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MOVEMENT ECOLOGY OF FEMALE ALPINE IBEX (*CAPRA IBEX*): INFLUENCE OF RESOURCES, CLIMATE, AND REPRODUCTIVE CONSTRAINTS

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ABSTRACT

There is now ample evidence of the ecological impacts of recent climate change on Alpine ecosystems. Animal populations, and in particular herbivores, can be affected directly, through modifications of the environmental temperature, and indirectly, through alteration of both distribution and phenology of plant communities. Understanding the behavioral strategies and tactics that populations and individuals use to buffer climatic variability and its impacts are particularly relevant in order to evaluate their vulnerability to climate change and develop incisive management and conservation actions. This dissertation investigates how females of Alpine ibex (Capra ibex) taken as a model for specialized Alpine large herbivore species, shape their behavior to deal with environmental and climatic variation and reproductive constraints during summer, a crucial period for the fitness of females of a capital breeder species. For this purpose, I used GPS locations and activity data of 22 females monitored in the Marmolada massif (northeastern Italian Alps) from 2010 to 2016. I tested for differences in space use and activity patterns of female ibex at different temporal scales (annual, intra-seasonal and hourly), in relation with changes in temperature, habitat type, and food resource availability -productivity (NDVI) and green up (ΔNDVI) of vegetation-. In addition, I evaluated anti-predator behavior contrasting the tactics of use of refuge areas and habitat types of females with different reproductive status. My findings showed how female ibex vary the use of space, habitat selection and rhythms of activity in a continuous trade off that allow them to fulfill different physiological needs in response to variation in environmental and climatic conditions, and under reproductive constraint. Female ibex responded to the altitudinal gradient in vegetation productivity with an altitudinal shift in spring and summer, to exploit the vegetation in earlier phenological stages. At the same time, females avoided thermal stress and maintained constant the daily foraging time through adjustments in circadian activity rhythms and altitudinal shifts. Moreover, during the reproductive period females with kids modified their movement patterns, feeding activity, and habitat use cope with increased energetic demands and the need of protecting kids with their limited locomotion capacity. My results have shown that the spatial behaviors that act at different scales were an effective strategy to optimize thermoregulation needs and forage acquisition while reducing predation risk. This thesis enriches knowledge on the influence of resources, climate, and reproductive constraints on behavioral strategies and tactics of female ibex. It represents the first attempt for this species, to my knowledge, to describe these behavioral responses as part of a complex trade-off mechanism, which occurs across different temporal scales, highlighting a presence of behavioral plasticity in female ibex. Such behavioral plasticity may allow them to buffer the environmental variations associated with current climate change.

RIASSUNTO

Risulta ormai evidente come il cambiamento climatico in atto stia avendo un forte impatto sull'ecosistema alpino. Le popolazioni animali, ed in particolare su gli erbivori possono essere influenzati direttamente, delle variazioni delle temperature ambientali, e indirettamente, dalle alterazioni nella distribuzione e nelle fasi fenologiche della vegetazione. La comprensione delle strategie comportamentali, utilizzate dagli animali per rispondere al cambiamento climatico è particolarmente rilevante per valutare la loro vulnerabilità a tali modifiche, permettendo così di sviluppare azioni di gestione e conservazione efficaci.

Questa tesi esamina come le femmine di stambecco *Capra ibex* (prese come specie modello specializzata all'ambiente alpino di alta quota) variano il loro comportamento spaziale e i ritmi di attività in risposta ai cambiamenti ambientali e climatici, nonché ai vincoli riproduttivi durante il periodo primaverile e estivo. Per raggiungere gli obiettivi della mia tesi, ho utilizzato le localizzazioni raccolte attraverso collari GPS e i dati di attività del sensore di movimento posizionato sui collari di 22 femmine monitorate dal 2010 al 2016 nel massiccio della Marmolada (Alpi nord-orientali). Ho analizzato le variazioni a diverse scale temporali (annuale, intra - stagionale e oraria) del comportamento spaziale e dei pattern di attività delle femmine di stambecco in relazione ai cambiamenti nella disponibilità delle risorse trofiche - produttività (NDVI) e green-up (ΔNDVI) della vegetazione -, della temperatura ambientale e all'uso dei diversi tipi di habitat. Inoltre, ho valutato il comportamento anti-predatorio confrontato l'uso delle aree di rifugio delle femmine a diverso stato riproduttivo. I risultati dimostrano come le femmine di stambecco abbiano variato l'uso dello spazio, della selezione degli habitat e dei ritmi di attività, in un meccanismo di trade-off, per soddisfare diverse esigenze fisiologiche in risposta alla variazione delle condizioni ambientali, climatiche e al loro stato riproduttivo. Durante la stagione primaverile e estiva le femmine di stambecco hanno risposto al gradiente altitudinale della produttività della vegetazione con uno spostamento verso le quote più alte, per sfruttare la vegetazione nei primi stadi fenologici. Allo stesso tempo, hanno evitato lo stress termico e hanno mantenuto costante l'attività di alimentazione regolando, a scala giornaliera, i ritmi di attività e gli spostamenti altitudinali.

Lo studio ha premesso di descrivere come la variazione circadiana e stagionale dell'uso dei diversi tipi di habitat rappresenti una strategia ottimale di uso dello spazio, minimizzando lo stress termico e massimizzando l'acquisizione delle risorse trofiche. Inoltre è stato messo in luce come, durante il periodo riproduttivo le femmine con il piccolo modifichino il loro comportamento spaziale e l'attività di alimentazione, variando altresì l'uso dell'habitat in risposta all'aumento delle esigenze energetiche e delle necessità di protezione dei piccoli, nonché la loro minore capacità di locomozione. I risultati hanno dimostrato come strategie comportamentali che agiscono a diverse scale rappresentano un modo efficace per ottimizzare le esigenze di termoregolazione, l'acquisizione di risorse alimentari e per ridurre il rischio di predazione.

Questa tesi arricchisce le conoscenze sull'influenza delle risorse trofiche, del clima e dei vincoli riproduttivi sulle strategie e tattiche comportamentali delle femmine di stambecco. Essa rappresenta il primo tentativo per questa specie, secondo le mie conoscenze, di descrivere queste risposte comportamentali come parte di un complesso trade-off che si verifica a diverse scale temporali, evidenziando una presenza di plasticità comportamentale nelle femmine di stambecco. Tale

plasticità comportamentale potrebbe consentire a questa specie di tamponare le variazioni ambientali associate agli attuali cambiamenti climatici.

