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INTER-INDIVIDUAL VARIATION OF BEHAVIOUR IN ALPINE IBEX (*CAPRA IBEX*): THE EFFECT OF BODY SIZE

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To my grandfather…

Index

Summary

[ENGLISH] In mammals, body size determines energetic requirements, the amount of food that can be gathered, and the vulnerability to predators. Moreover, in polygynous species, body size is one of the major factors contributing to male reproductive success. Alpine ibex (*Capra ibex*) is an ungulate characterised by an evident dimorphism between sexes, but also among males of different age. Hence it is an ideal study case to shed light on the effects of body size in individuals of the same species, avoiding implications linked to sex. My findings suggest that for male ibex to reach a large body size is a benefit under different points of view, involving feeding, predator avoidance and reproductive success. While foraging, larger males were less selective than younger and smaller ones, thus suggesting that large body size provides to males the possibility to use a poorer quality of food, which is typically more readily available in the environment. Results on antipredator behaviour (related to vigilance, group size and use of safe areas) showed that larger males are generally less sensible to predation risk. These findings strongly suggest that adult males benefit from more time for feeding (they showed lower vigilance frequency) and from higher quality and quantity of forage (they used riskier and high-quality meadow far from rock and steep slopes). However, an increase of predation risk, related to the recovery of a wolf (*Canis lupus*) pack in the study area, led to important behavioural changes, even if large male ibex were little affected by direct lethal effects of wolves predation. In fact, after wolf recolonization male ibex changed their habitat use in favour of safer areas, at the expenses of a less rewarding food intake. Finally, I found that old and full-grown males had higher mating opportunities as, thanks to their large body size, they were more competitive. This was particularly true during rut seasons with abundant snow, when only the tactic successfully used by large males (*tending tactic*) was adopted. Moreover, large body size provides adult males with more fat reserves that gave them the possibility to substantially reduce food intake during the rut. As consequence, adult large-bodied males had more time to invest in mating related activities and, thus, had more chance to mate. In conclusion, the findings of this study showed that the evolution of large body in male ibex is probably to be favoured because it increases, directly and indirectly, their reproductive success.

Riassunto

[ITALIAN] Lo scopo di questa tesi è stato quello di analizzare gli effetti delle dimensioni corporee sui *pattern* comportamentali dello stambecco alpino (*Capra ibex*). E' noto come le dimensioni corporee degli animali influenzino le loro richieste energetiche, la qualità e la quantità del cibo utilizzato e il rischio di predazione cui possono essere sottoposti. Inoltre, nelle specie poliginiche, la taglia corporea sembra essere uno dei fattori che maggiormente contribuisce ad aumentare il successo riproduttivo maschile. Lo stambecco alpino è un ungulato caratterizzato da un evidente dimorfismo fra i sessi e fra maschi di età diversa; esso è quindi un ottimo modello di studio per indagare come, all'interno della stessa specie e dello stesso sesso, le differenze della taglia corporea tra gli individuali possano influenzarne il comportamento. I risultati di questo studio suggeriscono che per un maschio di stambecco raggiungere grosse dimensioni corporee è vantaggioso sotto differenti punti di vista, che coinvolgono strategie alimentari, anti-predatorie e riproduttive. Dalle analisi del comportamento alimentare è risultato che i maschi adulti, di grosse dimensioni, hanno la possibilità di tollerare una dieta qualitativamente più povera, e quindi più facilmente reperibile nell'ambiente in cui vivono. I risultati relativi al comportamento anti-predatorio dimostrano che i maschi più grossi erano meno vulnerabili al rischio di predazione. In particolare, i maschi di dimensioni corporee maggiori, eseguivano meno eventi di vigilanza e così avevano più tempo a disposizione per l'assunzione di nutrienti e, utilizzando pascoli maggiormente lontani dalle pareti rocciose, potevano nutrirsi di un foraggio di più alta qualità. Nonostante le più grandi dimensioni fisiche ed i benefici connessi in termini di comportamento alimentare, il ritorno di un grande carnivoro, il lupo (*Canis lupus*), ha causato importanti modificazioni anche sul comportamento dei maschi adulti. Dopo il ritorno del predatore, i gruppi maschili utilizzavano siti di foraggiamento più prossimi alle aree rifugio, anche se a discapito della qualità del foraggio di cui alimentarsi. Infine, i maschi di stambecco di grosse dimensioni corporee potevano avere maggior successo riproduttivo, poiché potevano essere più competitivi

per l'accesso alle femmine in estro. Tale tendenza era più evidente durante le stagioni riproduttive caratterizzate da più alta copertura nevosa, durante le quali solo la strategia riproduttiva statica (*tending tactic*), utilizzata esclusivamente dai maschi adulti, poteva essere adottata. Inoltre, i maschi adulti, accumulando maggiori riserve di grasso in estate, potevano permettersi di ridurre maggiormente il tempo speso in alimentazione durante la stagione degli amori. Essi avevano così più tempo a disposizione per il corteggiamento e così più possibilità di incrementare il loro successo riproduttivo. In conclusione, i maschi di stambecco alpino di maggiori dimensioni corporee attuano una serie di adattamenti comportamentali tali da favorire sia, direttamente sia indirettamente, il loro successo riproduttivo, lasciando intuire una selezione positiva verso maschi con sviluppo ponderale più accentuato.

Introduction

Body size is one of the most obvious features of any animal and one of the most important (Calder 1984; Peters 1983; Reiss 1989; Schmidt-Nielsen 1984). Many physiological and ecological attributes of animals scale significantly with body mass. Since these attributes influence behaviour, it is to be expected that behavioural patterns should also scale in some ways with animal size (Peters 1983).

Large body size provides a number of ecological advantages. The advantage most often cited is a reduced relative energy requirement for maintenance, due to a relative increase in gastrointestinal capacity in relation to energy requirements (Demment and Van Soest 1985). A large body can facilitate larger movement ranges (Altman 1987). Moreover, it enables large species to successfully compete with smaller ones for the same resource (e.g. elephants: Fritz et al. 2002) and it provides an organism with the ability to avoid predation (Owen-Smith 1988). On the other hand, large animals have high absolute energy requirements and therefore need more abundant forage (Demment and Van Soest 1985). Due to their low surface-to-volume ratio, they can have difficulties in dissipating heat (Owen-Smith 1988). Lastly, larger animals tend to have fewer offspring, mature sexually at a later age, and have longer gestation times (Peters 1983), all of which lead to long generation intervals, which drastically prolongs the evolutionary reaction time of species.

In ungulate, a lot of researches have analysed the influence of body size on animal behaviour comparing species of different sizes. Many work has been done on foraging behaviour (e.g. Demment and Van Soest 1985; Illius and Gordon 1987; Shipley and Spalinger 1995; Clauss et al. 2003), on anti-predator behaviour (e.g. Berger and Cunningham 1988; Sinclair et al. 2003; Fortin et al. 2004) and on specific habitat selection resulting from the trade off between food acquisition and safety from predators (e.g. Grignolio et al 2007; Hopcraft et al. 2012). Within the same species, where males and females are dimorphic, the interactions between body size and digestive strategies and/or the anti-predator behaviour have been used to explain, for example, the phenomenon of sexual segregation (e.g. Barboza and Bowyer 2000; Ruckstuhl and Neuhaus 2005). Here I proposed a study in which I analysed how differences in body size may affect different behavioural patterns among dimorphic males of the same species. In so doing, it is possible to highlight the effect of body size per se, free from constraints related to specific aspect of species or of gender. Alpine ibex (*Capra ibex*) is an ungulate characterised by extreme sexual dimorphism (more than 100% in body mass - Loison et al. 1999) and a peculiar body growth. Females reach their maximum weight at the age of 4-5, while males show a slow and progressive increase of body mass until the age of 9-10. As a consequence, males present a remarkable dimorphism among different age classes (Bassano et al. 2003). For these reasons, the ibex is an ideal case study for investigating behavioural polymorphism resulting from differences in animal body size.

Size influences how much energy an animal needs and determines the quality of forage it is capable of processing (Owen-Smith 1988). The conventional expression of animal requirements assumes that energy requirements are proportional to body weight raised to the 0.75 power (Thonney et al. 1976). This means that large animals generally require more total energy, but small animals require more energy per unit of body weight for maintenance and general functions (VanSoest 1994). In ruminant ungulate, the capacity to process food into nutrients is determined, in part, by the gastrointestinal capacity, which scale isometrically with body weight. Thus, larger animals have larger rumen and a relatively lower rumen turnover ratio, allowing the food to stay longer in the stomach (Demment and Van Soest 1985). Longer retention of digesta increases digestive efficiency and would permit larger animals to survive on lower-quality foods compared with smaller ones (Demment and Van Soest 1985; Illius and Gordon 1992). On the other hand, since small animals have lower total metabolic requirements, they have a greater ability to fulfil their energetic requirements with high-quality foods, which are generally scarce and discretely distributed in the environment. Because small ungulates are obliged to seek out rare high quality foods, they are expected to increase their diet selection by means of increased searching time while foraging (Demment and Van Soest 1985).

The concept of search time for a generalist herbivore has been taken to be different from that of a predator. Rather than seeking specific prey, an herbivore is usually assumed to travel an environment containing a superabundance of potential foods varying greatly in their potential nutritional value (Hanley 1997). Search time for a particular type of food is then considered simply the inverse of its encounter rate (function of its density in the feeding patch), spatial distribution (clumped, uniform, ect.), and the speed of travel and search-path width of the foraging animal (Roese et al. 1991; Spalinger and Hobbs 1992). Each animal may determine the quality of its diet selecting the forage with each bite; whereas, it can regulate the quantity of its food intake modifying the number of bites and their size (Parker et al. 1996). Food intake rate of grazing herbivores feeding in food-saturated patches is typically negative related to bite size (Spalinger and Hobbs 1992). In turns, the size of the bite cropped on grasses is a function of height and density of available plants and incisor bar width and shape of the herbivore (Illius and Gordon 1987; Spalinger and Hobbs 1992; Gross et al. 1993), which usually scale with its body mass (Shipley et al. 1994).

Thus, the body size of ruminant ungulates strongly constrains individual' feeding behaviour. Besides its influence on feeding behaviour, body size may also determine the individual responses to changing environmental conditions, as in the case of variable quality and quantity of forage. A first aim of this thesis was to describe and understand the connection between male ibex body size, their feeding behaviour and the characteristics of patches were they feed (**chapter 1**).

The size of an herbivore also affects the rates at which it is predated (Cohen et al. 1993; Sinclair et al. 2003). Sinclair et al. (2003) showed that smaller-bodied ungulates suffer predation from many more predators than do larger ungulates. Moreover, small herbivores and juveniles are exposed to greater rates of predation as large predators, in addition to eating large prey, also tend to supplement their diet with small preys (Cohen et al. 1993).

Predation is an important agent of natural selection and can have a strong influence on the evolution of behavioural patterns in herbivore species (Lima and Dill 1990). Herbivores, during all their lifetime have constantly to solve the trade-offs between the need of forage and protection from predators (Lawton and McNeill 1979; Sinclair and Arcese 1995). An individual foraging under predation risk has several options to solve the conflicting demands of food versus safety. A forager can influence its safety by the way it allocates time among different activities that differ in risk and in food intake opportunities (Brown 1999). While foraging, an individual should choose primarily when and where to eat but also how long it should stay in a food patch (Lima and Dill 1990). Patch choice requires a trade-off between feeding rate and predation risk. Factors that influence whether to opt for a riskier patch include the state of the forager (e.g. non-pregnant adult females are more willing to take risks than pregnant females or females with kids; Festa-Bianchet 1988; Grignolio et al. 2007), direct or indirect cues of predation risk (Brown 1988), time since last exposure to a predator (Kotler 1992) and the body size of the forager (Hopcraft et al. 2012). A second option for managing risk of predation is the choice of the vigilance level. Vigilance is often defined as time spent scanning the surroundings with the head up (scanning behaviour) during which time no foraging takes place (Hochman and Kotler 2007). The importance of vigilance in the detection of predators has been well established in numerous theoretical and empirical studies (i.e. reviewed most recently by Treves 2000; Bednekoff and Lima 2002). Despite the demonstrable benefits of vigilance behaviour, its performance by animals is limited because it requires exclusive visual attention, reducing the time available for other activities such as foraging or mating (Pulliam and Caraco 1982). Studies of vigilance have shown sex-age class and body size to be important factors influencing vigilance behaviour (Berger and Cunningham 1988; Laundré et al. 2001). Aggregation with conspecifics is a further behaviour that can help to reduce predation risk (Hamilton 1971; Treisman 1975). Individuals in a group of conspecifics can potentially benefit by coordinated group defence, increased probability of escape or decreased probability of death per encounter (Bertram 1978; Turner and Pitcher 1986). Moreover, groups of vigilant individuals potentially benefit by a collective ability to detect predators sooner than solitary individuals, allowing for reduced levels of individual scanning and increased foraging effort (Pulliam 1973; Elcavage and Caraco 1983).

Given such scenario, the second goal of this thesis was to examine vigilance behaviour of male ibex while foraging. I analysed the effect of body size, forage quality and quantity, and group size on scan frequency of feeding males (**chapter 1**).

The Gran Paradiso National Park (where this study was conduced) was a "predator free" area for ungulates until 2006, when a resident wolf (*Canis lupus*) pack was confirmed. This event gave the rare opportunity to monitor the behavioural response of preys in face of a change in predation risk. Thus, in the second part of this thesis I investigate which behavioural mechanism was used by individuals of different body size (between and within species) in reaction to the return of their main predator (**chapter 2**).

The evolution of male large body size is generally under control of sexual selection, deriving from the advantages conferred to males during competition for mates by a larger body (Andersson 1994). In fact, body size has often been found to be a major contributing factor to male reproductive success (reviewed in Höglund and Alatalo 1995). This is especially true in species with large variation in body size. These species include several insects (where larger males occupy the sites favoured by incoming females), amphibia (e.g. frogs, where spectral properties of male mating calls are associated with body size: Friedl and Klump 2005), and, particularly, polygynous ungulates, where body mass is generally considered to be the main determinant of social rank or territorial acquisition (e.g., *Kobus kob thomasi*, Balmford et al. 1992; *Dama dama* and *Ovis canadensis* Clutton-Brock et al. 1988; Pelletier and Festa-Bianchet 2006; *Bison bison*, Bowyer et al. 2007).

In polygynous ungulates, yearly reproductive success of males is often skewed, because a few males mate with many females and several males do not mate at all (Apollonio et . al 1989, Hogg and Forbes 1997; Preston et al. 2003). The monopolization of females in oestrus appears to be mainly determined by the ability of males to keep other males away, which is strongly correlated with fighting abilities and often with social rank (Roed et al. 2002; Pelletier and Festa-Bianchet 2006). Social rank is often linked to conspicuous secondary traits such as body mass, body size and antler or horn size (Clutton-Brock et al. 1980; Pelletier and Festa-Bianchet 2006; Bergeron et al. 2010). Common male tactics to monopolize receptive females are the direct defence of potential mates (Clutton-Brock et al. 1982; Hogg 1987) or the defence of territories on which females reside (Clutton-Brock et al. 1988; Von Hardenberg et al. 2000). The successful defence of females or territories is usually restricted to a small number of large-size and dominant males that can compete more effectively in keeping other males away (Isvaran 2005; Wolff 2008). Subordinated males, often smaller and younger individuals, must resort to alternative cryptic or satellite tactics, including abducting oestrous females or sneaking copulations when the opportunity arises, in order to achieve reproductive success (e.g. Hogg 1987; Apollonio et al 1992). Male alternative mating tactics (AMTs) commonly coexist between and within populations of a huge ungulates species (Isvaran 2005). It has been demonstrated that male AMTs commonly change according to internal factors (age, body size, condition) and external conditions (weather, resources, predation, animal density: Isvaran 2005).

In the third part of this thesis I investigated ibex males rutting behaviour with the aim to assessed the presence of male AMTs in its only native population. I analysed the influence of male body size on the adoption of AMTs. Moreover, since weather and environmental conditions are commonly thought to affect the use of different mating tactics, I analysed the effect of weather on male reproductive behaviour and on the adoption of AMTs, giving the first quantitative example of such influence on the mating behaviour of a mammals (**chapter 3**).

Reproduction generally leads to high energy expenditure and imply severe trade-off between energetic costs of mate and other fitness components such as survival (Descamps et al. 2006). One of the major costs commonly reported is related to changes in animal activity budget that often imply a reduction in food intake during the rut. Rut-induced hypophagia has been reported across a wide range of ungulate species (*Alces alces*: Miquelle 1990; *Bison bison:* Komers et al. 1994; *Dama dama:* Apollonio and Di Vittorio 2004; *Ovis Canadensis*: Pelletier 2005; *Rupicapra rupicapra*: Willisch and Ingold 2007; *Oreamnos americanus*: Mainguy and Côté 2008; *Cervus elaphus*: Mysterud et al. 2008). Several studies pointed out that the degree of forage reduction during the rut varies according to male age, with adult males foraging less than young males (Maher and Byers 1987; Miquelle 1990; Apollonio and Di Vittorio 2004; Mainguy and Côté 2008; Mysterud et al. 2008). Younger and smaller males have less chance of immediate reproduction when competing with larger adult males (see also Chapter 3). Therefore, they might give priority to growth in order to increase their future chances of reproduction (Maher and Byers 1987; Miquelle 1990; Mainguy and Côté 2008). This could be particularly important for Alpine ibex male, in which male dimorphism is at the highest levels. Accordingly, it is particularly interesting to ascertain whether males show a rut-induced hypophagia or not, and to investigate the proximate mechanism accounting for it. In the last chapter of this thesis (**Chapter 4**) I analysed and compared the activity budgets of ibex before, during, and after the breeding season (from October to February) in order to evaluate if male ibex incur in hypophagia during the rut, trying to understand the proximate mechanisms leading with it.

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FIRST PART

Foraging and antipredator behaviour

Chapter 1

Effects of body size on foraging behaviour in dimorphic males

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ABSTRACT

Foraging behaviour exerts an important influence on herbivore biology, as it affects population distribution and dynamics, use of ecological niches and impact on the environment. Animal body mass and forage quality and quantity are key elements of the foraging ecology of wild herbivores. Since the body size could influence the animal's sensitivity to predation risk, it is to be expected that the vigilance behaviour will also be affected, particularly during foraging. Alpine ibex (*Capra ibex*) is characterised by a strong dimorphism among males of different ages. Hence, it is an ideal case study for investigating the effect of body size per se, in individuals of the same species and sex. We analysed the fine-scale foraging behaviour of ibex males in order to assess: 1) the effect of body size on male behaviour, and 2) the effects of vegetation quality and quantity on both foraging and vigilance behaviour. Results showed that young and small males seemed to be more selective than older ones, presumably on account of their lower capability of digesting plant material and their higher energetic requirements for growth. While feeding, young males scanned the environment more frequently than older males, therefore probably paying a greater cost for vigilance. All foraging ibex males seemed to graze more selectively in sites with high quality forage and their biting rate increased as forage biomass decreased, thus suggesting that male ibex have a behavioural flexibility that enables them to adjust their foraging decisions in response to changes in the quality of the patches where they feed. Forage quality and quantity also affected vigilance behaviour. Scan frequency increased with increasing forage biomass, arguably because, in these conditions, they should be able to scan the environment while chewing bites that have already been cropped. Finally, our findings showed that for male ibex feeding in group is rewarding, because individual vigilance behaviour decreased without any apparent negative effects of intra-group competition on foraging behaviour.

Key words: Alpine ibex, body size, diet selection, forage quality, vigilance behaviour

INTRODUCTION

Foraging behaviour is a highly influential process in many respects of herbivore ecology. It motivates animal movements, controls energy and nutrients intake and therefore affects the individual's body condition, reproductive success and survival (Senft et al. 1987; Festa-Bianchet 1988; Spalinger and Hobbs 1992). The study of the factors driving foraging behaviour may provide valuable insights about the mechanisms of resource selection and may thus improve our understanding of animal distribution and population dynamics (Bailey et al. 1996; Wilmshurst et al. 1999; Fryxell et al. 2004).

For ruminant ungulates, the primary constraints on foraging behaviour result from the interplay between the individual morphological and physiological limitations and the characteristics of the plant resource under exploitation (Arnold 1975). Morphological and physiological limitations are strongly related to the animal's body mass: digestive efficiency and, consequently, the feeding niche selected (i.e., the minimum quality and quantity of food necessary for survival) have been proven to be strongly related to body mass (Illius and Gordon 1992). Whereas specific metabolic rate decreases with increasing body weight, gut capacity remains a constant fraction of the body weight. Hence, larger ungulates should be able to tolerate a lower minimum dietary quality than smaller ones (*Bell-Jarman principle* in Geist 1974). Large animals have large rumens and a relatively slow rumen turnover ratio, which allows the food to stay longer in the stomach. A longer retention of digesta increases the digestive efficiency and enables larger animals to survive on lower-quality food more easily than smaller ones (Demment and Van Soest 1985; Illius and Gordon 1992). The theory, thus, predicts that small-bodied animals should compensate by selecting food that is more readily digested.

