shorter its horn length (Table 3).

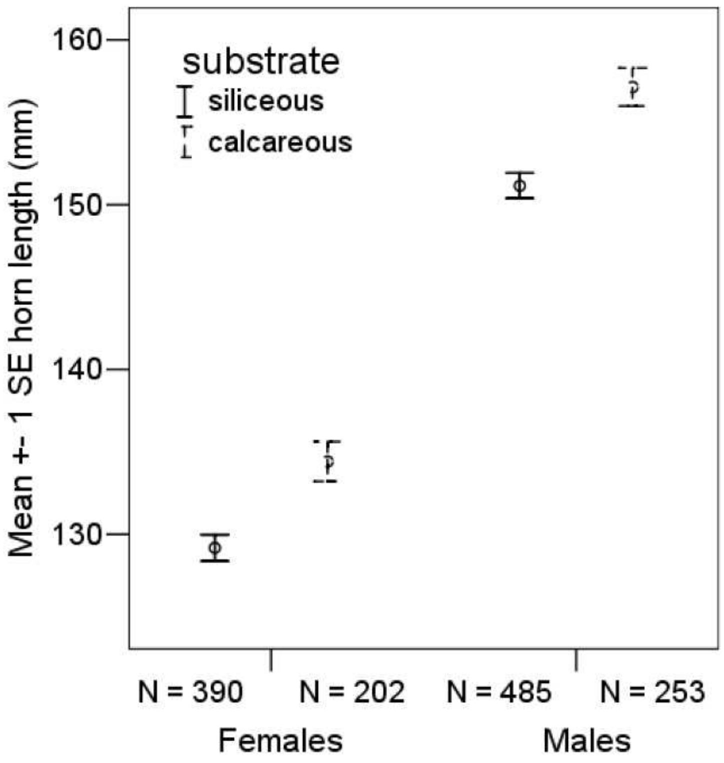

Figure 2 - Comparison of horn length on different soil types.
Horn length (mean mm ± SE) recorded for male and female yearling chamois shot for 4 consecutive years in the province of Trento (Italy) according to the soil type of the shooting place (either siliceous or calcareous substrate).

As the cos-mountainside value decreased (i.e. the shooting occurred on a mountainside increasingly facing the South), the horn length increased (Table 3). The hunting day also played a significant role in the model, given that the later a chamois was shot during the hunting season, the longer was the horn length.

Spring-summer rainfalls recorded in April-May I, June-July I, and August-September I (i.e. during late pregnancy, birth period, and when sampled individuals were kids) and those recorded in April-May II (i.e. when sampled individuals were about 1 y.o.) positively affected horn size (Table 3).

Average maximum July temperature positively affected horn size during the first year, while it negatively affected horn size during the second year of life of shot individuals (Table 3). The higher the average temperature recorded in March-May I, i.e. during late gestation and early lactation, the shorter the horn length.

Sex – F	**Substrate – F**	**Snow cover days – C**	**Rain Apr-May I – C**	**Rain Jun-Jul I – C**	**Rain Aug-Sep I – C**	**Rain Apr-May II – C**	Rain Jun-Jul II – C	Rain Aug-Sep II – C	**Max temperature Dec-Feb – C**	**Max temperature Jul I – C**	**Max temperature Jul II – C**	**Mean temperature Mar-May I – C**	**Mean temperature Mar-May II – C**	**Cos-mountainside – C**	**Maximum elevation – C**	**Hunting day – C**	**Density – C**	**Sex*Substrate**	Sex*Snow cover days	**Sex* Cos-mountainside**	Sex*Maximum elevation	**Substrate*Snow cover days**	Substrate*Maximum elevation	**Substrate* Cos-mountainside**	Snow cover days*Cos-mountainside	Maximum elevation*Cos-mountainside	Snow cover days*Density	Substrate*Snow cover days * Cos-mountainside	Substrate*Maximum elevation* Cos-mountainside	AIC	ΔAIC
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	11289.61	57.13
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		11281.16	48.68
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			11279.40	46.92
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				11274.35	41.88
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x				11264.28	31.80
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x		x	x	x	x	x				11263.02	30.54
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				x	x	x	x	x				11262.61	30.13
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x	x	x				11259.74	27.27
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x		x				11256.80	24.32
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x						11248.58	16.10
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x								11246.99	14.51
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x		x						11240.72	8.24
x	x	x	x	x	x	x			x	x	x	x		x	x	x	x	x		x		x		x						11239.32	6.84
x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x		x		x		x						11236.87	4.39
x	x	x	x	x	x	x				x	x	x	x	x	x	x	x	x		x		x		x						11234.32	1.84
x	x	x	x	x	x	x			x	x	x	x	x	x	x	x		x		x		x		x						11233.56	1.08
x	**x**	**x**	**x**	**x**	**x**	**x**			**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**		**x**		**x**		**x**						**11232.48**	**0.00**

Table 2 - Model selection.

Selection of models explaining horn length variation (dependent variable) in yearling chamois shot during 4 consecutive years in the Trento province, Italy. [x = terms included in each model. AIC = Akaike information criterion; ΔAIC = difference in the AIC value between a given model and the most parsimonious one (with the lowest AIC)]. Parameter estimate was run for the most parsimonious model (in bold) (see Table 3). See the text for details on predictor variables and their computation.

Parameter	Estimate	SE	t	P
Intercept	**140.756**	**31.651**	**4.447**	**<0.001**
Sex [females]	**-23.370**	**1.530**	**-15.273**	**<0.001**
Substrate [siliceous]	**-18.809**	**7.171**	**-2.623**	**0.009**
Snow cover days	**-0.298**	**0.076**	**-3.928**	**<0.001**
Rain Apr-May I	**0.484**	**0.141**	**3.430**	**0.001**
Rain Jun-Jul I	**0.107**	**0.052**	**2.081**	**0.038**
Rain Aug-Sep I	**0.186**	**0.055**	**3.368**	**0.001**
Rain Apr-May II	**0.052**	**0.015**	**3.614**	**<0.001**
Mean temperature Mar-May I	**-7.509**	**1.847**	**-4.066**	**<0.001**
Mean temperature Mar-May II	3.569	1.833	1.947	0.052
Max temperature Jul I	**0.765**	**0.259**	**2.953**	**0.003**
Max temperature Jul II	**-2.013**	**0.788**	**-2.554**	**0.011**
Max temperature Dec-Feb	0.565	0.440	1.283	0.200
Cos-mountainside	**-5.748**	**1.800**	**-3.192**	**0.001**
Maximum elevation	**-0.004**	**0.002**	**-2.636**	**0.008**
Hunting day	**0.100**	**0.019**	**5.351**	**<0.001**
Density	-0.086	0.679	-0.127	0.899
Sex [females] *Substrate [siliceous]	0.931	1.853	0.502	0.616
Sex [females] * Cos(mountainside)	-0.615	1.630	0.377	0.706
Substrate [siliceous] * Snow cover days	**0.101**	**0.048**	**2.093**	**0.037**
Substrate [siliceous] * Cos-mountainside	**4.050**	**1.961**	**2.065**	**0.039**

Table 3 - Parameter estimates and test statistics.
Parameter estimates and test statistics for the best model characterized by the lowest AIC value (AIC = 11232.48, see Table 2) and explaining horn length variation in yearling chamois. See the text for details on predictor variables and their computation.

Only 2 two-way interactions significantly affected horn size (Table 3, Figure 3). Environmental variables such as snow cover (number of days with more than 10 cm of snow cover) and cos-mountainside had effects which varied according to soil type. During an average winter (about 100 days with more than 10 cm of snow cover, Figure 3a) chamois horns were recorded to be longer in individuals living in calcareous areas than in individuals living in siliceous areas. The increase of snow cover duration seemed to affect horn length in chamois only shot in areas with calcareous soil. The horn length was affected by the cos-mountainside to a different degree which varied according to the soil type (Figure 3b), the difference being greater in the northernmost mountainside where the horns of chamois shot in calcareous areas were found to grow longer and, in contrast, those of chamois shot in siliceous areas were found to be shorter.

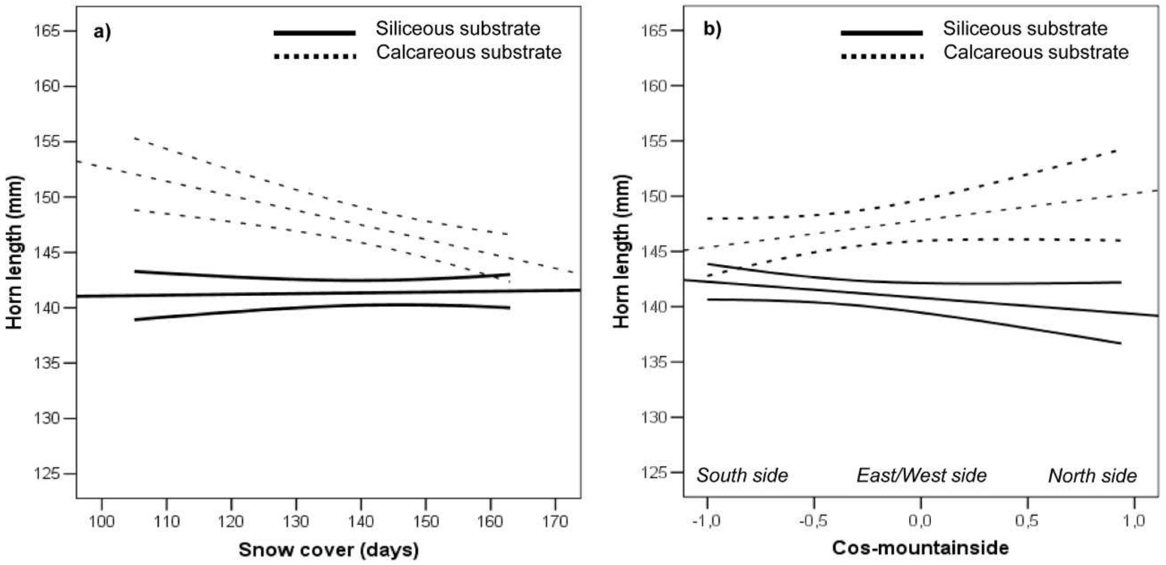

Figure 3 - Effect of interaction factors (substrate*snow cover and substrate*mountainside) on horn length.
(a) Combined effect of snow cover (i.e, number of days from November to April with more than 10 cm of snow cover) and soil type (either calcareous or siliceous substrate) of the shooting place on the left horn length in yearling chamois shot during 4 consecutive years in the province of Trento, Italy.
(b) Combined effect of mountainside and soil type of the shooting place on the left horn length in yearling chamois. Mountainside (originally expressed within the 0-360° range) was cos-transformed, thus assuming values from -1 (i.e. shooting place on the southern mountainside) to 1 (i.e. on the northern mountainside).
Linear regression lines and 95% Confidence Intervals describing horn length variations were reported on both graphs.

DISCUSSION

In ungulates, much attention has been paid to the role of horns and antlers as secondary sexual traits. In polygynous species males with large horns usually dominate other males and have a greater chance to reproduce (Coltman et al. 2002, Bergeron et al. 2010). Consequently, large-horned males enjoy a substantial reproductive advantage. Among *Rupicaprinae*, the horns of males are usually only 10 to 20% longer and thicker than those of females, and sexual dimorphism is mostly due to the greater horn growth reported in males during the first few years of life (Pérez-Barberia et al. 1996). This sexual dimorphism was confirmed by our study on Alpine chamois, with male yearlings showing 15% longer horns than females of the same age. We also found a positive relationship between hunting day, calculated as the number of days following the beginning of the hunting season (7th September), and horn length. This result is consistent with a study on Cantabrian chamois (Pérez-Barberia et al. 1996), which showed an inertial horn growth (before the winter break) also in late autumn, especially in subadults. The finding that even young Alpine chamois were able to invest in horn growth in the face of unfavourable climate shows that this species is highly adapted to mountain environments.

Horns were found to be longer in chamois shot in calcareous areas than in siliceous ones, confirming that soil type can indirectly constrain their growth. The quality of grassland communities to be found on calcareous substrates is higher than that of communities on siliceous ones (i.e. species richness; Grime 1979, Cavallero et al. 2007). As suggested by several authors (Duchaufour 1989, 1997, Gensac 1990, Rameau et al. 1993), the higher nutrient availability on calcareous soils when compared to siliceous soils is accompanied by higher plant productivity. Plant communities growing on siliceous soil have structural characteristics that can also reduce digestion efficiency (Laca et al. 2001), and, consequently, may negatively affect the energy intake of the animals feeding on them. This propriety can also have a negative effect on horn growth and size in chamois. Winnie et al. (2008) showed that the African buffalo modified spatial behaviour and foraging strategies according to the geologic substrate features (granite *versus* basalt) and to the corresponding differences in food quality and quantity. Indeed, granite areas are generally less fertile than areas characterized by other substrates, due to small nitrogen pools that tend to slowly turn over (Winnie et al. 2008). Winnie et al. (2008) argued for the varying effects of different soils on buffalo herd dynamics, distribution, and population dynamics.

As predicted, snow cover recorded during the winter before the shooting negatively affected horn length. Harsh winters are generally thought to affect juvenile body condition and survival by increasing the probability of starvation, through a combination of higher thermoregulatory costs and decreased forage availability due to a deep snow cover (Forchhammer et al. 1998). In our study, winter temperatures were included in the best model but did not significantly affect horn sizes. Therefore, snow cover was the only winter variable which was found to negatively affect body condition and indirectly limit the investment in secondary sexual traits. Therefore, we argued that the decrease in food availability due to persistent snow cover may prove more costly to chamois than the thermoregulatory costs linked to low winter temperatures. Winters are harsher in northern mountainsides on account of the lower solar radiation reported there and this aspect may negatively affect horn growth, also by virtue of the longer duration of snow cover (Jonas et al. 2008), as confirmed by the significant results of the mountainside predictor variable in our best model.

Moreover we found two interactions between substrate type and both snow cover and mountainside (Figure 3a and 3b). There were differences in horn length between substrate types in southern exposure but they become pronounced in northern exposures with longer horn length on calcareous rocks than on siliceous ones: horn size on calcareous rocks decreases when turning from North to South exposure (Figure 3b). Furthermore we found that horn length decreased with increasing snow cover on calcareous substrates but not on siliceous substrates (Figure 3a). As Michalet et al. (2002) argued in damp conditions (high rainfall and/or deep soils and/or northern exposure) calcareous soils are more nitrogen rich than siliceous ones because of higher amount in clay in the former (enhancing organic matter decomposition and thus nitrogen availability), whereas in dry conditions calcareous soils are less or as nitrogen-rich than siliceous ones, because the mesh of the former induces a high water stress for plants. Thus our results showed that horn length was positively affected by calcareous substrates especially in wet conditions, i.e. in North exposure, and that snow cover duration plays an important role because increasing snow cover in North exposure decreases the length of the growing season and thus the positive fertility effect due to calcareous soils in wet conditions. As North exposed slopes are deciding to promote the marked differences observed between calcareous and siliceous environment the whole system is very sensitive to weather condition and finely tuned on the amount of snow cover: North slopes are the best environment on calcareous soil but they are also the one which may suffer most for a strong winter with high snow cover. As shown by Cavallero et al. (2007), vegetation communities growing on siliceous substrates in the Italian Alps show a higher resistance to winter conditions than vegetation of higher quality growing on calcareous soil, ensuring a constant trophic level availability in different environmental conditions as confirmed by Michalet et al. (2002) who found an increase in crude biomass and vegetation cover from calcareous to siliceous substrate. Moreover, opal silica improves plant resistance to mechanical stress and pathogens (Raven 1983). So siliceous and calcareous soils seem to represent two extremes of environmental sensitivity of plant communities. In the former we may expect more constant conditions whether calcareous communities may draw pronounced variability in plant biomass and quality. It is likely that Alpine chamois population dynamics (with special reference to population recruitment and survival) in our study would differ from area to area according to their different geological features. Accordingly, further studies on this topic would be valuable.

Another variable able to affect horn size was the elevation of the areas where chamois were shot (i.e. autumn-winter ranges): the higher the elevation of such areas, the higher the probability to find snow cover. The depth and persistence of snow cover were reported to affect the costs of locomotion (Parker et al. 1984) and availability of browsing (Post and Stenseth 1999). Snow cover was already shown to be correlated with winter mortality of Alpine chamois (Jonas et al. 2008) and Pyrenean chamois (*Rupicapra pyrenaica*, Gonzalez and Crampe 2001). Similarly, as resources became scarce, young bighorn rams were reported to allocate an increasing proportion of those resources to body growth, rather than to horn growth (Festa-Bianchet et al. 2004). This suggest that chamois living at higher elevation pay the cost of living in a suboptimal environment possibly as a pay off for a safer environment and reduced intraguild competition. It is well known that this species can live as low as 400 m a.s.l. (Apollonio et al. 2010) however this implies a stronger vulnerability to predators (e.g. wolves), that usually has a limited share of this ungulates in their diet (Gazzola et al. 2005) in high altitude environments, and the coexistence with a number of other wild ungulate species.

As shown by our analyses on yearling chamois and unlike antlers in cervids, horn growth in bovids is a cumulative process able to reflect environmental and body conditions experienced throughout the individual’s life history. Diverse environmental factors recorded during both years of life of shot individuals as well as during the late pregnancy of mothers, influenced horn growth and size. For instance, abundant spring rainfalls had been shown to favour horn growth through the increase of primary production (Lesage et al. 2000) and our results confirmed the importance of precipitation during this critical period of the year, with the rainfall recorded in April-May of both years being able to positively enhance horn growth. In mountain goats (*Oreamnos americanus*) of both sexes, horn length increased as early-June faecal crude proteins increased, as a consequence of improved meadow quality (Gendreau et al. 2005). Interestingly, rainfall recorded in April-May I (late pregnancy-birth-early lactation) enhanced meadow quality and quantity thus improving mothers' milk quality and favouring the horn growth of kids. As reported by Oftedal (1984), one major determinant of juvenile phenotypic quality in mammals is the quantity and quality of food resources available to the mother during lactation and the last third of gestation. The importance of maternal lactation (total milk production and percent weight milk protein) in relation to the length of secondary sexual traits was also confirmed by Gómez (2004). However, high temperatures recorded in March-May may be a constraint on the latter phenomenon, accounting for the early degradation of meadows and the lower quality of mothers' milk, as indicated by the significant role played by spring temperatures recorded during the first year in the best model. On this subject, Toïgo et al. (1999) found the horn growth in young male ibexes to be limited in those years when climatic conditions favoured early vegetation growth (e.g. high temperatures). In these years, the onset of vegetation on alpine meadows occurred earlier (Toïgo et al. 1999), and, consequently, when kids were able to feed on them the quantity of protein available was lower than usual. The influence of spring climatic conditions on meadow quality and, consequently, on life history and population dynamics of ungulates, was confirmed by Pettorelli et al.'s (2007) findings: warmer winters and springs were shown to affect green-up and timing of vegetation onset, thus influencing juvenile growth in three alpine ungulate populations.