CONTENTS

1. General Introduction

1.1. Background and State-of-the-art

Changes in space use and activity patterns of animals are behavioral responses to environmental and climatic spatio-temporal heterogeneity (Brockmann, 2001; Nathan *et al.*, 2008). These behaviors reflect the dynamic relation between internal states of animals (physiological state or biological cycle phase) and external factors (set of abiotic and biotic environmental factors, e.g., climatic parameters, and interaction with other species; see Nathan *et al.* 2008).

Climate change directly affects the growth and survival of individuals and, hence, population dynamics and distribution (Parmesan, 2006, 2007; IPCC, 2007). Consequently, researchers are endeavoring to develop robust ways to evaluate the vulnerability of organisms to climate change (Turner *et al.*, 2003; Williams *et al.*, 2008; IPCC, 2014; Wong & Candolin, 2015) and to develop management strategies tailored for vulnerable species and populations (Thomas *et al.*, 2004). In order to assess vulnerability of a population it is necessary to evaluate, in addition to the exposure to climate-related risk factors, the population'sensitivity to expected environmental changes and its potential to adapt to such changes (Turner *et al.*, 2003; Thuiller *et al.*, 2005; Williams *et al.*, 2008; Huey *et al.*, 2012). In the simplest form, sensitivity of individuals/populations to a set of environmental changes will be determined by intrinsic factors including physiological tolerance limits, life history traits, and genetic diversity (Williams *et al.*, 2008; Huey *et al.*, 2012), whereas adaptive capacity includes both rapid evolutionary changes (e.g., Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011) and plastic behavioral responses (Walther *et al.*, 2002; Slabbekoorn & Peet, 2003; Dowding *et al.*, 2010; Legagneux & Ducatez, 2013; Wong & Candolin, 2015). In general, behavioral plasticity allows individuals and populations to buffer the spatio-temporal heterogeneity of abiotic conditions (Thuiller *et al.*, 2005; Morin & Lechowicz, 2008; Araújo *et al.*, 2011), but specialist species (with restricted fundamental niche, Hutchinson, 1957) are likely to be particularly vulnerable to changes with respect to generalist species that rely on broader tolerance limits (Thuiller *et al.*, 2005).

Behavioral responses of animals to variation of environmental and climatic factors affect their fitness, and hence these behavioral phenotypes are subject to natural selection (Sih, Ferrari & Harris, 2011). From a conservation point of view, the spectrum of behavioral responses contributes to the capacity of animal species to buffer environmental perturbations and especially climate change (Williams *et al.*, 2008; Huey *et al.*, 2012). In long-lived species, behavioral plasticity is likely to be more important than evolutionary potential in order to minimize impacts in the short term. This is because climatic changes are too fast to allow an adaptive evolutionary response that involves multiple generations, whereas plasticity acts within a generation, at the individual or population level. Movement and foraging activity, in particular, are primary behavioral adaptation by which individuals cope with spatio-temporal heterogeneity of resources and limiting factors (Sih & Gleeson, 1995; Nathan *et al.*, 2008).

This dissertation is framed within this theoretical and applied framework, with the purpose of improving understanding of how changes in climatic and environmental condition might affect the ability of specialized mountain ungulate species to persist in the Alpine environment. The choice of studying behavioral adaptations, and in particular the movement ecology, of mountain ungulates is based on their peculiar ecological and life-history traits, that make them potentially more vulnerable to climate change than other less specialized groups (Walther *et al.*, 2002; Weladji *et al.*, 2002; Rivrud *et al.*, 2010; Mason *et al.*, 2014). Mountain ungulates have developed specific physiological mechanisms (Heldmaier *et al.*, 2004; Arnold *et al.*, 2006) and behavioral tactics (Nicholson *et al.*, 1997; Arnold *et al.*, 2006; Rice, 2008; Aublet *et al.*, 2009; Mason *et al.*, 2014) to cope with climatic constraints and extreme seasonality of resources availability. Many mountain ungulates exhibit seasonal movements, that generally consists of upward altitudinal shifts in summer to enhance access to high quality food, while trading off for predation risk (Festa-Bianchet, 1988; Hebblewhite & Merrill, 2009; Bischof *et al.*, 2012) and thermoregulation needs (Aublet *et al.*, 2009; Mason *et al.*, 2017). Climate change can have a strong impact on Alpine habitats, in particular, altering distribution and succession of plant communities structure, composition, and phenological stages (Parolo & Rossi, 2008; Rammig *et al.*, 2010; Ernakovich *et al.*, 2014). As primary consumers, large herbivores are particularly sensitive to variations in vegetation distribution, and they are expected to be among the first to respond to changes on plant communities because of global warming (Post & Stenseth, 1999; Pettorelli *et al.*, 2007). Climate change may thus act indirectly on individual condition through its effect on the distribution and phenology of plants. Increases in late winter-spring temperatures may favor early plant growth and potentially increase the length of the growing season (Ernakovich *et al.*, 2014). Nevertheless, in alpine regions, photoperiod limits plant productivity and the extent to which the growing season can lengthen, thus reducing the advantage of early snowmelt (Keller & Körner, 2003; Ernakovich *et al.*, 2014) and possibly causing an earlier plant senescence (Ernakovich *et al.*, 2014). These changes might reduce the period of access to high-quality forage by mountain ungulates, and especially create a mismatch between the peak of resource demands by reproducing herbivores and the peak of resource availability (Post & Forchhammer, 2008; Plard *et al.*, 2014). This mismatch might have profound effects on the energy balance during late pregnancy and lactation, with consequences on growth, body mass, and survival of kids (Pettorelli *et al.*, 2007; Rughetti & Festa-Bianchet, 2012; Tveraa *et al.*, 2013).

Moreover, climate change can affect mountain ungulate species directly, because in many cases they are heat sensitive (Renecker & Hudson, 1986; Aublet *et al.*, 2009; Signer *et al.*, 2011; Mason *et al.*, 2014, 2017). To buffer environmental temperature fluctuations, animals use a range of thermoregulatory behaviors to keep within tolerated thermal margins and avoid for example heat stress (Signer *et al.*, 2011). These adaptive behaviors include adjustment of activity patterns (Aublet *et al.*, 2009; Bourgoin *et al.*, 2011) and selection of habitats providing thermal cover (Bowyer &

Kie, 2009; van Beest *et al.*, 2012). Indeed, mountain ungulates move in altitude not only to follow the gradient of food resource availability but also to take advantage of decreasing isotherms. For example, high altitude areas in summer can be functionally compared to cover habitats for protection from heat stress in chamois (Mason *et al.*, 2014) and Alpine ibex (Aublet *et al.*, 2009).