Body size in ungulates could also affect the forager's intake rate (Shipley et al. 1994): when herbivores graze in food-saturated patches, such as alpine meadows, their intake rate is negatively related with the mass of plant tissue that an animal can remove from the plant with a single jaw movement (Spalinger and Hobbs 1992), that is defined as bite size (Gross et al. 1993). The size of the bite cropped on grasses is a function of the plant height and density, and on the width and shape of the incisor bar (Illius and Gordon 1987; Spalinger and Hobbs 1992; Gross et al. 1993), which are usually proportioned to the body mass (Shipley et al. 1994). An individual's bite rate can be affected by several other factors, such as satiation level and reproductive status, but also by the trade-off between foraging and social conflicts and security from predation (Ruckstuhl et al. 2003). The predation risk perception is another important factor that adds to the influence of body size on foraging behaviour. While foraging, animals usually scan the environment in order to increase the probability of detecting predators (Brown 1999; Treves 2000; Bergman et al. 2001). Despite its well-established benefits (Treves 2000), this vigilance performance is limited because it requires exclusive visual attention, thus reducing the time available for other activities, such as foraging or mating (Pulliam and Caraco 1982). The fundamental importance of foraging cost is recognized in many theoretical models of vigilance, where foraging and scanning are considered as mutually incompatible (Lima 1988). However, some authors have questioned this assumption, showing that vigilance and foraging can occur simultaneously when foragers are able to scan the environment while chewing vegetation (Illius and Fitzgibbon 1994, Cowlishaw et al. 2004).

Several studies have analysed the influence of body size on ungulate foraging behaviour (e.g. Demment and Van Soest 1985; Illius and Gordon 1987; Illius and Gordon 1992; Shipley and Spalinger 1995; Clauss et al. 2003). The interactions among body size, digestive efficiency and diet selection have been used to explain diverse foraging strategies and competitive interactions among different ungulate species (e.g. Demment and Van Soest 1985; Illius and Gordon 1992; Shipley and Spalinger 1995), as well as to compare dissimilar foraging behaviours between males and females in sexually dimorphic species (e.g. Gross et al. 1996; Ruckstuhl et al. 2003; St-Louis and Côte 2012) and to explain sexual segregation (cf. Barboza and Bowyer 2000; Ruckstuhl and Neuhaus 2005). Our study investigates how differences in body size may affect the foraging behaviour in Alpine ibex males (*Capra ibex*) of various ages, in order to shed light on the effect of body size per se, studying individuals of the same species and the same sex.

Alpine ibex is a mountain ungulate characterised by a strong dimorphism among males of different ages. Males show a slow and progressive increase of body mass until the age of 9–10. As a consequence, old males (>9 years old) have twice the weight and body mass than 3-5 years old males (Bassano et al. 2003). Ibex mainly live in homogeneous habitats above the tree line and they typically select alpine meadows and rocky slopes (Grignolio et al. 2003). Like other mountain ungulates (e.g., *Rangifer tarandus*: Oosenbrug and Theberge 1980; *Rupicapra rupicapra*: Hamr 1984; *Ovis Canadensis*: Festa-Bianchet 1988; *Cervus elaphus*: Hebblewhite et al. 2008), during the vegetation growing season ibex typically undertake altitudinal migrations (Grignolio et al. 2003; Parrini et al. 2003) in order to have prolonged access to nutritious growing forage. Moreover, summer temperatures highly affect the behaviour of male ibex: as daily temperature and solar radiation increase, ibex reduce the time allocated to feeding during daylight hours and move to higher elevations (Aublet et al. 2009). Under temperature constrains it is possible that ibex males are forced to forage in areas where forage quality or quantity are sub-optimal, so it could be interesting to study how they adjust their foraging strategies in accordance with the characteristics of the feeding site.

Given such premises, we studied fine-scale foraging behaviour of Alpine ibex males considering: (1) fine-scale selectivity of focal individuals; (2) the instantaneous intake rate (bite rate); (3) vigilance behaviour. We hypothesised that:

1a) young males should be more selective than older ones, on account of their smaller body size and their lower digestive efficiency; b) forage quality and quantity should influence male foraging selectivity;

2a) bite rate should decrease with increasing male age and body size, since usually the bite rate is negatively related to bite size (Spalinger and Hobbs 1992); b) bite rate should decrease with decreasing forage biomass in the feeding site, since in grasslands the bite size is generally positively related to plant biomass (Illius 2006);

3a) young males should be more vigilant than older ones, since, on account of their smaller body size, they should perceive an higher risk of predation; b) vigilance should increase with increasing forage biomass. In these conditions, foraging costs of vigilance are likely to be reduced because ungulates may be able to scan the environment while chewing vegetation (Illius and Fitzgibbon 1994; Cowlishaw et al. 2004; Fortin et al. 2004).

METHODS

Study area and population

The study was carried out in the Gran Paradiso National Park (GPNP; 45°35’N, 7°12’E), in the northwestern Italian Alps. The study area (1700 ha) lay between 1600 m and 3100 m a.s.l. and consisted mainly of cliffs, slopes, and alpine meadows. The woods (mainly *Picea abies*, *Larix decidua*, and *Pinus cembra*) represented less than 15% of the area and were not common in the areas selected by ibex. Ibex mainly selected homogeneous habitats, like secondary pastures or alpine meadows, where the most common grass plant genera were *Festuca*, *Carex*, *Poa, Achillea,* and *Trifolium* (Grignolio et al. 2003; Grignolio et al. 2007). During data collection, temperatures ranged from a minimum of -9.5 °C (20 October at 2900 m a.s.l.) to a maximum of 29.5 °C (9 August at 1700 m a.s.l.). In 2010, mean annual precipitation was 2.22 mm/day (Data from Regione Autonoma Valle d’Aosta). Hunting was not allowed in the Park and the presence of a wolf pack (*Canis lupus*) has been confirmed since 2006.

The ibex population in the study area has been intensively monitored since 1999. Every year, the wardens and vets of the GPNP captured some ibex to check for the presence of infectious diseases. At capture, males were aged by counting the horn annuli (Ratti and Habermehl 1977;

von Hardenberg et al. 2004) and marked with different coloured plastic ear tags. Our study sample consisted of 42 marked males, aged from 4 to 14 years.

Data collection

Behavioural observation

From May to October 2010, ibex males were observed with the *Focal Animal Sampling* method (Altmann 1974), in order to monitor fine-scale foraging behaviour. Observations were conducted during the first hours in the morning and the last hours before dusk, because previous studies have shown that ibex are usually most active at this time of day (see also Aublet et al. 2009). In GPNP ibex are used to the presence of people and therefore easy to observe. However, all observations were made with binoculars (10x42) from such a distance so as to minimize disturbance. Focal individuals were selected randomly from a group of foraging animals, making sure that each marked male present in the study area would be sampled every 2-3 week. Date, hour, localization, and group size were recorded at the beginning of each observation. Ibex position was determined by mapping the study area onto a grid of 62.5 x 62.5 m squares and locating each animal observed in the centre of the corresponding square. The focal individual was then observed continuously for 15 minutes, during which we recorded the number of bites, steps, lateral head movements made while feeding and number of vigilance postures by means of a hand-held digital recorder. A bite consisted of gathering vegetation with the muzzle followed by an upward jerking movement of the head. A step was defined as a forward movement of any of the front legs done while foraging with the head lowered below the shoulders. A head lateral movement was defined as a sideward movement of the neck turning the head over the shoulders side-line. Finally, ibex males were considered to be vigilant when they interrupted foraging and raised their head above shoulder height (Frid 1997). The observation was considered valid if the focal male spent the majority (at least 80%) of the 15-min foraging; otherwise the observation was discarded. A total of 512 focal observations were collected. For each month, 24±0.02% of them were on 3-5 y.o. males, 39±0.01% on 6-8 y.o. males, 26±0.02% on 9-11 y.o. males and 11±0.01% on males older than 11 yrs.

We used the free software JWatcher v.0.9 (http://www.jwatcher.ucla.edu/) to digitize and process voice records. We calculated bite rate (number of bite/min foraging), step rate (number of steps/min foraging), the rate of lateral head movements (number of movement/min foraging), and the number of vigilance events (number of alerts during a 15-min focal sample) for each observation. The number of steps taken per minute while feeding was used as a proxy of forage selectivity following Risenhood and Bailer (1985), Alados and Escos (1987), Ruckstuhl (2003) and Komers et al. (1993). Moreover, the rate of lateral head movements while foraging was used as a further proxy of forage selectivity.

Vegetation quality and biomass

Forage quality was assessed using the Normalized Difference Vegetation Index (NDVI) data acquired by the moderate-resolution imaging spectroradiometer (MODIS) on board of the AQUA satellite. We obtained a 16-day NDVI composite in 250 m resolution from Earth Resources Observation and Science Center (EROS-http://glovis.usgs.gov/). We used these data as a measure of the change in vegetation quality in the study area. These data were then re-projected (ED50 / UTM zone 32N), in order to match the position of each observed ibex and the NDVI value of the corresponding feeding patch.

In addition, we evaluated the quality of the foraging patches by calculating an index of biomass, so as to assess the characteristic forage abundance of the alpine meadows in the study area. From May to October of three consecutive years, forage quality was measured following Carranza and Valencia (1999), by selecting ten sampling sites, homogeneously distributed in meadows where ibex males were observed foraging. In each sampling site, all observations were made along the same fixed linear transect, at five sampling points set every 10 m. We dropped a 30 x 30 cm sampling square subdivided into four squares, at four randomly selected locations within approximately 1 m of each sampling point, in order to measure: 1) grass cover: a visual estimate of the proportion of area covered by grass within the 30 x 30 cm sampling square; and 2) grass length: at the spot with the most grass cover within the sampling square, we measured the length of the longest aerial part of the grass. In agreement with the findings of Carranza and Valencia (1999), these data proved to be strongly correlated with biomass, and were thus considered a useful means of evaluating meadow productivity. With these data, we calculated a biomass index for each sampling site, for each month, defined as the mathematical product of grass cover and grass length. We then matched each ibex localisation with the corresponding biomass index, and we used this measure as a proxy of the forage biomass of the patch where ibex were observed foraging.

Data analyses

In order to evaluate ibex males foraging behaviour, we modelled three different behaviours (i.e., bite rate, step rate, and lateral head movement rate) using generalised linear mixed models (GLMM) with Gaussian distribution of errors. Step rate was log-transformed (natural logarithm transformation) to improve normality of residuals and to reduce skewness. We modelled vigilance behaviour was modelled using GLMM, with the Poisson distribution. In all the models developed, ibex identity was used as a random factor to control for repeated measurements of the same individual (Pinheiro and Bates 2000). We defined a set of alternative hypotheses based on previous research on related species, on theory, and on biological relevance, using the information-theoretic approach (Dochtermann and Jenkins 2011). Predictor variables used in the models were: 1) AGE: males age; 2) FOOD QUALITY: NDVI value and biomass index corresponding to the localization of the observed males; 3) SOCIALITY: size of the group within which each ibex male was observed foraging; and 4) SEASONALITY: month of data collection. For each dependent variable we constructed twenty-seven *a priori* models. An analysis of the full model (i.e., the model with all the predictor variables) indicated substantial tolerance between variables, suggesting that all the variables were sufficiently independent. There was no indication of overdispersion in the data set.

For each response variable we ranked and weighed the alternative models using the minimum AIC criterion (Symonds and Moussalli 2011). For each response variable, models with delta AIC values less than 6 were considered to be essentially as good as the best model (reported in bold in the tables 1, 2, 3, and 4 - Richards 2005; Symonds and Moussalli 2011). Parameters and variance were estimated from the selected top-ranked models by means of model averaging technique (Burnham and Anderson 2002). Statistical analyses were implemented using R 2.14.1, while GIS analyses were performed with ARCMAP 9.2.

Table 1. Sets of models predicting step rate in ibex males.

Model #	*Dep. variable: step rate, n = 486 focal ibex males*	AIC	ΔAIC	w_i	ER	*logLik*
21	**age+ndvi+month**	**450.7**	**0**	**0.613**	**1**	**-215.36**
23	**age+ndvi+gr. size+month**	**452.2**	**1.5**	**0.285**	**2.15**	**-215.12**
11	**ndvi+month**	**455.9**	**5.2**	**0.047**	**13.14**	**-218.93**
22	age+ndvi+biomass index+month	457.0	6.2	0.027	22.72	-217.48
24	age+ndvi+biomass index+gr. size+month	457.9	7.2	0.017	36.41	-216.95
25	age+ndvi+gr. size+month+age*ndvi	459.0	8.3	0.010	622.66	-217.49
12	ndvi+biomass index+month	462.1	11.4	0.002	294.75	-221.04
26	age+ndvi+biom index+gr. size+month+age*ndvi	464.7	14.0	0.001	10^3	-219.34
5	age+ndvi	483.9	33.1	<0.001	10^7	-236.93
6	age+ndvi+biomass index	488.2	37.5	<0.001	10^8	-238.10
8	age+ndvi+age*ndvi	489.5	38.8	<0.001	10^8	-238.76
17	age+ndvi+gr. size	489.7	39.0	<0.001	10^8	-238.86
3	age	490.4	39.7	<0.001	10^8	-241.21
1	ndvi	490.7	40.0	<0.001	10^8	-241.37
18	age+ndvi+biomass index+gr. size	492.8	42.1	<0.001	10^9	-239.40
7	age+ndvi+biomass index+age*ndvi	494.0	43.3	<0.001	10^9	-240.00
9	age+gr. size	494.3	43.5	<0.001	10^9	-242.13
2	ndvi+biomass index	494.8	44.0	<0.001	10^9	-242.38
13	ndvi+gr. size	494.8	44.1	<0.001	10^9	-242.42
27	intercept only	494.9	44.2	<0.001	10^9	-244.45
4	gr. size	496.9	46.2	<0.001	10^{10}	-244.45
14	ndvi+biomass index+gr. size	497.1	46.4	<0.001	10^{10}	-242.54
15	ndvi+gr. size+gr.size*ndvi	499.6	48.9	<0.001	10^{10}	-243.79
19	age+ndvi+gr. size+age*ndvi+gr. size*ndvi	500.0	49.3	<0.001	10^{10}	-242.02
16	ndvi+biomass index+gr. size+gr. size*ndvi	501.8	51.1	<0.001	10^{11}	-243.89
10	age+gr.size+age*gr. size	503.6	52.9	<0.001	10^{11}	-245.80
20	age+ndvi+biomass index+ gr. size+age*ndvi+age*gr.	508.0	57.3	<0.001	10^{12}	-245.02

Sets of linear mixed models fit to predict step rate in ibex males observed in the Gran Paradiso National Park, Italy. Best models (in bold, first rows) were selected with the ΔAIC < 6 criterion.[AIC = Akaike information criterion; ΔAIC = difference in AIC value between the AIC of a given model and the best model (lowest AIC); wi = Akaike weights; ER = evidence ratio; logLik = log-likelihood value]

Table 2. Sets of models predicting lateral head movement rate in ibex males.

Model #	*Dep. variable: rate of head lateral movements, n = 350 focal ibex males*	AIC	ΔAIC	w_i	ER	*logLik*
21	**age+ndvi+month**	**824.8**	**0**	**0.524**	**1.000**	**-402.40**
22	**age+ndvi+biomass index+month**	**827.6**	**2.74**	**0.133**	**3.94**	**-402.78**
3	**age**	**829.0**	**4.15**	**0.066**	**7.98**	**-410.48**
5	**age+ndvi**	**829.1**	**4.30**	**0.061**	**8.60**	**-409.56**
23	**age+ndvi+gr. size+month**	**829.3**	**4.50**	**0.055**	**9.50**	**-403.66**
6	**age+ndvi+biomass index**	**829.6**	**4.80**	**0.047**	**11.05**	**-408.81**
11	ndvi+month	831.4	6.56	0.020	26.64	-406.69
7	age+ndvi+biomass index+age*ndvi	831.4	6.64	0.019	27.67	-408.72
8	age+ndvi+age*ndvi	831.5	6.67	0.019	28.11	-409.74
26	age+ndvi+biom index+gr. size+month+age*ndvi	832.3	7.48	0.012	42.02	-404.14
24	age+ndvi+biomass index+gr. size+month	832.3	7.54	0.012	43.41	-404.17
27	intercept only	833.5	8.65	0.007	75.49	-413.73
12	ndvi+biomass index+month	834.4	9.59	0.004	121.10	-407.20
9	age+gr. size	834.5	9.69	0.004	127.19	-412.25
1	ndvi	834.7	9.92	0.004	142.47	-413.36
25	age+ndvi+gr. size+month+age*ndvi	835.1	10.30	0.003	172.60	-404.56
17	age+ndvi+gr. size	835.2	10.39	0.003	180.75	411.60
18	age+ndvi+biomass index+gr. size	835.8	11.00	0.002	244.77	-410.90
2	ndvi+biomass index	835.9	11.08	0.002	254.86	-412.94
4	gr. size	837.7	12.92	<0.001	638.17	-414.86
19	age+ndvi+gr. size+age*ndvi+gr. size*ndvi	839.0	14.17	<0.001	10^3	410.49
15	ndvi+gr. size+gr. size*ndvi	839.1	14.30	<0.001	10^3	-413.56
13	ndvi+gr. size	839.8	14.94	<0.001	10^3	-414.88
16	ndvi+biomass index+gr. size+gr. size*ndvi	841.1	16.25	<0.001	10^3	-413.53
14	ndvi+biomass index+gr. size	841.2	16.35	<0.001	10^3	-414.58
10	age+gr. size+age*gr. size	842.8	18.01	<0.001	10^3	-415.41
20	age+ndvi+biomass index+ gr. size+age*ndvi+age*gr.	845.9	21.05	<0.001	10^4	-413.93

Sets of linear mixed models fit to predict rate of head lateral movements in ibex males observed in the Gran Paradiso National Park, Italy. Best models (in bold, first rows) were selected with the *ΔAIC* < 6 criterion.[*AIC* = Akaike information criterion; *ΔAIC* = difference in AIC value between the AIC of a given model and the best model (lowest AIC); w_i = Akaike weights; *ER* = evidence ratio; *logLik* = log-likelihood value]

Table 3. Sets of models predicting bite rate in ibex males.

Model #	*Dep. variable: bite rate, n = 486 focal ibex males*	*AIC*	*ΔAIC*	w_i	*ER*	*logLik*
26	**age+ndvi+biomass index+gr.**	**3691.1**	**0.0**	**0.474**	**1**	**-1832.53**
24	**age+ndvi+biomass index+gr. size+month**	**3692.6**	**1.5**	**0.222**	**2.134**	**-1834.29**
12	**ndvi+biomass index+month**	**3692.7**	**1.7**	**0.206**	**2.292**	**-1836.36**
22	**age+ndvi+biomass index+month**	**3694.2**	**3.2**	**0.097**	**4.901**	**-1836.12**
25	age+ndvi+gr. size+month+age*ndvi+gr.	3774.5	83.4	<0.001	10^{18}	-1874.25
23	age+ndvi+gr. size+month	3779.0	87.9	<0.001	10^{19}	-1878.49
11	ndvi+month	3790.3	99.2	<0.001	10^{21}	-1886.16
21	age+ndvi+month	3791.9	100.8	<0.001	10^{21}	-1885.93
16	ndvi+biomass index+gr. size+gr. size*ndvi	3850.7	159.7	<0.001	10^{34}	-1918.36
20	age+ndvi+biomass index+ gr.	3850.9	159.9	<0.001	10^{34}	-1916.46
2	ndvi+biomass index	3852.6	161.5	<0.001	10^{35}	-1921.29
18	age+ndvi+biomass index+gr. size	3852.6	161.6	<0.001	10^{35}	-1919.31
14	ndvi+biomass index+gr. size	3853.2	162.1	<0.001	10^{35}	-1920.59
7	age+ndvi+biomass index+age*ndvi	3872.7	181.6	<0.001	10^{39}	-1929.34
6	age+ndvi+biomass index	3874.9	183.9	<0.001	10^{39}	-1931.47
19	age+ndvi+gr. size+age*ndvi+gr. size*ndvi	4007.2	316.2	<0.001	10^{68}	-1995.61
17	age+ndvi+gr.size	4010.3	319.2	<0.001	10^{69}	-1999.14
15	ndvi+gr. size+gr. size*ndvi	4011.2	320.1	<0.001	10^{70}	-1999.58
13	ndvi+gr. size	4013.7	322.6	<0.001	10^{70}	-2001.83
9	age+gr. size	4016.2	325.1	<0.001	10^{69}	-2003.08
10	age+gr.size+age*gr. size	4018.8	327.7	<0.001	10^{71}	-2003.40
8	age+ndvi+age*ndvi	4020.1	329.1	<0.001	10^{71}	-2004.07
4	group size	4020.8	329.7	<0.001	10^{71}	-2006.39
5	age+ndvi	4020.9	329.9	<0.001	10^{71}	-2005.47
1	ndvi	4021.4	330.3	<0.001	10^{71}	-2006.70
3	age	4029.1	338.1	<0.001	10^{73}	-2010.57
27	intercept only	4030.5	339.4	<0.001	10^{73}	-2012.23

Sets of linear mixed models fit to predict bite rate in ibex males observed in the Gran Paradiso National Park, Italy. Best models (in bold, first rows) were selected with the *ΔAIC* < 6 criterion.[*AIC* = Akaike information criterion; *ΔAIC* = difference in AIC value between the AIC of a given model and the best model (lowest AIC); w_i = Akaike weights; *ER* = evidence ratio; *logLik* = log-likelihood value]

Table 4. Sets of models predicting scan frequency in ibex males.