Our results confirm that environmental factors may have contrasting effects on body condition and horn size according to age, especially during the early phases of the individual life history. For instance, summer precipitation positively affected horn growth in chamois when they were kids (rainfalls in June-July I and August-September I), but not in the following year, when they had grown into yearlings. Likewise, the high temperatures recorded during the first summer seemed to favour the horn growth, presumably on account of the low thermoregulatory costs kids had to pay to avoid hypothermia. Undoubtedly, hypothermia and risk of infection are the most important causes of death after predation in juvenile ungulates (Dwyer 2008). In the second year, summer temperatures had an opposite effect, with lower temperatures favouring the horn growth. It can thus be argued that during the first year high temperatures helped kids to avoid hypothermia (positive effect), whereas in the second year it decreased productivity of meadows (negative effect).

In our study, horn growth did not appear to be density-dependent. Even though we included chamois as a variable in our best model, its contribution to explaining horn size variation was not significant. In ungulates, juveniles are more susceptible than adults to density-dependent resource limitations (Gaillard et al. 1998), and shorter horns may be expected in highly populated areas. In fact, high densities could negatively affect ungulate populations through increased forage competition (Post and Stenseth 1999). Be that as it may, the density variation in our hunting districts was not pronounced, ranging from 8.4 to 15.4 heads/100 ha. Further investigations on this topic (including low- and high- density populations, i.e. 1-2 heads/100 ha and 30 heads/100 ha, respectively) are needed to explain if and how density-dependent processes may affect resource availability and, consequently, body size and horn size in the Alpine chamois.

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Chapter 2

Differential investment in horn length and body mass in male and female yearling Alpine chamois (*Rupicapra rupicapra*)

Differential investment in horn length and body mass in male and female yearling Alpine chamois (*Rupicapra rupicapra*)

Roberta Chirichella[1,2], Simone Ciuti[1], Michele Rocca[3], and Marco Apollonio[1]

1 - Department of Zoology and Evolutionary Genetics, University of Sassari,
via Muroni 25, I-07100, Sassari, Italy

2 - Adamello Brenta Nature Park,
via Nazionale 24, I-38080, Strembo (TN), Italy

3 - Hunting association of the Trento province (Associazione Cacciatori Trentini),
via Guardini 41, I-38121, Trento, Italy

ABSTRACT

The role of ecological processes able to drive the trade off between body mass and horn size development in the early stages of individual life histories in ungulates is particularly interesting, as it is often crucial for yearlings to quickly gain body mass rather than horn size. Consequently, it is important to disentangle the factors which may either promote or restrain the ratio of horn length to body mass (H/W).

Given that there are many ecological factors able to modify horn length in yearling Alpine chamois after the lactation period, in this study we analysed if males and females performed the same trade off between horn and body growth. More in detail, we described how this bovid allocates resources in body mass and horn development living in different environmental and climatic conditions, and with a variable density rate. We modelled 1,685 yearling Alpine chamois (756 females and 929 males) shot during 5 consecutive hunting season (5 years, from 2005 to 2009) in 5 hunting districts in the central-eastern Italian Alps. We found that environmental characteristic (i.e. substrate type), winter weather conditions (i.e. snow cover duration and winter temperature), and local density rates may modify H/W ratio. More in details on siliceous substrate, with harsher winter condition and living in higher density rates, the H/W ratio were lower, that is horns were shorter for a given body mass. Moreover, either males or females showed a high investment in secondary sexual traits (i.e. horn growth) in good conditions but females on siliceous substrate and after winter with longer snow cover duration reduced this investment. In general, the trade off between body weight and horn size confirmed that the early stage of development is a deciding step in the individual life history of ungulate. Thus, the ecological factors able to modify H/W ratio may negatively affect the gain of a proper body size of chamois, especially in males, and it could have strong impacts on the winter survival of both sexes, and, more in general, on its population dynamic parameters.

INTRODUCTION

The importance of body mass and secondary sexual traits in ecology and life history evolution cannot be understated (Peters 1983, von Hardenberg et al. 2004), especially in herbivores polygynous species. Among ungulates, it is often crucial for juveniles and yearlings to quickly gain body size and, at the same time, to allocate resources to antlers or horns growth (e.g. Pérez-Barberia et al. 1996). This is especially valid for those bovid species where horns grow mainly in the first years of life and their size can be deciding for future individual success. As shown for species living in temperate areas, large and heavy juveniles of both sexes enjoy higher survival rates over their first winter than lighter and smaller ones (Loison et al. 1999, Côté and Festa-Bianchet 2001). Moreover, unlike cervids' antlers, which are renewed year after year, the early development of permanent horns is a critical life-step for bovids. Given that the development of horns and body size is massive during the first years of life (Festa-Bianchet and Côté 2008), it is crucial analysing the factors affecting the choice to invest more resources in body mass rather than in horn size.

Fecundity of females is strongly influenced by body mass so that fast-growing females reproduce earlier in life than slow-growing females (Sadleir 1969, Albon et al. 1983, Sæther and Haagenrud 1983, Reimers 1983, Gaillard et al. 1992, Garel et al. 2005). For males of polygynous species, access to females depends on intrasexual competition and body size positively influences male reproductive success (Clutton-Brock et al. 1988, Skogland 1989, McElligott et al. 2001). Moreover, males with large horns usually dominate other males and have a greater chance to reproduce (Coltman et al. 2002, Bergeron et al. 2010). Consequently, large-horned males enjoy a substantial reproductive advantage.

In mountain goats (*Oreamnos americanus*; Festa-Bianchet and Côté 2008) in both sexes, horn length of yearlings is positively correlated with body mass, but even when effects of sex and mass were considered, horn length increased with early-June fecal crude protein. That may suggest that yearlings allocated more resources to body rather than to horn growth when resource were scarce, as reported in bighorn rams (*Ovis canadensis*, Festa-Bianchet et al. 2004).

Among *Rupicaprinae*, the horns of males are usually only 10 to 20% longer and thicker than those of females, and sexual dimorphism is mostly due to the greater horn growth reported in males during the first few years of life (Pérez-Barberia et al. 1996). In this context, Alpine chamois (*Rupicapra rupicapra*) is an ideal case study for investigating the trade off between body mass and secondary sexual traits investment. As a matter of fact, 60-70% of horn growth takes place in the first 2 years of life in both males and females (Schröder 1971, Bassano et al. 2003). Moreover, horns have an importance in intrasexual and intersexual social relationship for both sexes (Krämer 1969), but little is known about the causes that lead an individual to choose how allocate resource during the first period of their life.

Given that there are many variables able to modify horn length in yearling Alpine chamois after the lactation period (see Chapter 1), in this study we analysed if males and females showed the same trade off between horn and body growth. More in detail, we described how this bovid allocates resources in body mass and horn development living in different environmental and climatic conditions, and with a variable density rate. We analysed 1,685 yearling Alpine chamois (756 females and 929 males) shot during 5 consecutive hunting season (5 years, from 2005 to 2009). Yearlings were legally shot in autumn-winter (when about 1.5 y.o.) in the central-eastern Italian Alps, in 5 hunting district with different local chamois density. Thus, by controlling the effect of the age (the same for the whole sample) and by comparing populations living on different substrate, in different climatic characteristic and with different local density condition, we investigated if males and females direct more resources to body growth rather than horn growth in worse conditions (i.e. shorter horn length for a given body mass). This aspect is crucial to be considered in population dynamic because the trade off between body mass and horn size investment might increase the yearling survival probability, possibly to the detriment of their short-term reproductive success, shaping demographic parameters of chamois populations.

METHODS

Study area

This study was carried out in the central-eastern Italian Alps (Figure 1), in a 121,906 ha-wide area of the Trento Province (46°02'N; 10°38'E). This mountainous area (Figure 1) was subdivided into 2 main sectors: the Adamello-Presanella Massif (51,847 ha), characterized by siliceous substrate, and the Brenta and Cadria Altissimo Massif (70,059 ha), characterized by calcareous substrate with sedimentary rocks (mainly limestone and dolomite). This soil composition accounts for the natural development of botanic endemisms and peculiar plant associations, especially in the area above the tree line. Two vegetation patterns were detectable corresponding to the two soil compositions. Typical primary grassland covering the calcareous substrate was mainly composed by *Sesleria albicans* and *Carex firma*, whereas grassland covering the siliceous substrate was composed by *Festuca scabriculmis* and *Carex curvula* (Adamello Brenta Nature Park – digitized official data). Elevation ranged from 65 to 3,558 m a.s.l., with a mean of 1,630 m a.s.l.. The tree line was around 2,000 m a.s.l.. The study area consisted of 5 hunting districts (Figure 1) where chamois hunting with rifles was allowed from mid-September to mid-December. In the Trento Province hunting was controlled through licenses issued by local wildlife boards, and shot chamois were checked in municipal reserves (n = 68) corresponding to further subdivisions of the 5 hunting districts.

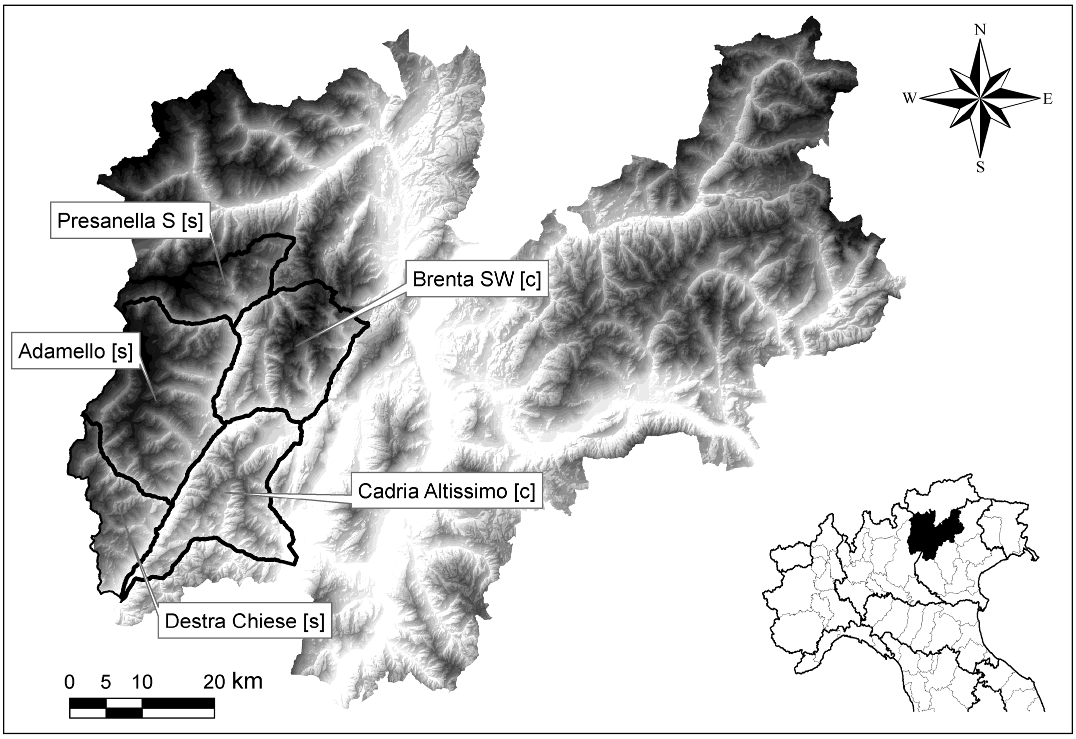

Figure 1 - Map of the Trento Province (Central-Eastern Alps, Italy).
The 5 hunting districts (and corresponding soil type, i.e. either [s] = siliceous substrate or [c] = calcareous substrate) where yearling chamois were legally shot (n = 1,685) during 5 consecutive years are indicated on the map. The darker the colour of the map surface, the higher the elevation (a.s.l.).

As regards other ungulates, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) were abundant but rarely used the areas above the tree line, which were commonly populated by the Alpine chamois. In contrast, mouflon (*Ovis orientalis musimon*) and Alpine ibex, which potentially used chamois areas, were limited to small areas, having been respectively introduced and reintroduced in the recent past only. Finally, the wild boar (*Sus scrofa*) was occasionally seen in the southern portion of the study area.

Potential terrestrial predators of chamois were represented by a small and yet stable population of brown bear (*Ursus arctos*) and a few lynx (*Lynx lynx*). Among birds of prey, the golden eagle (*Aquila chrysäetos*) was the only one which might prey upon kids in their first weeks of life.

Data collection and analyses

From 2005 to 2009, we measured the left horn length of 1,685 yearling Alpine chamois shot during 5 consecutive hunting seasons (see Table 1 for sample size). The length of the left horn was measured to the nearest 0.5 millimetre along front side using a flexible ruler. For each shot chamois, we also collected empty body weight, recorded with a digital balance to the nearest 0.1 kilogram.

Kids of chamois were usually born in May (Schröder 1971), and, consequently, yearling Alpine chamois were about 16-19 months old when shot. In order to model the differential investment in horn size and body mass in male and female yearling chamois, we considered the ratio of horn length (mm) to eviscerated weight (kg) (H/W). Each yearling chamois (and its H/W) was assigned to a large data set according to the variable able to modify horn length in yearling Alpine chamois after the lactation period (see Chapter 1).

Such data were available on a broad scale (i.e. for the 5 hunting districts) or on a finer scale (i.e. for the 68 municipal reserves) depending on their accuracy. The following independent variables were initially included in the model:

- main substrate type: either calcareous or siliceous;
- chamois population density (number of heads per 100 ha); censuses were performed in each hunting district by both hunters and game keepers, using the block count census technique during the summer, i.e. after the birth period and prior to the hunting season;
- maximum elevation (meters a.s.l.) of the municipal reserve (n = 68) where chamois were shot in autumn-winter;

		Sample size		
Year	**Hunting districts**	**Females**	**Males**	**Total**
2005	Adamello [s]	57	67	**124**
	Brenta SW [c]	40	48	**88**
	Cadria Altissimo [c]	10	18	**28**
	Destra Chiese [s]	10	9	**19**
	Presanella S [s]	25	32	**57**
2006	Adamello [s]	61	76	**137**
	Brenta SW [c]	39	45	**84**
	Cadria Altissimo [c]	14	17	**31**
	Destra Chiese [s]	6	11	**17**
	Presanella S [s]	26	33	**59**
2007	Adamello [s]	81	91	**172**
	Brenta SW [c]	36	45	**81**
	Cadria Altissimo [c]	14	19	**33**
	Destra Chiese [s]	8	13	**21**
	Presanella S [s]	20	24	**44**
2008	Adamello [s]	58	85	**143**
	Brenta SW [c]	34	45	**79**
	Cadria Altissimo [c]	15	16	**31**
	Destra Chiese [s]	12	11	**23**
	Presanella S [s]	26	33	**59**
2009	Adamello [s]	69	80	**149**
	Brenta SW [c]	40	55	**95**
	Cadria Altissimo [c]	12	20	**32**
	Destra Chiese [s]	10	15	**25**
	Presanella S [s]	33	21	**54**
	Total	**756**	**929**	**1685**

Table 1 - Sample size.
Yearling chamois (n = 1,685) shot in a south-western area of Trento province, Italy. The sample was split according to hunting season (5 consecutive years), hunting district (with corresponding soil type, i.e. either [s] = siliceous substrate or [c] = calcareous substrate) and sex.

- aspect of the shooting place: i.e. the expression of the average mountainside exposure with respect to the North. Originally expressed within the 0-360° range, it was cosine transformed, therefore assuming values from -1 (i.e. shooting place totally on the southern mountainside) to 1 (i.e. totally on the northern mountainside). These data were available on a fine scale, i.e. the average exposure was calculated for each of the 68 council municipal reserves;

- snow data: number of days with snow cover of more than 10 cm from November to April (broad scale);

- winter temperatures: average maximum temperatures (°C) during the coldest months (December-February) of the year (broad scale);

- spring temperatures: average temperatures (°C) in spring (March-May, broad scale);

- precipitations: total precipitations (mm) in April-May (broad scale);

- July temperatures (°C): average maximum temperatures during the hottest month of the year (July) (broad scale);

- hunting day: calculated as the number of days following the beginning of the hunting season (7th September);

Five weather stations and snow-gauges supplied data on temperatures, precipitations and depth of snow cover (Forecasts and Organization Office - Civil Protection and Infrastructures Department – Trento Province, official data). The independent variables were assigned to each chamois by means of ArcGIS 9.3 (ESRI inc. 1999-2008) (Trento Province geological maps, official data).

We modelled the variation of the H/W by fitting a Linear Mixed Effect (LME) model with Restricted Maximum Likelihood (REML) method. Fixed factors in the model were sex (male, female) and substrate (calcareous, siliceous). The other independent variables were included in the model as covariates (see Table 2 for a complete list of variables). We considered the hunting districts repeated among different years as a random factor in order to avoid pseudo-replication of data (Machlis et al. 1985).

As a starting point, we included all the main effects and all two-way interactions between sex and each other independent variable in the LME model. Then, we modelled the dependent variable excluding not significant interaction terms and including a lower number of fixed factors (see Table 2). Akaike information criterion values (AIC; Burnham and Anderson 1998) were reported for each model. Following Mysterud et al. (2005), we chose the model with the lowest AIC value as the best model, for which we calculated parameter estimates. All data were successfully checked for normality and homoscedasticity. All analyses were run using the SPSS 13.0 program (SPSS inc. 1989-2004), and all means were reported with standard errors.

RESULTS

Among all the factors able to modify the yearling chamois horn size, not all of them drove a differential investment in horn size and body mass and only two of them generated a different tactic in male and female yearling chamois. In particular, the model with the lowest AIC value (Table 2) included substrate and sex as fixed factors. As regards to covariates, the best model included the following: local density, snow cover days (number of days between November and April with more than 10 cm of snow cover), average maximum temperature recorded in December-February, and hunting day (Table 2). Only 2 two-way interactions significantly affected the ratio of horn length to eviscerated weight: sex * substrate and sex * snow cover (Table 2).