Therefore, mountain ungulates developed behavioral strategies (for example, movement), that likely trade-off resource acquisition, and thermoregulation (e.g., Boyles *et al.*, 2011; van Beest *et al.*, 2012). Although endotherms are able to maintain a relatively constant body temperature, independently of ambient temperature, the energetic cost increases dramatically when an individual is outside its thermoneutral zone (Boyles *et al.*, 2011). Furthermore, food intake is often inversely related to high environmental temperatures (Renecker & Hudson, 1986). The effects on energy budgets and body condition of a reduced feed intake might affect also reproduction and survival of individuals, which directly correlate with the body mass acquired during summer (Cameron *et al.*, 1993; Testa & Adams, 1998; Lenart *et al.*, 2002; Bender *et al.*, 2008).

The behavioral trade-off to buffer variation in temperature and resource availability may also be influenced by predator avoidance (Hebblewhite & Merrill, 2009). Predators may affect spatial use of preys, frequently leading them to use suboptimal habitats (e.g., Fortin *et al.*, 2005). For instance, moose and reindeer with calves, i.e. more exposed to predation, may be deterred from migrating to areas with the best forage conditions in case of high predation risk (Edwards, 1983; Bergerud *et al.*, 1984). Many European Alpine ungulate populations have been living in the absence of large mammal predators for a long time, since wolves (*Canis lupus*), brown bears (*Ursus arctos*) and lynx (*Lynx lynx*) were locally extirpated during the 19th century (Chapron *et al.*, 2014). The present recolonization process of Alpine areas by large carnivores (Chapron *et al.*, 2014) may therefore introduce a further element in the thermoregulation-food acquisition trade-off.

This dissertation specifically aims to address the resource acquisition tactics of female Alpine ibex (*Capra ibex*) in response to the variation of resource availability, predation risk perception, and heat stress compensation needs during summer. I chose the Alpine ibex as a model for specialized large herbivore species living in high mountain habitats. The Alpine ibex is a highly sexually dimorphic species of the Caprinae subfamily adapted to extreme environmental conditions, with a distribution range that typically encompasses altitudes between 1600 and 3200 m a.s.l. (Pedrotti *et al.*, 2009). Hence, this species faces the most extreme environmental conditions of all European Alpine ungulates (Pedrotti *et al.*, 2009). By setting specific thermoregulatory physiological and behavioral tactics, individuals are able to survive through long, cold and snowy winters and exploit the spring steep temperature rise (Signer *et al.*, 2011). A very low metabolic rate in winter is followed by intense resource acquisition and activity in spring and summer (Signer *et al.*, 2011). The species is a capital breeder, i.e. individuals accumulate body fat throughout spring and summer to face the mating season at the beginning of the winter, as well as to overwinter (Toïgo *et al.*, 2002; Signer *et al.*, 2011). After winter, females have only a short period to regain body reserves before engaging into parturition and have then to meet enhanced nutritional requirements due to lactation and kids raising (Toïgo *et al.*, 2006). This condition makes them very sensitive to modifications of vegetation distribution and phenology caused by climate change.

It is also important to emphasize the relevance of studying an ibex population in the Eastern Alps. Indeed, most of the knowledge available on this species derives from the population in the Gran Paradiso National Park-Western Alps. The Western\Central Alps markedly differ in topography and vegetation composition from the Eastern Alps, in which this study has been developed, specifically in the Marmolada-Monzoni massif groups. The Dolomitic substrate of this massifs results in a dramatic topography, with extensive steep rock and scree areas and limited high-altitude grasslands, with important effects on forage and cover-habitats distribution.

Moreover, the study of ibex behavioral adaptations is important for planning conservation actions for the species. Although Alpine ibex is no longer considered a species at risk of extinction (it is classified as “least concern” by IUCN; Aulagnier *et al.*, 2008), its highly fragmented distribution (Dupré *et al.*, 2001) and the low genetic variability (Grossen *et al.*), as well as its importance as a flagship species for many Alpine areas, require conservation and management actions based on solid knowledge (EEA, 2015).

1.2. Objectives and outline, with summary of chapters

My PhD project investigates the movement ecology of female Alpine ibex (*Capra ibex*), in the colony of the Marmolada massif (see below for details on the colony), in particular focusing on movement and activity patterns of female ibex in response to resource availability, temperature and predation risk, in summer. I chose to focus the analysis mainly on the reproductive period, that is highly demanding for females of a capital breeder species because of the high energy costs associated with pregnancy and lactation and the need of kid protection (e.g., Loudon, 1985; Ciuti *et al.*, 2006; Hamel *et al.*, 2010). In addition, the study was designed to highlight how different behavioral tactics occur at different temporal scales, implementing the analyses at the annual, intra-season and daily scales. This has been possible thanks to the use of GPS collars and activity sensor that collected data at high spatial and temporal resolutions (for details see Chapter 2). This is the first study, to my knowledge, that uses high-temporal resolution movement and activity data to study the behavioral adaptations of female Alpine ibex.

I structured my dissertation into four main sections. After a brief overview of the Alpine ibex biology, the characteristics of the study area and population (Chapter 1), and of the datasets used and their management (Chapter 2), I explore how variation of resource availability and temperature (Chapter 3), and reproductive constraints (Chapter 4) affect movement behavior, habitat use and activity levels (Chapter 3, Chapter 5; see below for summaries of chapters).

To reach the aim of my dissertation, I used GPS and activity data of 22 radio-collared females from 2010 to 2016 monitored in Marmolada massif, within the project "*Movement ecology of Female Alpine ibex*" coordinated by Prof. Maurizio Ramanzin (Department of Agronomy Food Natural resources Animal Environment, Padova University), and since 2014 in collaboration with Dr Francesca Cagnacci (Biodiversity and Molecular Ecology Department, Research and Innovation Centre, Fondazione Edmund Mach).

Summer movement and activity patterns in female Alpine ibex: a case for temperature stress compensation? (Chapter 3)

Many mountain ungulates exhibit seasonal movements, that generally consists of altitudinal shifts to enhance access to high-quality food while trading off for predation risk (Festa-Bianchet, 1988; Hebblewhite & Merrill, 2009). The forage-maturation hypothesis (Hebblewhite *et al.*, 2008; Bischof *et al.*, 2012) states that during the vegetation season herbivores migrate along a phenological gradient of plant growth in order to maximize energy intake. Ungulates optimize forage acquisition also by adjusting feeding behavior, i.e. time spent feeding (Bergman *et al.*, 2001).