Model #	*Dep. variable: scan frequency, n = 488 focal ibex males*	*AIC*	*ΔAIC*	w_i	*ER*	*logLik*
26	**age+ndvi+biom index+gr. size+month+age*ndvi**	**1943**	**0**	**0.781**	**1.00**	**-959.70**
24	**age+ndvi+biomass index+gr. size+month**	**1946**	**3**	**0.174**	**4.48**	**-962.10**
25	age+ndvi+gr. size+month+age*ndvi	1949	6	0.039	20.09	-963.70
23	age+ndvi+gr. size+month	1953	10	0.005	148.41	-966.50
20	age+ndvi+biomass index+ gr. size+age*ndvi+age*gr.	1994	51	$6.6\ e^{-12}$	10^{11}	-989.20
21	age+ndvi+month	1997	54	$1.5\ e^{-12}$	10^{11}	-989.60
22	age+ndvi+biomass index+month	1998	55	$8.9\ e^{-13}$	10^{11}	-989.10
11	ndvi+month	1999	56	$5.4\ e^{-13}$	10^{12}	-991.30
12	ndvi+biomass index+month	2000	57	$3.3\ e^{-13}$	10^{12}	-990.80
18	age+ndvi+biomass index+gr. size	2009	66	$3.6\ e^{-15}$	10^{14}	-998.40
14	ndvi+biomass index+gr. size	2013	70	$4.9\ e^{-16}$	10^{15}	-1002.00
16	ndvi+biomass index+gr. size+gr.size*ndvi	2015	72	$1.8\ e^{-16}$	10^{15}	-1001.00
19	age+ndvi+gr. size+age*ndvi+gr. size*ndvi	2034	91	$1.4\ e^{-20}$	10^{19}	-1010.00
17	age+ndvi+gr. size	2038	95	$1.8\ e^{-21}$	10^{20}	-1014.00
13	ndvi+gr. size	2041	98	$4.1\ e^{-22}$	10^{21}	-1016.00
15	ndvi+gr. size+gr. size*ndvi	2042	99	$2.5\ e^{-22}$	10^{21}	-1016.00
7	age+ndvi+biomass index+age*ndvi	2067	124	$9.3\ e^{-28}$	10^{26}	-1027.00
6	age+ndvi+biomass index	2074	131	$2.8\ e^{-29}$	10^{28}	-1032.00
2	ndvi+biomass index	2075	132	$1.7\ e^{-29}$	10^{28}	-1033.00
8	age+ndvi+age*ndvi	2077	134	$6.2\ e^{-30}$	10^{29}	-1033.00
1	ndvi	2085	142	$1.1\ e^{-31}$	10^{30}	-1040.00
5	age+ndvi	2085	142	$1.1\ e^{-31}$	10^{30}	-1038.00
10	age+gr. size+age*gr. size	2087	144	$4.2\ e^{-32}$	10^{31}	-1039.00
4	gr. size	2102	159	$2.3\ e^{-35}$	10^{34}	-1048.00
9	age+gr. size	2102	159	$2.3\ e^{-35}$	10^{34}	-1047.00
27	intercept only	2131	188	$1.2\ e^{-41}$	10^{40}	-1064.00
3	age	2132	189	$7.1\ e^{-42}$	10^{41}	-1063.00

Sets of linear mixed models fit to predict scan frequency in ibex males observed in the Gran Paradiso National Park, Italy. Best models (in bold, first rows) were selected with the *ΔAIC* < 6 criterion.[*AIC* = Akaike information criterion; *ΔAIC* = difference in AIC value between the AIC of a given model and the best model (lowest AIC); w_i = Akaike weights; *ER* = evidence ratio; *logLik* = log-likelihood value]

RESULTS

Diet selection

Diet selection was estimated analysing step rate and frequency of lateral head movements. A comparison of models predicting step rate and frequency of lateral head movements is reported in Tables 1 and 2. For these two dependent variables we identified a confidence set of 4 and 6 best models, respectively. The top-ranked models for step rate included four predictor variables: age, NDVI, group size, and month of data collection. Top-ranked models for rate of lateral head movements included all predictor variables (biomass index included) but no interaction factors. According to predictions of the multimodel-based inference, selectivity decreased with the increasing of ibex male age (step rate: β = -0.035, SE = 0.009 [Fig.1]; lateral head movement rate: β = -0.079, SE = 0.019). Instead, diet selection increased with increasing NDVI values of the feeding site (step rate: β = 0.608, SE = 0.125; lateral head movement rate: β = 0.782, SE = 0.349). With respect to May, step rate were particularly intensified in July (β = 0.608, SE = 0.095) and in August (β = 0.578, SE = 0.089). In June (β = 0.341, SE = 0.080), in September (β = 0.375, SE = 0.092), and in October (β = 0.418, SE = 0.099) males moved more frequently than in May. Lateral head movements rate increased progressively in June (β = 0.256, SE = 0.145), in August (β = 0.406, SE = 0.195), September (β = 0.494, SE = 0.190) and October (β = 0.731, SE = 0.236), but not in July (β = 0.226, SE = 0.170). Group size and Biomass index (in the case of lateral head movements rate) were also included in the set of best models, but the large estimated standard error indicated that the parameter was not reliable for predicting diet selection of ibex males.

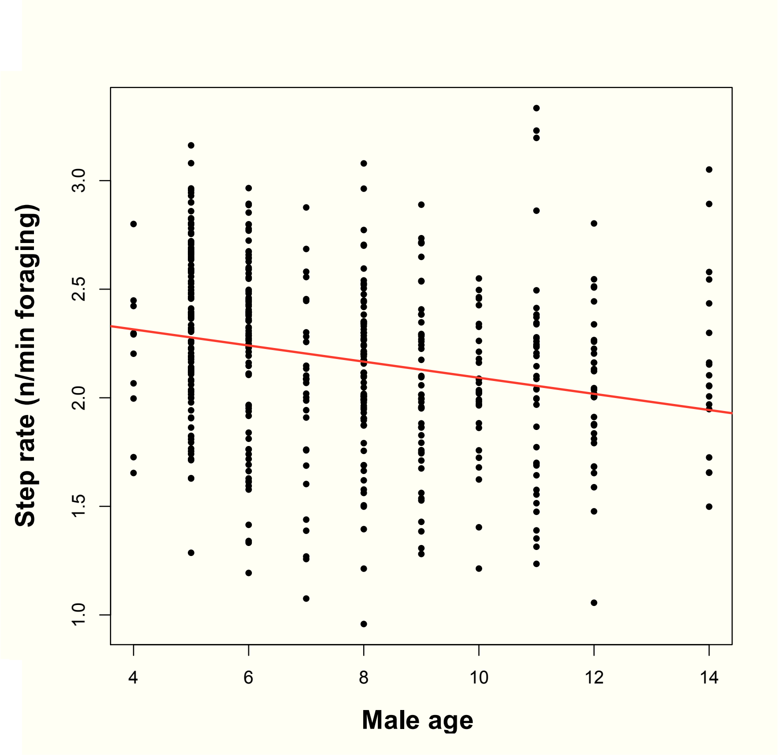

Fig. 1 - Step rate taken by male ibex while foraging in relation to male age in the Gran Paradiso National Park, Italy, May- October 2010

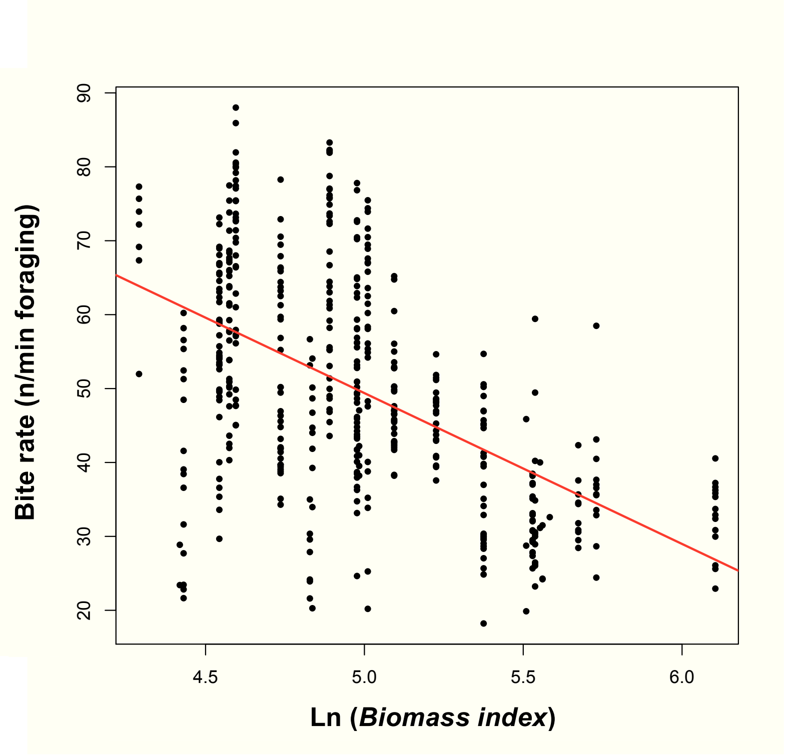

Fig. 2 - Bite rate taken by male ibex while foraging in relation to forage biomass on the feeding sites (ln transformed) in the Gran Paradiso National Park, Italy, May- October 2010

Bite rate

A comparison of models predicting bite rate is reported in Table 3. A confidence set of four best models was identified (Table 3). Top-ranked models included all predictor variables: age, NDVI, biomass index, group size, and month of data collection. According to predictions of the multimodel-based inference, bite rate decreased in proportion to the increasing biomass index of the feeding site (β = -14.636, SE = 1.495; Fig.2). With respect to May, bite rate increased in June (β = 12.387, SE = 2.519) and even more in July (β = 24.692, SE = 2.948), then it decreased in August (β = 11.254, SE = 2.750) and in September (β = 12.931, SE = 2.847). In October, bite rate was similar to that recorded in May (β = 1.160, SE = 3.109). Male age, NDVI, group size and the interaction between age and NDVI were also included in the set of best models, but the large estimated standard errors indicated that the parameter estimates were not reliable for predicting bite rate.

Vigilance behaviour

A comparison of models predicting vigilance events is reported in Table 4. For these dependent variables we identified a confidence set of two best models, which included age, NDVI, biomass index, group size, month of data collection and the interaction between age and NDVI. According to predictions of the multimodel-based inference, vigilance decreased with increasing age of ibex males (β = -0.054, SE = 0.018; Fig 3) as well as with the increasing group size (β = -0.107, SE = 0.015; Fig. 5). Males increased vigilance events when they fed in patches of increasing quality and biomass (NDVI: β = 0.482, SE = 0.279, biomass index: β = 0.113, SE = 0.039; Fig 4). Scan frequency was significantly higher in July (β = 0183, SE = 0.075) and in October (β = 0.339, SE = 0.078) than in May.

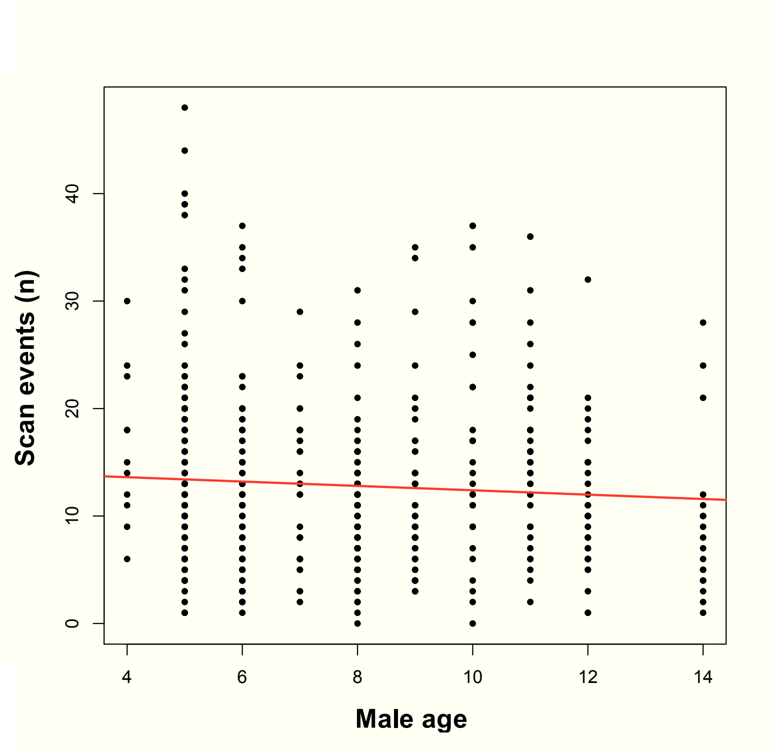

Fig. 3 - Number of scan events taken by male ibex while foraging during 15 minutes sampling in relation to male age in the Gran Paradiso National Park, Italy, May- October 2010

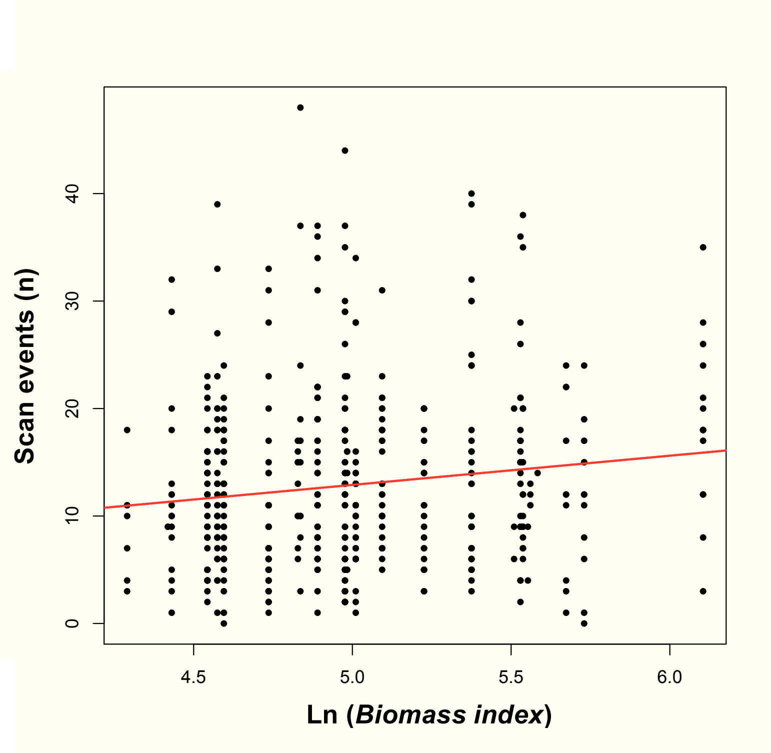

Fig. 4 - Number of standing events taken by male ibex while foraging during 15 minutes sampling in relation to forage biomass on the feeding sites (ln transformed) in the Gran Paradiso National Park, Italy, May- October 2010

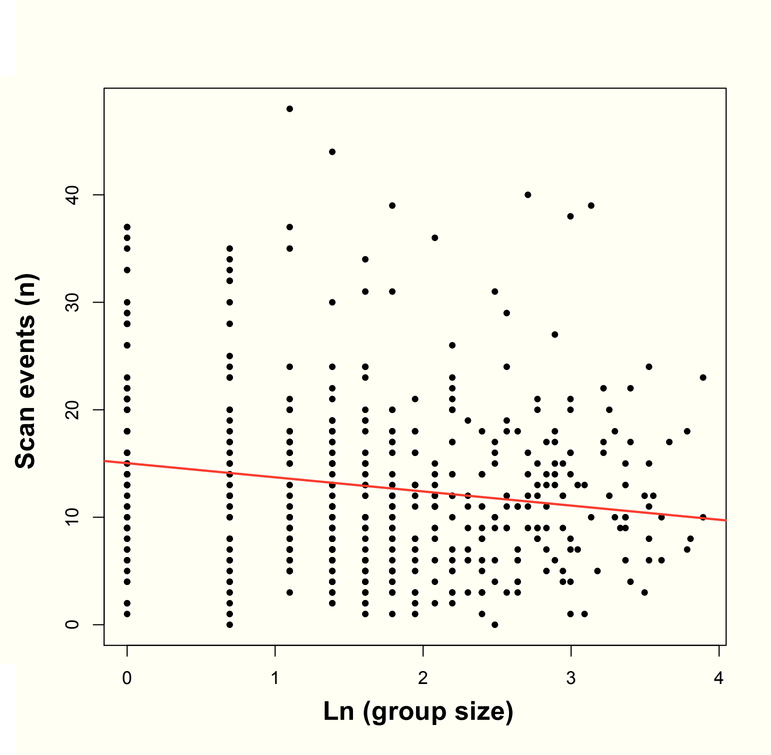

Fig. 5 - Number of standing events taken by male ibex while foraging during 15 minutes sampling in relation to group size among which each ibex male was observed (ln transformed) in the Gran Paradiso National Park, Italy, May- October 2010

DISCUSSION

Several authors have emphasized the importance of body size on the foraging strategies of ungulates comparing data on different species or different sex. In this paper, we proved evidence for the influence of body size and vegetation quality on fine-scale foraging behaviour by analysing individuals of the same species and sex. Our results showed that age and size of the male ibex actually have important effects on diet selection, as searching movements (i.e., step rate and frequency of lateral head movements) significantly increased as age decreased. These results are consistent with our hypothesis (1a) and in accordance with previous theories on ungulates species (Demment and Van Soest 1985; Illius and Gordon 1987; Illius and Gordon 1992). The basic pattern shared by these theories is that ruminant species differentiate ecologically, primarily along a body size gradient, which determines metabolic requirements, digestive system morphology and diet selection (Hanley 1997). This pattern seems also true for ibex males of different sizes. Larger adult males are able to tolerate food of poorer quality more than smaller young males, thanks to their lower specific metabolic rate and their higher gut capacity (Demment and Van Soest 1985). Since the retention of a food particle within the gut is proportional to the ratio between metabolic requirement and gut capacity, the extent to which nutrients are digested is related to body size (Demment and Van Soest 1985). As a consequence, small, young males are less efficient in extracting energy from plant fiber than larger adult males. Young ibex males seemed to compensate their lower capability in digesting plant material by an increasing diet selection.

Contrary to our hypothesis (2a) age had no effect on males' bite rate. A difference in bite rate among males of different ages was expected because of their dissimilar body size. Shipley et al. (1994) showed that bite size scales with herbivores' body mass. Since bite rate is typically negatively related to bite size (Spalinger and Hobbs 1992), we expected that smaller males should have a higher bite rate. But this is not the case in our study, probably because in mature males, despite the strong dimorphism in body mass, width of the incisor bar could be similar to that of growing and younger males, due to tooth wear. Tooth wear with age is well known in ruminants (e.g. Carranza et al. 2004). A reduction in height of the incisors due to tooth wear would consequently reduce the dimensions of the incisor arcade, as documented, for example, in adult bighorn ewes (*Ovis Canadensis*: von Hardenberg et al. 2003). Young males need energy to grow and reach a large body size, so as to be more competitive during social interactions and maximise their reproductive success. Other studies on bighorn sheep (Ruckstuhl et al. 2003) and zebras (*Equus burchelli*: Neuhaus and Ruckstuhl 2002) suggest that the bite rate should be highly flexible, so as to adapt to and compensate for the higher energy demands of growth or reproduction. Instead, our results showed a non-significant effect of age male on bite rate, suggesting that young males presumably managed to meet their energetic requirements by spending more time feeding during the day, as shown by Aublet et al. (2009) and by increasing diet selection.

Our results suggest that male ibex have the behavioural flexibility to adjust their foraging decisions in response to changes in the quality of the patches where they feed, as already demonstrated in other ungulate species in a study where environmental conditions were hand-controlled by researchers (*Alces alces* and *Odocoileus virginianus*: Shipley and Spalinger 1995). We did not find a differential response in males of different ages, but we found a common pattern in behavioural modifications influenced by forage biomass and quality. While foraging, ibex males showed a bite rate that increased when forage biomass decreased, presumably as a result of a decreasing bite size. This result is consistent with our hypothesis (2b) and in accordance with theories advanced on animals that forage in food-saturated patches, such as alpine meadows (Penning et al. 1991; Spalinger and Hobbs 1992; Shipley et al. 1994). The decrease in bite rate is likely related to a larger bite size due to higher grass cover and a consequent increase in handling time (Bunnell and Gillingham 1985; Parsons et al. 1994). Moreover, as quality of forage in feeding sites became higher, males seemed to graze more selectively, since the frequency of searching movements increased (i.e., step rate and lateral head movements; hypothesis 1b). An intensification of selectivity in foraging sites with increasing forage quality has been observed also in other ungulate species *(Rangifer tarandus tarandus*: Trudell and White 1981; *Capra pyrenaica*: Alados and Escos 1987).

Previous studies suggested that predation risk and temperature constraints are important factors that contribute substantially to shape ibex habitat selection (Grignolio et al. 2007; Aublet et al. 2009). It is likely that under predation and temperature constraints ibex males are forced to forage in sub-optimal patches, where forage quality and quantity are lower (Grignolio et al. 2007; Aublet et al. 2009). In order to satisfy their daily energetic requirements, ruminants in northern or mountain environments must accumulate enough fat during the growing seasons to reproduce and to survive the shortage of food during winter (Bruno and Lovari 1989). Our results suggest that male ibex could adjust their total energy intake by modifying bite rate and diet selection. In fact, since bite size and bite rate are usually inversely related (Spalinger and Hobbs 1992), adopting a higher cropping rate could be a strategy used by ibex males to compensate for reduced bite size in lower biomass patches. Moreover, the tendency of ibex to increase forage selection in patches characterized by high nutritional values is possibly a mechanism to maximize their nutrients intake in a highly seasonal and forage-limited environment.

Ibex males' age was found to affect their vigilance behaviour significantly (i.e., in lifting the head to scan for predators), with a decrease in scan frequency as age increased (hypothesis 3a). Young males seemed to be more sensitive to predation risk than older ones, as a potential consequence of their lower body size. Studies on vigilance behaviour in ungulates have shown that body size is an influencing factor (Underwood 1982; Berger and Cunningham 1988; Laundré et al. 2001). For example, Berger and Cunningham (1988) found that differences in predator scanning among females of four different ungulate species were positively related to their body size. Also, Grignolio et al. (2007) found that anti-predator behaviour in ibex varies according to body size: smaller young males preferred to keep closer to refuge areas and farther from disturbed areas than adult males, thus suggesting that age and, consequently, weight, could influence sensitivity to predation risk.