There are some variables able to modify the H/W ratio in the same way for males and females: local density (parameter estimate for the best model: -0.044 ± 0.018), snow cover days (parameter estimate for the best model: -0.003 ± 0.002), average maximum temperature recorded in December-February (parameter estimate for the best model: 0.029 ± 0.014), and hunting day (parameter estimate for the best model: 0.001 ± 0.001) (Figure 2).

Sex	X	X	X	X	X	X	X	X	X	X	X	X	**X**
Substrate	X	X	X	X	X	X	X	X	X	X	X	X	**X**
Density	X	X	X	X	X	X	X	X	X	X	X	X	**X**
Altitude	X	X	X	X	X	X	X	X	X				
Aspect	X	X	X	X	X	X	X	X	X	X	X	X	
Snow cover	X	X	X	X	X	X	X	X	X	X	X	X	**X**
T max winter	X	X	X	X	X	X	X	X	X	X	X	X	**X**
T spring	X	X	X	X	X	X	X	X	X	X	X		
Rain April-May	X	X	X	X	X	X	X	X	X	X			
T max July	X	X	X	X	X	X	X	X					
Hunt day	X	X	X	X	X	X	X	X	X	X	X	X	**X**
Substrate * Sex	X	X	X	X	X	X	X	X	X	X	X	X	**X**
Density * Sex	X	X	X	X	X	X	X						
Altitude * Sex	X	X	X	X	X								
Aspect * Sex	X												
Snow cover * Sex	X	X	X	X	X	X	X	X	X	X	X	X	**X**
T max winter * Sex	X	X	X	X	X	X							
T spring * Sex	X	X											
Rain Apr-May * Sex	X	X	X	X									
T max July * Sex	X	X	X										
AIC	5503.814	5500.957	5497.306	5492.663	5482.422	5478.708	5469.776	5465.696	5459.144	5454.359	5447.394	5446.055	**5443.707**
ΔAIC	60.107	57.250	53.599	48.956	38.715	35.001	26.069	21.989	15.437	10.652	3.687	2.348	**0**

Table 2 - Model selection.

Selection of models explaining horn length / eviscerated weight variation (H/W mm/kg; dependent variable) in yearling chamois shot during 5 consecutive years in the Trento province, Italy. [x = terms included in each model. AIC = Akaike information criterion; ΔAIC = difference in the AIC value between a given model and the most parsimonious one (with the lowest AIC)]. Parameter estimate was run for the most parsimonious model (in bold). See the text for details on predictor variables and their computation.

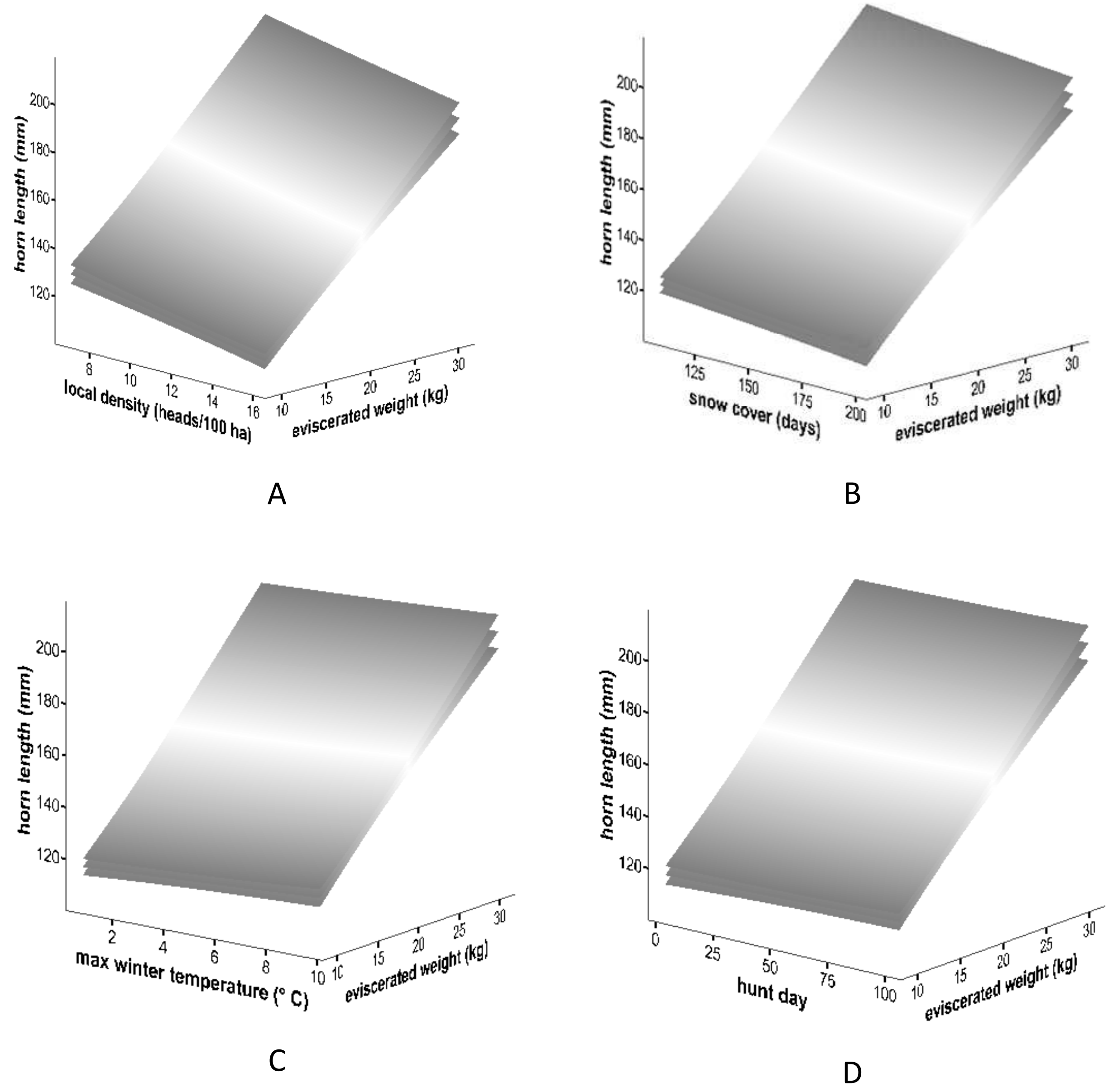

Figure 2 - Relationship between horn length and eviscerated weight in different conditions.
Effect of local density (panel A), snow cover (panel B), average of maximum temperature in November-February period (panel C), and hunting day (panel D) on horn length (mm) and eviscerated weight (kg) recorded for yearling chamois shot for 5 consecutive years in the province of Trento (Italy). Linear regression surface and 95% Confidence Intervals describing horn length variations were reported in the graphs.

Two factors induced a differential investment in horn length and body mass for males and females: living on different substrate (Figure 3) and spending the previous winter in harsh snow conditions (Figure 4). More in details, as the local density and the snow cover value increased, the dependent variable decreased, that is shorter horns for a given body mass; on the contrary, as the average of maximum temperature during the coldest months increased, the H/W value increased (i.e. longer horns for a given body mass). The hunting day also played a significant role in the model, given that the later a chamois was shot during the hunting season, the longer was the horn length and the lower was the eviscerated weight.

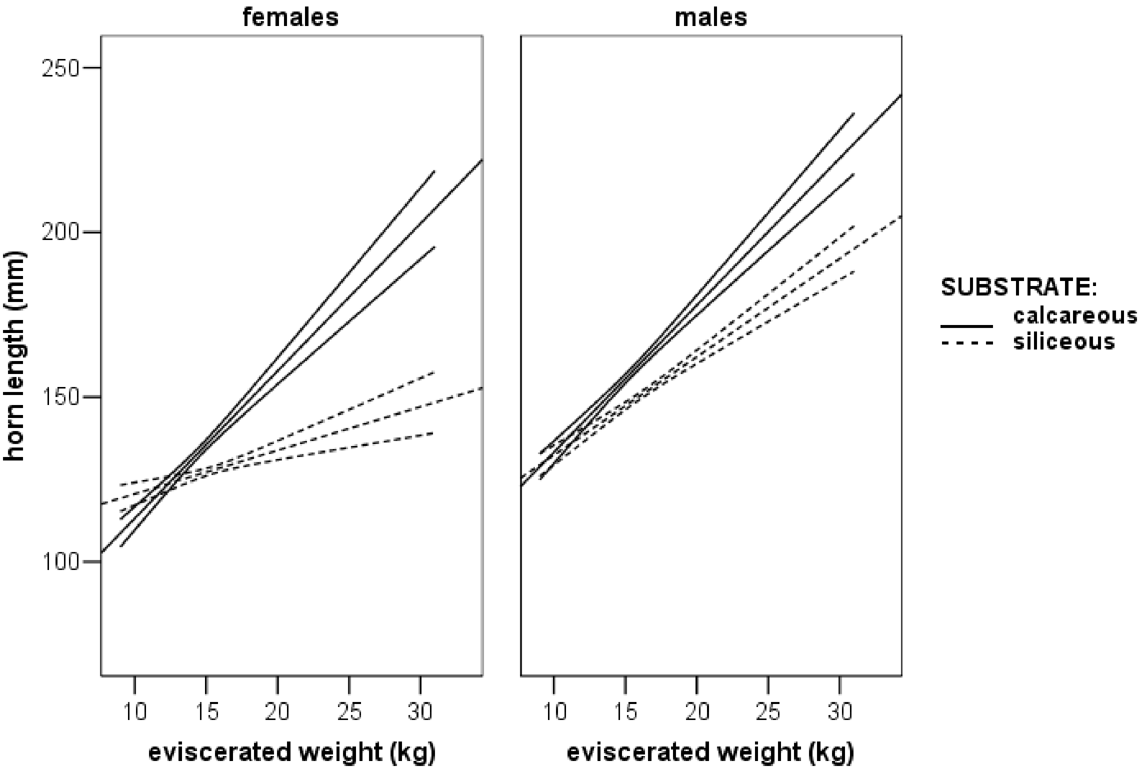

Figure 3 - Relationship between horn length and eviscerated weight on different soil type.
Effect of different substrate on the horn length (mm) and eviscerated weight (kg) ratio recorded for male (right panel) and female (left panel) yearling chamois shot for 5 consecutive years in the province of Trento (Italy). Linear regression lines and 95% Confidence Intervals describing horn length variations were reported in the graphs.

Either males (H/W: n = 929, 9.2 ± 0.04 mm/kg) or females (H/W: n = 756, 8.8 ± 0.05 mm/kg) showed an higher investment in secondary sexual traits (i.e. horn growth) in relation to more productive substrate type (i.e. calcareous soil [males: N = 387, 10.3 ± 0.07; females: N = 300, 9.3 ± 0.07] and milder winter [parameter estimate for the best model: $\text{sex}_{(\text{female})}$*winter snow cover -0.006 ± 0.002]), but females reduced their investment in poor substrate type conditions (i.e. siliceous soil [males: N = 542, 9.4 ± 0.05; females: N = 456, 8.4 ± 0.06]) and harsher winter.

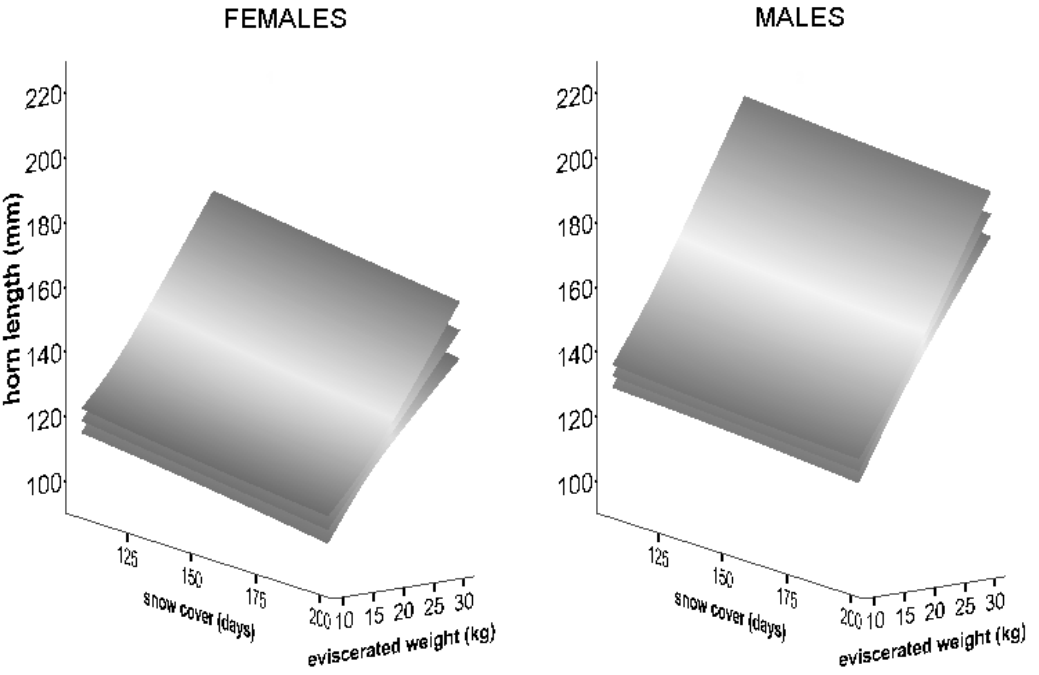

Figure 4 - Effect of two-way interactions (snow cover * sex) on the dependent variable.
Effect of snow cover duration on the horn length (mm) and eviscerated weight (kg) recorded for male (right panel) and female (left panel) yearling chamois shot for 5 consecutive years in the province of Trento (Italy). Linear regression surface and 95% Confidence Intervals describing horn length variations were reported in the graphs.

DISCUSSION

As suggested for the antlers of some deer species (Folstad and Karter 1992, Ditchkoff et al. 2001, Ciuti and Apollonio in press), horns too may be an honest signal of individual quality, given that they are energetically costly and are a major source of heat loss during winter (Picard et al. 1996). Antler and horn size are strongly related with body mass and condition in many ungulate species (*Rupicapra pyrenaica parva*, Pérez-Barberia et al. 1996; *Rupicapra rupicapra rupicapra*, Bassano et al. 2003; *Oreamnus americanus*, Côté et al. 1998; *Capra ibex*, von Hardenberg et al. 2004; *Ovis canadensis*, Festa-Bianchet et al. 2000, 2004; *Cervus elaphus hispanicus*, Gaspar-López et al. 2008; *Alces alces,* Nygren et al. 2007).

As shown in Chapter 1, yearling chamois horn length is affect by many environmental, climatic and local density conditions: among this factors only substrate type, local density, snow cover and average maximum temperature recorded in December-February drove a differential investment in horn size and body mass. More in details, worse conditions (i.e. siliceous substrate, winter with longer snow cover duration, lower maximum temperature and higher density rates) promoted a reduction in H/W ratio, that is shorter horns for a given body mass. Beyond, only substrate type and snow cover generated a different tactic in male and female yearling chamois.

Considering the different soil type, the quality of grassland communities to be found on calcareous substrates is higher than that of communities on siliceous ones (i.e. species richness; Grime 1979, Cavallero et al. 2007). As suggested by several authors (Duchaufour 1989, 1997, Gensac 1990, Rameau et al. 1993), the higher nutrient availability on calcareous soils when compared to siliceous substrate is accompanied by higher plant productivity. Plant communities growing on siliceous soil have structural characteristics that can also reduce digestion efficiency (Laca et al. 2001), and, consequently, may negatively affect the energy intake of the animals feeding on them. As evidenced in mountain goats (*Oreamnos americanus*, Festa-Bianchet and Côté 2008) for both sexes, in worse condition (e.g. decreasing early-June fecal crude protein) yearlings allocated more resources to body rather than to horn growth. That may suggest that in different condition (i.e. calcareous *vs* siliceous substrate), individuals can acquire resources and decide to allocate them in a different way: the trade off between body mass and secondary sexual traits priority investment shows the use of alternative life history tactics. Thus, living on siliceous substrate may induce a lower investment in horn growth and size in yearling chamois.

Another factor able to influence the quantity and quality of resource availability, and therefore the H/W ratio (i.e. a reduction of horn length for a given body mass), is the local population density. Moreover, young animals are more susceptible than adults to density-dependent resource limitations (Gaillard et al. 1998), and high densities could negatively affect ungulate populations through increased forage competition (Post and Stenseth 1999). As reported for bighorn sheep (*Ovis canadensis*), population density has a negative effect on resource allocation of young males and females (LeBlanc et al. 2001).

According to climatic conditions only the winter snow cover and the average maximum temperature during the coldest months play an important role in shaping the H/W ratio (i.e. a reduction of horn length for a given body mass with longer snow cover duration and lower maximum temperature). Our results confirmed that winter condition is one of the most important factors limiting the secondary sexual traits investment in Alpine area. Harsh winters (i.e. with longer snow cover duration and lower maximum temperature) are generally thought to affect juvenile body condition and survival by increasing the probability of starvation, through a combination of higher thermoregulatory costs and decreased forage availability due to a deep snow cover (Forchhammer et al. 1998). Therefore, we argued that the decrease in food availability due to persistent snow cover may prove more costly to chamois than the thermoregulatory costs linked to low winter temperatures. Moreover individuals between 1 and 2 years of age are in a more critical physical condition than juveniles, because they are burdened with the legacy of a poor body condition developed throughout their first winter (De Ross at al. 2009). The allocation strategy may increase the probability of survival, possibly at the cost of decreased lifetime reproductive success and consequently by allocating more resource to body growth rather than to horn growth, yearlings may not compromise their short-term survival.

As expected, the hunting day, calculated as the number of days following the beginning of the hunting season (7th September), also played a significant role in the model, given that the later a chamois was shot during the hunting season, the longer was the horn length and the lower was the eviscerated weight. Thus, the positive relationship between hunting day and H/W ratio is in accordance with a study on Cantabrian chamois (Pérez-Barberia et al. 1996), which showed an inertial horn growth (before the winter break) also in late autumn, especially in subadults, and a physiological reduction of weight in late autumn (Xue et al. 2005).