In mountain ungulates, the temperature gradient is a major limiting factor for food resource acquisition tactics (Grignolio *et al.*, 2004; Aublet *et al.*, 2009; Signer *et al.*, 2011), since feeding activity is depressed at high temperatures (Dussault *et al.*, 2004). In turn, habitats offering optimal thermal-cover and high-quality food may not coincide, hence thermal shelter-food trade-offs are common in ungulates, either by selecting habitats (Mysterud & Østbye, 1999; Dussault *et al.*, 2005; Hebblewhite & Merrill, 2009; van Beest *et al.*, 2012), or by adjusting activity budgets to maximize energy intake (Aublet *et al.*, 2009; Bourgoin *et al.*, 2011).

The aim of this chapter is to study the behavioral tactics adopted by female ibex to cope with strong daily and seasonal variation in temperature and resource availability in the Alpine environment. For this purpose, I investigated the behavioral responses of 21 female Alpine ibex to the variation of resource availability and temperature fluctuations at different spatio-temporal scales (annual/seasonal, daily/hourly) by means of high-frequency GPS locations and accelerometer data throughout the year and the 24 hours cycle. The results showed how female ibex adopted a complex behavior that acts at different scales to respond both to thermal constraint and forage availability. At the annual scale, they exhibited strong seasonal patterns of activity (which I used as a proxy for foraging behavior, see Chapter 3), and altitude use, in relation to vegetation productivity and temperature. They increased activity and performed altitudinal migration in spring and summer to exploit the vegetation in earlier phenological stages. At the daily scale, in the spring-summer period, female ibex reacted to thermal stress by reducing activity and shifting to higher altitude areas, that functioned as thermal-cover. This behavior was not fixed, but plastic in relation with daily mean temperature and was paralleled by adjusted activity rhythms to compensate for foraging time during cooler hours when thermoregulation costs were lower. In this way, the females were able to keep the total daily foraging time constant across a wide range of temperatures (-6.9/+17.7 °C). Moreover, they showed a daily pattern of the relative probability of use of habitat types in relation to daily altitudinal shifts. This pattern of use seems to be a space use tactic to maximize thermal cover and resource acquisition, selecting forage habitats during the daily movement periods to and from higher elevations. To my knowledge, this study is the first example demonstrating how seasonal and daily altitudinal migrations combine with adjustments in feeding activity in response to food acquisition and exposure to thermal stress, laying the basis to assess the potential of this species to adapt to the conditions of climate change scenarios.

Better safe than sorry: anti-predatory response of ibex reproductive females under multiple environmental and life-history constraints (Chapter 4)

In ungulates, predation risk often forces prey to trade-off safety for other ecological needs, as forage and thermal-cover (Hebblewhite & Merrill, 2009). Ungulates may be able to adjust their behavioral tactics within or between spatial and temporal scales to avoid predation while gaining access to forage (Hebblewhite & Merrill, 2009). Anti-predator behaviors should be more pronounced in individuals more exposed to predation (“predation risk hypothesis” (Main & Coblentz, 1996), as females with dependent offspring. In particular, reproducing females should adopt anti-predator tactics more than non-reproducing females, because of the higher vulnerability of kids, and the fitness cost due to offspring loss. Reproductive females are also constrained by other factors than predation risk, such as increased energy demand due to lactation (Loudon, 1985), and limited mobility of offspring, in case of 'followers' species (Ralls *et al.*, 1986; Grignolio *et al.*, 2004; Ramanzin *et al.* unpublished data). Hence, behavioral tactics of reproductive females will have to respond to environmental factors common to all individuals, as forage availability and climatic constraints, as well as to specific needs linked to reproduction.

In this chapter, I studied the occurrence of anti-predatory response on female ibex with different reproductive status in presence of steep environmental and climatic gradients, at different temporal scales. Specifically, I contrasted the movement behavior of 11 lactating and 11 non-lactating females, monitored from 2010 to 2016, during different periods of the reproductive cycle and between daytime and nighttime. To consider the main environmental constraints (temperature and food resource) to which females have to respond I used altitude use as a proxy, because of the strong altitudinal gradients in temperature and food availability of the study area and the Alpine environment in general. To assess the occurrence of anti-predator behavior I estimated the use of refuge areas, defined as steep rocky patches.

Even though ibex is a gregarious species, my results showed a more pronounce antipredator behavior in lactating female than in non-lactating females. The probability to be inside or closer to refuge areas peaked in the period immediately after birth, with higher absolute values for lactating than for non-lactating females starting from this period and continuing through summer.

Instead, no difference in daily patterns of use of refuge areas was found between lactating and non-lactating females. All female ibex had a higher probability to be inside and closer to refuge areas during daytime than during nighttime. Lactating and non-lactating females shifted away from refuge areas at night in a similar proportion, so that the relative distance from refuge was maintained constant. The results also confirmed that female ibex performed seasonal altitudinal shifts (annual altitudinal shift: Chapter 3; Parrini *et al.*, 2003; Mason *et al.*, 2017), as well as daily movements between different altitudes (daily altitudinal shift: Chapter 3; Aublet *et al.*, 2009), with a peak of altitudes in early lactation, and higher altitudes used during daylight. Interestingly, however, I found that the daily altitudinal shift after births was different in relation with the reproductive status, with the lactating females shifting less, and therefore keeping at higher altitudes than non-lactating ones, at night. This can be explained as a response to specific requirements of their kids, such as less efficient locomotion capacities while accounting for thermoregulation and forage availability. In other words, lactating females used a range of altitudes that contemporarily allowed to reach refuge and forage areas, while compensating for thermoregulation needs and kids specific needs. The marked difference in movement behavior between lactating and non-lactating females is also an evidence of individual behavioral plasticity in dependence on life-history traits.