Scan frequency is also affected by the quality and quantity of forage in the feeding patches. In fact, we found that male vigilance increased with increasing forage biomass (hypothesis 3b). A similar pattern was found in other ungulate species in North America *(Bison bison, Cervus Canadensis*: Fortin et al. 2004). While foraging on patches of high biomass, ibex may be able to scan the environment while chewing bites that have already been cropped (Illius and Fitzgibbon 1994). In contrast, while foraging on patches of low biomass, where cropping and chewing may be simultaneous (Laca et al. 1994), male may have to slow down or stop foraging altogether in order to lift the head and scan for predators (Illius and Fitzgibbon 1994). The importance of vigilance in the detection of predators has been well established in numerous theoretical and empirical studies (cf. Treves 2000; Bednekoff and Lima 2002). Despite the demonstrated benefits of vigilance behaviour, its performance is limited, because it requires exclusive visual attention, thereby interrupting other fitness-enhancing activities (i.e. on reduction of feeding rates: Saino 1994; Beauchamp and Livoreil 1997; Fritz et al. 2002). This trade-off is believed to underlie many classical patterns of vigilance behaviour, such as the group–size effect: animals in smaller groups are more vigilant because they are at higher risk of predation and therefore more willing to reduce foraging success in order to increase vigilance (Elgar 1989; Roberts 1996; Lima et al. 1999). Accordingly, we found that ibex scan frequency decreased with increasing group size. This group size effect may be the result of individuals responding to a decreased perception of predation risk, due to the dilution effect or to the safety of group predator detection (Lima 1995; Roberts 1996). Living in group, though, may also entail negative effects on foraging individuals: in large groups there will likely be more interference, competition for food access and scrounging (competition hypothesis, Lima et al. 1999). The competition hypothesis is that, as group size increases in a food-limited environment, an animal will increase its feeding rate (consequently reducing vigilance) in order to gain a greater portion of the food supply. Our results, though, did not reveal any influence of group size neither on bite rate, nor on searching movements while foraging. In conclusion, our findings showed that feeding in group is particularly rewarding for male Alpine ibex. They should obviously face a trade-off between the positive (i.e., reduced predation risk) and the negative (i.e., intra-group competition and interaction) effects, but it is clear that this trade-off is advantageous. In fact, each individual spends less time scanning the environment without incurring in a decrease of intake rate.

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Chapter 2

A natural modification of landscape of fear induces different antipredator behaviour responses between sexes.

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ABSTRACT

The natural expansion of the wolf (*Canis lupus*) in North-Western Alps gave the rare opportunity to monitor the response to a modification in landscape of fear in a prey species that lived fully free from terrestrial predators since a long period (about a century). Predators may influence their prey populations not only through direct lethal effects, but also through indirect behavioural changes. Here we examined the effects of wolf recolonization on antipredator behaviour (use of safe areas and group size) of Alpine ibex (*Capra ibex*) in the Gran Paradiso National Park (Italy), the only natural population of this species. We found that the return of the wolf, i.e. the more important ungulate predators in Europe, induced quick modifications in ibex behaviour after a few years only. Females, increased their propensity to aggregate with conspecifics, especially when followed by young, but didn't modify distance from refuge sites. On contrary, male groups decreased in size and moved closer to safer areas. These results showed that female and male ibex, which are characterized by a strong dimorphism, adopt different strategies to solve the conflicting demands of nutrient intake versus safety. The results also strongly suggest that in polyginous species maximization of reproductive success drives differentially male and female behavioural choice. Despite sexual differences, behavioural modifications induced by wolf presence are likely to cause a reduction of nutrients intake, thus a reduction of body conditions and growth. The influences of risk effects on individual life history may be important especially in a species, like Alpine ibex, already characterised by a negative trend of its population dynamic.

Keys words: Alpine ibex, antipredator behaviour, behavioural modification, risk effects, wolf recolonization

INTRODUCTION

Before that Holling (1959) had contemplated behaviour in predator-prey models, the effects of predation on biology of preys were only focused on the lethal events (predation). More recently, ecologists reconsidered the importance of indirect effects of predator on population dynamic of preys (prey behaviour alterations or physiological modifications, cf. Creel and Christianson 2008). While the benefit of antipredator behaviours is obvious (decreased risk of predation), conversely their costs (risk effects) are less apparent, and they have been ignored in several analyses of vertebrate predator–prey dynamics (Creel and Christianson 2008). Instead, to take into account also risk effects may be useful in order to better understand prey ecology and dynamics. For example, Hebbelwhite et al. (2002) showed 50-70% declines in the elk (*Cervus elaphus*) population of Banff National Park (Alberta), while the predator-prey models predicted a decline of 10-25% after the recolonisation of wolf (*Canis lupus*, Boyce and Gaillard 1992; Garton and Crabtree 1992). The difference between the estimation assessed by the theoretic models in Yellowstone National Park and the elk population dynamic of Banff National Park was explained by the interaction between wolf predation and snow depth, probably due to modifications in grouping behaviour (Hebblewhite and Pletscher 2002). A change in predation risk induces prey to alter their habitat use, trading security for a reduction in forage quality, quantity, or both (Brown 1999). At finer temporal and spatial scales, ungulate responses include changes in activity patterns (Fenn and Macdonald 1995), variation in vigilance levels (Ciuti et al. 2012), changes in group size (Lima 1995), or interaction vigilance and group size (Roberts 1996; Childress and Lung 2003).

The synergism between morphological and behavioural traits constrains the antipredator strategy adopted by animals (Cott 1940). Different individuals of the same species, even of the same age-sex classes, may use different defences versus the same predator (Caro 2005). The exhibition of different antipredator strategies among individuals of the same species is a phenomenon relatively rare in homeotherms (Caro 2005), but it should consider that body size generally influences predation risk sensitivity (Cohen et al. 1993; Sinclair et al. 2003). Ungulates adopting polygynous mating systems are often characterised by sexual body size dimorphism (Weckerly 1998). Thus, it may be assumed that, in species with high sexual dimorphism, sexes adopted different antipredator strategies.

At yet, little works have examined simultaneously how group size and use of safe areas respond to natural variation in predation risk. Several papers have measured the effects of modification in predation risk on habitat selection or on vigilance behaviour, but in most cases group size was considered only as an independent variable. More recently, researchers have related the group size, considered as dependent variable, to independent measures of risk (see for example Creel and Winnie 2005).

The response of prey species to a modification in the landscape of fear was at yet mostly evaluated on the ground of the information obtained after the reintroduction of grey wolf in the Yellowstone National Park, Wyoming. This study site was free of wolves for about 50 years. Before the wolf reintroduction (1994-1995) the principal predators for ungulates (i.e., elk and bison, *Bison bison*) were grizzly bears (*Ursus arctos horribilus*), coyotes (*Canis latrans*), and mountain lion (*Puma concolor*). The study case of Yellowstone National Park (Fortin et al. 2005), as well as the case of reintroduction of lion in Serengeti National Park, Tanzania (Hunter and Skinner 1998), documented how prey species changed their behaviour when the landscape of fear was modified in presence of other predators. What can happen if a predator re-establishes where prey species have been living free from terrestrial predators since a long time? The natural wolf expansion in North-Western Alps (Scandura et al. 2001; Fabbri et al. 2007; Marucco and McIntire 2010; Palmegiani et al. in press) is an opportunity for ecologists to accept the challenge, proposed by Creel & Christianson (2008), to design field studies that determine the relative magnitudes of risk effects and direct predation in wild populations that are not manipulated. Here we disentangle the effects of the natural expansion of the grey wolf on the antipredator behaviour (use of safe sites and grouping patterns) of Alpine ibex (*Capra ibex*) in the Gran Paradiso National

Park (PNGP, Italy), the only natural population of this species. Alpine ibex is a good model species because it is characterised by high dimorphism between the sexes and among males of different age (Bassano et al. 2003).

METHODS

Study area and population

The study was conducted in the PNGP (northwestern Italian Alps; 45° 25′ N, 07° 34′ E) in the Levionaz basin. The main habitats of the study area were rocks, glaciers, stone ravines and alpine meadows. The forests represented less than 10% of the area and were below 2000-2300 meter above sea level. In the area where data sampling occurred, the upper forest vegetation was mainly composed of conifers (*Picea abies* and *Larix decidua*). Above the timberline, slopes were covered by meadows (*Festuca spp* and *Carex curvula*) with shrubs (*Rhododendron ssp., Vaccinium vitis-idaea, Vaccinum myrtillus* and *Juniperus nana*). Areas used by ibex range from 1500 m to 3300 m a.s.l.. Hunting was not allowed in the Park and the most relevant predators, such as lynx (*Lynx lynx*) and wolf have been absent for about a century. During summer 2006 first signs of presence of a wolf breeding pair were found and the presence of a wolf pack have been confirmed in the following years (Palmegiani et al. in press).

The Alpine ibex population at GPNP is the only surviving natural population of this species (Passerin D'Entrëves 2000). This population grew to almost 5000 individuals in the 1990s, and then began to decline (Jacobson et al. 2004). Since 1999, ibex have been intensively monitored inside the Levionaz surveillance area, where individually marked animals were present (see Grignolio et al. 2007a for more details). Ibex density in Levionaz valley ranged from 19.0 individuals/Km^2 (in 2004) to 9.0 individuals/Km^2 (in 2008).

Data collection

The data collection was conduced during two distinct periods: before (2000-2005) and after wolf re-colonization (2008-2010) from May to October. In order to monitor habitat use and grouping patterns we used ten line transects of 3-6 km each The transects were designed to reach an adequate coverage of the study area and a proper sampling of the habitat types typically used by female and male ibex. Each transect was repeated at least 3 times per month during morning and evening hours when animals were most active, resulting in overall 1460 km walked. One or more animals of the same species within 50 m of each other were considered as a group (Frid 1997). For each sighting, we recorded the following data:

1. Species, group size and composition.
2. Position of the group. Localization was determined subdividing the study area into a grid of squares of 125 x 125 m, and locating each group and each fix in the centre of the corresponding square (see Grignolio et al. 2007a for more details).

Ibex groups were distinguished following Grignolio et al. (2007a), accordingly we identified 5 different groups: adult males (at least 75% of the group members being males, more than 50% of the males being >5 years of age), subadult males (at least 75% of the group members being males, more than 50% of the males being <5 years of age), females with young (at least 75% of the group members being females, at least 1 kid or 1 yearling was present), females without kids (at least 75% of the group members being females, no young present) and mixed groups (when the ratio of both sexes was lower than 75%).

We measured the distance between each group location and the nearest rocky slope using the same methodology described by Grignolio et al. (2007a) by means of geographic information system software (ArcGis 9.3).

Data analyses

In order to evaluate the response of Alpine ibex to the return of the wolf, we analysed group size and distance from refuge areas using General Linear Model (GLM). Since ibex density in the study area varied during the years of data collection, we decided to weight the group size on the density of ibex of each year: we calculated the ratio between number of individuals of each group observed and the total number of ibex of the same sex counted during census in the study area (standardised group size - SGS), and we used it as dependent variable in the model. We compared the effect of the presence of the wolf on ibex SGS using period of data collection (before and after wolf re-colonization) as categorical fixed effect in the model. We introduced group type and month of data collection as fixed effects; distance from refuge areas was integrated in the model as covariate. Distance from refuge areas of each ibex group was modelled following the same assumptions (same fixed effects) used for SGS. In this case, we introduced group size as covariate in the model. In both models we included all main effects and all two-way interactions in the GLMs and subsequently modelled the dependent variable excluding the interaction terms that were not found to be significant. Estimate of marginal means were performed to show differences among values of significant variables

RESULTS

We recorded 3267 ibex locations including 1639 collected before and 1628 after wolf re-colonization. Group size ranged from 1 to 56 and mean distance from refuge sites was 135.19m (ranging from 0 to 557.38m). Standardised group size (SGS) was analysed by means of a General Linear Model (GLM) that, after model simplification, included period of data collection (before and after wolf re-colonization), group type, distance from refuge areas and month of data collection. Moreover, the followed 2-way interaction between factors were included in the model: period x group type, group type x month. SGS significantly differed from the first to the second period of data collection (GLM: $F_{1,3266}$= 10.134; P = 0.001). Specifically, group size increased from the period before (SGS = 0.048 ± 0.003, mean ± standard error) to the period after wolf re-colonization (SGS = 0.060 ± 0.003). Moreover we found that group composition significantly affected group size (GLM: $F_{4,3266}$ = 67.523; P < 0.001;). Groups of females with young were significantly the largest group type observed (SGS = 0.097 ± 0.003), then followed by groups of males (prevalence of adult males: SGS = 0.068 ± 0.002; prevalence of subadult males: SGS = 0.046 ± 0.005). Female groups without young (SGS = 0.030 ± 0.003) and mixed groups (SGS = 0.028 ± 0.008) were the smallest ones contacted (Fig. 1). During May, June and July ibex formed significantly larger groups than during other months of data collection (GLM: $F_{5,3266}$= 3.835; P = 0.002). The two-way interaction term period x group type was significant (GLM: $F_{4,3266}$= 19.773, P< 0.001). More precisely, female group size significantly increased from the period without predator to the period after wolf re-colonization, on the contrary dimension of groups formed prevalently of adult males decreased. Subadult male group and mixed group size did not significantly change in the two periods (Fig. 1). Distance from refuge area did not affect ibex group size.

Distance of groups from the refuge sites was analysed by means of a General Linear Model (GLM) that included period of data collection (before and after wolf re-colonization), group type, group size and month of data collection. Two interaction factors were also included in the model: period x group type and month x group type. Group type (GLM: $F_{4,3266}$ = 145.586; P < 0.001), month (GLM: $F_{5,3266}$ = 7.284; P < 0.001) and their two-way interaction term (GLM: $F_{20,3266}$ = 3.712; P< 0.001) significantly affected group distance from refuge sites. Groups of females were the closest to refuge areas (females with young: distance = 82.370 ± 4.581 m, females without young: distance = 89.604 ± 4.418 m), whereas male groups were the farthest (prevalence of adult males: distance = 186.847 ± 2.857 m; prevalence of subadult males: distance = 155.947 ± 6.683 m; Fig. 2). Moreover, ibex were closer to the refuge sites in May (distance = 106.563 ± 6.055 m) and October (distance = 102.889 ± 7.019 m), and they are further on July (distance = 142.959 ± 6.698) and August (distance = 147.510 ± 7.684). Distance from refuge areas did not significantly change from the period before to the period after predator re-colonization. But, the combined effect of presence of wolf and group type had a significant effect on group distance (GLM: $F_{4,3266} = 3.574$; P= 0.006). In particular, groups mainly composed by adult males were observed closer to refuge areas after wolf re-colonization, whereas others group type did not significantly change their behaviour (Fig. 2).

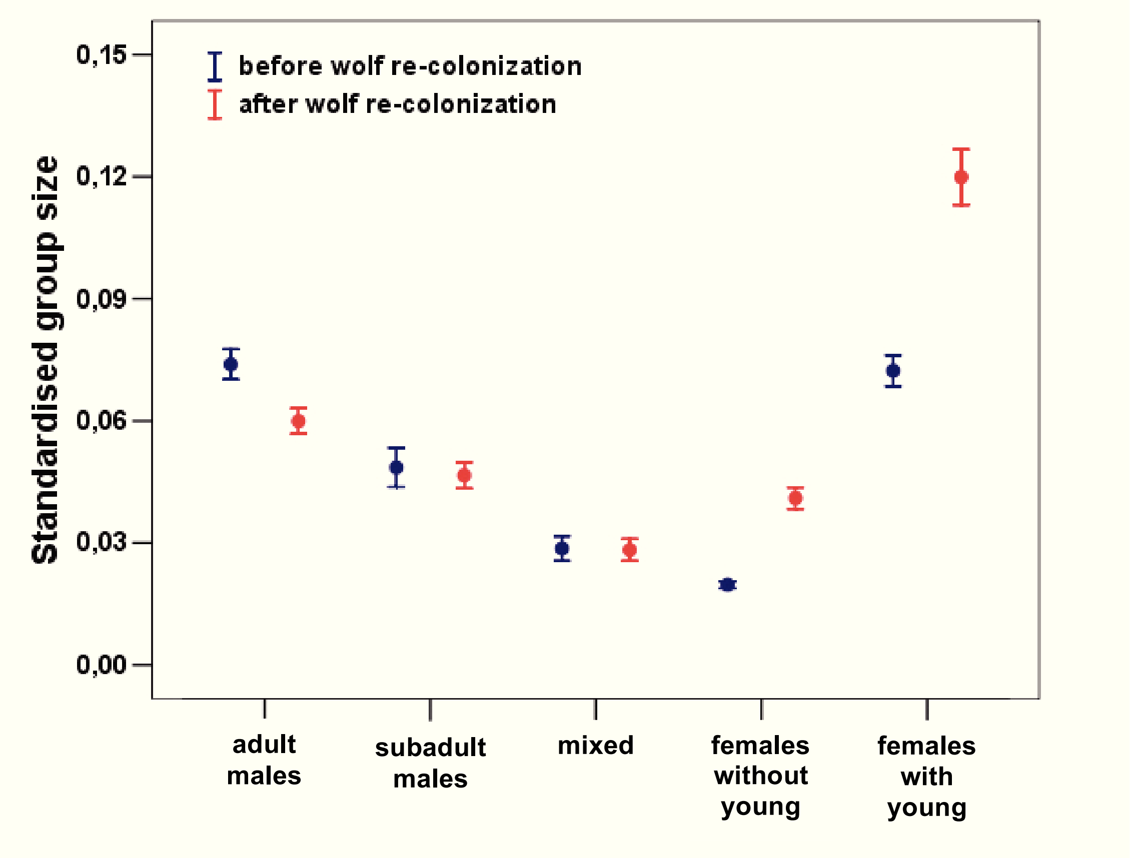

Fig. 1 – Mean group size (with SE) of ibex groups standardised on their anual density (total number of ibex in the study area for each year of data collection) A) in relation to group composition (adult males= group composed prevalently of males > 5 y.o.; subadult males= group composed prevalently of males ≤ 5 y.o.; mixed= groups in which the ratio of both sexes was lower than 75%; females without young= groups composed prevalently of females, no young present; females with young= groups composed prevalently of females and with at least 1 young) and B) in relation to group composition and to the period of data collection (before the re-colonization of the predator and after the re-colonization of the predator) in the Gran Paradiso National Park, Italy.

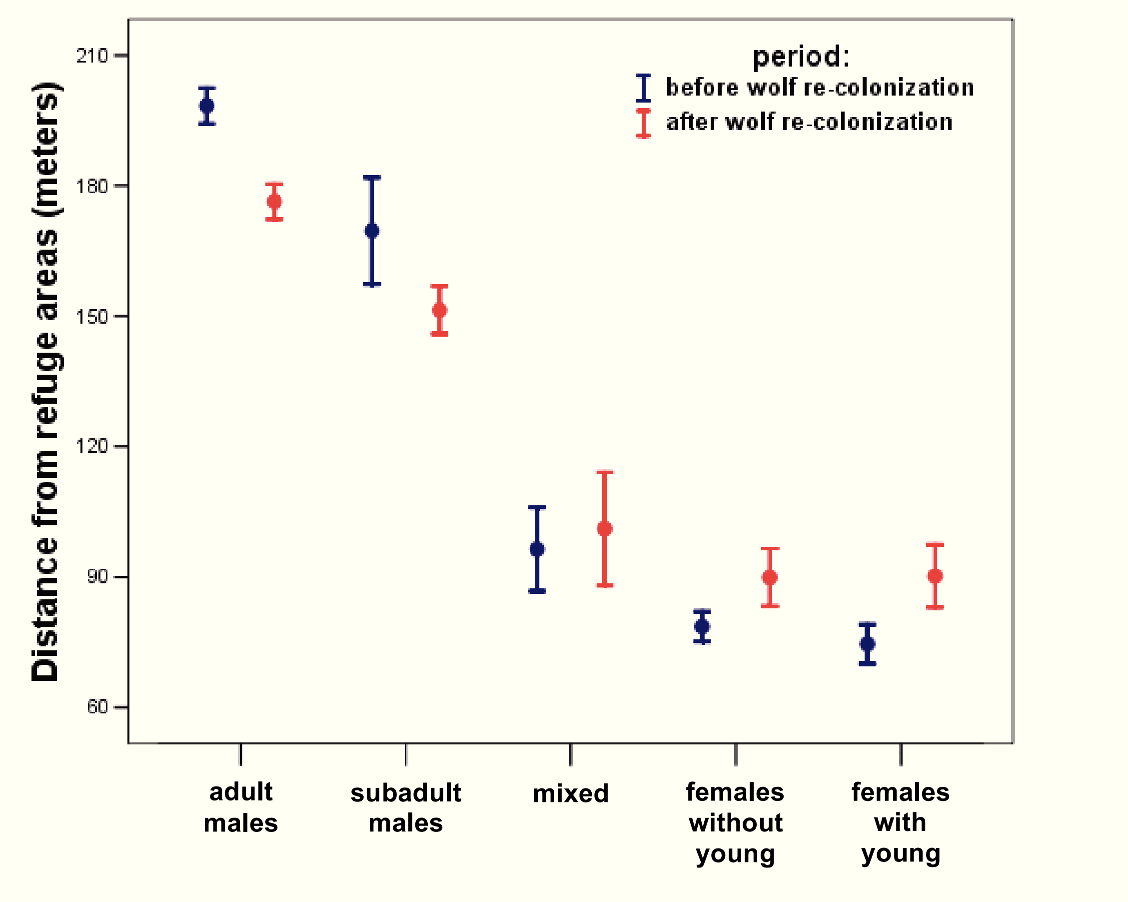

Fig. 3 – Mean distance (with SE) from refuge areas of ibex groups A) in relation to group composition (adult males= group composed prevalently of males > 5 y.o.; subadult males= group composed prevalently of males ≤ 5 y.o.; mixed= groups in which the ratio of both sexes was lower than 75%; females without young= groups composed prevalently of females, no young present; females with young= groups composed prevalently of females and with at least 1 young) and B) in relation to group composition and to the period of data collection (before the re-colonization of the predator and after the re-colonization of the predator) in the Gran Paradiso National Park, Italy.