Among all these variables, only substrate type and snow cover duration play a different role in females and males. This can be considered as a use of dissimilar life history tactics between sexes (Stearns 1992). Indeed, in worse conditions, yearling females allocate an increasing proportion of resources to body growth rather than to horn growth while yearling males continue to promote a greater investment in secondary sexual traits. The sex-specific differences observed in our study may have been due to sex-specific differences in resource allocation for growth and reproduction. In both males and females natural selection and sexual selection are expected to favour rapid development to sexual maturity (Fisher 1930, Andersson 1994). Among female ungulates, sexual maturity depends closely on reaching a threshold body mass (reviewed by Gaillard et al. 2000), after which energy is primarily allocated to reproduction (Clutton-Brock et al. 1982). As reported for other species of large ungulates (Gaillard et al. 2000), this threshold in body mass corresponded to ~80% of asymptotic carcass mass of adult female alpine chamois, indicating that female chamois begin reproducing before they reach asymptotic growth. Thus, body weight plays a decisive role in reproductive potential (Reimers 1983, Gaillard et al. 1992, Sæther and Heim 1993). In contrast, in social systems that promote intrasexual competition for mates (Weckerly 1998), males tend to delay social maturity and consequently access to females because early reproduction is likely to have negative effects on body growth (Mysterud et al. 2003, Garel et al. 2006). During the rutting season, males defend areas within which they attempt to keep a varying number of females. In this period, male chamois engage in intra-sexual contests showing direct and indirect forms of aggressive behaviour (Krämer 1969), in which both body mass and horn size likely play an important role. Because male reproductive success typically depends on male-male combat, males are generally expected to adopt a riskier strategy than females to achieve the greatest possible development of weapons (antlers and horns) used in competition for estrous females, and consequently suffer a survival cost, particularly when resources are scarce (Clutton-Brock 1988). If males directed more resources to body growth rather than horn or antler growth when food was scarce, they might increase their survival probability, possibly to the detriment of their future reproductive success. As resources become scarce, male yearling chamois allocate an increasing proportion of those resources to body growth but, as a matter of fact, 60-70% of horn growth takes place in the first 2 years of life (Schröder 1971, Bassano et al. 2003) and males, compared to females with the same body mass, continue to promote a greater investment in horn size. This allocation strategy may decrease the probability of survival, possibly at the result of increased lifetime reproductive success.

In general, the trade off between body weight and horn size confirmed that the early stage of development is a crucial step in the individual life history of ungulate. Thus, the ecological factors able to modify H/W ratio may negatively affect the gain of a proper body size of chamois, especially in males, and it could have strong impacts on the winter survival of both sexes, and, more in general, on its population dynamic parameters.

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SECOND PART

Male reproductive strategies

Chapter 3

Older males invest more in reproduction: evidence for an important life history tactic

Older males invest more in reproduction: evidence for an important life history tactic

Roberta Chirichella[1,2], Tom H.E. Mason[3], Marco Apollonio[1], Philip A. Stephens[3], Stephen G. Willis[3]

1 - Department of Zoology and Evolutionary Genetics, University of Sassari,
via Muroni 25, I-07100, Sassari, Italy

2 - Adamello Brenta Nature Park,
via Nazionale 24, I-38080, Strembo (TN), Italy

3 - School of Biological and Biomedical Sciences, University of Durham,
South road, Durham, DH1 3LE, UK

ABSTRACT

A fundamental life history question is how to allocate reproductive investment optimally over time. The 'terminal investment' hypothesis predicts that individuals should continue to invest more energy in reproduction after prime age, owing to a decreasing residual reproductive value (RRV). Consistent with the theory of terminal investment, we found that reproductive investment in male Alpine chamois *Rupicapra rupicapra* increased with age and continued to do so even after the onset of apparent senescence. Terminal investment is an important concept but has rarely been verified reliably before, particularly in males. As such, our results provide an important contrast to accelerating support for reproductive restraint in later life. We also found highly male skewed mortality rates, likely a result of hunting pressure. By reducing the RRV of males, hunting will be a strong driver of terminal investment, illustrating the pervasive effects of human harvesting on demography, population dynamics and life histories.

INTRODUCTION

The question of how long-lived iteroparous animals should allocate resources to reproduction over their lives is of great ecological importance (Williams 1966, Stearns 1992). Trade-offs exist not only between survival and reproduction, but also between current and future reproduction (Williams 1966, Clutton-Brock 1984, Stearns 1992). For instance, in order to maximise lifetime reproductive success, an individual may forego mating in the present if conditions are unfavourable and there is a good chance of breeding in the future. Prime-aged individuals generally have the highest competitive ability and, thus, might be expected to benefit most from investing energy in reproduction (Yoccoz et al. 2002). Indeed, the 'mating strategy-effort' hypothesis (Yoccoz et al. 2002), which predicts that reproductive investment (the investment of energy in current reproduction rather than in future reproduction, growth or survival) peaks in prime-aged adults before decreasing in older individuals, has received support from studies on a range of taxa (Cameron et al. 2000, Billing et al. 2007, Mainguy and Côté 2008). A contrasting hypothesis, the theory of 'terminal investment', predicts that reproductive investment should continue to increase after prime age due to a diminishing residual reproductive value (RRV) (Williams 1966). Despite the theoretical appeal of the terminal investment hypothesis, it has rarely been empirically proven. Indeed, the results of a recent modelling study suggest that, under most conditions, a decline in reproductive investment after prime age is favoured (McNamara et al. 2009).

Ungulate species provide good model systems in which to study the allocation of reproductive investment over time. Males and females often have strongly contrasting life histories, investing in reproduction in different ways and over different periods of the mating season (Clutton-Brock et al. 1985, Stearns 1992). Generally, females invest heavily in gestation, lactation and parental care, with their reproductive success strongly dependent on raising young successfully (Krebs and Davies 1993). In contrast, male reproductive success depends on competing for access to females during a short rutting season (Clutton-Brock et al. 1988). Specifically, male reproductive behaviour consists of competing with other males for access to estrous females and performing courtship behaviours to attract females (McElligott et al. 2001, Yoccoz et al. 2002, Forsyth et al. 2005). Male reproductive investment can be relatively easily studied over the rut by measuring the somatic costs of reproductive behaviour. Male ungulates often adopt a strategy of 'appetite suppression' during the rut, meaning that they are 'capital breeders' (or rather, towards the capital end of the capital-income breeder continuum) and are reliant on stored energy to breed (Stearns 1992, Jonsson 1997, Willisch and Ingold 2007, Stephens et al. 2009). As such, the proportion of mass lost by a male during the rut can be used as an estimate of the energy invested in reproductive behaviour (Doughty and Shine 1997). Mass loss is an informative indicator of current reproductive investment as males that invest more energy during the rut and consequently lose more mass will enter winter in poorer condition and will thus be more susceptible to mortality (there tends to be a positive relationship between body mass and survival in ungulates of seasonal environments [Berube et al. 1999, Loison et al. 1999c]). As such, rutting males that lose more body mass may be less likely to breed the following season, highlighting the important life history trade-off between current and future reproduction.

The allocation of reproductive investment has been studied in a number of male ungulates. Findings have tended to support the 'mating strategy-effort' hypothesis. Reproductive investment peaks in prime-aged male red deer *Cervus elaphus* before declining; this is probably explained by a reduced ability of older males to hold a harem (Clutton-Brock et al. 1985, Yoccoz et al. 2002). Declines in investment in older individuals have also been observed in male bison *Bison bison* (Maher and Byers 1987) and mountain goats *Oreamnos americanus* (Mainguy and Côté 2008). It is thought that, because males often adopt alternative mating strategies as they senesce and become less competitive, an increase in reproductive investment is unlikely to be observed after prime age (Yoccoz et al. 2002, Mainguy and Côté 2008). To date, there is a lack of strong evidence supporting terminal investment in a male ungulate. Intriguingly, Mysterud et al. (2005) put forward evidence of increasing reproductive investment with age in male moose *Alces alces*; however, they found that the investment of the oldest males actually tended to stabilise or decrease (Mysterud et al. 2005).

Here, we analyse the relationship between age and reproductive investment among male Alpine chamois *Rupicapra rupicapra*. Chamois are a polygynous (Loison et al. 1999b, von Hardenberg et al. 2000) yet relatively sexually monomorphic mountain-dwelling ungulate (only modest sexual dimorphism exists with respect to body mass and horn size [Couturier 1938, Kramer 1969, Knaus and Schröder 1983]). Breeding male chamois defend small clustered territories during the rut, excluding rival males and defending estrous females (Kramer 1969, von Hardenberg et al. 2000). Male rutting behaviour consists of agonistic interactions with rival males such as chasing and posturing; and interactions with sexually mature females, including herding and copulation (Kramer 1969). During the rut, males allocate much of their non-rutting time to rest rather than foraging; they are thus capital breeders (Willisch and Ingold 2007). We tested variation in male reproductive investment across age classes using relative body mass change as an estimate of investment. We found that reproductive investment increased significantly with age, even after prime age, providing strong support for the terminal investment hypothesis.

MATERIALS AND METHODS

Data collection

Data were collected in the central-eastern Italian Alps, across a 1,333km^2 area of Trento Province (46°02’N, 10°38’E). The elevation of the study area ranges from 52 to 3,558m above sea level, with a mean altitude of 1,586m. It is forested up to the tree-line at about 2,000m, above which habitat consists of alpine meadows and open rock faces. The study area consists of six chamois hunting districts (Figure 1) which are subdivided further into 68 municipal reserves. Chamois are hunted with rifles every year from mid-September to mid-December. Hunting is controlled through licenses issued by local wildlife boards. Data were collected on the eviscerated body mass, sex, age and date shot of 28,011 Alpine chamois (14,627 males and 13,384 females) culled over 37 consecutive hunting seasons between 1973 and 2009. Ages were estimated from counts of horn growth annuli (Schröder and Von Elsner-Schak 1985) and were recorded to the nearest 0.5 years. The ages of males varied between 1.5 and 18.5 years; the ages of females between 1.5 and 21.5 years. Dates of shooting were converted to the Julian calendar and ranged from day 247 to 365.

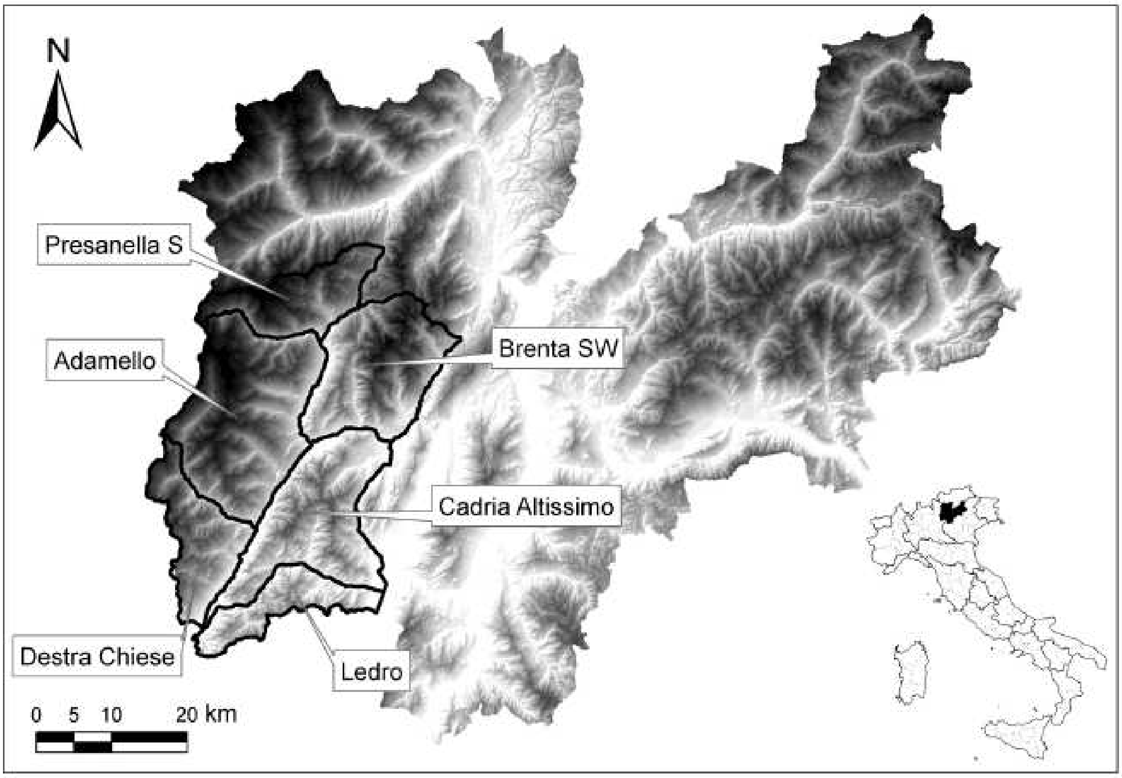

Figure 1 - Map of the Trento Province (Central-Eastern Alps, Italy).
Map displaying Trento Province and boundaries of hunting districts. Darker colours indicate areas of higher altitude.

Statistical analysis

We analysed both male and female relative body mass change during the rut. Female mass change was analysed to provide a control (female reproductive investment occurs later in the breeding season). We focussed on individuals shot during the period of most intense rutting behaviour between days 300 and 340 of the year. Individuals were separated into four age classes: yearlings (1.5 years), sub-adults (2.5 - 4.5 years), prime adults (5.5 - 7.5 years) and old adults (≥ 8.5 years). This categorisation ensured that there were sufficiently large sample sizes in even the oldest age class. The boundaries for age classes were chosen based on body mass reaching a maximum between 5.5 and 7.5 years (prime adults) and steadily declining thereafter (see Figure S1, supplementary materials). To estimate reproductive investment, the eviscerated body masses of shot individuals were regressed against date for each age class, within each hunting district. Linear regressions were performed for each combination of age class, district and year for which there were sufficient data. To ensure robustness, we only used regressions with at least ten individuals shot over a period spanning a minimum of 20 days. Our proxy for reproductive investment,

$RI_{a,y,d}$, for any age class (*a*), year (*y*) and hunting district (*d*) was percentage relative mass change during the rut, and was given by:

$$RI_{a,y,d} = \frac{40m_{a,y,d}}{300m_{a,y,d} + c_{a,y,d}} \times 100$$

where $m_{a,y,d}$ is the gradient of the regression slope and $c_{a,y,d}$ is the intercept. $40m_{a,y,d}$ is the change in body mass during the rut and $300m_{a,y,d} + c_{a,y,d}$ is body mass at the start of the rut (on day 300). ANOVAs were used to test for differences in $RI_{a,y,d}$ between age classes within each sex, followed by *post hoc* testing using Tukey's HSD test to determine which age classes were significantly different to each other.

To account for between-site variation in reproductive investment, we looked at variation in reproductive investment within the two hunting districts with the most data: Adamello (3,533 males shot during the rut) and Brenta (2,442 males shot during the rut); these were also the only two hunting districts within which meaningful numbers of older males (≥ 8.5 years) had been shot. We calculated reproductive investment as before; however, in order to visualise patterns of investment within the final age class, we performed our analyses by age, rather than by age class. To provide sufficient data for this analysis, we relaxed our sample size threshold for regressions of body mass against date; specifically, we performed regressions for any combination of district, year and age with at least three individuals (again shot over at least a 20 day period). To emphasise the contribution of the more reliable regressions for each age, regressions were weighted by $\frac{1}{SE}$ and weighted means were calculated for each age within each district as follows:

$$\overline{RI}_{a,d} = \frac{\sum\left(\frac{RI_{a,y,d}}{SE_{a,y,d}}\right)}{\sum\left(\frac{1}{SE_{a,y,d}}\right)}$$

where $\overline{RI}_{a,d}$ is mean weighted reproductive investment for a given age (a) and hunting district (d) and $SE_{a,y,d}$ is the standard error of the regression from which $RI_{a,y,d}$ is calculated. Weighted means were only calculated for ages with at least five regressions. For both districts, we regressed weighted mean reproductive investment on age, using 1,000 bootstrapped replicates (Efron and Tibshirani 1991) stratified by age to determine 95%

confidence intervals for the regressions. Statistical analyses were performed using R version 2.11.1 (R Core Development Team, 2010). Results are reported with standard errors.

RESULTS

There was a somatic cost of reproduction during the rut for all male age classes (mean body mass loss = 12.5 ± 0.8 %). In each age class, male reproductive investment was significantly greater than in the age class below ($F_{3,275}$ = 58.8, *P* <0.001; differences between individual age classes: Tukey's HSD test: yearlings *vs* sub-adults, *P* <0.001; sub-adults *vs* prime adults, *P* <0.001; prime adults *vs* old adults, *P* = 0.01, Figure 2a). Old adult males lost, on average, 7% more of their body mass than did prime adult males (prime male mean body mass loss = 20.3 ± 1.1 %; old male mean body mass loss = 27.6 ± 2.1 %). In comparison, female mass loss was low and did not vary significantly with age ($F_{3,287}$ = 1.5, *P* = 0.2, mean body mass loss = 4.4 ± 0.9 %, Figure 2b).