Feed first, forage later: spatio-temporal tactics for habitat use under life-history constraints in female Alpine ibex (Chapter 5)

Ungulates adopt behavioral tactics to trade-off access to forage against other constraints, forcing them, in some cases, to use sub-optimal habitat types. A common tactic in ungulate species is to move among different habitats in order to maximize access to forage resources while minimizing the limiting conditions imposed by climate variation and predation risk (Hebblewhite & Merrill, 2009). The costs and benefits deriving from the limiting or favorable conditions associated with different habitats vary not only in relation to temporal variability of climatic and environmental factors but also in interaction with life-history traits, as reproductive status or age. For example, newborns are more sensitive to predation and less able to move than adults, while the mothers' energetic demands increase because of lactation. Therefore, habitats used by reproductive females reflect a trade-off between the total fitness costs and benefits associated with different habitats, i.e. including kids' survival and growth (Ciuti *et al.*, 2006; Dussault *et al.*, 2005). For a better understanding of this trade-off, it is important to contrast the quality of habitats, e.g., in terms of forage productivity, with their functional role, i.e. which main function a habitat plays for an individual according to its life history.

The purpose of this study was to evaluate the functional role of different habitat types for lactating *vs* non-lactating females, by analyzing the use of different habitats in relation with activity (as a proxy for foraging, see Chapter 3) patterns. I evaluated in particular whether lactating females 1) used sub-optimal forage habitat types with respect to non-lactating females under reproductive constraints (e.g., risk of predation; kids' reduced locomotion capacity); 2) compensated the use of these sub-optimal habitats by more intense foraging. I, therefore, analyzed habitat use and activity patterns of 11 lactating and 11 non-lactating females, monitored throughout the reproductive phases, and the 24 hours cycle, from 2010 to 2016.

The analysis of habitat use and foraging activity showed that female ibex were mainly inactive in "rock", which they used increasingly with increasing slope, confirming the function of refuge of this habitat (Chapter 4), while feeding activity was concentrated in "grassland" and "grassland mixed with rock" habitats. However, use of these habitats differed according to reproductive status, with lactating females using "grassland" less, and "grassland mixed with rock" more, than non-lactating females, especially at gentler slopes. Moreover, my results highlighted that "scree" habitats, although poor in vegetation, were also used as feeding areas especially by lactating females during lactation. This role of screes is in contrast with that found in other studies conducted in the western Alps where screes were much less extensive (e.g., Villaret & Bon, 1995; Grignolio *et al.*, 2007). Arguably, the use of "scree" and "grassland mixed with rock" by lactating females may be a compromise between foraging and protection needs, since these habitats are closer to refuge areas than "grassland". Indeed, lactating females kept constantly closer to refuge areas than non-lactating females (see Chapter 4), that instead mainly use grassland as a forage habitat. Finally, my results confirm that "forest" is a habitat with a marginal importance for female Alpine ibex during summer.

Furthermore, my results demonstrated that activity patterns varied across reproductive phases, but that this variation was mediated by the habitat used. In relation with the kid limitation hypothesis, reproducing females showed a lower activity than non-reproducing females especially during birth and, less, during lactation, but only when they were in steep rock. This might be related to the mobility of kids, which is presumably limited especially in this usually steep habitat and might also allow females to reduce energy expenditure. Conversely, lactating females maintained activity levels similar to those of non-reproducing females in all periods in forage-rich habitats, and higher activity levels in scree during lactation. In addition, circadian patterns of activity showed that reproducing females were more active than non-reproducing females during the mid-day resting period, presumably because they foraged more and rested less in a period where surveillance of kids was easier.

In conclusion, my results supported life-history mediated individual plasticity, where lactating females adjusted habitat use and activity to respond to the multiple constraints imposed by reproduction, and specifically to access forage resources while trading for protection and limited movement ability of kids. However, in order to fully understand whether or not an investment on kid protection implied the use of possibly sub-optimal habitats with consequential potential negative cumulative effect on energy intake, data on the biomass and quality of vegetation of the different habitats should be acquired. Furthermore, lactating females could have adopted other behavioral tactics, like increasing bite rate during feeding, to increase food intake, and/or rumination time and chewing time, to increase digestion efficiency, which I did not address here.

1.3. **Alpine ibex**

1.3.1. Systematic, history and current status of conservation

The genus Capra belongs to the family Bovidae and to the subfamily Caprinae, including several forms of wild goats present in mountain habitats of Europe, Asia and North Africa, and a cosmopolitan domestic form. The systematics of this genus is very controversial. According to the classification of Schaller (1977) and Shackleton (1997) I can distinguish five different subspecies of *Capra ibex*: Alpine ibex (*C.ibex ibex*), Siberian ibex (*C.i. sibirica*), Nubian ibex (*C.i. nubiana*), Walia ibex (*C.i. walie*) and West Caucasian tur (*C.i. caucasica*). Alpine ibex was present in Italy during the Pleistocene, and reached its maximum expansion during the Wurm glaciation when occurring throughout the Alps and the Apennines (for a review, Tosi & Pedrotti, 2003). At the end of the last glacial stage, Alpine ibex was confined to all the Alps. During the 16th-19th century, over-hunting progressively reduced the Alpine ibex population to few hundred individuals, which survived in the north-western Italian Alps, in the Gran Paradiso area. At the beginning of the XIX century, the Alpine ibex was on the verge of extinction. In 1821, the king of Savoy proclaimed the first banning of hunting for ibex. In 1856, King Vittorio Emanuele II reserved the exclusive hunting rights of Alpine ibex for himself, establishing a Royal preserve. Owing to the strict control of poaching from that time on, the population of Alpine ibex in the Gran Paradiso area recovered rapidly even with royal hunting continuing. In 1922, the preserve was transformed into a protected area, the Gran Paradiso National Park (GPNP). Since the beginning of the twentieth century, reintroduction actions have rebuilt colonies of the species throughout all the Alps, mostly using as source of translocated individuals the GPNP colony. Currently, the Alpine ibex occur in Austria, France, Germany, Italy, and Switzerland. It has also been introduced in Slovenia and Bulgaria (Tosi & Pedrotti, 2003). The total Alpine population's size has been growing ever since the sixties of the last century (with a growth rate between 3% and 6%) and is estimated at more than 47,000 heads, distributed into about 150-160 separate colonies (Raganella Pelliccioni *et al.*, 2013). In Italy, there are 63 colonies (about 15,600 individuals - data for the 2010-2012 period) (Raganella Pelliccioni *et al.*, 2013). Based on the wide distribution, large population size, and favorable trend in the last decades, the species is now considered as not threatened ("Least Concern" by IUCN), (Aulagnier *et al.*, 2008). However, it needs conservation action to prevent future decline.