DISCUSSION

We found that the return of a large predator induced quick modifications in antipredator behaviour of Alpine ibex. Toward the end of the 19th century, the GPNP was free from predators for adult ibex and golden eagles (*Aquila chrysäetos*) exerted only a very scarce impact on young. Nevertheless, Alpine ibex showed typical antipredator behaviour, i.e. use of "predator-safe" habitats (Grignolio et al. 2007a; Grignolio et al. 2007b), in the absence of predators (“ghost of predators past” Byers 1997). The explanation could be that behavioural patterns coevolved in this species and their predators for thousands of years and the absence of predators for a few centuries was not sufficient to remove them. However, a few years after the settlement of a reproductive wolf pack in the area of GPNP, males and females modified their strategies adopting safer behaviours. Several authors documented behavioural modifications in ungulate populations after the reintroduction of a predator (e.g. Hunter and Skinner 1998; Hebblewhite and Pletscher 2002), but in these cases they were not living in predator free area. Differently, our study case allows to achieve new information about ungulate antipredator responses when a modification of landscape of fear occur in an area totally free from predators. We documented the importance of the phenomenon of the “ghost of predator past ascertaining the ability of preys to quickly modify their behaviour (3-4 years) in face of the recent arrival of wolves in spite of an absence of predators dating a century.

Habitat selection may be viewed as a complex of scale-dependent behavioural decisions concerning environmental factors, the state of the individual animal, and intra and interspecific interactions (Senft et al. 1987; Rettie and Messier 2000; Boyce et al. 2003; Ciuti et al. 2006; Kittle et al. 2008). Factors commonly thought to be primary drivers of antipredator behaviour (i.e. selection of areas near rocky slopes) of ibex are sex, age, and reproductive status (Grignolio et al. 2007a; Grignolio et al. 2007b). The presence of the wolf induced only male ibex groups to modify their habitat use in favour of sites near the safe areas. Female did not adapt their habitat selection, notwithstanding the presence of kids. Animals should compromise between the choice of food-rich sites and the reduction of perceived risk. We conjectured that female couldn’t move nearer to rocky areas because they already used sites and meadows very close to these safe sites. The quality of forage in these meadows was lower compared to the flat areas (Grignolio et al. 2007a). Hence, females were probably unable to increase their antipredator behaviour without paying a critical energy cost. Moreover, it is possible that females considered their used areas secure enough to avoid the risk of wolf predation and therefore they had no need to shift their groups in a safer area.

Preys may try to reduce predation risk by grouping. Several authors have shown that individuals in larger groups are still safer, because they benefits of dilution effect (Creel and Creel 2002; Hebblewhite and Pletscher 2002), collective detection or cooperation in escape (Krause and Godin 1995), or combinations of these effects (Cresswell 1994; Uetz and Hieber 1994). Notwithstanding, some researches have reported that larger groups are more often detected and attacked; they also showed that higher predator success increase when attacking large groups (Hirsch and Morrell 2011). Creel & Winnie (2005) documented that elk herd size decreases when wolves are present, even if groups were far from timber (safe areas), thus suggesting that elk may disaggregate to reduce the likelihood of being detected by the predator. As a matter of fact, Hebblewhite & Pletscher (2002) found that wolves encountered larger groups more often than expected by chance. Only Alpine ibex males responded in the same way to the arrival of wolves: their group sizes decreased with the presence of wolf. The trade-offs between encounters with predators and dilution provide a coherent explanation for these social responses. Hence, males may need to avoid large groups (despite associate benefits), particularly when they forage in flat and more dangerous areas.

On the other hand, the presence of wolf affected female' aggregation propensity. Females did not modify their habitat selection but, taking into account their density in the study area, an increase of group size was detected. Our findings highlighted the importance of this social behaviour for this sex, also under an antipredator perspective.

We argued that different behavioural patterns of female and males are due to high sexual dimorphism of this species. Adult males weigh twice as females and have longer weapons (Bassano et al. 2003). These significant body size differences between the sexes may contribute to understand the different behavioural responses to a change of landscape of fair. The sexes should seek a different trade-off between maximizing foraging benefits and minimizing predation risk. Larger males seemed to respond to this trade-off by favouring food, even if their should reduce the distance from refuge areas. Instead, the reduction of predation risk played a key role for smaller females already before the presence of wolf pack. When the perceived risk increased, they could not allow themselves to further modify their habitat selection. Hence, females increased aggregation with conspecifics. In other words, they accepted a stronger foraging intrasexual competition to obtain an individual reduction of predation risk.

These antipredator responses can cause indirect costs of predation that may affect prey demography through individual' survival or reproduction. Results of this study showed that, even if ibex were little affected by direct lethal effects (Palmegiani et al. in press), they suffered from important indirect effects (i.e. alteration of their behaviour). As recently showed by empirical researches, risk effects (i.e. costs of antipredator behaviours) on prey dynamics can be as large as direct effects, or even larger (Schmitz et al. 1997; Nelson et al. 2004; Preisser et al. 2005; Pangle et al. 2007). Our results showed that male ibex were forced to forage in meadows characterised by worst forage quality and quantity (i.e. near rocks and slopes), while females were forced to forage under a stronger intraspecific competition for food (i.e. feeding in larger groups). Both these factors are likely to lead with a reduction of nutrients intake, thus a reduction of individual body conditions and growth. In addition, the landscape of fear may affect behaviours other than foraging, for example, movements (Fortin et al. 2005; Frair et al. 2005; Winnie et al. 2006), activity rhythms (Jeppesen 1987; Yarmoloy et al. 1988), or individual physiology (Bateson and Bradshaw 1997; Creel and Christianson 2008). Indeed, Creel et al. (2007) provided evidence that wolf predation risk alters reproductive physiology and demography of elk. The influences of risk effects on individual life history may play a relevant role especially in a species, like Alpine ibex, already characterised by a negative trend of its population dynamic (Jacobson et al. 2004).

Finally, it may be interesting to evaluate how ibex behavioural modifications evidenced in this work could influence trophic cascades. Trophic cascades generally arise through direct population-level effects, in which predators prey on herbivores, decreasing the abundance of herbivores that impact plant trophic levels (Schmitz et al. 1997). Trophic cascades could also arise through prey behavioural shifts that can result in reduced feeding intake, again lowering the impact of herbivores on plants. Ripple et al. (2001) showed that in Yellowstone ecosystem aspen benefited from the reintroduction of wolves because elk were forced to modify their distribution as well as their foraging strategy, thus reducing browsing pressure on that tree species. So, it is possible that ibex responses to the predator presence modify their pressure on Alpine meadows. Future studies may be implemented in order to evaluate the influence of this ungulate on Alpine ecosystem.

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SECOND PART

Reproductive behaviour

Chapter 3

Consequences of snowy winters on male mating strategies and reproduction in a mountain ungulate.

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ABSTRACT

Alternative mating tactics (AMTs) are intrasexual variants in mating behaviour of several species ranging from arthropods to mammals. Male AMTs coexist between and within populations. In particular, male ungulates rarely adopt just one tactic throughout their lifetime. Tactics commonly change according to internal factors (age, body size, condition) and external conditions (weather, resources, predation, animal density). However, the influence of weather has not yet been investigated in upper vertebrates. Such influence may be relevant in species whose rutting period occurs late in fall or in winter, when environmental conditions and the snow cover in particular may vary considerably. We detected two AMTs in Alpine ibex (*Capra ibex*) males: older and full-grown males mainly adopted the tending tactic, while younger males usually pursued an alternative one (coursing tactic). Weather was found to influence the adoptability of male AMTs: in snowy mating seasons, the coursing tactic disappeared due to difficulties in moving through deep snow. In snowy rutting periods, males appeared to delay or even avoid mating activities and a decrease of births was reported in the second part of the following birth season. Snow cover may have a negative effect on population dynamics by reducing the recruitment and on population genetic variability, as a consequence of poorer mating opportunities. Studies on factors affecting mating behaviour and leading to a reduced availability of mates and a decrease in female productivity are especially relevant in species, like Alpine ibex, whose genetic variability is low.

Key words: Alpine ibex, alternative mating tactics, female productivity, genetic variability, snow cover, weather conditions.

INTRODUCTION

Animal mating systems show a remarkable variation among species, whereas a degree of plasticity in reproductive behaviours was reported among (Emlen and Oring 1977; Lott 1991) and within (Austad 1984; Gross 1984; Shuster 1989; Zimmerer and Kallman 1989) populations, also on account of distinct male alternative mating tactics (AMTs). AMTs occur when conspecifics find different solutions to face intrasexual reproductive competition (Taborsky et al. 2008). These variations in mating behaviour are seen in diverse animal taxa, from arthropods to mammals (Alcock 1979; Taborsky 1994; Lank et al. 1995; Brockmann 2001; Calsbeek et al. 2002; Schradin and Lindholm 2011). Among mammals, variations in rutting behaviour within populations are particularly common in ungulates (Isvaran 2005 and references therein).

In polygynous species, males' reproductive success depends mostly on their fighting with other males so as to gain access to potential mates (Clutton-Brock et al. 1982; Gosling et al. 1987; Clutton-Brock et al. 1988; Festa-Bianchet et al. 1990; Komers et al. 1994). Larger or more powerful males may be able to monopolize mating access to females, thereby restricting the reproductive opportunity of less competitive rivals. Less successful males may thus be prevented from contributing to the species' gene pool (Dunbar et al. 1990). In such a situation, low-ranking animals can opt between giving up mating altogether and trying to find different solutions to gain access to oestrous females. Sexual selection is expected to favour any tactics that help less successful males to achieve mating success and this would likely contribute to the enhancement of the population's genetic variability (Coltman et al. 1999). Male ungulates rarely adopt just one AMT throughout their lifetime, as they commonly switch between two or more tactics, often within the same breeding season (Isvaran 2005). AMTs adoption commonly change according to internal factors (age, body size and condition), as well as to external conditions (resources, predation, and animal density - Isvaran 2005). In this regard, weather and environmental conditions are thought to affect the use of different mating tactics within a population, even though no specific study has been carried out as yet.

In mountainous environments, when females are widely and unpredictably distributed during the mating season, males rove broadly in search of oestrous females (roving strategy - Clutton-Brock 1989). Mate guarding is the conventional mating tactic (the so-called tending tactic) used by dominant males. During tending courtship, males persistently follow a female during her foraging activity, courting and defending her from other competing males. Young and/or subordinate males try to obtain mating opportunities by means of an alternative tactic (the so-called coursing tactic) which consists in the coursing and rapid chase of an oestrous female by a cohort of males that lined up behind the female. The first male (the one being closer to the female) could attempt a mount, clinching with the front legs on the female flanks (Hogg 1984; Lovari and Ale 2001; Saunders et al. 2005; Mainguy and Côté 2008; Willisch and Neuhaus 2009).

Alpine ibex (*Capra ibex*) is a polygynous ungulate that inhabits mountainous environments with marked seasonal changes. The roving strategy is used by males and two mating tactics have been identified: tending and coursing (Willisch and Neuhaus 2009).This species suffered from severe genetic bottlenecks through its peculiar history: in the 18th century, Alpine ibex appeared to be almost extinct and its distribution was reduced to a small population in the Gran Paradiso massif in Italy. As a result, its genetic variability is reported to be one of the lowest among mammal species (Maudet et al. 2002). Females give birth in late spring/early summer to match the green-up of vegetation and allow offspring to benefit from the entire vegetation growing season (Pettorelli et al. 2007). Hence, the mating season occurs from late autumn to early winter, when food availability is scarce and hard winter conditions typically persist for a long time (at least for three months). Studies on the Gran Paradiso population revealed that snow cover has important effects on both ibex population dynamics and behaviour. Jacobson et al. (2004) suggested that a deep snow cover may cause direct mortality of individuals from all age classes and/or affect survival of aging individuals. In addition, snow cover reduces ibex movements and limits the extension of their winter ranges (Parrini et al. 2003; Grignolio et al. 2004).

Under these premises, we investigated ibex males rutting behaviour over ten different mating seasons within the Gran Paradiso National Park. In particular:

1. we assessed the presence of AMTs in the only native and unmanaged population of Alpine ibex which is therefore characterized by a natural structure. As the body size of ibex males is still increasing at 9-11 years of age (Bassano et al. 2003; von Hardenberg 2005), we assumed that, where present, older males were more competitive. Accordingly, we predicted that the role of age in the adoption of AMTs is relative to the age structure of the population;
2. as snow cover causes mobility difficulties and an increase in energetic expenditure, we expected a reduction in the number of males involved in mating activities during snowy winters. Moreover, as males adopting the coursing tactic have to run behind females, we supposed that the adoption of this tactic would decrease when heavy snow was reported;
3. should snow cover be found to influence male reproductive performances (prediction 2), we expected that the amount of snow cover during the rut could influence the timing of the following birth season and female productivity.

METHODS

Study area and population

We studied ibex behaviour in the Gran Paradiso National Park, Italy (GPNP; 45°35'N, 7°12'E; north-western Italian Alps). We collected data from the Valnontey valley (VNV) from 1993 to 1998, and from the Valsavarenche valley (VSV) from 2000 to 2010. The two study areas are similar, consisting of steep glacial valleys running N-S, and featuring similar environments. In both study areas the habitat used by ibex ranges from 1500 m to 3300 m a.s.l., and is dominated by alpine meadows, rocky slopes, and stone ravines (Grignolio et al. 2003; Parrini et al. 2003).

The two areas were characterized by similar male ibex density (census 2000: 7.6 male/km2 in VNV; 6.4 male/km2 in VSV).

Every year the wardens and vets of the GPNP captured some ibex to check the presence of infectious diseases and marked the animals. Thanks to a long experience (more than 40 years), the mortality rate during these captures was very low (<2%, Bassano et al. 2004). In order to reduce the considerable distress to animals during the first part of the capture, only one operator with a darting gun would approach the ibex and walk away right after the shot. We used a mixture of xylazine (Rompun, Bayer: about 70 mg per ibex) and ketamine (Ketavet, about 50 mg per ibex) in a dose that has not been proven to cause any adverse effect. The use of this mixture in wild ungulates is widely described in literature. The drug-sedated ibex was observed by means of binoculars and about 10 minutes after the injection the ibex would lay down. After 5 more minutes an operator approached the animal and if this did not show any sign of alert, three operators joined in, tied the ibex and covered its eyes. After the capture we collected biometric data and biological samples. In order to define the exact ibex age we counted the clearly separated annuli (Ratti and Habermehl 1977; von Hardenberg et al. 2004), then we marked the ibex and injected an antagonist of xilazin (Atipamezole: 1 ml per ibex) to accelerate the recovery of the animal. During the operation the ibex did not show any sign of distress. We freed it after about 20 minutes. We used radio-collars (VHF Televilt, Sweden, 285g corresponding to 0.4 % of adult male mean weight) and livestock (sheep and goats) ear tags (Allflex, USA: 5.5 x 6.8cm) to mark the animals. We used radio-collars only on adult animals and therefore we did not need to remove them. In 15 years of ibex behavioural research we did not record any adverse effects of radio-collars and ear tags on animals. The research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. The Italian National Wildlife Institute approved the handling protocols.

In VSV study area we followed 28 marked males in 2000, 49 in 2001, 57 in 2002, 24 in 2007 and 2010. Throughout the year a proportion of marked males used both areas (authors' personal observations). Snow cover depth was measured each day, starting from the first day of snow, which usually occurred in November (Fig. 1 – Data from Regione Autonoma Valle d'Aosta).

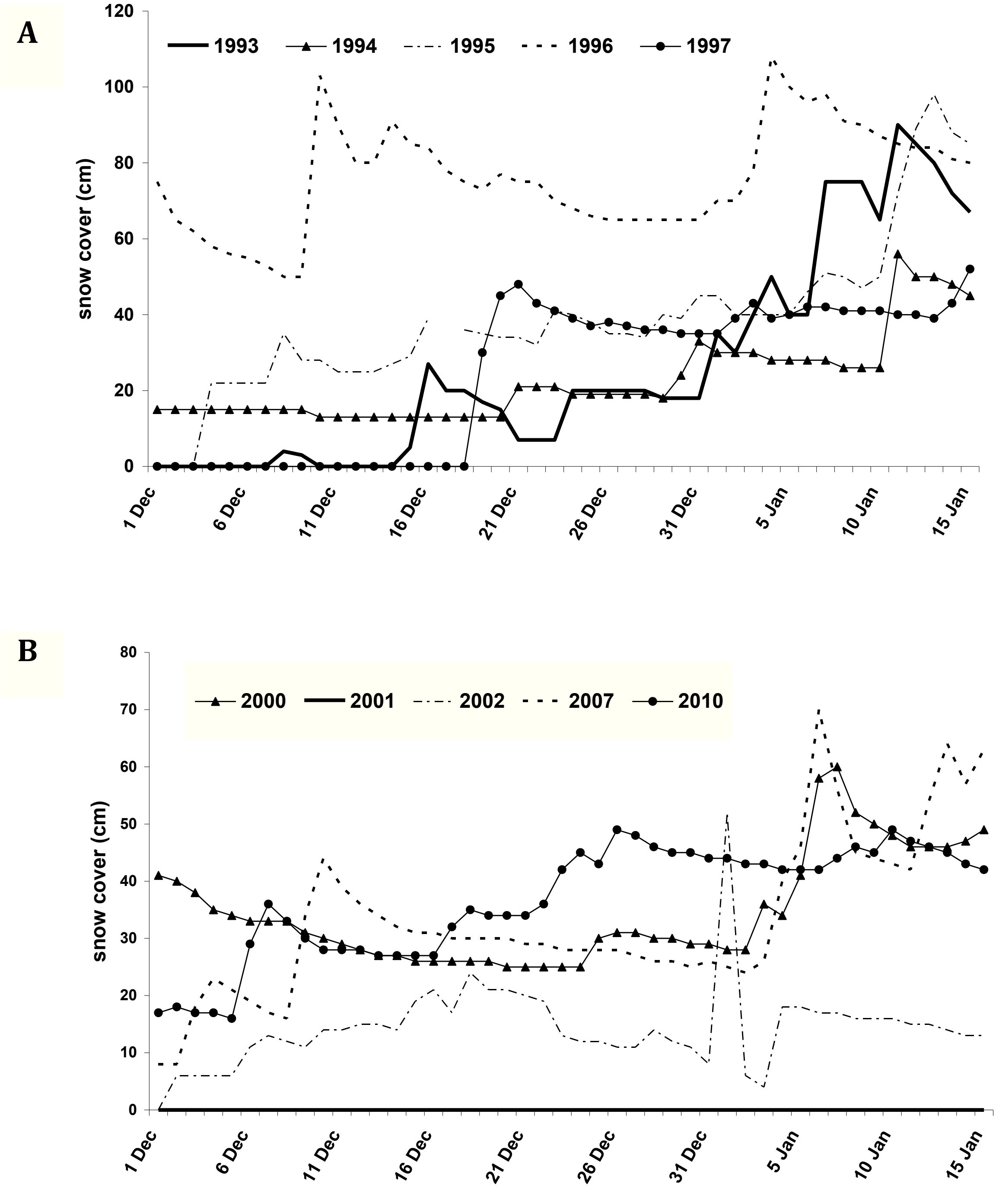

Figure 1 - snow cover depth in Valnontey Valley (A) and Valsavarenche Valley (B), Gran Paradiso National Park, Italy. During the 2001 rut period snow cover was absent.

Data collection and analysis

Behavioural observation

Ibex were observed during the rut period (1st Dec. – 15th Jan.) of 10 mating seasons (from 1993 to 1997 in VNV; 2000, 2001, 2002, 2007, and 2010 in VSV). In VNV observations were conducted on courting animals (no marked ibex was present) using the "sampling all occurrences method" (Altmann 1974). In VSV observations were conducted on marked animals using the "focal animal sampling" over continuous periods (Altmann 1974). Observations were made for at least one hour by means of binoculars (10 x) and spotting scopes (20-60 x). We recorded group size and composition, as well as all behavioural patterns performed by the focal animal and the times of transition between different patterns. In addition, the behaviour of courting males was recorded in detail by means of audio recorders, as described by Couturier (1962) and Aeschbacher (1978). When a courtship involved more males, we also recorded the position of each male with respect to the courted female. Focal watches were distributed over daylight hours (from 8:30 to 17:00 approximately) and on all marked ibex present in the study area.

We used logistic regression to evaluate if the male age affected the occurrence probability of a tending or coursing courtship. Moreover, we applied the same analysis to assess if the age influenced the probability for a male to be in the first or last position with respect to the courted female. In all the logistic regression models, we included the age class (3-5 y.o. - 6-8 y.o. - 9-11 y.o. - >11 y.o., as suggested by Grignolio et al. 2007), as a categorical variable.

During the rut period only, ibex males typically raise their tail and lay it over their back, thus showing a behavioural pattern which is associated to the activity of the subcaudal gland (Couturier 1962; Aeschbacher 1978). We considered the males which laid their tails over their back to be engaged in sexual activities. For this reason, during three years (2000, 2001 and 2002) we also recorded the position of the tail each time we observed a marked male. We did not consider observations made after 30 Dec. because as the end of the rut approaches, males tend to alternatively raise up and lower down their tails (Aeschbacher 1978; authors personal observations).