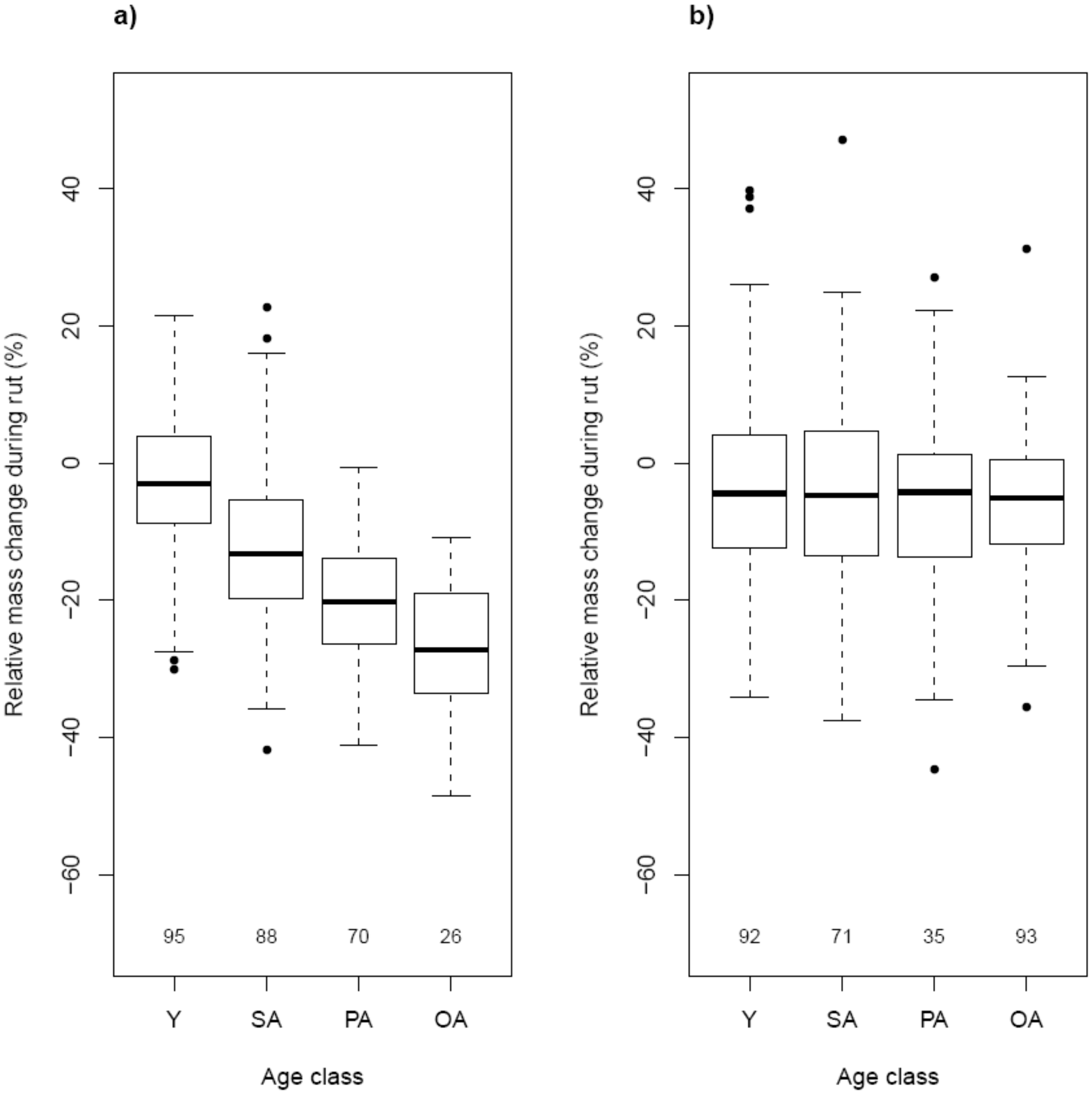

Figure 2 - Boxplots comparing the distributions of relative mass change during the rut between different age classes in a) males and b) females.

Thick lines represent median values, boxes display inter-quartile ranges (IQRs) and the extents of dashed lines show maximum and minimum values. Outliers represent values more than 1.5 of the IQR higher or lower than the mean and, in such cases, the extents of dashed lines represent maximum and minimum values within 1.5 of the IQR. 'Y' displays data for yearlings, 'SA' for sub-adults, 'PA' for prime adults and 'OA' for old adults. Sample sizes of regressions (with each based on at least 10 individuals) for each age class are displayed under data.

Linear regressions of weighted mean reproductive investment against age were significant in both Adamello ($F_{1,7}$ = 145.1, P <0.001, Figure 3a) and Brenta ($F_{1,7}$ = 18.1, P = 0.004, Figure 3b).

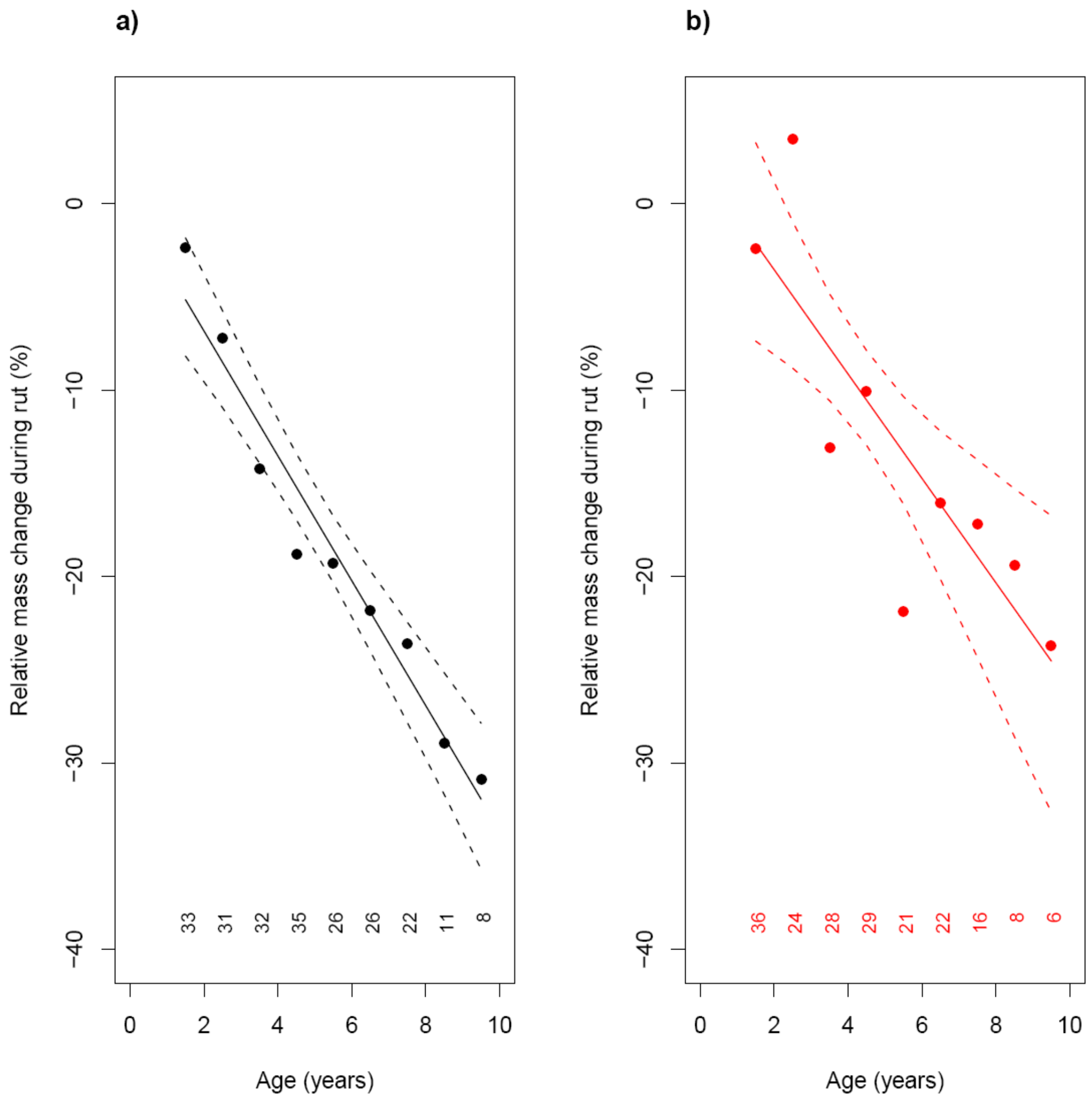

Figure 3 - Plots showing variation with age in weighted mean relative mass change during the rut for males shot in a) Adamello and b) Brenta.
Solid straight lines are linear regressions. Dashed lines are 95% Confidence Intervals from 1,000 bootstrapped replicates (Efron and Tibshirani 1991). Samples sizes are shown at bottom of plot.

Assuming that proportions shot reflect population age structure, we inferred structure from the collated hunting records. In spite of the apparent equity in the ratio of males to females in the earliest age classes, older age classes have substantially skewed sex ratios, with females outliving males (Figure 4).

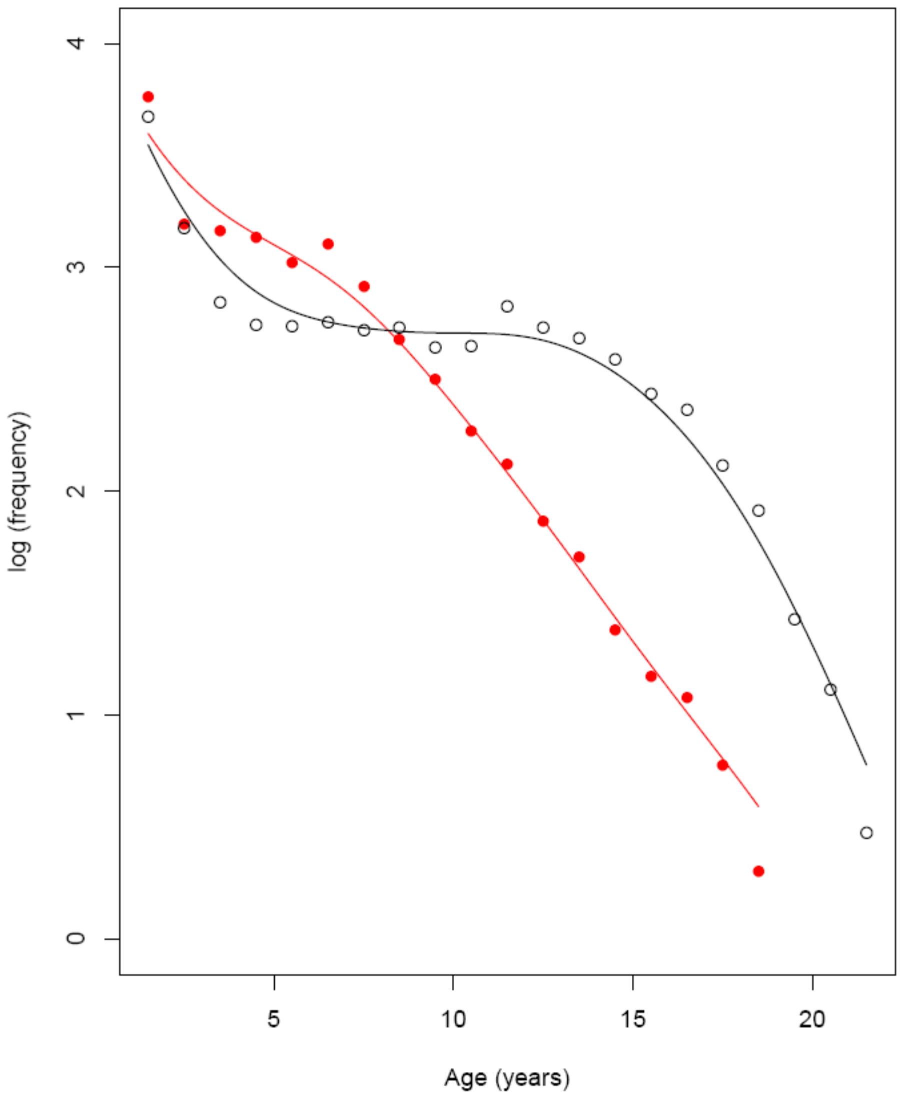

Figure 4 - Plot comparing log (frequency) of all shot males and females, across different ages. Solid circles show male data and open circles show female data. The red curve is fitted to male data and the black curve to female data. The curves were fitted using local polynomial regression. Bandwidths were set using direct plug-in methodology (Ruppert et al. 1995).

DISCUSSION

Our analyses showed that male reproductive investment during the rut increased significantly with age, even after prime age (Figure 2a). Old adult males, despite generally being in poorer condition (see Figure S1, supplementary materials), invested relatively more energy in current reproduction than prime adult males did. The results shown in Figure 2 could be vulnerable to the concern that they show only that increasing proportions of males within successive age classes are taking part in the rut. However, for sites in which older males were more commonly shot, our results suggest that male reproductive investment continues to increase within the oldest age class (Figure 3). These findings provide compelling support for the terminal investment hypothesis, suggesting that old males compensate for a lower chance of breeding in the future by investing more in current reproduction.

Our findings contrast with results from a range of taxa, particularly in males (Cameron et al. 2000, Yoccoz et al. 2002, Billing et al. 2007). Generally, reproductive restraint is thought to be favoured after prime age due to a trade-off between current reproduction and survival. This strategy enables senescent individuals to continue to breed for a number of years, albeit with a lower reproductive output within any given breeding season. McNamara et al. (2009) used a modelling approach to highlight broad conditions under which reproductive restraint is likely to occur, suggesting that terminal investment should rarely be observed. McNamara et al. argued that time pressure may be weaker on an individual that has already accumulated significant damage because extrinsic mortality risk, such as from disease or predation, is low relative to the risk of death from intrinsic causes. When the risk of extrinsic mortality is lower than that of intrinsic mortality (due to the accumulation of cellular and physical damage), restraint should be optimal because high reproductive investment could lead to rapid damage accumulation and death. However, extrinsic and intrinsic mortality are concepts which are difficult to separate (and are particularly difficult to measure separately in the field [Nussey et al. 2008]). In reality, different sources of mortality are tightly linked and the accumulation of damage due to senescence is likely to increase the risk of both intrinsic and extrinsic mortality (Williams and Day 2003, Reznick et al. 2004). For example, whilst disease and predation are extrinsic mortality sources, they are more likely to kill individuals that have already accumulated significant levels of intrinsic damage (Ashman et al. 1999, Moller and De Lope 1999, Wright et al. 2006).

Declines in reproductive investment in old males may be a result of males adopting alternative mating strategies as they senesce and become less competitive (Yoccoz et al. 2002, Mysterud et al. 2005). For instance, old red deer males are no longer able to defend harems and consequently adopt the less costly (but less profitable) 'sneaker' strategy (Clutton-Brock et al. 1985, Yoccoz et al. 2002). In chamois, there is no evidence of senescent individuals adopting alternative strategies. Both prime and senescent chamois males are able to defend territories before and during the rut (von Hardenberg et al. 2000). The fact that older males can still maintain breeding territories, despite being in poorer condition, may result from a 'prior residence advantage' in territory ownership (von Hardenberg et al. 2000). Chamois males show high levels of site-fidelity year by year and experienced males that have defended a given territory in the previous year's rut may be more likely to defend it successfully in the present rut (von Hardenberg et al. 2000). As such, in contrast to species in which males are forced to adopt less profitable mating strategies, old male chamois have the potential to increase their reproductive investment in response to their diminishing RRV.

We identified an increasingly pronounced skew in the sex ratio of shot individuals with age (Figure 4). Assuming that the sex ratio of shot individuals reflects the population sex ratio, this suggests that after prime age, the number of males drops significantly, whilst the number of females remains stable until about 14.5 years of age. This skew suggests that the intrinsic mortality rates of adult males are much higher than those of females. It is surprising to see this pattern in a sexually relatively monomorphic species such as chamois, as inter-sexual survival differences are generally associated with high levels of sexual dimorphism (Promislow 1992, Promislow et al. 1992) and costly male mating tactics (Loison et al. 1999a, Toïgo and Gaillard 2003). However, studies on other chamois populations subjected to hunting have found similar levels of skewed mortality to that seen in our population (Schröder 1971, Loison et al. 1999a). In contrast, research on non-hunted populations of chamois and isard *Rupicapra pyrenaica* has found even sex-ratios and inter-sexual mortality rates (Gonzalez and Crampe 2001, Bocci et al. 2010). This suggests that hunting may be responsible for the high levels of male intrinsic mortality in this population. Specifically, a positive feedback loop may exist between extrinsic and intrinsic sources of mortality: as males invest more heavily in reproduction due to high extrinsic mortality, they incur increased levels of intrinsic damage, thus further decreasing their RRV. This process could explain the evolution of terminal investment in this population, because it would lead to males investing increasingly more energy in reproduction as they age, impacting on their rate of damage accumulation and increasing their pace of life. This highlights the profound impacts harvesting can have on the life histories and population dynamics of natural populations.

An interesting future avenue for research would be to adopt a longitudinal approach (taking repeated measurements from the same individuals over time) to investigate reproductive investment. By weighing known individuals at regular intervals during the rut, fine-scale individual mass change profiles could be created. A non-invasive methodology for weighing free-ranging ungulates has already been developed and could be applied to this end (Bassano et al. 2003). This would ensure that results were not affected by within-cohort selection, which can lead to older cohorts containing a higher proportion of high quality individuals because low quality individuals die earlier (Service 2000, Cam et al. 2002). Within-cohort selection is a common concern in transversal studies. Where it occurs, one expectation would be that the strategies followed by individuals would become more consistent as the cohort ages (because the cohort composition becomes increasingly skewed towards individuals that actively participate in the rut). Our analyses suggest that no such increase in behavioural consistency occurs between prime and old males (see Figure S2 and Table S1, supplementary materials). Our study does highlight the limitation, common to studies of senescence (Nussey et al. 2008), of low sample sizes among the oldest age classes. Despite our large dataset, consisting of 14,627 males (of which 8,046 were shot during the rut), we had to categorise males into broad age classes in order to examine the reproductive investment of the oldest individuals. Furthermore, in our second analysis focussing on variation with age within separate sites, reproductive investment could only be reliably calculated for males up to 9.5 years. Despite this, we feel that our results show that comprehensive transversal datasets can still be of great value to ecological research. Whilst longitudinal field studies have the advantage of being focussed on within-individual changes, they can be limited by a focus on relatively small numbers of known individuals (e.g. Cameron et al. 2000, Willisch and Ingold 2007). In comparison, whilst data on old individuals is invariably limited, transversal data can contain information on thousands of individuals (e.g. Yoccoz et al. 2002, Mysterud et al. 2005). Ideally, transversal and longitudinal studies should be combined to provide definitive answers to important life history questions.

We have found rare evidence for a life history strategy of substantial theoretical and practical importance. Our research also highlights a novel mechanism by which hunting may impact on the life histories of harvested species. Currently, much research is focussed on the effects of human harvesting on population fluctuations in natural populations (Anderson et al. 2008, Fryxell et al. 2010). Studies have also discovered unexpected evolutionary impacts resulting from harvesting, such as reductions in body size and secondary sexual traits in male ungulates (Coltman et al. 2003, Carlson et al. 2007). Our findings highlight the influence harvesting can have on life histories, compounding increased extrinsic mortality by the life history response of increasing intrinsic mortality. Further research, comparing populations subjected to different hunting pressures, is required in order to test how profoundly patterns of harvesting influence reproductive behaviour.