Hunting of Alpine ibex is allowed in Switzerland, Austria, and Slovenia, while in Italy the National law (157/92) does not allow it. Although hunting did not prevent the numerical increase of the populations, there is concern for its potential evolutionary consequences (Festa-Bianchet, 2017). In addition, conservation problems for the Alpine ibex arise mainly from the low genetic variability and fragmented distribution, especially in the Eastern Alps, where the range is still far from reflecting the potentialities expressed by the Alpine Arc (Boitani *et al.*, 2002). The risks of small populations constitute a critical issue for their conservation since environmental, demographic or genetic stochasticity may increase the probability of extinction (Soulé, 1985). Genetic variability in ibex populations is among the lowest reported from microsatellites in mammal species (Maudet *et al.*, 2002), and all the reintroduced populations, because of inbreeding, genetic drift, bottleneck and founder events, have lower genetic diversity than the founder populations (Grossen *et al.*; Randi *et al.*, 1990; Biebach & Keller, 2009), with possible consequence on the long-term evolutionary potential. An additional risk factor for ibex is the development of epizootics, linked to the small size of the colonies. In the 2000s, a parasitic infection by the scabies mite (*Sarcoptes scabiei*) led to a steep decline in some isolated populations in the Eastern Italian Alps, such as the colony of the Marmolada massif (Rossi *et al.*, 2006). High densities of domestic goats and sheep may also have a negative impact on the ibex through parasite and disease transmission (Guberti *et al.*, 2014); Hybridization can be a threat where populations are small and sympatric with high densities of domestic goats, as is the case in Italy (Randi *et al.*, 1990). Finally, changes in alpine ecosystems, caused by climate change, can have a major impact on ibex populations. The global warming has an indirect impact on dynamic of population, altering habitats and the vegetation successions, and a direct impact on thermoregulation capacity of individuals (see Chapter 4).

1.3.2. Alpine ibex is a mountain ungulate

Alpine ibex is an ungulate species with physiological and behavioral characteristics that make them adapted to live in extreme Alpine, high-elevation environments (Loison *et al.*, 2003). In such environments, the pronounced topographic gradients and extreme changes in climatic conditions and food availability require morphological adjustments (Lovegrove, 2005). Relatively short and solid legs, a compact body shape, a dark and well-insulating winter fur, the shape of hoof as well as high haematocrit are the main adaptations in Alpine ibex to high mountain environments (Tosi & Pedrotti, 2003; Signer *et al.*, 2011).

Morphological and behavioral adaptations allow ibex to cope with strong seasonality and variation in food availability. Based on the ruminant digestive system morpho-physiology and feeding behavior, the Alpine ibex has been classified as an intermediate feeder, close to grazers (Hofmann, 1989). The diet of this species is mostly composed of herbaceous species, with conifers and shrubs being present in small proportions especially during winter and transition seasons, but is almost absent in summer (Trutmann, 2009; Zingg, 2009). As an intermediate ruminant feeder, ibex can increase food intake two or three-fold when food is plentiful to meet peaks of nutrient requirements corresponding to changes in metabolism (Ostrowski *et al.*, 2006; Signer *et al.*, 2011). Moreover, as capital breeders (Toïgo *et al.*, 2002) the reproduction is financed using stored capital. Female ibex accumulate body fat mainly in spring before birth to face reproduction period, when daily energy costs are highest. For male ibex, seasonal energy requirements are typically highest during the breeding period when animals are most active. A first avenue of seasonal acclimatization that is employed by large mammals is a voluntary reduction of food intake and body size towards winter, which results in reduced overall energy expenditure (Worden & Pekins, 1995; Mesteig *et* *al.*, 2000). Secondly, endotherms may adjust to conditions of cold and scarcity of food by lowering the body temperature set-point (Signer *et al.*, 2011).

Ibex is a gregarious species, with a strong sexual segregation (Villaret *et al.*, 1997; Bon *et al.*, 2001; Ruckstuhl & Neuhaus, 2002; Tosi & Pedrotti, 2003) and a great sexual dimorphism (male/female body weight ratio close to 2; Loison *et al.*, 1999). Adult males and female groups segregate until the reproductive season in winter (from December to January) (Tosi & Pedrotti, 2003). Female groups are composed of adult females, kids of the year and young individuals of both sexes (Tosi & Pedrotti, 2003). Births occur mainly in June, the kids following their mother soon after birth (Tosi & Pedrotti, 2003). The follower strategy is characterized by the use of open habitats, the larger size of the groups of animals, and the use of collective antipredator strategies (i.e., vigilance(Toïgo, 1999) as occurs in Alpine ibex.

1.3.3. The Marmolada colony

The colony was founded from 1978 to 1979, with a translocation, operated by the Autonomous Province of Trento, of 5 females and 5 males from the Gran Paradiso National Park to the Marmolada-Monzoni massif group, in the Eastern Italian Alps (Dolomites - 46°26’ 13” N, 11°51’ 54” E) (Figure 1-1). The size of the colony has been monitored since foundation with the ground counts method, that is capable of detecting Alpine ibex population trend (Largo *et al.*, 2008). Until 2002 the population size increased steadily to more than 450 individuals, with an estimated growth rate (λ) of 1.24, close to the maximum rate of increase for the species (Loison *et al.*, 2002). In 2003, the Marmolada colony was, therefore, one of the biggest of the eastern Italian Alps (Monaco *et al.*, 2004).