For each marked male we calculated the number of days elapsed between the 1 Dec. and the first day on which he was observed with his tail up. We used this as a dependent variable and developed a LMM with age class and year of data collection as categorical fixed factors. In all the LMM models developed and reported in this manuscript, ibex identity was used as a random term to control for repeated measurements of the same individual (Pinheiro and Bates 2000). We included all main effects and all two-way interactions in the LMM and subsequently modelled the dependent variable excluding the interaction terms that were not found to be significant. LMM pairwise comparisons with adjustment for multiple comparisons were performed to show differences among values of significant variables.

Spatial behaviour

From October to February 2000, 2001, and 2002 we collected locations of 59 marked ibex males. We tracked each individual either by direct observation (90%) or by triangulation using radio-techniques, at least 10 times over each biological period. In this respect, we considered three biological periods: pre-rut (from 15 Oct. to 30 Nov.), rut (from 1 Dec. to 15 Jan.), and post-rut (from 16 Jan. to 28 Feb.), as suggested by Brivio et al. (2010). We uniformly distributed the observation times over the daylight hours and separated them by an interval of at least 4 hours to achieve independence of fixes (Swihart and Slade 1985). We collected direct observations by means of binoculars, telescopes, and homing-in radio-tracking in order to locate ibex groups (MacDonald et al. 1980; White and Garrott 1990).

Home ranges of 45 days (pre-rut, rut and post-rut period; n° fix/individual/period: 12.13 ± 0.57) were estimated by the 90% Kernel method (Börger et al. 2006), using the software program Ranges VI (Kenward et al. 2003). We analysed the effect of independent variables on the spatial behaviour by fitting LMM to natural logarithm transformed 45-day period home range sizes (ln

HR) as response variables. We considered biological period (pre-rut, rut, post-rut), age class, and year of data collection as categorical fixed effects in the models. Then, we computed the ratio between distance (meters) of two consecutive fixes and the time (hours) elapsed between them. By means of LMM we fitted the ln-transformed of this ratio (ln distance) considering the influence of year, biological period, age class (categorical fixed factors) and daily snow cover (covariate).

Female productivity and timing of birth period

From 1 June to 10 July of 6 years (2001-2003 and 2008-2010) we monitored the area selected by females to give birth and during the early weeks of life of the kids every 3-4 days (Grignolio et al. 2007). Observations were made by means of binoculars and spotting scopes during the last two hours of light before dusk. We recorded the number of kids and females in order to estimate female productivity and timing of birth period.

For each day of data collection we evaluated female productivity as the ratio between number of kids and number of females observed. Then, for each year of data collection we calculated the best regression (in all cases logarithmic) between day of observation (considered as the number of days after 1 June) and the respective female productivity. We solved the equations resulting from the logarithmic regressions in order to estimate: 1) annual productivity until 20 June, i.e. in the first half of the birth season; 2) annual productivity in the second half of the birth season, calculated as the difference between productivity as of 10 July and productivity as of 20 June. In conclusion, we calculated a linear regression using the estimated productivity for the first half of the birth season of each year of data collection (dependent variable) and the mean snow cover recorded during the previous mating season (independent variable). Then, we computed a similar linear regression using the estimated annual productivity for the second half of the birth season.

RESULTS

Description of courtships and relative activity budgets

Based on a total of 610 hours of observation, our results confirmed that male ibex adopted two AMTs: tending and coursing. During both types of courtship, the group size varied (minimum 1 male, maximum 12 males) and both composition and rank line changed quite often. Moreover, a tending courtship could evolve into a coursing one and vice versa.

Coursing courtships were observed in VNV throughout the years of data collection, except for 1996, whereas no coursing courtship was recorded in VSV in 2000, 2007 and 2010: in these four years, winters were characterised by deep snow cover (Fig. 3). Our results revealed that the logistic regression with age class as predictor of the event probability of coursing courtships fits the data well ($\chi^2 = 53.041$, df = 3, $P < 0.001$). Males of all age classes were involved in the coursing mating tactic, but the probability for a male to perform a coursing courtship was significantly higher for 3-5 y.o. males than for 6-8 y.o. males (odds ratio = 0.214, $P < 0.001$), 9-11 y.o. males (odds ratio = 0.226, $P < 0.001$), and males older than 11 yrs (odds ratio = 0.121, $P < 0.001$; Fig. 2B). Within coursing parties, the probability to be in the first or in the last position behind the pursued female were well predicted by male age class (first position: $\chi^2 = 32.255$, df = 3, $P < 0.001$; last position: $\chi^2 = 52.696$, df = 3, $P < 0.001$). The probability to be in first position was significantly higher for 3-5 y.o. males than for 9-11 y.o. males (odds ratio = 0.077, $P = 0.002$) and for males older than 11 (never observed in the first position; Fig. 2B). On the contrary, males older than 11 yrs had a significantly higher probability to be in the last position than 3-5 y.o. males (odds ratio = 0.006, $P < 0.001$), 6-8 y.o. males (odds ratio = 0.007, $P < 0.001$), and 9-11 y.o. males (odds ratio = 0.067, $P = 0.002$; Fig. 2B). When males used the tending tactic, their position with respect to the courted female was significantly affected by their age ($\chi^2 = 58.140$, df = 3, $P < 0.001$): males older than 11 yrs had a significantly higher probability to be closer to the female than 3-5 y.o. males (odds ratio = 0.074, P < 0.001), 6-8 y.o. males (odds ratio = 0.094, P < 0.001), and 9-11 y.o. males (odds ratio = 0.291, P = 0.003; Fig. 2A).

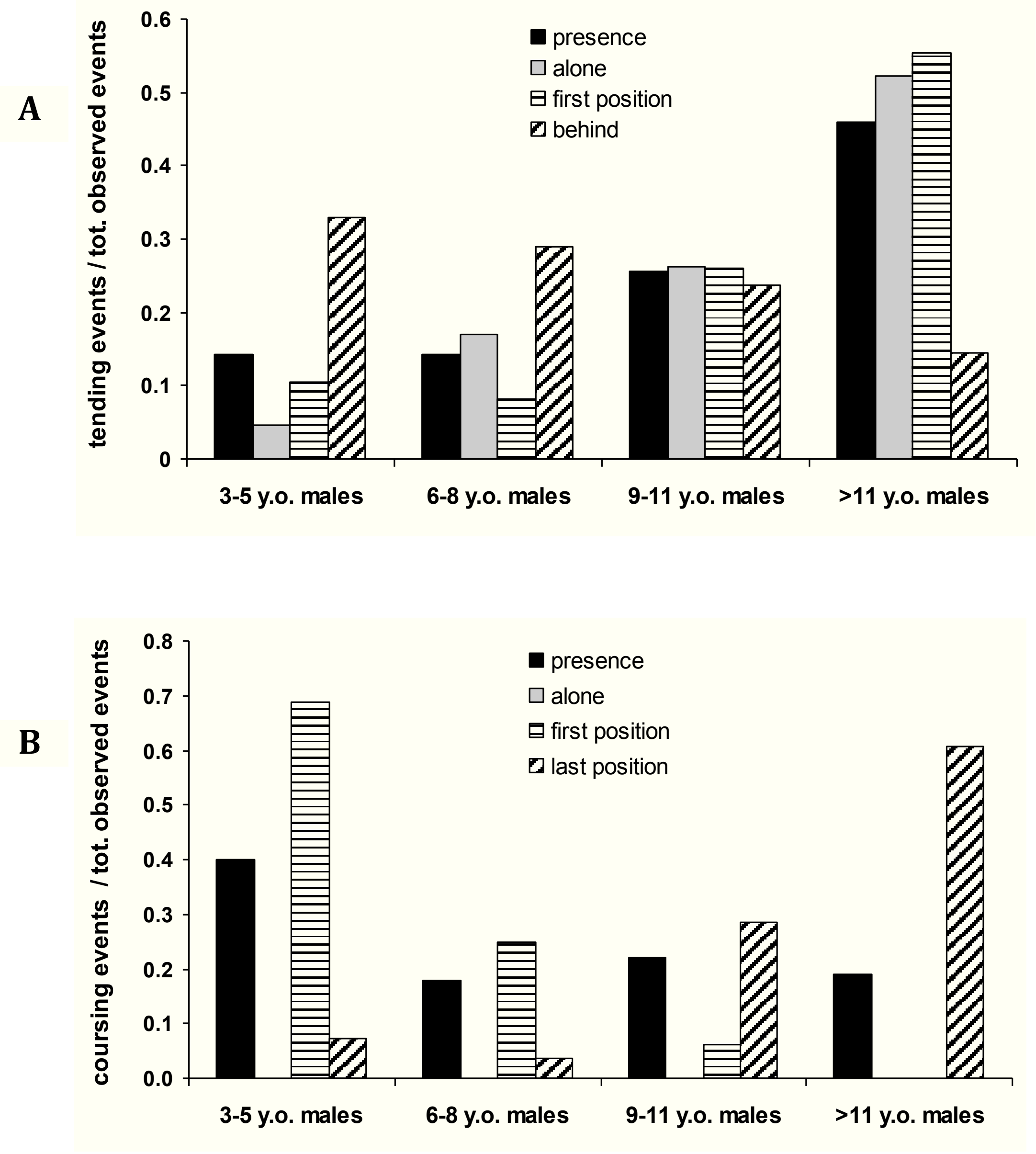

Figure 2 - percentages of males from different age classes observed to be engaged in tending (A) and coursing (B) courtships, and their position with respect to the courted female, in Gran Paradiso National Park, Italy.

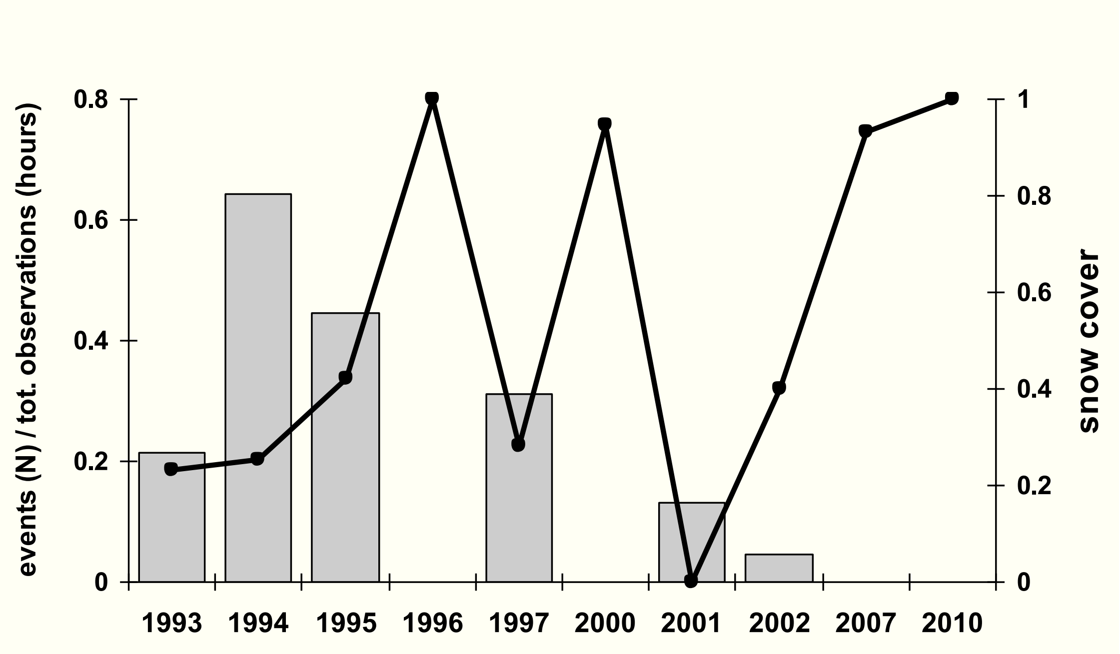

Figure 3 - number of coursing courtships observed on total hours of observations (bars) and standardized mean snow cover (line) during the rut period (1 Dec. – 15 Jan.) in Valnontey Valley (from 1993 to 1997) and in Valsavarenche Valley (from 2000 to 2010), Gran Paradiso National Park, Italy. For each study area, yearly mean snow cover was standardized with respect to the maximum value.

The analysis of the first day on which ibex males were reported to raise their tail above their back showed significant differences among years of data collection (LMM: $F_{2,56} = 9.647$; $P < 0.001$) as well as among age classes (LMM: $F_{3,55} = 3.668$; $P = 0.017$). In 2000, which was characterized by deep snow cover, males raised their tail later (X ± SE: 1.43 ± 0.25 days after 1 Dec.) than in 2002 (0.81 ± 0.16 days after 1 Dec.), while in 2002 it occurred later than in 2001 (0.26 ± 0.15 days after 1 Dec.), when snow cover was absent. Moreover, males younger than 9 yrs started to raise the tail earlier than males of 9-11 y.o., which in turn raised their tail earlier than males older than 11 yrs.

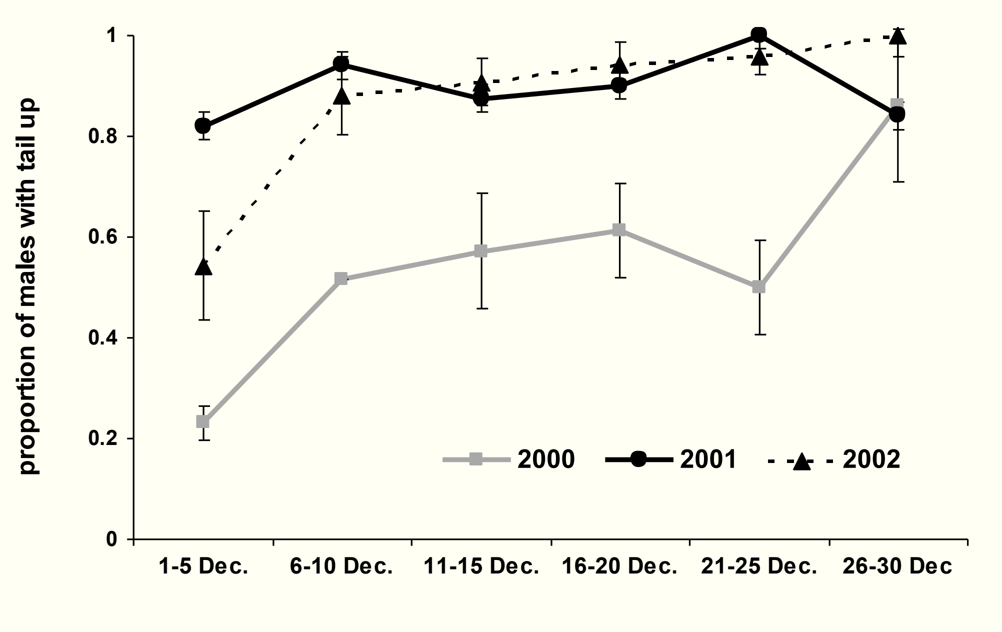

Figure 4 - proportion of males with tail up (X ± SE) in 5-day periods in 2000 (gray line), 2001 (black line), and 2002 (hatching line) in Gran Paradiso National Park, Italy.

Spatial behaviour

The home range size of males did not vary according to age class (LMM: $F_{3,120} = 0.359$; $P = 0.783$). Males significantly reduced their home range size from the pre-rut (LMM: $F_{2,120} = 17.774$; $P < 0.001$; ln HR = 4.36 ± 0.15 ha) to the rut (ln HR = 3.66 ± 0.12 ha; $P < 0.001$), and again from the rut to the post-rut (ln HR = 2.66 ± 0.25 ha; $P < 0.001$). We found an almost significant effect of year of data collection (LMM: $F_{2,120} = 2.817$; $P = 0.064$). During the year 2000, which was characterized by deep snow cover, the home range size of males (ln HR = 3.18 ± 0.24) was significantly smaller than in 2001, when no snow cover was reported (ln HR = 3.82 ± 0.14; $P = 0.019$). The combined effect of year and biological period had a significant effect on home range size (LMM: $F_{4,120} = 9.954$; $P < 0.001$). In particular, during the rut period the smallest home range sizes were recorded in 2000 (ln HR= 3.03 ± 0.29) and the largest ones in 2001 (ln HR = 4.37 ± 0.17).

The distance covered by ibex differed significantly among years (LMM: $F_{2,3286} = 23.520$; $P < 0.001$): males moved less in 2000, with deep snow cover (ln distance = 2.23 ± 0.09 m/h), than in the year without snow (2001: ln distance = 2.48 ± 0.04 m/h; $P = 0.016$). Distances were significantly longer during the rut (LMM: $F_{2,3286} = 8.611$; $P < 0.001$; ln distance = 2.47 ± 0.04 m/h) than during the pre-rut (ln distance = 2.28 ± 0.05 m/h; $P = 0.003$) and the post-rut period (ln distance = 2.04 ± 0.07 m/h; $P < 0.001$); likewise, they were significantly longer during the pre-rut than during the post-rut period ($P = 0.005$). The model showed a significantly negative effect of snow cover on the distance covered by males (LMM: $F_{1,3286} = 8.017$; $P = 0.005$).

Female productivity and timing of birth period

Logarithmic curve was the best regression to fit timing of birth period in each year of data collection. Regressions were significant in all cases (at least $P < 0.02$). R^2 values were 0.86, 0.91, 0.55, 0.84, 0.61, and 0.75 in 2001, 2002, 2003, 2008, 2009, and 2010, respectively. We found a negative relationship between estimated annual productivity in the first half of the birth season and snow depth in the previous rut period, but with no statistical significance ($R^2 = 0.04$, $P = 0.708$; Fig 5). Instead, in years with deep snow cover, female productivity was found to decrease significantly in the second half of the birth period ($R^2 = 0.78$; $P = 0.01$; Fig. 5).

DISCUSSION

In the only natural population of Alpine ibex, males adopted two distinct alternative tactics to gain access to receptive females: tending and coursing. The occurrence of these AMTs has been reported in a range of mountain ungulates (e.g., *Ovis canadensis*, Hogg 1984; *Pseudois nayaur*, Lovari and Ale 2001; *Capra hircus*, Saunders et al. 2005; *Oreamnos americanus*, Mainguy and Côté 2008), and even in a reintroduced population of Alpine ibex in Switzerland (Willisch and Neuhaus 2009). Sexual selection of these tactics is likely related to differences in male body size as well as

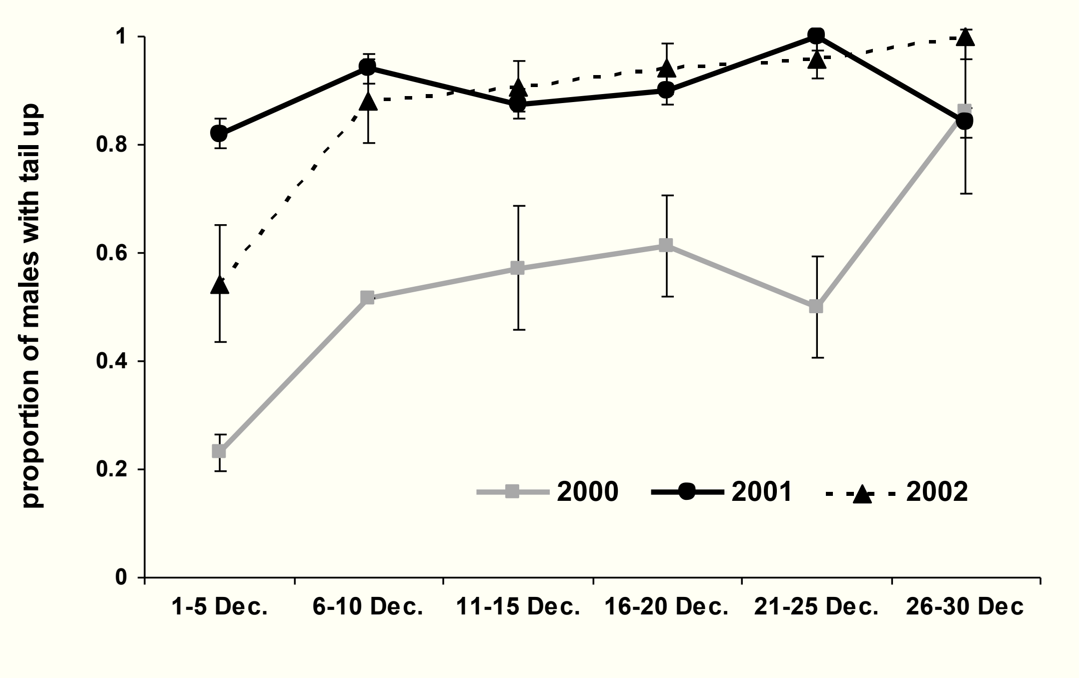

Figure 5 - relationship between the estimated productivity of female ibex and mean snow cover during the previous rut period in Gran Paradiso National Park, Italy. Grey line is linear regressions of estimated productivity in the first half of the birth period. Black line is the productivity in the second half of the birth period, calculated as the difference between productivity, as calculated on 10 July and 20 June.

to the mountain environment. Small and young males suffer from a severe disadvantage when the tending tactic is adopted, because they cannot effectively defend the oestrous females from older males that may attempt to approach them. In order not to be prevented from contributing to the species' gene pool, they have to adopt an AMT (coursing) in which their small and slight mass turns into an asset. Moreover, particularly over rugged and discontinuous terrains, a small body size accounts for above-the-average agility, endurance and speed, that are likely to be important factors for a successful coursing (Hogg and Forbes 1997). Male ibex are characterized by a slow and progressive growth of body mass that results in a strong dimorphism among age classes (about 40% of body mass between 3-5 y.o. males and fully grown males older than 9 yrs – Bassano et al. 2003). The weight of young male ibex (3-5 y.o.) is similar to that of adult females. Accordingly, young males are quicker, can follow females during a coursing chase, and stand a good chance to mate with them. Our findings, relative to a protected population with a natural age structure, are consistent with the results reported by Willisch and Neuhaus (2009) for a hunted and younger population in the Swiss Alps. The comparison between these two studies pointed out that the role of age in the adoption of AMTs is correlates to the age structure of the population (prediction 1). In the Swiss population, the proportion of time spent tending and the percentage of tending courtships peaked for 9-11 y.o. males (Willisch and Neuhaus 2009), while in our population the peak was recorded for males older than 11 yrs (46% of males from this age class were observed to participate in tending events). Given that the body size of Alpine ibex keeps on growing in the period between 9 and 11 years of age, it is clear that where older males are present, these result to be the most successful.