ACKNOWLEDGEMENTS

We are grateful to Trento Province, the Adamello Brenta Nature Park, and the "*Associazione Cacciatori Trentini*" (Trento provincial hunting association), as well as to the hunting reserve of "*Regole Spinale e Manez*" for supplying data. We are indebted to Michele Rocca, Alessandro Brugnoli and all the game wardens who collected Alpine chamois measurements. We thank Shane Richards, Oliver Beveridge and Georgina Palmer for insightful comments on analytical methods. We thank Chris Carbone for helpful comments on an earlier draft.

The study complies with all relevant national, regional and provincial Italian laws.

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SUPPLEMENTARY MATERIALS

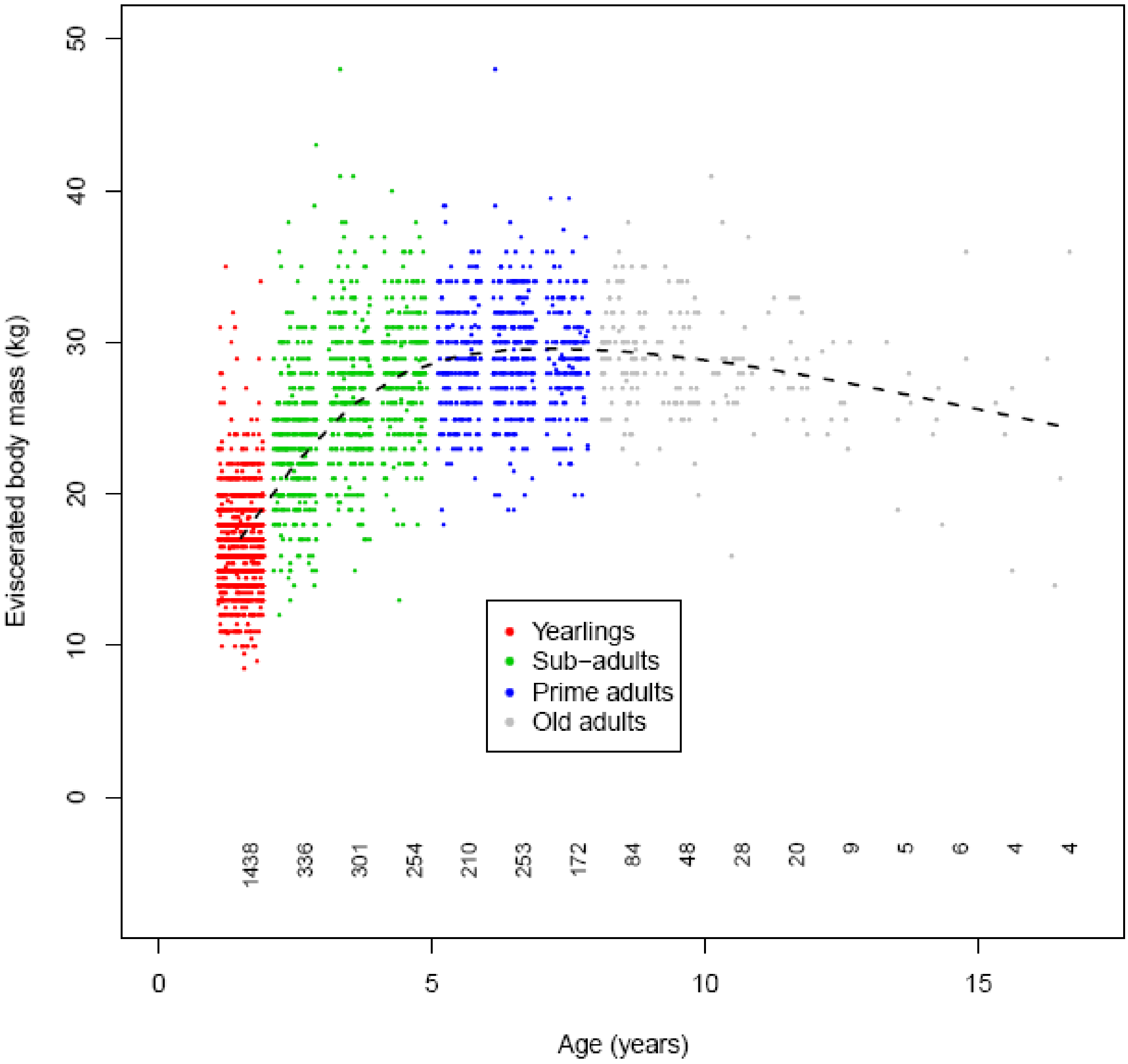

Figure S1 - Plot showing the relationship between body mass and age of males shot shortly before the rut (between days 280 and 300).
A small amount of noise has been added to the x-axis to visualise better the distribution of points within each age. Sample sizes of each age are displayed under data. A cubic smoothing spline was fitted to the data to illustrate the relationship. Bandwidth was set using cross-validation (Craven and Wahba 1979).

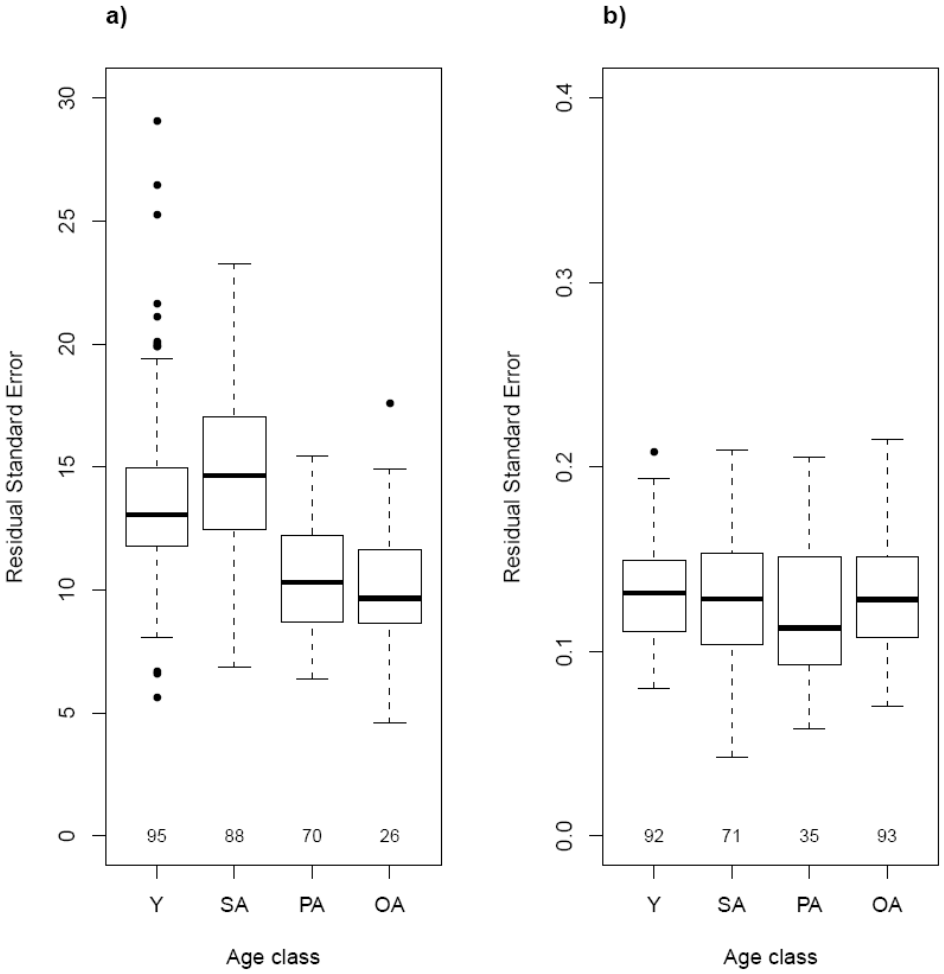

Figure S2 - Boxplot comparing the distributions of proportional residual standard error (PRSE) between males and b) females of different age classes.
Boxplot comparing the distributions of proportional residual standard error (PRSE) between males of different age classes. PRSE is a measure of variation around a regression and was calculated from each regression as follows:

$$PRSE = \frac{\sqrt{\frac{\sum (y - \bar{y})^2}{n-2}}}{\bar{y}} \times 100$$

where y is the body mass of a given individual, $\bar{y}$ is mean body mass and n is the number of individuals. The plot shows that the amount of variation around regressions is similar for prime males and old males, suggesting that the level of behavioural consistency does not vary significantly between these cohorts (the higher levels of PRSE in younger age classes are unsurprising as many younger individuals do not participate in the rut but, among sub-adults in particular, some might be beginning to do so; thus, behaviour may be less consistent across the cohort). Thick lines represent median values, boxes display inter-quartile ranges (IQRs) and the extents of dashed lines show maximum and minimum values. Outliers represent values more than 1.5 of the IQR higher or lower than the mean and, in such cases, the extents of dashed lines represent maximum and minimum values within 1.5 of the IQR. 'Y' displays data for yearlings, 'SA' for sub-adults, 'PA' for prime adults and 'OA' for old adults. Sample sizes of regressions (with each based on at least 10 individuals) for each age class are displayed under data.

Age class 1	Age class 2	Mean difference in PRSE (%)	*P*
Yearlings	Sub-adults	-0.9	0.02
Yearlings	Prime adults	3.05	<0.001
Yearlings	Old adults	3.05	<0.001
Sub-adults	Prime adults	4.04	<0.001
Sub-adults	Old adults	4.05	<0.001
Prime adults	Old adults	0.01	1

Table S1 - Table showing Tukey's HSD test output for tests of differences in proportional residual standard error (PRSE) between male age classes.

The output shows that PRSE doesn't vary significantly between prime and old males, confirming that behavioural consistency doesn't vary significantly between adult cohorts.

THIRD PART

Ecological factors affecting a low investment in body size: resource competition among different ungulate species

Chapter 4

Interactions among Alpine chamois, mouflon and livestock in the Alps

Interactions among Alpine chamois, mouflon and livestock in the Alps

Roberta Chirichella[1,2], Simone Ciuti[1], Marco Apollonio[1]

1 - Department of Zoology and Evolutionary Genetics, University of Sassari,
via Muroni 25, I-07100, Sassari, Italy

2 - Adamello Brenta Nature Park,
via Nazionale 24, I-38080, Strembo (TN), Italy

ABSTRACT

The interaction between native and introduced wildlife is an issue widespread on a global scale. For instance, the competition for resources between the native Alpine chamois (*Rupicapra rupicapra*), the non native mouflon (*Ovis orientalis musimon*) and livestock at large is still an unsolved dilemma in the Alps. Empirical data on such a phenomenon are urgently needed to plan proper management strategies aimed to protect native species. We aimed to disentangle if and how the presence of livestock and mouflon could negatively affect the access by Alpine chamois to high-quality meadows during the summer. We performed this research in a 4,550-ha wide area covered by Alpine meadows in north-eastern Alps, Italy, where chamois, mouflon, and free-ranging sheep and goat occurred simultaneously. During summer 2007 and 2008, we walked every 15 days 5 hiking trails (25 km) and we localized each group of free-ranging ungulates, as well as we recorded data on the grass quality and availability. Given that we recorded that the forage availability increased linearly as the distance from rocks did, we modelled the distance of chamois from rocks to understand how it was shaped by the co-presence of free-ranging livestock and/or mouflon. Our results showed that chamois were forced to be closest to rocks (thus having access to areas with lower food availability) as livestock groups were larger and closer to them. This was highly pronounced when shepherds' dogs were also present with livestock at large. At the same time, large and close group of mouflons forced chamois near to rocks. Indeed, the presence of adult males within mouflon aggregations evoked such a response in chamois, suggesting the likely occurrence of a direct competition for the access to best foraging sites between male mouflons (larger and more aggressive than female mouflons) and chamois. The use by chamois of low availability food areas due to mouflon and livestock can negatively affect chamois feed intake and the related gain of a proper body size during the summer, i.e a crucial period for mountain ungulates to store reserves needed to face the winter. This, in turn, could have strong impacts on the productivity of females, on the winter survival of both sexes, and, more in general, on chamois population dynamics parameters.

INTRODUCTION

In theoretical ecology the relationship between different species which are adversely affected by having the same living requirements is a well debated issue (Shoener 1985, Loreau 2000, Vellend 2010). Among large herbivores, competition is a central mechanism of interaction, which plays a significant role when a high overlap of habitat use and a similar diet occurs between at least two species (Latham et al. 1999, Bertolino et al. 2009), especially when shared resources are limited (Belovski 1986, Latham 1999). In general, inter-specific competition may occur directly when a species interfere with foraging, survival, reproduction or preventing their physical establishment in a portion of the habitat of others, or indirectly through a common limiting resource which acts as an intermediate (Illius and Gordon 1992, Feldhamer and Armstrong 1993, Hulbert and Andersen 2001).

Among ungulates, interactions between different species have been the object of several studies (Gordon and Illius 1989, Homolka 1996, Putman 1996, Bartos et al. 2002). Moreover, competition can be strongly enhanced when we consider ecosystems where wild ungulates coexist and likely compete with non-native ungulate species and/or domestic livestock (Chapman et al. 1993, Vázquez 2002, La Morgia and Bassano 2009). Indeed, while native sympatric species commonly show low negative interactions as a consequence of niche separation and resource partitioning (Hartnett et al. 1997), the introduction of non native species can dramatically change previous set up in the herbivore community. These kinds of phenomena can interfere with mechanisms of competitive equilibrium and could lead to competition with one or more native species (Chapman et al. 1993, Vázquez 2002). At the same time, livestock grazing impact on native herbivores is an important conservation concern on a global scale (Prins 1992, Fleischner 1994, Noss 1994, Voeten 1999) and the compatibility among wild and domestic ungulates has been studied both to gain insight into coexistence processes in general and to solve practical management problems, such as the compatibility between wild and domestic ungulates (Mishra et al. 2004, La Morgia and Bassano 2009, Brown et al. 2010).

Moreover, the wildlife-livestock compatibility issue recently increased because of the rise in distribution and population size of many ungulate species in Europe (Apollonio et al. 2010). As interactions between wildlife and human activities become more relevant, the use of mountain ranges for grazing of domestic ungulates (cattle, sheep and goats) is a potential source of conflict of interests. In fact, the presence of domestic livestock can adversely affect the spatial distribution, activity budgets and/or the diets of wild ungulates (Kie et al. 1991, Loft et al. 1991, Kie 1996, Putman 1996, Matiello et al. 2002, Brown et al. 2010). Domestic animals are often abundant and potentially competitors of wild ungulates and, likely, domestic animals prevail in such a competition (Latham 1999). This contest for space and food may also have negative consequences for reproductive success and long-term population dynamics of wildlife species (Forsyth and Hickling 1998, Forsyth 2000, Madhusudan 2004, Mishra et al. 2004).

It is therefore arguable that the cumulative presence of livestock and alien species can be a more complicated issue for native ungulates. Little is known about the competitive interactions among ungulates, especially between native and exotic species, with the possible co-presence of domestic ungulates as a further additive factor. This problem seems to be pronounced in rural and mountainous areas, where the conditions for this competition occur (Apollonio et al. 2010). In the Alps, for instance, it is still unknown if Alpine chamois (*Rupicapra rupicapra*), a native species, is excluded from best foraging areas by mouflon (*Ovis orientalis musimon*) and domestic species. Empirical data on this phenomenon are urgently needed to improve the management of current natural ungulate populations. Indeed, the introduction of the mouflon in the Alps begun in 1962 and the alpine population in Italy has grown to over 5000 animals (Bertolino et al. 1998, Apollonio et al. 2010). The effects of these introductions have been poorly assessed, and some insights were given in the Pyrenees, where *Rupicapra pyrenaica* have apparently been displaced by the presence of introduced mouflons (Gonzales 1984, 1986). Moreover, preliminary researches performed in the Alpine meadows showed a marked spatial segregation between Alpine chamois and livestock, suggesting a direct negative interaction between the two species (Berdoucou 1986, Garcia-Gonzales et al. 1990), as well as chamois avoided sheep ranges when occurring in the same areas (Rebollo et al. 1993).

Under these circumstances, we studied the effect of non-native wild and domestic ungulates on the Alpine chamois spatial behavior. Our main prediction was that the free access by Alpine chamois to high-quality meadows during summer was negatively affected by the presence of mouflon and/or livestock. We predicted that the effect of such competitors can be additive on the native species. We also predicted that the presence of

Shepherds' dogs along with livestock can further decrease the use of high-quality meadows by chamois due to direct disturbance.

METHODS

Study area

We carried out this study in a 4,550 ha wide area of the Trento Province (46°05'N; 10°50'E) of the central-eastern Italian Alps, in the Southern slope of the Brenta Massif (Figure 1). Elevation of the area ranged from 950 to 2,850 m a.s.l., with a mean altitude of 2,005 m a.s.l. Direct observations were carried out above the tree line (2,000 m a.s.l.), where typical primary grassland were composed by meadows of *Sesleria albicans* and *Carex firma*.