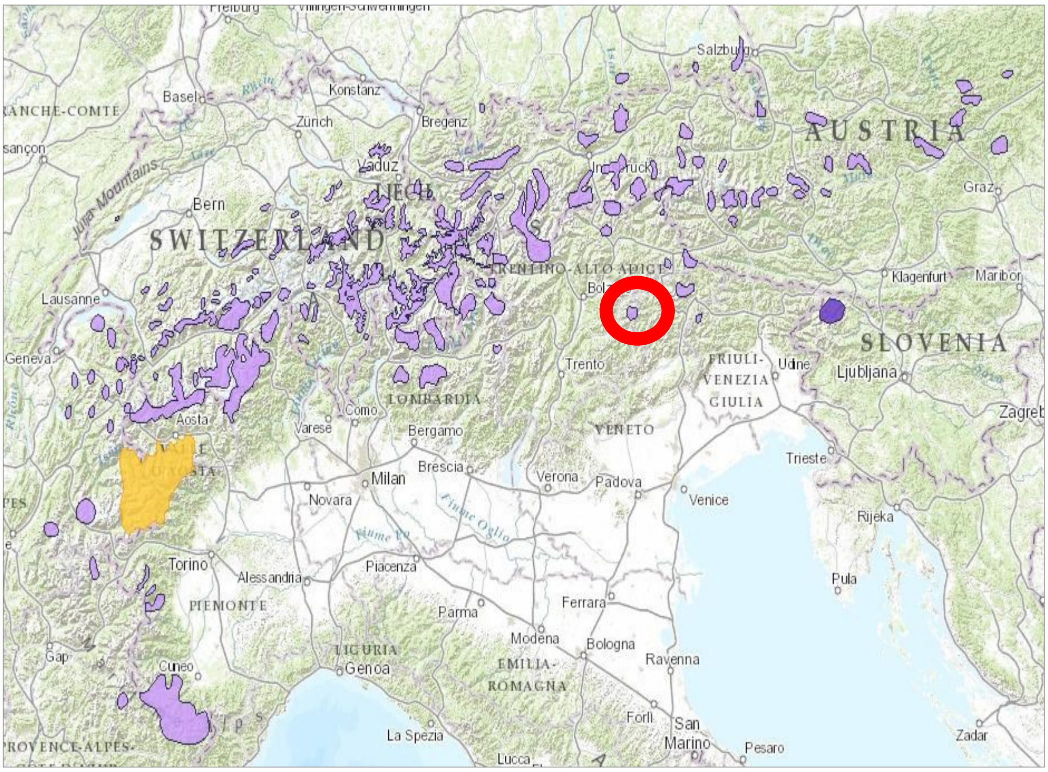

Figure 1-1 Distribution of the Alpine ibex colonies, with the Marmolada colony (red circle) and the Gran Paradiso National Park (in yellow). The map is taken from Aulagnier *et al.*, 2008.

During the winter 2003 – 2004, the combined effects of a sarcoptic mange epidemic (*Sarcoptes scabiei var. Rupicaprae*) and harsh weather conditions caused a dramatic crash of population (Monaco *et al.*, 2005), with an estimated loss of 75% of the individuals (Monaco *et al.*, 2004). The epizootic of sarcoptic mange was carried in the area by chamois and went to infect the ibex population (Rossi *et al.*, 2006). In 2006, only 114 individuals were counted. A project for sanitary treatment was carried out by the province of Belluno and the University of Torino with the aim of limiting the short-term effects of the epidemic (Rossi *et al.*, 2006). In 2006 and 2007, 14 males were translocated from the colony of Jof-Fuart Montasio (Giulie Alps). Alpine ibex in this colony had already overcome previous scabies epidemic, therefore they were presumably more resistant to the disease since scabies resistance could be an inheritable trait (Guberti & Zamboni, 2000; Leung & Grenfell, 2003; Scillitani *et al.*, 2009). Afterwards, the size of the population began to grow again. In the summer of 2017, a minimum number of 288 individuals were counted (Vendrami Stefano 2017, personal communication). The local ibex colony ranges over approximately 150 km^2, within 1700 to 2.900 m a.s.l., across two different administrative units: the province of Belluno (Veneto Region), and the autonomous province of Trento.

1.4. Study Area

The Marmolada-Monzoni massif extends over about 150 km^2 and is composed of several summits of Dolomitic limestone rising above 3000 m a.s.l.. The main peaks are: Punta Penia (3,343 m a. s.l.), Punta Rocca (3,250 m a.s.l.), Monte Serauta (3,009 m a.s.l.), all in the Marmolada massif, Cima dell'Auta (2,623 m a.s.l.), Padon (2,520 m a.s.l.) and Cima dell'Uomo (3,010 m a.s.l.).

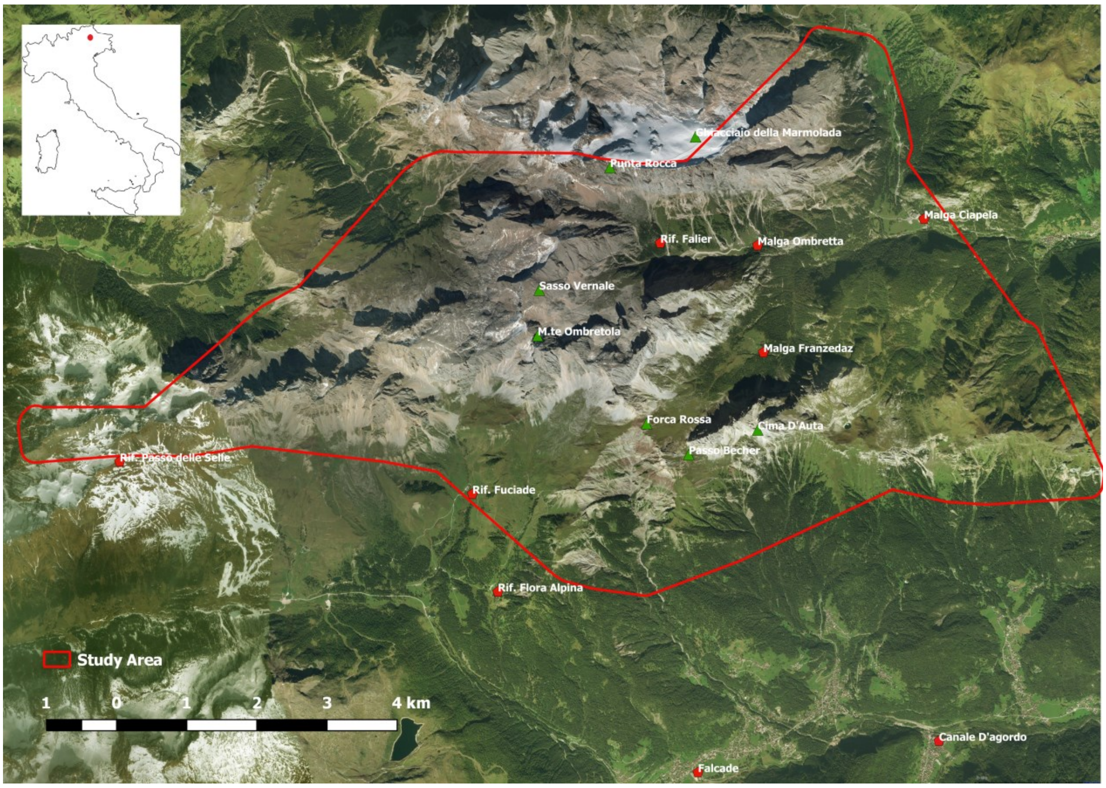

Figure 1-2 The study area, coinciding with the range used by 22 female, monitored in the Marmolada massif from 2010 to 2016, delimited as the minimum concave polygon encompassing all the GPS locations

Land topography in the range used by ibex is characterized by high elevation, narrow valleys with steep slopes delimited by rocky ridges (Figure 1-3). The main ridges orientation is east-west, therefore the slopes are mostly exposed either to north or south, with very different climatic conditions. Vegetation follows a strong altitudinal gradient. At the lowest elevations (≥1600 m) woodlands are mainly composed by Norway spruce and larch (*Larix decidua*). Above the timberline (1900 m) shrubs as mountain pine (*Pinus mugus*), hairy alpine rose (*Rhododendrum hirsutum*), willows (*Salix sp.*), and green alder (*Alnus viridis*) merge into Alpine grasslands, composed by different herbaceous species (mainly *Sesleria varia, Carex sempervirens, Nardus stricta, Carex firma*). Further up in elevation (2200-2300 m), screes and rock interrupt the vegetation patches and dominate above 2500 m.