Despite the 610 hours of ibex observation, we detected only a very little number of mounting and copulatory events. We estimated male reproductive opportunities on the basis of their rutting behaviour and considered that in a courtship group the individual which is observed to be closer to the courted female is most likely to mate. Our results showed that older males could achieve more matings in tending groups, while young males were more successful when the coursing tactic was adopted. In several ungulate populations, the matings achieved by young males are often attributed to their sneaky or coercive mating strategies (Clutton-Brock and Parker 1995), such as the coursing tactic. This tactic was less frequent in ibex (e.g., no courting events in 1997, 2000, and 2010) and associated with low reproductive success (Willisch et al. 2012). Hence, to contribute to the species' gene pool, young males seemed to start courting females before the older ones: males younger than 9 yrs raised their tail well in advance when compared to older males. Thus, at the beginning of the rut, when the competition with older males was lower, younger males could have increased their chances to access receptive females. We proposed that this could be a further strategy by means of which young ibex males may gain access to potential mates and improve population genetic variability, thus increasing the number of breeding males. Earlier mating attempts by young males have also been observed in other species, but females' ovulation at the beginning of the rut was found not to result in pregnancy (e.g. Lincoln and Guinness 1973; Thomas and Cowan 1975; Bartos and Perner 1998). Hence, these attempts presumably failed to increase young males' reproductive success. This seems not to be the case of Alpine ibex, since we observed some females giving birth right at the beginning of June, the gestation period lasting about 180 days in this species.

Our results on rutting behaviour are in accordance with Isvaran (2005): males of different age and status could follow different AMTs. Isvaran (2005) also proposed that weather conditions may affect the adoption of different tactics by males, but no study has yet investigated this aspect. Our findings showed that snow cover had remarkable effects on the Alpine ibex rutting behaviour: reduction in the use of AMTs, delay or even abandonment of mating activities, potential influence on population dynamic and presumably also on population genetic variability. We proposed that all these modifications were primarily linked to the influence of snow cover on ibex movement.

The analysis of spatial behaviour pointed out that deep snow cover reduced the home range size of males as well as their mobility, as previously reported for other ungulates species (e.g. *Cervus elaphus*, Georgii and Schroeder 1983; *Capra ibex sibirica*, Fox et al. 1992; *Bison bonasus*, Krasinska et al. 2000). Movement through deep snow causes higher energy expenditure for large mammals: the deeper the snow, the higher the energetic costs (Parker et al. 1984). The negative relationship between snow depth and mobility is likely a result of animal conserving energy when snow depth exceeds normal levels (Rivrud et al. 2010). Alpine ibex breeding season occurs from late autumn to early winter (it peaks around 20 Dec.), when the conditions in mountain environments can be very hard on account of low temperatures and the presence of snow cover in particular. In Alpine habitats, the snow generally falls first in November and persists on the ground till spring. However, these habitats are typically characterized by a strong variability from year to year, ranging from snowless winters to winters with constant heavy snow cover. Ibex had to approach the period after the rut in not too poor conditions, because at that stage they still had to face the long Alpine winter that requires considerable energy reserves.

In ibex mating strategy, mobility was a key factor. From the pre-rut (15 Oct.- 30 Nov.) to the rut (1 Dec. – 15 Jun.) period, male ibex reduced their home range sizes but at the same time increased their mobility. This is presumably due to the mating system based on the roving strategy: during the pre-rut, males had to reach females' winter home ranges, and then, during the rut, they had to rove intensively in order to increase the likelihood to meet with oestrous females. As snow depth can modify ibex mobility, snow cover likely influences male mating performances. First of all, our results showed that snow depth had consequences on the adoption of the two AMTs. During breeding seasons with deep snow cover, male ibex only adopted the tending tactic, while the coursing tactic disappeared (prediction 2). Coursing courtships consisted in running after females, often over long distances. The presence of deep snow made it difficult to run through rugged areas. Therefore, the costs of this tactic were presumably too high and young males were forced to give up reproduction and to invest their energy in maintenance activities.

Snow cover also influenced the timing of males' interest in rutting activities. During the breeding seasons when higher snow cover was reported, males started to raise their tail later. Moreover, our observations showed that the proportion of males that were involved in rutting activities each year was influenced by the amount of snow present on the ground: in years with deep snow, the proportion of males with tail up decreased (prediction 2, Fig. 4). During snowy mating seasons, males increased the use of energy-saving areas, characterized by less snow cover (e.g., rocky slopes, Grignolio et al. 2003), thus taking a long time to reach female areas or even avoiding to participate in the rut. In winters with abundant snow, ibex survival rate decreased (Jacobson et al. 2004), presumably as a consequence of both lower food availability and the increase in energy expenditures related to locomotion. Males seemed to be able to regulate their energy allocation when environmental conditions became hard by reducing the time spent in mating activities and increasing the energy allocated to survival. Possibly, in snowy winters there was a lower number of males with outstanding body conditions and this gave them the possibility to invest energy in rutting activities and to reduce the time normally allocated to maintenance activities (e.g., feeding and lying); moreover, Alpine winter environmental conditions forced all males to keep on foraging during the rut (Brivio et al. 2010). Male ibex cannot stop feeding completely as other ungulate species do (e.g., *Alces alces*, Miquelle 1990; *Dama dama*, Apollonio and Di Vittorio 2004).

Behavioural modifications related to snow cover had consequences on the number of breeding opportunities. Our analyses on female productivity partially supported the hypothesis that snowy mating seasons influenced the timing of the following birth period (prediction 3). After snowy winters, a decrease of births was reported in the second half of birth season (after 20 June), thus suggesting a reduction in the females mated when ovulation was late. Arguably, during snowy winters males' condition worsened faster, so that they seemed to give up investing in reproduction and to save energy for survival during the second part of the breeding season.

The aforementioned effects of snow cover on ibex reproduction may result in a reduction in the genetic variability of the cohort which will be born after snowy winters. This is particularly relevant in a species like Alpine ibex, whose genetic variability is among the lowest reported in mammal species (Maudet et al. 2002).

Alpine ibex is a species with evident morphological and behavioural adaptations to live in rocky areas, whereas it did not evolve morphological adaptations to snow, as is the case for Alpine chamois (Rupicapra rupicapra) and its interdigital membrane. In absence of morphological or physiological adjustments, ibex males can react to difficulties due to snow cover only with behavioural modifications. In large herbivores, behavioural adjustments are likely to be the quickest response to environmental pressure and, as a consequence, they presumably are under strong selective pressure.

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Chapter 4

To feed or not to feed? Testing different hypotheses on rut-induced hypophagia in a mountain ungulate.

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RESEARCH PAPER

To Feed or Not to Feed? Testing Different Hypotheses on Rut-Induced Hypophagia in a Mountain Ungulate

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Abstract

In many ruminant species, males dramatically reduce forage intake during the rut. To date, different hypotheses have been suggested to explain this rut-induced hypophagia. To assess the predictions of the main hypotheses, we analysed Alpine ibex (*Capra ibex*) activity budget and compared the behaviour of males and females before, during, and after the rut. Only males spent significantly less time foraging during the rut than outside of it, whereas females allocated a similar proportion of time to foraging before, during, and after the rut. Our results showed that during the rut males also reduced lying time, while the ratio of time spent feeding to time spent lying did not change for males among periods. In conclusion, during the breeding season males maximized energy intake when not actively engaged in mating activities and rut-induced hypophagia appeared to result from time budget constraints generated by mating-related activities. Accordingly, the *foraging constraint hypothesis* seems appropriate to explain this phenomenon in Alpine ibex males.

Introduction

In capital breeder species, a temporal separation exists between the phase of energy acquisition and investment in reproduction (Drent & Daan 1980; Jönsson 1997). Mammal males are often engaged in polygynic mating systems (Clutton-Brock 1989) that lead to high energy expenditure and imply severe trade-off between energetic costs of reproduction and other fitness components such as survival (Descamps et al. 2006). One of the major costs is probably related to changes in their activity budget that imply a reduction in food intake during the rut. Rut-induced hypophagia has been reported across a wide range of ruminants species living in different habitats and climate conditions: *Alces alces* (Miquelle 1990), *Bison bison* (Maher & Byers 1987; Komers et al. 1994), *Cervus elaphus* (Clutton-Brock et al. 1982; Mysterud et al. 2008), *Dama dama* (Apollonio & Di Vittorio 2004), *Oreamnos americanus* (Mainguy & Côté 2008), *Ovis canadensis* (Pelletier 2005), *Rupicapra rupicapra* (Willisch & Ingold 2007).

As Pelletier et al. (2009) recently pointed out, appetite suppression during the breeding season is a paradoxical phenomenon because it occurs at a time of the year when energy expenditure by males reaches its highest level. This applies particularly to species of temperate and arctic climates, whose mating periods occur late in fall or at the onset of winter. In these species, reduction in feeding during the rut may cause males to enter winter while in poor conditions. As a consequence, they will be more likely to die from predation, disease or starvation (Pelletier 2005).

To date, different hypotheses have been suggested to explain the proximate mechanism governing feeding time reduction in male ruminants (see Table 1, for a detailed description of the predictions):

1. *Foraging constraint hypothesis*: Time normally allocated to feeding is rather allocated to rutting activities (Geist 1982). Because the rut is generally short in ungulates, time spent for mating activities is expected to increase at the expense of maintenance activities, i.e. the time spent foraging and lying (Pelletier 2005; Pelletier et al. 2009). As the rut

Table 1: Hypotheses explaining hypophagia and related behavioural predictions in ungulate rutting males compared with the outcomes of our study

	Predictions					
	Rest (from the pre-rut to the rut period)	Foraging/lying (from the pre-rut to the rut period)	Foraging vs. rutting	Lying vs. rutting	Notes	Citations
The foraging constraint hypothesis	↓	↔	Negatively correlated	Negatively correlated		Pelletier et al. (2009)
The energy-saving hypothesis	↔ or ↑	↓	Threshold–like relationship	Negatively correlated	Males allocate most of their non-rutting time to lying	Willisch & Ingold (2007); Mysterud et al. (2008)
The physical rest hypothesis	↔ or ↑	↓	Negative linear relationship	Positively correlated		Mysterud et al. (2008)
The physiological hypothesis	↑	↓	No relationship	No relationship	Correlation with a physiological process	Miquelle (1990); Apollonio & Di Vittorio (2004)
The parasite hypothesis	↔	↓	No relationship	No relationship	Negative correlation between time spent foraging and parasite burden	Mysterud et al. (2008)
Observed outcome	↓	↔	Negatively correlated	Negatively correlated		

requires high energy expenditures (Yoccoz et al. 2002; McElligott et al. 2003), when they are not engaged in mating-related activities males are expected to allocate most of their available time to maximizing energy intake, i.e. to feeding. Given that rumination and food intake are equally important to ensure an optimal use of food resources, in species whose rumination mainly occurs while lying, the ratio of foraging to lying time (F/L) during the rut is supposed to be similar to the same ratio recorded outside the breeding season.

2. *Energy-saving hypothesis* (Willisch & Ingold 2007): During the breeding season, the males that are most involved in the rutting stop eating because efficient digestion is not possible with the limited time available for feeding. In this period, ruminant males might be unable to maintain the basic cyclic pattern of ingesting and ruminating food to ensure an efficient microbial fermentation in the foregut (van Soest 1994). Under these conditions, efficiency to assimilate energy would fall below the level necessary to meet basal energetic requirements. This would apply especially to those species whose mating periods occur when the forage quality is low. During the rut, the cost of foraging is potentially higher than the relative energy gain. Therefore, animals might choose to allocate most of their non-rutting time to lying rather than to foraging.

3. *Physical rest hypothesis* (Mysterud et al. 2008): Males need to rest their muscles to compete successfully for access to females. Thus, time for physical rest constrains the time for feeding. In fact, active time is rather devoted to rut-related activities and non-rutting time to recover from the consequent physical stress.

4. *Physiological hypothesis*: Hypophagia is a physiological process mediated through either a hormonal change, probably associated with annual cycle of photoperiod (McMillin et al. 1980; Simpson et al. 1984), or an effect of endogenous opiate antagonist (Plotka et al. 1985). Miquelle (1990) and Apollonio & Di Vittorio (2004) proposed an association between 'scent-urination' and hypophagia (*the scent-urination hypothesis* sensu Pelletier et al. 2009). They suggested that the physiological process inducing scent-urination may be the same that induces appetite suppression. Scent-urination, which is responsible for the pungent odour of adult males' urine during the rut and plays an important role in intra- and inter-sexual olfactory communication (Coblentz 1976), is also argued to increase reproductive success.

5. *Parasite hypothesis* (Mysterud et al. 2008): The males that are most involved in the rutting may avoid eating because they are less able to fight ingested parasites on account of their reduced immune system. This hypothesis assumes a trade-off between investing in immunity and investing in reproduction (Kyriazakis et al. 1998).

Several studies pointed out that the degree of forage reduction during the rut varies according to male age, with adult males foraging less than young males (Maher & Byers 1987; Miquelle 1990; Apollonio & Di Vittorio 2004; Mainguy & Côté 2008; Mysterud et al. 2008). Younger males have less chance of immediate reproduction when competing with larger adult males. Therefore, they might give priority to growth to increase their future chances of reproduction (Maher & Byers 1987; Miquelle 1990; Mysterud et al. 2003; Mainguy & Côté 2008) and might adopt less costly mating strategies, thus gaining at least some copulations (e.g. Hogg 1984; Willisch & Neuhaus 2009).

Alpine ibex (*Capra ibex*) is a polygynous alpine ungulate characterized by extreme sexual dimorphism (more than 100% in body mass – Loison et al. 1999) and a peculiar body growth. Females reach their maximum weight at the age of 4–5, whereas males show a slow and progressive increase of body mass until the age of 9–10. As a consequence, males present a remarkable dimorphism among different age classes (Bassano et al. 2003), and, for this reason, the ibex is an ideal case study for investigating behavioural differences between sexes and among male age classes. Alpine ibex is a capital breeder species (Toïgo et al. 2002). Its mating season occurs from late fall to early winter (it peaks around 20 Dec.), when food availability is low and movements more difficult because of snow cover (Parrini et al. 2003). Accordingly, it is particularly interesting to ascertain whether males show a rut-induced hypophagia or not, and to investigate the proximate mechanism accounting for it. Therefore, we analysed and compared the activity budgets of male and female ibex before, during, and after the breeding season (from Oct. to Feb.). To date, several authors have studied rut-induced hypophagia in male ungulates but neglected data from female ungulates. In contrast, we assessed the activity budgets of females to exclude that the reduction in feeding time was a consequence of environmental factors such as the scarce availability of forage. Finally, we assessed the predictions of the five main hypotheses on rut-induced hypophagia (reported in Table 1) in Alpine ibex.

Methods

Study Area

The study was conducted in the Valsavarenche Valley, within the Gran Paradiso National Park (GPNP; 45°35′N, 7°12′E; northwestern Italian Alps). The habitat used by ibex ranges from 1500 to 3300 m a.s.l., and is dominated by rock cliffs, slops, alpine meadows (*Carex curvula* and *Festuca* spp.), and conifer woods (*Picea abies, Larix decidua* and *Pinus cembra*); see Grignolio et al. (2007b) for more details. An automatic station recorded temperature (24 records/d) and precipitation data (Property of Meteorological Service of Aosta Valley Region). Temperatures from Oct. through Feb. ranged from a minimum of −18.7°C (26 Jan. 2005) to a maximum of 16.4°C (27 Oct. 2006). Considering daily minimum values, Jan. was the coldest month with −5.8 ± 0.26°C ($\bar{x} \pm$ SE) and Oct. the hottest with 2.4 ± 0.19°C. Snow usually first appeared in Nov. and melted away in spring. During the data collection performed over eight consecutive ibex mating seasons (from 1 Dec. to 15 Jan.), snow cover averaged 37.3 d (±5.4) out of the 46 d of the entire period.

Data Collection

The studied population was monitored from Dec. 2000 to Jan. 2008: during this period, activity budget data were collected on a sampled population of marked females and males that could be recognized by means of radio-collars and ear tags. The age of marked animals was accurately determined by counting the annual horn growth rings (*annuli*) at capture (Ratti & Habermehl 1977; von Hardenberg et al. 2004). More details about the capture and marking of ibex in GPNP can be found in Grignolio et al. (2007a).

Ibex were observed with binoculars and spotting scopes from such a distance (at least 200 m) that their behaviour would not be influenced by the presence of the observers. The main features of each animal (identity, sex, and age) were determined and recorded at the beginning of the observations. We uniformly distributed the observation times over the daylight hours. Animals' behaviour was observed using scan sampling at 2-min intervals, as described by Altmann (1974). When an animal was observed for <30 min, the observation was discarded.

Activity budgets included six behaviours: foraging, lying, moving, standing, social activity, and others. Foraging was defined as the animal standing or advancing slowly while grazing or browsing, with the head lowered below the shoulders. Lying was defined as the animal lying down; it typically included rumination. Moving was defined as a direct walk or run with the head above the shoulders. Standing was defined as the animal being still with the head above the shoulders and included all behaviours that could be performed while standing, e.g. vigilance. Social activity included interactions with individuals of the same sex and courtship of females. Others was defined as all the activities that could not be classified into any of the first five categories. In a limited number of short-distance observations, we could distinguish whether males ruminated or not. We considered activity budget data from Oct. to Feb., and grouped them into three periods: pre-rut period (from 15 Oct. to 30 Nov.), rut period (from 1 Dec. to 15 Jan.), and post-rut period (from 16 Jan. to 28 Feb.).

We used the male age classification proposed by Grignolio et al. (2007a), though slightly modified to gain a better understanding of the behaviour of adult males. Willisch & Neuhaus (2009) showed that <9-yr-old males were more likely to use a coursing strategy, whereas >9-yr-old males were more likely to use a tending strategy. Accordingly, we grouped males into three age classes as follows: <9, 9 to 11, and >11 yr-old males.

Given the rugged terrain and the necessity to keep far apart from the observed animals, ibex often moved out of the observers' visual angle. As a consequence, duration of the observations varied significantly and starting time could not be used as a variable in analyses assessing behavioural differences according to time of the day. Consequently, for the purpose of analysis, we preferred to divide the day into three parts (morning, midday, and afternoon) of equal length and varying according to each month. When more than 50% of the duration of the observation fell into the time span of one of these three parts of the day, the observation was assigned to that specific part.

Data Analysis

We used the statistical approach proposed by Pelletier et al. (2009) to obtain comparable results. For each individual, we assessed the overall proportion of the time spent performing each of the five main behaviours (foraging, lying, standing, moving, and social activities) in each period-year and used such proportions as sampling units. We did not analyse the data falling into the category 'others', because of the tiny proportion of time spent by animals in activities that fell into this category (0.8 ± 0.08%). The mean proportion of time spent performing each behaviour was arc-sin square-root transformed to approximate a normal distribution. Ibex identity was fitted as a random term to control for repeated measurements of the same individual (Pinheiro & Bates 2000) using a linear-mixed model (LMM). We compared the effect of biological period (pre-rut, rut, and post-rut) and sex–age class (female, <9, 9 to 11, and >11 yr-old male) on the time spent performing each behaviour. Biological period and sex–age class were thus fitted as categorical fixed effects. Given that the year of data collection could affect activity budgets, we included this variable too as a categorical fixed effect in the models. Finally, we tested whether ibex activity patterns differed according to the parts of the day (morning, midday, and afternoon) and eventually incorporated also this variable as a categorical fixed effect in the models. LMM pairwise comparisons with adjustment for multiple comparisons were performed to test the differences among biological periods, sex–age classes, and parts of the day.

We analysed the effects of year of observation, male age class, and biological period (as categorical fixed effects) on the variation of F/L by means of LMM. Also in this case, males' identity was fitted as a random term to control for repeated measurements. A constant ($k = 1$) was added to the proportions of time spent foraging and time spent lying to avoid a ratio of 0, when an individual was not observed to forage, and a division by 0, when an individual was not observed to rest.

To asses the relationship between time spent either foraging or lying and time spent rutting in males, we calculated the best curve estimation (logarithmic regression in both cases). We considered time spent rutting as the total amount of time spent in social activity, moving, and standing. Moving and standing were classified as male rutting activities because we considered them important behaviours to males that aimed to gain and ensure access to the females in estrus (Willisch & Ingold 2007; Pelletier et al. 2009). In these analyses, we considered individual mean values to avoid pseudo-replications.

Results

A total of 1045 (on 78 marked males) and 360 (on 21 marked females) hours of observations were collected. The proportion of time spent performing each activity was analysed by means of models that included sex, male age, period, year, and part of the day (Table 2).