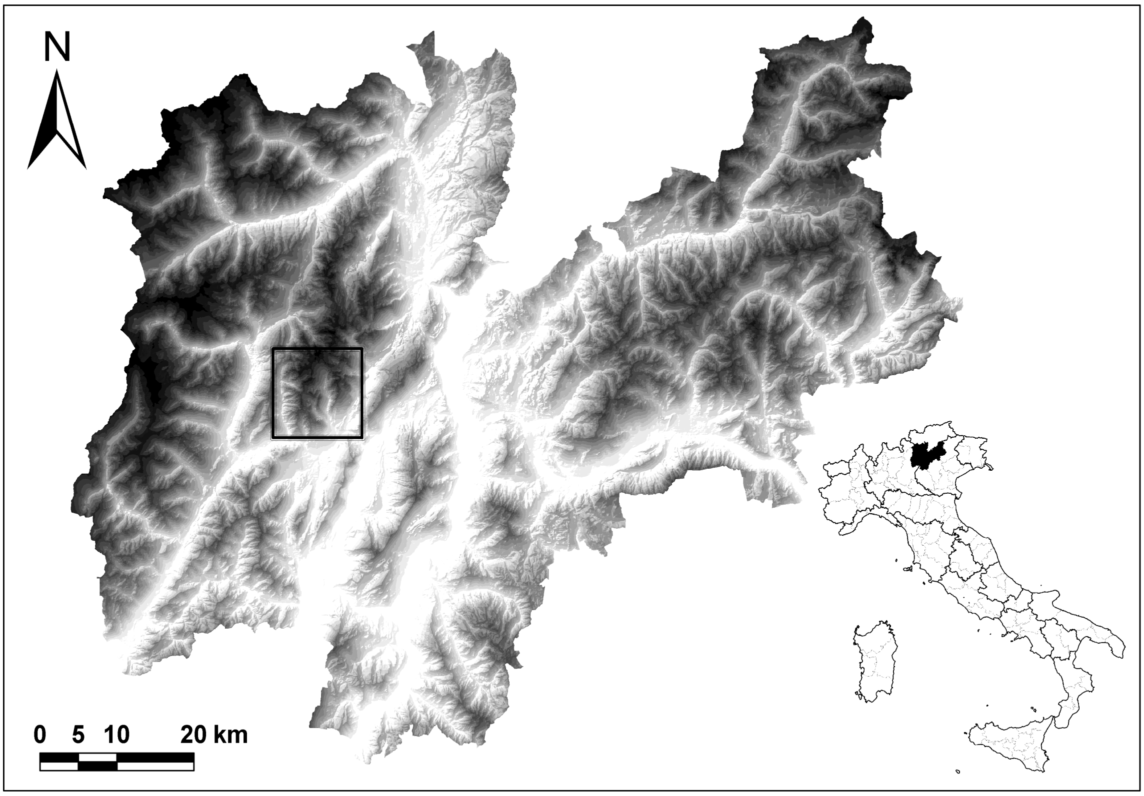

Figure 1 - Map of the Trento Province (eastern Italian Alps, Italy).
The study area is a 4,550 ha-wide area of the Brenta Massif (indicated by a square). Darker is the colour of the map surface, higher is the altitude a.s.l..

These areas were commonly used in summer by the Alpine chamois (12 head/100 ha), mouflon (introduced in 1970s, 4.5 head/100 ha), and large flocks of domestic sheep and goats often cared by shepherds and their dogs. Red deer (*Cervus elaphus*) and roe deer

(*Capreolus capreolus*) were abundant in this area, but commonly using areas below the tree line. Chamois and mouflon can be rarely predated by brown bear (*Ursus arctos*) and lynx (*Linx linx*) in this area, while the golden eagle (*Aquila chrysäetos*) may prey upon kids and lambs in their first weeks of life.

Data collection and analyses

During summer 2007 and 2008, between 15 June and 15 September, we walked 5 hiking trails (25 km) every 15 days. During each survey, we localized and mapped all groups of free-ranging ungulates by means of binocular 10×50, telescope 45×, Global Positioning System (GPS) device, hand compass, and rangefinder. Individuals of each group of mouflon or chamois were identified according to age and sex classes defined by previous researches (for mouflon see Ciuti et al. 2008, Pipia et al. 2009; for chamois see Gerard et al. 1992, Herrero et al. 2002). At the same time, we recorded the position and the group size of domestic ungulates' herds, and, if present, we took note of the shepherd's dogs presence.

During the same period, every 15 days, according to Carranza and Valencia (1999) we measured the quality of grass as well as we quantified the forage availability of meadows in 18 randomly selected sampling areas (1 sampling point every 137.22 ha). For each sampling site, we collected grass measurements along a linear transect at five sampling points which were set every 10 m (total sampling points = 90). At each sampling point and in the area of approximately 1 m around it, for four times we dropped a square of 30 x 30 cm (total samplings: 360 every 15 days). At each sampling point we measured the following (Carranza and Valencia 1999): (1) grass cover: a visual estimate of percentage area covered by grass in the square; (2) green index: the four corner tips of the square touched a leaf blade, which could be either green or brown. The green index was the number of tips touching green leaves (from 0 to 4) in proportion to the tips touching any blade (0 to 4); (3) grass length: at one point with most cover within the square, we measured the length of the longest aerial part of the grass. In agreement with the findings of Carranza and Valencia (1999), these kinds of grass measurements and forage availability (in terms of dry mass) proved to be strongly correlated.

First, we verified how the grass quality and availability changed as a function of the distance from rocks. We modelled both the normalized grass quality (arcsin[sqrt(green index/100)]) and forage availability (grass cover×grass length/100) of meadows by fitting two

Linear Mixed Effect (LME) models with Restricted Maximum Likelihood (REML) method. In both models, the log-transformed distance from the nearest rock was fitted as a covariate (Table 1).

Parameter	**Estimate**	**SE**	**t**	**P**
Intercept	1.354	0.050	27.197	<0.001
Log-distance from rocks	-0.001	0.009	-0.132	0.895

Parameter	**Estimate**	**SE**	**t**	**P**
Intercept	59.124	27.765	2.129	0.034
Log-distance from rocks	25.019	4.827	5.183	<0.001

Table 1 - Forage quality and quantity.
Parameter estimates and test statistics (Linear Mixed Effect LME models) for the normalized grass quality (green index = arcsin[sqrt(green index/100)], top panel) and forage quantity (forage availability = grass cover×grass length/100, low panel) of meadows in the Eastern Alps, Italy.

In such analyses we considered the sampling period (15 days) repeated among the summer and two years (2007 and 2008) as a random factor in the models in order to avoid pseudo-replication of data (Machlis et al. 1985). The quality (green index) of meadows did not change as the distance from rocks increased (Table 1, Figure 2), but this was true and statistically significant in the case of the availability of forage. The higher was the distance from rocks, the higher was the forage availability (Table 1, Figure 2). Therefore, we found patent collinearity occurring between the distance from rocks of a meadow and its grass availability. Consequently, higher was the distance of a chamois from rocks, higher was the food availability. Under these circumstances, we selected the distance (log-transformed) of chamois from rocks as the dependant variable in our analyses. From an ecological perspective, our starting assumption was that lower was the distance of a chamois from the rocks, lower was the grass availability there. At the same time, from a behavioural perspective, lower was the distance of a chamois from the rocks, higher was the perception of a safe place (Grignolio et al. 2007a).

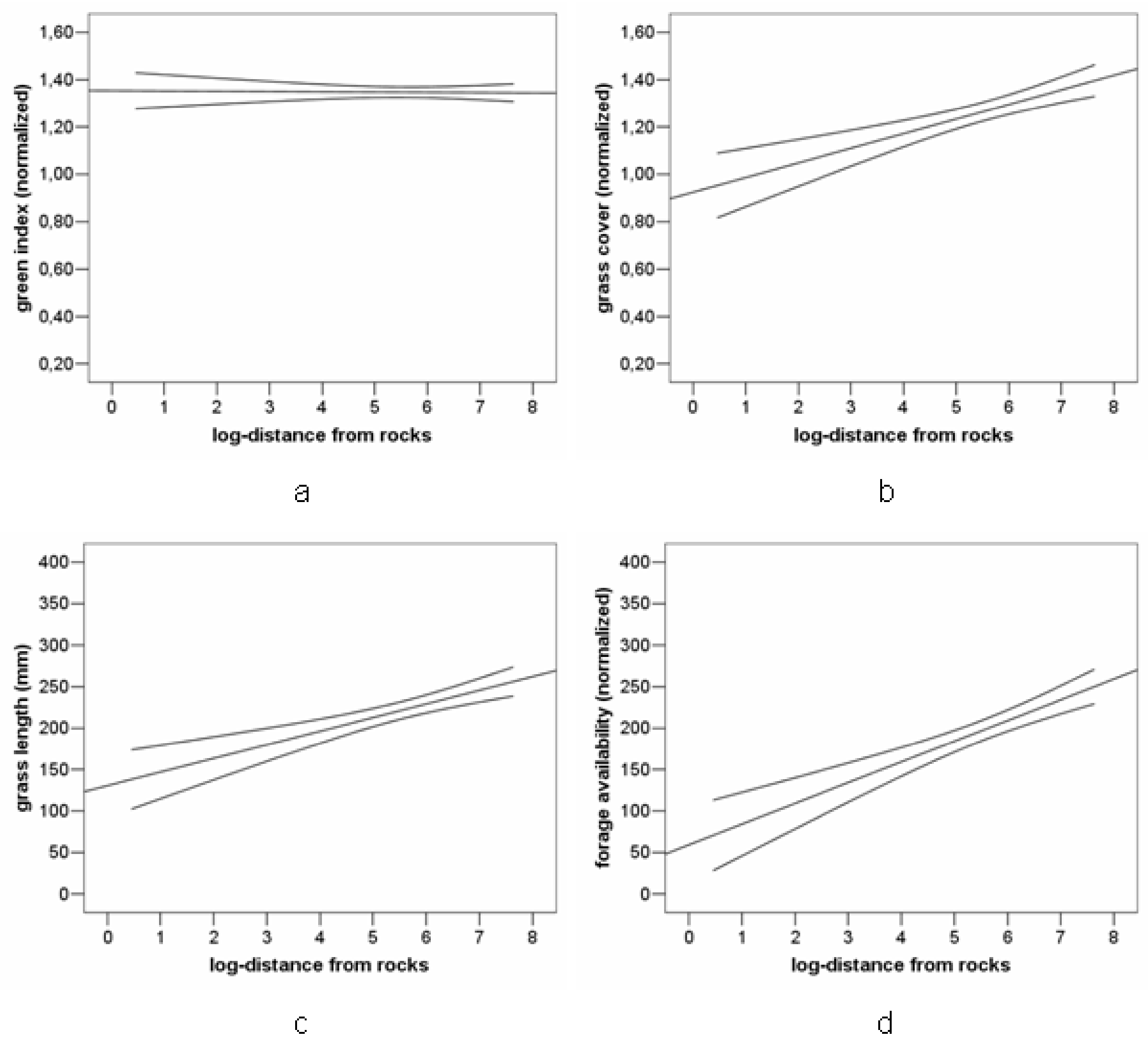

Figure 2 - Forage quality and quantity in relation to distance from rocks.
Effect of log-distance from rocks on the normalized green index (a), on the normalized grass cover (b), on the grass length (c), and on the normalized forage availability (grass cover×grass length/100) (d) recorded in 18 meadows randomly selected in the study area in the Eastern Alps, Italy. Linear regression lines and 95% Confidence Intervals were shown on each graph.

Thus, we modelled how the log-distance of chamois groups from rocks was affected by the co-presence of other ungulate species (domestic ungulates and/or mouflon) present in the area. We selected a large set of candidate independent variables to be fitted as predictor variables in our model. We associated to each chamois group observed (by means of ArcGIS 9.3, ESRI inc. 1999-2008) the following covariates: percentage of adult males within the chamois group; chamois group size (log-transformed); percentage of adult males within the nearest mouflon group; group size (log-transformed) of the nearest group of mouflon; distance (log-transformed) of the nearest group of mouflon; group size (log-transformed) of the nearest group of livestock; distance (meters; log-transformed) of the nearest group of livestock. We used the percentage of adult males within a group to define the type of aggregation in order to avoid collinearity issues between group size and number of adult males in our model. Moreover, among environmental variables, we considered the slope of the terrain where the chamois group was observed expressed within the 0-90° range, its altitude (meters a.s.l.), and its aspect (cos-mountainside, i.e. the expression of the mountain side exposure with respect to the north). The latter variable, originally expressed within the 0-360° range, it was cosine transformed, therefore assuming values from -1 (i.e. chamois group on the south aspect) to 1 (i.e. north aspect). We modelled the variation of log-distance of chamois groups from rocks by fitting a set LME models with REML method. The fixed factors in the models were shepherds' dogs presence within the nearest livestock group, and the month in which we carried out the observations. The other variables (mentioned above) were included in the models as covariates. (see Table 2 for the complete list of variables). We considered the 15-day period repeated among different years (2007 and 2008) as a random factor in the models in order to avoid pseudo-replication of data (Machlis et al. 1985). As a starting point, we included all main effects and all two-way interactions in the starting LME model. Then, we produced further LMEs by modelling the dependent variable excluding not significant interactions terms and including step by step a lower number of fixed factors or covariates. Akaike information criterion values (AIC) (Burnham and Anderson 1998) were reported for each single model. Among the final set of LMEs, in accordance with Mysterud et al. (2005), we chose as the best model the one with the lowest AIC value, for which we performed parameter estimations. All analyses were run using the SPSS 13.0 program (SPSS inc. 1989-2004), and all means were reported with standard errors.

RESULTS

We reported how we modelled the log-distance of chamois groups from rocks in Table 2. The best model characterized by the lowest AIC value included shepherds' dogs presence within the nearest livestock group, and the month in which we carried out observations as fixed categorical factors. The best model included the following covariates: the percentage of adult males within the nearest mouflon group, the size (log-transformed) of the nearest mouflon group, the distance (log-transformed) of the nearest mouflon group, the size (log-transformed) of the nearest livestock group, the distance (log-transfromed) of the nearest livestock group, and the slope of the terrain where chamois group were observed. The best model included one two-way interaction only (Table 2).

Parameters estimation (Table 3) of the most parsimonious model showed the single role of predictor variables in explaining the log-distance of chamois groups from rocks. Considering the fixed factors included in our best model, the presence of shepherds' dogs within the nearest livestock group induced the chamois groups to get closer to the rocks (mean ± SE; 250.35 m ± 66.01) while without this factor the distance increased (378.27 m ± 64.15). Moreover, the month of data collection was a factor able to contribute to the most parsimonious model in affecting the variability of distance of chamois groups from rocks. In particular during July and August the distance from rocks of chamois groups was lower than in June and September (June: 472.92 m ± 72.25; July: 319.58 m ± 53.34; August: 275.81 m ± 43.32; September: 454.63 m ± 52.57). Taking into account the covariates, higher was the percentage presence of adult males within mouflon aggregations or larger was the size of the nearest group of mouflons, lower was the distance from rocks of chamois. As regards to livestock, larger was the group of livestock, as well as closer it was from the chamois groups, lower was the distance of chamois from the rocks.

As regards to environmental variables, only the slope of the terrain where chamois were observed had a significant effect in the best model. Higher was the slope, higher was the distance of chamois group from rocks.

Shepherds' dogs presence - F	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Month - F	x	x	x	x	x	x	x	x	x	x	x	x		x	**x**
Males within chamois group (%) - C	x	x	x	x	x	x	x	x	x	x					
Log-chamois group size - C	x	x	x	x	x	x	x	x	x	x	x	x		x	
Males within mouflon group (%) - C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Log-mouflon group size - C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Log-distance from mouflon group - C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Log-livestock group size - C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Log-distance from livestock group - C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Slope - C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Altitude - C	x	x	x	x	x	x	x	x	x	x	x				
Aspect - C	x	x	x	x	x	x	x	x	x	x	x	x			
Log-chamois group size * Males within chamois group (%)	x	x	x	x	x	x	x	x							
Log- mouflon group size * Males within mouflon group (%)	x	x	x	x	x	x									
Log-distance from mouflon group * Males within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**
Log-distance from mouflon group * Log-mouflon group size	x	x	x	x	x										
Log-distance from livestock group * Log-livestock group size	x	x	x	x											
Log-distance from livestock group * Shepherds' dogs presence	x	x	x	x	x	x	x								
Log-livestock group size * Shepherds' dogs presence	x	x	x												
Log-distance from mouflon group * Males within chamois group (%)	x	x	x	x	x	x	x	x	x						
Log-distance from livestock group * Males within chamois group (%)	x	x													
Log-livestock group size * Males within chamois group (%)	x														
AIC	1571.492	1570.456	1568.836	1567.851	1563.874	1562.513	1560.853	1560.011	1559.976	1559.713	1558.723	1557.066	1556.009	1555.247	**1553.726**
Δ AIC	17.766	16.730	15.110	14.125	10.148	8.787	7.127	6.285	6.250	5.987	4.997	3.340	2.283	1.521	**0.000**

Table 2 - Model selection.

Model selection of a set of Linear Mixed Effect models fitted to explain chamois groups' distance from rocks (log-transformed) observed in the Eastern Alps, Italy, from 2007 to 2008. Each column corresponds to a model. [x = terms included in a model. AIC = Akaike information criterion value; ΔAIC = difference in the AIC value between a given model and the most parsimonious one (with the lowest AIC)]. Parameter estimation was run for the most parsimonious model (in bold, last column on the right) (see Table 3).

Parameter	Estimate	SE	t	P
Intercept	**-2.132**	**1.191**	**-1.779**	**0.006**
Shepherds' dogs presence	**1.187**	**0.368**	**5.078**	**<0.001**
Month [June]	**0.742**	**0.364**	**2.041**	**0.004**
Month [July]	0.009	0.306	0.028	0.978
Month [August]	-0.059	0.320	-0.185	0.853
Month [September]	0	0	-	-
Males within mouflon group (%)	**-7.738**	**2.218**	**-3.488**	**0.001**
Log-mouflon group size	**-0.282**	**0.104**	**3.215**	**0.002**
Log-distance from mouflon group	0.073	0.095	0.769	0.443
Log-livestock group size	**-0.272**	**0.058**	**-4.678**	**<0.001**
Log-distance from livestock group	**0.693**	**0.093**	**7.445**	**<0.001**
Slope	**0.019**	**0.008**	**2.344**	**0.020**
Log-distance from mouflon group * Males within mouflon group (%)	**1.159**	**0.360**	**3.215**	**0.008**

Table 3 - Parameter estimates and test statistics.
Parameter estimates and test statistics of the best model (Akaike information criterion value [AIC] = 1553.726; see Table 2) explaining the variation of distance (log-transformed) of chamois groups from rocks in the Eastern Alps, Italy, from 2007 to 2008.

Only 1 two-way interactions had a significant role in affecting the log-distance of chamois groups from rocks (Table 3). Indeed, chamois groups got closer to the rocks when mouflon groups were closer and at the same time including a higher percentage of adult males (Figure 3), but mouflon groups with lower percentage of adult males did not have the same effect on affecting the distance of chamois to rocks.

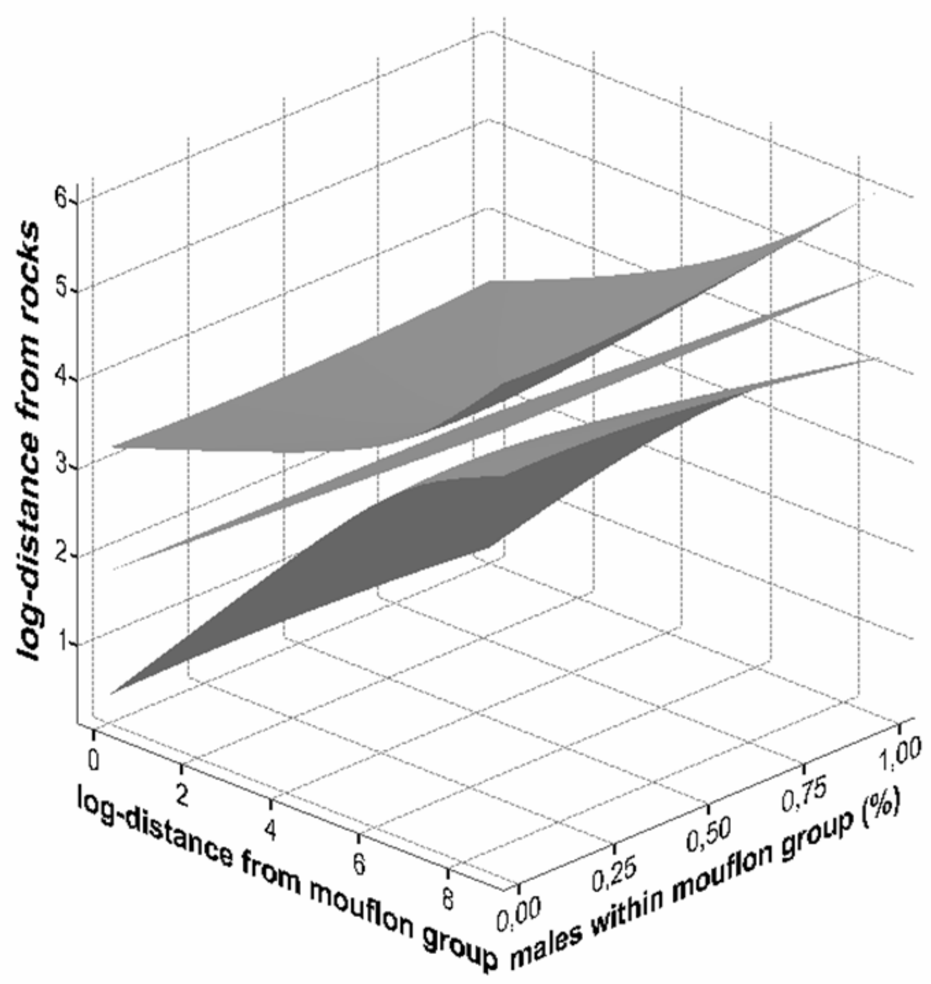

Figure 3 - Effect of two-way interactions on the dependent variable.
Combined effect of the distance (log-transformed) of the nearest mouflon group and the percentage of males in it on the dependent variable (i.e. log-distance from rocks of the chamois groups).
Linear regression surface and 95% Confidence Intervals describing log-distance from rocks variations were reported in the graph.

DISCUSSION

Our study showed that chamois were forced to use sub-optimal meadows (near rocks) as groups of mouflon were closer to them. Indeed, larger was the mouflon group size as well as higher was the presence of adult males within mouflon groups, lower was the distance of chamois from rocks. However, female groups of mouflon did not evoke the same behavioural response in chamois. At the same time the proximity and the size of livestock herd at large affected the distance of chamois from rocks, inducing the latter to find refuge there. Moreover, not only larger was the group of livestock, shorter was the distance of chamois from rocks, but this was highly pronounced when shepherds' dogs were also present.

The chamois group composition, represented by the fraction of males included within chamois aggregations, and its size did not play a significant role in our analyses, and were excluded by our best model. According to previous researches (Main et al. 1996, Grignolio et al 2007*a*, Ciuti et al. 2008) we could expect a different behaviour between male and female chamois groups in taking up high-quality meadows, with females supposed to get closer to rocks than males in the presence of sources of disturbances. In fact, the use of suboptimal meadows was not affected by chamois group type and this allows us to draw general considerations on the use of grazing areas for the species, with no differences between sexes. Indeed, the Alpine chamois is a relatively sexually monomorphic mountain-dwelling ungulate: only modest sexual dimorphism exists with respect to body mass and horn size (Couturier 1938, Schröder 1971, Knaus and Schröder 1983) and males couldn't be generally considered more aggressive and heavy than females. As regards to group size, we could expect that higher was the chamois group, lower was the effect of competitive species on its behaviour, but this did not occur as well. With relation to the group size, the predation factor might be the main driving force, as reported in many birds and mammals (Elgar 1989, Lima 1995, Roberts 1996, Zhongqiu and Zhigang 2008), in determining the right dimension able to increase detection ability and dilution of predation risk. So, we could expect that, for instance, higher was the chamois group, lower was the effect of dogs on the decrease of chamois distance from rocks (to find refuge), but this was not the case.

Different ungulate species that co-occur over evolutionary time have been hypothesized to develop mechanisms to limit the degree to which they directly compete for the same limited resources (i.e. resource partitioning). In situations where an exotic ungulate has been recently introduced to an ecological system, resource partitioning has not likely developed (Latham 1999). In Italian Alps, the mouflon showed a considerable dietary overlap with the chamois in all seasons and overlapping of the mouflon diet with those of the chamois was mainly due to a similar use of graminoids and dicotyledons (Bertolino et al. 2009). High food–niche overlap can imply competition (Belovski 1986, Putman 1996) but as Bertolino et al. (2009) argued only if resources are limited, and data on space use and habitat selection are also necessary to better understand resource sharing.

In our study case, the proximity of groups of mouflon and their group size affected the distance of chamois from rocks, and these data showed as in the presence of a non indigenous species, chamois made use of suboptimal meadows. Among ungulates Danilkin (1996) gave insights of sika deer (*Cervus nippon*) chasing roe deer from feeding sites and related that to a decline in roe deer population size after sika deer was introduced. In our study case, higher was the presence of males within mouflon groups, lower was the distance of chamois from rocks. However, female groups of mouflon did not evoke the same behaviour in chamois. This phenomenon can be arguably due to the direct competition for high-quality meadows between male mouflons (more aggressive and heavy than females) and chamois. While chamois's sexual dimorphism is low, mouflon shows high differences either in body size or in horn presence and size in the Alps (Ruckstuhl and Neuhaus 2002). Moreover, comparing male body mass and horn size in the two species, adult mouflon males have larger body size and horns than adult chamois males (see Pérez-Barberia et al. [1996] for *Rupicaprinae* and LeBlanc et al. [2001] for *Caprinae*). At the same time, the presence of livestock can influence distribution and behaviour of native ungulates (Kie 1996, Coe et al. 2001, 2004, Brown et al. 2010), as ungulates could move away from the areas occupied by livestock due to visual and acoustic disturbance (Matiello et al. 2002). Moreover, the diet overlap between domestic sheep and chamois (Berdoucou 1986, Garcia-Gonzales et al. 1990, La Morgia and Bassano 2009) and the spatial segregation of some population of *Rupicapra pyrenaica* (Rebollo at al. 1993) during summer suggested a direct negative interaction with domestic ungulates. In a recent study on Iberian ibex (*Capra pyrenaica*) in central Spain, the presence of a potential competitor, the domestic goat (*Capra hircus*), had a negative effect on ibex relative abundance, causing the ibex to select suboptimal habitat (Acevedo et al. 2007). According to that, our study case showed that chamois were forced to use sub-optimal meadows (near rocks) as livestock were closer to them. Moreover, larger was the group of livestock, shorter was the distance of chamois from rocks, and this was highly pronounced when shepherds' dogs were also present. In a similar way Ruttimann et al. (2008) reported all the encounters between chamois and sheep happened when sheep moved into areas occupied by chamois and the ending of the most of these encounters by the chamois demonstrated their intolerance towards sheep in close proximity. According to the effect of livestock group size, Kie (1991) demonstrated that female mule deer (*Odocoileua hemionus*) competed with cattle particularly at high stocking rates. There are no specific studies on the disturbance caused by shepherds' dogs to wild ungulates, but Lenth et al. (2008) reported that the presence of domestic dogs (*Canis familiaris*) along recreational trails is correlated with altered patterns of habitat utilization by several species and mule deer activity was significantly lower within 100 m of trails in areas that allowed dogs than in areas that prohibited dogs. Moreover Herbold et al. (1992) reported physiological change in red deer and roe deer due to dogs barking.

As regards to environmental variable tested in our set of models, only the slope positively affected the dependent variable: chamois took advantage of better pastures when it is found in situations of steeper slope, areas that can be considered of greater shelter (Grignolio et al. 2007*b*). Not so surprising this native ungulate showed a wider adaptation level to mountain environment. Finally, the month of data collection play a significant role in shaping the position of chamois, showing the importance of weather condition in determining the position of chamois groups. In July and August chamois groups were closer to rocks probably in accordance to meteorological conditions. As Grignolio et al. (2007b) reported for Alpine Ibex, in high temperature and scarce precipitation conditions during summer, weaning females modified habitat selection (i.e. use of suboptimal habitat in rocky areas).

In conclusion, our study showed for the first time how livestock, along with shepherds' dogs presence, and wild non native ungulates may force chamois in the use of meadows closer to rocks, where the availability of grass is lower than elsewhere through a direct and indirect competition process. This, in turn, may negatively affect the gain of a proper body size of chamois during summer due to reduction of feed intake, and it could have strong impacts on the productivity of females, on the winter survival of both sexes, and, more in general, on its population dynamic (Gaillard et al. 1998, Festa-Bianchet et al. 2000, Côté and Festa-Bianchet 2001).

MANAGEMENT IMPLICATIONS

The wildlife-livestock compatibility issue is very important either in conservation (Acevedo 2007, Fleischner 1994) or in management practice (Kie et al. 1991, Loft 1991, Ruttimann et al. 2008, Brown et al. 2010). Recently, the global warming topic with the resulting lower quality of Alpine meadows (Sanz-Elorza 2003) exacerbate this issue. In this context, our study showed how domestic and wild non native ungulates forced chamois to use forage areas with lower productivity. According to this, managers should account for the presence of domestic ungulate when carrying out chamois management plans because we showed that their presence may reduce the food intake for the native species. Moreover, when there are evidences of competitive interaction between native and non-native ungulate management plans should account for the status (i.e. demographic trend) of native species. In our study the co-presence of introduced ungulate species was a further factor negatively affecting the free access to resources for native ungulates and management practice should take it in account. Finally, managers should consider habitat use in summer as an important aspect for management activities. Management plans should also account for summers with anomalous weather conditions, which may directly reduce the pasture quality, and indirectly alter the population dynamic of this species forced in sub-optimal habitat.

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CONCLUSIONS

The results of the **First Part** show for the first time a different investment in horn length in chamois of both sexes shot on siliceous soil than on calcareous one. Horns were found to be longer in chamois shot in calcareous areas than in siliceous ones, thus confirming that the soil type can indirectly constrain their growth. The quality of grassland communities to be found on calcareous substrates is higher than that of communities on siliceous ones (i.e. species richness; Grime 1979, Cavallero et al. 2007). As suggested by several authors (Duchaufour 1989, Gensac 1990, Rameau et al. 1993, Duchaufour 1997), the higher nutrient availability on calcareous soils when compared to siliceous soils is accompanied by higher plant productivity. Plant communities growing on siliceous soil have structural characteristics that can also reduce digestion efficiency (Laca et al. 2001), and, consequently, may negatively affect the energy intake of the animals feeding on them. This propriety can also have a negative effect on horn growth and size in chamois. Adverse environmental and climatic conditions (e.g. elevation, snow cover, northern mountainsides) negatively affected horn lengths in yearling chamois of both sexes. I found significant interactions between substrate type and both snow cover and aspect, with significantly longer horn length on calcareous rocks only with low snow cover and North exposure. This was likely due to the high-quality grasslands growing over calcareous soils in wet conditions and to the more negative impact of high snow cover in calcareous environment. Moreover I found that, rainfalls positively affected horn growth not only in kids, but also later, when 1 y.o. individuals directly benefited from high quality meadows, confirming that horn growth is a cumulative process which reflects environmental condition. In general, ecological factors such as temperature and precipitations positively affected horn size during the first year of life more than during the second, thus confirming that the early stage of development is a crucial step in the individual life history of ungulates (**Chapter 1**).

As evidenced in mountain goats (*Oreamnos americanus*; Festa-Bianchet and Côté 2008) for both sexes and in bighorn rams (*Ovis canadensis*; Festa-Bianchet et al. 2004), in worse condition (e.g. decreasing early-June fecal crude protein) yearlings allocated more resources to body rather than to horn growth. In my study (**Chapter 2**) I demonstrate that in different climatic and environmental conditions, individuals can acquire resources and decide to allocate them in a different way: the trade off between body mass and secondary sexual traits priority investment showes the use of alternative life history tactics. The allocation strategy may increase the probability of survival, possibly at the cost of decreased lifetime reproductive success and consequently by allocating more resource to body growth rather than to horn growth, yearlings may not compromise their short-term survival.

Another factor able to influence the quantity and quality of resource availability is the local population density, especially for yearlings. As reported for bighorn sheep (*Ovis canadensis*), population density has a negative effect on body mass and seasonal mass changes of young males and females (LeBlanc et al. 2001).

In ungulates, juveniles are more susceptible than adults to density-dependent resource limitations (Gaillard et al. 1998), and high densities could negatively affect ungulate populations through increased forage competition (Post and Stenseth 1999).

Differences in environmental characteristics or in local population density may play a different role in females or males life history tactics (Stearns 1992).

According to females, body weight and population density therefore play a decisive role in reproductive potential (Reimers 1983, Gaillard et al. 1992, Sæther and Heim 1993). In bighorn sheep (*Ovis canadensis*) both factors have a significant effect upon the probability of ewes lactating at 2 years of age (Jorgenson et al. 1993). Even young bighorn ewes postpone primiparity when resources are scarce (Jorgenson et al. 1993), and age of primiparity is often the first vital rate affected by increasing population density in ungulates (Gaillard et al. 2000).

During the rutting season, males defend areas within which they attempt to keep a varying number of females. In this period, male chamois engage in intra-sexual contests showing direct and indirect forms of aggressive behaviour (Krämer 1969), in which body mass and horn size likely play an important role. Because male reproductive success typically depends on male-male combat, males are generally expected to adopt a riskier strategy than females to achieve the greatest possible development of weapons (antlers and horns) used in competition for estrous females, and consequently suffer a survival cost, particularly when resources are scarce (Clutton-Brock 1988). By directing more resources to body growth rather than horn or antler growth when food is scarce, males might increase their survival probability, possibly to the detriment of their short-term reproductive success. As resources become scarce, young rams allocate an increasing proportion of those resources to body growth rather than to horn growth. Rams 2 years of age and older can father lambs

(Coltman et al. 2002, Hogg and Forbes 1997), but horn length does not affect reproductive success of rams younger than about 7 years (Coltman et al. 2002). Consequently, by allocating more resources to body growth rather than to horn growth, young rams may not compromise their short-term reproductive success.

A fundamental life history question is how to allocate reproductive investment optimally over time. The 'terminal investment' hypothesis predicts that individuals should continue to invest more energy in reproduction after prime age, owing to a decreasing residual reproductive value (RRV). Consistent with the theory of terminal investment, we found that reproductive investment in male Alpine chamois *Rupicapra rupicapra* increased with age and continued to do so even after the onset of apparent senescence. Terminal investment is an important concept but has rarely been verified reliably before, particularly in males. As such, our results provide an important contrast to accelerating support for reproductive restraint in later life. We also found highly male skewed mortality rates, likely a result of hunting pressure. By reducing the RRV of males, hunting will be a strong driver of terminal investment, illustrating the pervasive effects of human harvesting on demography, population dynamics and life histories. The analyses in the **Second Part** (**Chapter 3**) show that reproductive investment in male Alpine chamois increases with age and males continue to invest more energy in reproduction after prime age, owing to a decreasing residual reproductive value (RRV).

These findings provide compelling support for the terminal investment hypothesis, suggesting that old males compensate for a lower chance of breeding in the future by investing more in current reproduction. My findings contrast with results from a range of taxa, particularly in males (Cameron et al. 2000, Yoccoz et al. 2002, Billing et al. 2007). Generally, reproductive restraint is thought to be favoured after prime age due to a trade-off between current reproduction and survival. This strategy enables senescent individuals to continue to breed for a number of years, albeit with a lower reproductive output within any given breeding season. McNamara et al. (2009) used a modelling approach to highlight broad conditions under which reproductive restraint is likely to occur, suggesting that terminal investment should rarely be observed. McNamara et al. argued that time pressure may be weaker on an individual that has already accumulated significant damage because extrinsic mortality risk, such as from disease or predation, is low relative to the risk of death from intrinsic causes. When the risk of extrinsic mortality is lower than that of intrinsic mortality (due to the accumulation of cellular and physical damage), restraint should be optimal because high reproductive investment could lead to rapid damage accumulation and death. However, extrinsic and intrinsic mortality are concepts which are difficult to separate (and are particularly difficult to measure separately in the field [Nussey et al. 2008]). In reality, different sources of mortality are tightly linked and the accumulation of damage due to senescence is likely to increase the risk of both intrinsic and extrinsic mortality (Williams and Day 2003, Reznick et al. 2004). For example, whilst disease and predation are extrinsic mortality sources, they are more likely to kill individuals that have already accumulated significant levels of intrinsic damage (Ashman et al. 1999, Moller and De Lope 1999, Wright et al. 2006).

Finally in the **Third Part** (**Chapter 4**) I demonstrate for the first time how livestock, along with shepherds' dogs presence, and wild non native ungulates may force chamois in the use of meadows closer to rocks, where the availability of grass is lower than elsewhere through a direct and indirect competition process. This, in turn, may negatively affect the gain of a proper body size of chamois during summer due to reduction of feed intake, and it could have strong impacts on the productivity of females, on the winter survival of both sexes, and, more in general, on its population dynamic (Gaillard et al. 1998, Festa-Bianchet et al. 2000, Côté and Festa-Bianchet 2001). My conclusion has an important role in wildlife management: managers should account for the presence of domestic and wild non-native ungulate when carrying out chamois management plans. Moreover, non-native ungulate management plans should account for the status (i.e. demographic trend) of native species. Managers should consider habitat use in summer as an important aspect for management activities. Management plans should also account for summers with anomalous weather conditions, which may directly reduce the pasture quality, and indirectly alter the population dynamic of this species forced in sub-optimal habitat.

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