The time spent foraging was not found to differ among years of data collection (LME: $F_{5,727} = 1.300$, $p = 0.262$). Females spent more time eating than males during all periods (LME pairwise-adjusted comparisons: $p < 0.001$ in all cases). Males older

Table 2: Linear models of the effects of sex–age classes (females vs. <9 yr-old males vs. 9 to 11 yr-old males vs. >11 yr-old males), biological periods (pre-rut vs. rut vs. post-rut), years of observation and parts of the day (morning vs. midday vs. afternoon) on five behaviours monitored in Alpine ibex in the Gran Paradiso National Park, Italy

Dependent variable	Variable	F-value	p-value
Foraging	Sex–age classes	15.449	<0.001
	Biological period	14.775	<0.001
	Year	1.300	0.262
	Part of the day	8.589	<0.001
Lying	Sex–age classes	5.793	0.001
	Biological period	10.200	<0.001
	Year	4.630	<0.001
	Part of the day	10.299	<0.001
Moving	Sex–age classes	1.524	0.207
	Biological period	39.741	<0.001
	Year	2.785	0.017
	Part of the day	6.025	0.003
Standing	Sex–age classes	3.444	0.016
	Biological period	37.041	<0.001
	Year	7.892	<0.001
	Part of the day	5.428	0.005
Social activities	Sex–age classes	3.170	0.024
	Biological period	16.558	<0.001
	Year	6.970	<0.001
	Part of the day	1.665	0.190

than 11 yr spent significantly less time feeding than other males (<9 yr-old males: $p = 0.12$; 9 to 11 yr-old males: $p = 0.002$; Fig. 1a). During the mating season, ibex ate less than during other periods (before rut: $p = 0.009$; after rut: $p < 0.001$). All males foraged less during the rut than before and after the rut, but never stopped eating completely (Fig 1a). On average, the proportion of time spent feeding decreased from the pre-rut to the rut by 36% (from 0.47 ± 0.08 to 0.30 ± 0.02) for >11 yr-old males, by 24% (from 0.51 ± 0.05 to 0.39 ± 0.02) for 9 to 11 yr-old males, and by 22% (from 0.47 ± 0.05 to 0.37 ± 0.02) for <9 yr-old males. In the post-rut period, the proportion of time spent feeding increased again to 0.48 ± 0.09, 0.69 ± 0.07, and 0.63 ± 0.05 for >11, 9 to 11, and <9 yr-old males, respectively. On the contrary, females showed a little but not significant increase in the proportion of time spent foraging through the three periods.

Ibex also spent less time lying during the rut than before and after the rut (before rut: $p < 0.001$; after rut: $p = 0.025$; Fig. 1b). The model showed significant differences in time spent lying between sexes and among age classes (LME: $F_{3,727} = 5.793$,

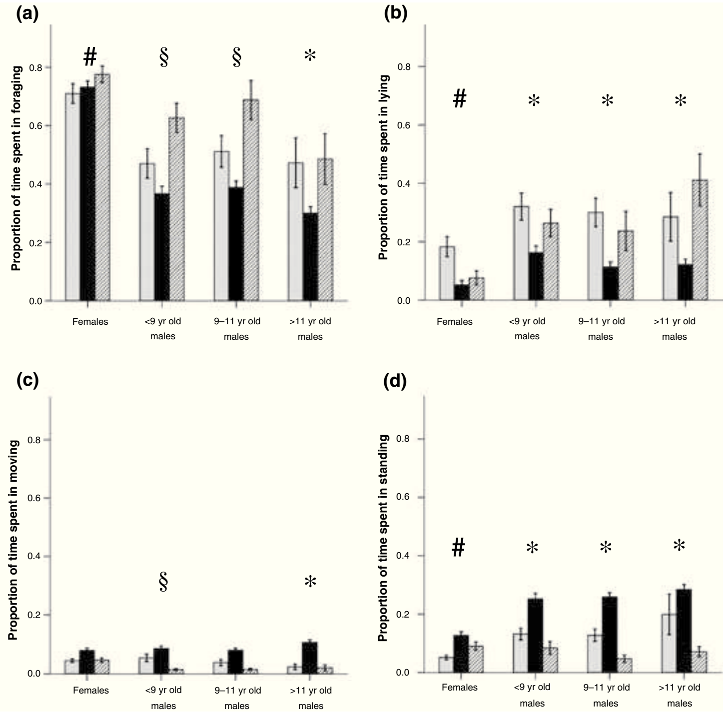

Fig. 1: Proportion of time spent foraging (a), lying (b), moving (c) and standing (d) during the pre-rut (grey bar), the rut (black bar) and the post-rut period (bar with oblique lines) by Alpine ibex in the Gran Paradiso National Park, Italy. Different symbols over the bars show statistically significant differences among sex–age classes.

p = 0.001), with females lying down less than all male classes (<9 and >11 yr-old males: $p < 0.001$; 9 to 11 yr-old males: p = 0.005). On average, the proportion of time spent lying from the pre-rut to the rut decreased from 0.30 ± 0.03 to 0.13 ± 0.01, and from 0.18 ± 0.03 to 0.05 ± 0.01, for males and females, respectively.

During the rut, both males and females spent more time moving, standing, and in social activities than during the pre-rut and post-rut periods (Table 2; Figs 1c–d and 2). Sex and age classes did not affect the time spent moving. In contrast, the model showed significant differences between females and males in time spent standing (<9 yr-old males: p = 0.023; 9 to 11 yr-old males: p = 0.014; >11 yr-old males: p = 0.001) but did not report significant differences among male age classes. Males obviously spent more time in social activities than females (<9 yr-old males: p = 0.013; 9 to 11 yr-old males: p = 0.007; >11 yr-old males: p = 0.002). No difference was found among male age classes in this respect.

All models showed that during the middle part of the day ibex were less active than during the rest of the day, foraged and moved less, and spent significantly more time lying than in the morning and in the afternoon. No significant difference was found among parts of the day as regards the time spent in social activities.

During 301 observation hours, we could record the ruminating time. Males averagely ruminated 45.74 ± 0.03% of their lying time. This ratio did not change among biological periods (ANOVA: $F_{2,116} = 0.234$, p = 0.792). Given this result, we chose to use lying time as a surrogate of ruminating time. In males the ratio F/L did not change among years of observation (LME: $F_{5,599} = 2.205$, p = 0.052) and biological periods (LME: $F_{2,599} = 1.534$, p = 0.217). During the rut, F/L was lower (1.38 ± 0.03) than before (1.45 ± 0.08), and after the rut (1.55 ± 0.09), but no significant statistical difference was found in either cases. Moreover, we did not find any significant difference among male age classes (LME: $F_{2,599} = 2.030$, p = 0.132).

Finally, the time spent foraging ($R^2 = 0.609$, $p < 0.001$; Fig. 3a) and lying ($R^2 = 0.510$, $p < 0.001$; Fig. 3b) by ibex males during the rut was negatively related to the time spent rutting (i.e. standing, moving, and engaged in social behaviours). During the breeding season, the non-rutting time was mainly used by males for feeding, averaging about 73% of it, whereas only about 25% was used for lying.

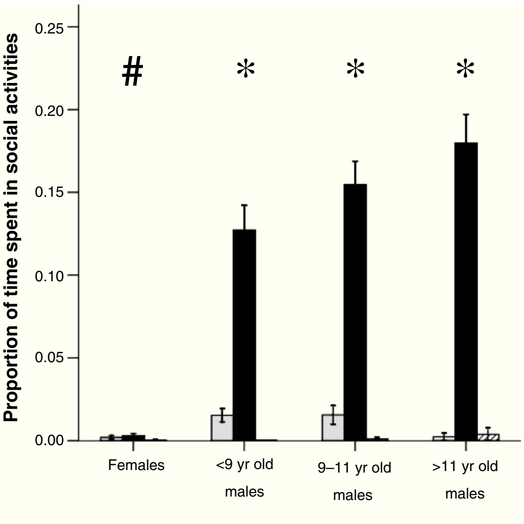

Fig. 2: Proportion of time spent in social activity during the pre-rut (grey bar), the rut (black bar) and the post-rut period (bar with oblique lines) by Alpine ibex in the Gran Paradiso National Park, Italy. Different symbols over the bars show statistically significant differences among sex–age classes. Please note that the *y*-axis scale differs from that in Fig. 1.

Discussion

Of the five hypotheses concerning rutting male ungulate hypophagia (Table 1), the foraging constraint hypothesis stands out as the only one whose predictions came all true.

Like in other ungulates, ibex activity budget varied greatly from the pre-rut to the post-rut period, as significant differences were found among periods for each of the behavioural categories taken into consideration. During the breeding season, ibex allocated more time to social activities, standing, and moving, while reduced the time spent feeding and lying. During the rut, the reduction in forage intake was sex- and age-dependent: while males decreased the time spent feeding, the time allocated by females to foraging did not vary before, during, and after the mating season. Males older than 11 yr substantially reduced food intake during the rut, with a decrease of 42% of the proportion of time devoted to feeding, while younger males reduced this activity to a smaller extent (22–24%). In our study, rut-induced hypophagia was also found in young male ibex, even though these generally adopted a less costly mating strategy (coursing) and were less likely to copulate (Willisch & Neuhaus 2009).

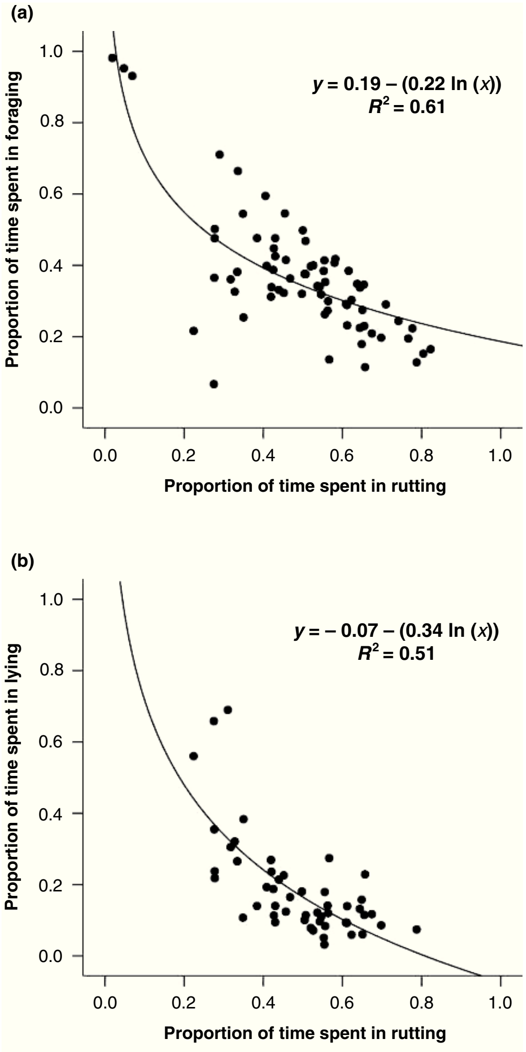

Fig. 3: Proportion of time spent foraging (a) or lying (b) in relation to time spent rutting in male Alpine ibex during the rut in the Gran Paradiso National Park, Italy. Line represents a logarithmic regression.

As females did not change their forage activity, rut-induced hypophagia in males cannot be explained by the environmental conditions that usually get worse during the breeding season (i.e. reduction of food availability due to snow cover and/or reduction of food quality). Accordingly, hypophagia seems to be somehow related to a need for males to ensure or improve their reproductive success.

Our data on ibex are similar to those recently reported in mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*, Pelletier et al. 2009), where daylight time budgets indicated that males tend to maximize energy intake when not actively engaged in mating activities. In fact, even though males reduced the time spent foraging, they still allocated the greatest part (average 73%) of their non-rutting time to feeding. Besides, when compared to other periods, during the rut males were reported to reduce the time spent lying. This decrease was comparable to the decrease of time allocated to foraging. This is further corroborated by a feeding-to-lying ratio approach: our analysis showed an unmodified F/L ratio before, during, and after the rut. Furthermore, during the rut the time spent foraging and the time spent lying were both negatively correlated to the time spent in rutting activities, thus confirming that a trade-off between reproduction and maintenance occurred at the expense of feeding and lying. All these results are consistent with the predictions of *the foraging constraint hypothesis*; in fact, only this hypothesis expects the F/L ratio not to change among biological periods (Table 1).

Our findings are in contrast with the predictions of both *the energy-saving hypothesis* and *the physical rest hypothesis*. These two hypotheses have been proposed to explain why, in some ungulates, rutting males apparently have much time for feeding but do not make use of it. Indeed, as recently shown in Alpine chamois (*Rupicapra rupicapra*), resting time is constant before, during, and after the rut. Therefore, rutting activities take place at the detriment of feeding time only (Willisch & Ingold 2007). *The energy-saving hypothesis* proposes that reduction in time spent foraging is an output of the digestive system: because of their diminished efficiency to assimilate energy, rutting males might yield a better energy balance by reducing the time spent feeding and thereby increasing the time spent resting. *The physical rest hypothesis* suggests that feeding time is constrained by the time devoted to muscle resting, which is necessary for males aiming to compete successfully for access to females. Both these hypotheses predict a reduction in foraging time, but not in lying time, during the rut, compared to both the pre-rut and post-rut periods, whereby the ratio of feeding to lying time would consequently decrease. These two hypotheses predict that most of the time spent in non-rutting activities is dedicated to lying. As our findings do not confirm almost any of the predictions of the last two hypotheses, both *the energy-saving hypothesis* and *the physical rest hypothesis* fail to explain this phenomenon in Alpine ibex.

Ultimately, male ibex hypophagia during the rut appeared to result not so much from strategies meant either to save energy or to get physical rest, as from time budget constraints generated by mating-related activities.

However, also other functional explanations entailing physiological processes might account for the reduction in foraging time observed in polygynous male ungulates during the rut. Hypophagia might be a by-product of changes related to other physiological processes and might amount to a cost that males have to pay to gain the benefits deriving from other physiological factors. For example, in moose (*Alces alces*) and fallow deer (*Dama dama*) hypophagia is temporally correlated and presumably physiologically tied to scent-urination (Miquelle 1990; Apollonio & Di Vittorio 2004). In these species, it seems likely that the costs of feeding suppression are offset for mature males that may take advantage of this scent so as to make themselves more attractive to females, and/or induce their ovulation (Miquelle 1991), and/or indicate age dominance and physical conditions to other males (Coblentz 1976). The typical odour and chemical composition of rutting males' urine might be explained by their hypophagic behaviour, as concentration of urinary compounds is correlated to the amount of food eaten (Whittle et al. 2000). Therefore, as Pelletier et al. (2009) suggested, *the scent-urination hypothesis* can explain the complete cessation of feeding during the rut in some ungulates, but does not provide a full understanding of hypophagia in those species, including Alpine ibex, in which males still forage during the rut (e.g. bighorn sheep and mountain goats – Pelletier 2005; Mainguy & Côté 2008). Lastly, but perhaps most importantly, if the reduction in forage intake was only a by-product of other physiological processes, such as hormonal changes or some gland activity (e.g. fallow deer – Kennaugh et al. 1977), no decrease in time spent lying should be expected. On the contrary, as observed in moose (Miquelle 1990) and fallow deer (Apollonio & Di Vittorio 2004), an increase in the proportion of time spent resting should be predicted. In contrast, in our study ibex were reported to reduce the proportion of time spent lying during the rut.

Another hypothesis proposed that hypophagia is a cost that males have to pay to minimize parasite infection risk: *the parasite hypothesis*. As Decristophoris et al. (2007) reported in the same population studied in this research, testosterone has an immunosuppressive effect. Following the results of Decristophoris's study, one might hypothesize that during the rut, when testosterone levels substantially increase (Pelletier et al. 2003; Mooring et al. 2004), hypophagia is a result of the reduced efficiency of the immune system of those males that are most involved in the rutting. The above-mentioned hypothesis, however, does not seem to account for ibex food intake reduction during the breeding season, as the level of testosterone in males peaks in the same period when parasite numbers are lowest in the environment (Lanfranchi et al. 1995; Zaffaroni et al. 2000).

The results of our analysis of activity budgets, as obtained through field observations, are in contrast with these two last hypotheses, but the data from physiological traits (e.g. testosterone levels) and parasite burden could help measure the contribution of physiological processes to generating males feeding reduction during the rut. In fact, different factors could concur to cause the rut-induced hypophagia observed in many ungulate species.

To the best of our knowledge, all studies on bovids showed that the reduction of time spent feeding is due to time constraints (*Bison bison* – Maher & Byers 1987; *Rupicapra rupicapra* – Willisch & Ingold 2007; *Ovis canadensis* and *Oreamnos americanus* – Pelletier et al. 2009; *Capra ibex* – this study). In contrast, three (*Odocoileus virginianus borealis* – McMillin et al. 1980; *Alces alces* – Miquelle 1990; *Dama dama* – Apollonio & Di Vittorio 2004) of the four studies (in addition to the above mentioned *Cervus elaphus* – Mysterud et al. 2008) on cervid species raised the possibility that appetite suppression may be a by-product of physiological processes. Further studies should therefore be encouraged so as to test whether rut-induced hypophagia is present in other ungulate species or not, considering that a variety of factors may account for it in bovids and cervids.

Drent & Daan (1980) defined capital breeders those species where storage represents the primary energy source for reproduction. Our findings suggest that to separate completely the phase of energy acquisition and that of investment in reproduction is not advantageous to Alpine ibex, even though males of this species seem to be capital breeders. In fact, during the breeding season male ibex still foraged from 30% to 39% (Fig. 1a) of their total amount of daylight time and never completely stopped feeding. This arguably indicates a more conservative reproductive strategy than those observed in other species (e.g. cervids – fallow deer and moose) and can be related to environmental conditions as well as to the mating strategy adopted. Specifically, this can be related to the fact that the rutting season occurs in late fall and early winter when the mountain environment is characterized by the low availability and quality of forage: in fact, under these conditions, males may not easily recover from energy expenditures and weight loss.

During courtship, ibex males can spend a considerable amount of time feeding, while guarding an oestrous female. As showed in another mountain ungulate (Pelletier 2005), in rugged terrains, it is often possible for a male to block all accesses to an oestrous female simply by positioning itself on a narrow cliff ledge, where it can spend time foraging. On the other hand, males that rut on a lek or defend a group of females may have to defend their territories continuously, and this could reduce the time available for feeding.

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Conclusion

The findings presented in this thesis suggest that individual differences in body size have important implications on different aspects of male Alpine ibex behaviour and, consequently, on individual life history and reproductive success. Several studies have paid attention to the direct effect of body size on reproductive success. My results showed that body size had also several indirect effects. In fact, to reach a large body size leads to advantages under different points of view, involving feeding, anti-predator and reproductive strategies.

Looking to the feeding behaviour, large body size means to be more efficient in digestion, thus to have the capability to tolerate a poorer quality of food (Demment and Van Soest 1985). This means to have the possibility to be less selective. Indeed, I found that during forage activity selective movements (step rate and rate of head lateral movements) significantly decreased as male age (and therefor size) increased (**chapter 1**).

Moreover, larger animals are less vulnerable to predation (Sinclair et al. 2003, Cohen et al. 1993), thus they can use behavioural patterns associated to higher risks. On one hand, they can be less vigilant during foraging. For example, Berger and Cunningham (1988) found that differences in predator scanning among females of four different ungulate species were positively related to their body size. I found that with increasing of male age, the frequency with which they scanned the environment during foraging activity decreased (**chapter 1**). Larger individuals have the possibility to feed in habitat of greater predation risk, characterised by higher quality and quantity of forage (Grignolio et al. 2007). This probably allows larger males to cope with the need of more abundant forage, associated to their higher absolute energy requirements (Demment and Van Soest 1985). However, it is important to note that with an increase of predation risk (as in the case of the return of the wolf in my study area), adult male ibex changed their behavioural patterns. They moved closer to safe areas (i.e. rock and steep slopes) at the expenses of a less rewarding food intake (**Chapter 2**). These results, in conjunction to what found by Grignolio et al.

(2007), show that under predation-risk constraints ibex were forced to forage in patches characterised by suboptimal food resources (Grignolio et al. 2007). This constrain could affect the life history and population dynamic of this species that, like other mountain ungulates, must accumulate enough fat during the growing season in order to reproduce and to survive the seasonal shortage of food during winter (Bruno and Lovari 1989). My results on male forage behaviour suggest that ibex have the behavioural flexibility to adjust their foraging decisions in response to changes in food quality, regardless of age and body size. This flexibility may help them to adjust their total energy intake during the growing season (**chapter 1**). When forage biomass is low, higher cropping rates could be a strategy used by male ibex to compensate the reduced bite sizes in lower biomass patches (Spalinger and Hobbs 1992). The tendency of ibex to increase forage selection in patches characterized by high nutritional values is possibly a mechanism to maximize their nutrients intake in a highly seasonal and forage-limited environment.

My findings on the male ibex rut-induced hypophagia (**chapter 4)** suggested that a further advantage related to large body size is that adult males, with more fat reserves, should have the possibility to reduce food intake during the rut to a greater extent with respect to young small-bodied males. I found that males older than 11 years substantially reduced food intake during the mating season (decrease of 42% of the proportion of time spent feeding), while younger males reduced this activity to a smaller extent (22-24%). Male ibex hypophagia during the rut appeared to be related to a need for males to ensure or improve their reproductive success. Indeed, the reduction of food intake in this species seemed to result from time budget constraints generated by mating-related activities. Consequently, adult large-bodied males had more time to invest in mating related activities and finally more chance to mate.

Finally, larger males have higher chance to win in intra-sexual competition for mate, thus gain a higher reproductive success. In my study (**chapter 3**) I found that old and full-grown males prevalently used tending, the mating tactic associated to higher reproductive success (Willisch et al. 2012). On contrary, younger and smaller males adopted an alternative less-successful tactic (coursing), because they cannot effectively defend the oestrous females during tending courtships. A further disadvantage for smaller and less-competitive males is that when environmental conditions become hard (i.e. high snow cover) coursing becomes a very high-cost tactic. I observed (**Chapter 3**) that during breeding seasons with deep snow cover the coursing tactic disappeared. The presence of deep snow made it difficult to run through rugged areas. Therefore, the costs of the coursing tactic were presumably too high and young males were forced to give up reproduction.

In conclusion, my findings showed that the evolution of large body in male ibex is likely to be favoured because it increases, directly and indirectly, their reproductive success.

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