Figure 1-3 Examples of Alpine ibex habitats in the study area located in Marmolada massif (Italy).

Other large herbivores present in the area are roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and Alpine chamois (*Rupicapra rupicapra*), the only species that can overlap its range with that of ibex. During summer (mid-June - mid-September), part of the grasslands in the area are locally grazed by domestic cattle, which however stay at lower elevations than those used by Ibex. No large predators were present during the study period.

The temperature of the study area may ranges on average between -20°C in winter to 20°C in summer with a mean annual temperature of 1.7°C the average monthly temperatures varying from about – 5°C in December – January to about 10°C in July-August (Figure 1-4). The total yearly precipitation is approximately 1400mm. The wintertime precipitation is mostly in the form of snow about from October-November to April-May, but the snow cover at highest altitudes lasts longer (Figure 1-4).

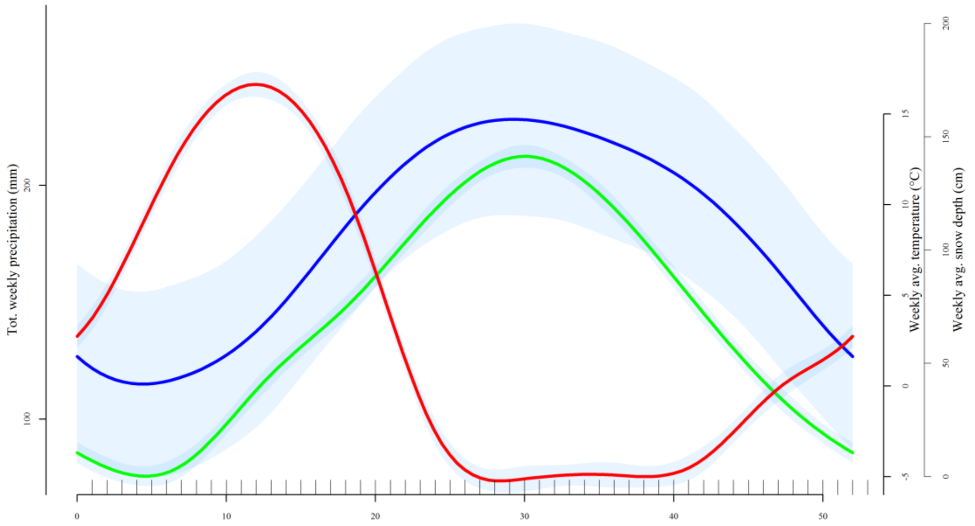

Figure 1-4 Annual pattern of weekly average temperatures (line green), weekly average of snow depth (line red) and total weekly precipitation (line blue) recorded by two meteorological stations (Monti Alti di Ornella e Malga Ciapela) located in proximity of the study area at elevations of 2250 and 1475 m a.sl. Grey bands indicate confidence intervals.

On the north side of the Marmolada lies a glacier, covering around 2% of the study area (Dupré *et al.*, 2001). This side is heavily exploited during the winter season for snow sports. On the opposite, on the southern side, the touristic pressure is mostly constant throughout the summer, when activities such as hiking or climbing take place, but very scarce during winter. From September to January, selective hunting by stalking is allowed on chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), and red deer (*Cervus elaphus*).

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2. Animal tracking data and spatial database

2.1. Introduction

In recent years, new global position system (GPS) technologies have boosted the potential for the remote tracking of free-ranging animals (Cooke *et al.*, 2004; Tomkiewicz *et al.*, 2010), allowing to record remote data with a very high spatial and temporal resolution from a wide number of species and individuals, and in areas and climate conditions otherwise non-accessible for direct observation or for the traditional hand held VHF tracking (Cagnacci *et al.*, 2010). Animal locations generated by GPS tracking allow describing individual movement trajectories, which in relation with individuals internal state (physiological needs), movement capacity, navigation (orientation) capacity and external conditions (climate and resources) permit to understand how individuals interact with their ecosystems (Nathan et al, 2008). This increases enormously the opportunities to study animals behavior, allowing a mechanistic understanding of the key concepts of behavioral and evolutionary ecology (Cooke *et al.*, 2004; Hooker *et al.*, 2007; Rutz & Hays, 2009; Cagnacci *et al.*, 2010). However, these very large data sets require powerful spatial relational database-management system (SRDBMS), with innovative and efficient data handling and analytical tools. The SRDBMS must allow managing these data sets securely, consistently and efficiently, in order to minimize errors, prevent error propagation, optimize modeling and analysis, improve the robustness of the results, and ensure data persistence. Last but not least, they must allow data sharing to the research community, for principle and opportunity (Urbano *et al.*, 2010).

The recent developments of new computing and analytical tools have opened new and ample opportunities for the construction and management of complex spatial databases. Today, most powerful data management and analysis tools are developed in open source environment. These software are part of a collective process of knowledge sharing for the development of science, and ensure a flexible development of research needs, with an increasing number of modeling and analytical tools developed ad hoc for specific topics of different scientific areas, an easy sharing and of scripts and algorithms for computing specific analyses between research groups, , a reduction of research costs.

The data management and analysis in this Ph.D. project were based, as much as possible, on open source tools. In particular, I used the open source software R (R Core Team, 2016), QuantumGIS (QGIS Development Team, 2017) and PostgreSQL (PostgreSQL Global Development Group, 2015), with its spatial extension PostGIS (PostGis Refractions Research Inc., 2015) and pgAdmin (pgAdmin Development Team, 2015) administration and development platform for PostgreSQL). Instead, I used a proprietary software GPSplusX of *Vectronic Aerospace GmbH©* (the company producing the GPS collars used in this project) to download raw GPS data. However, this software has been developed to efficiently interact with PoastgreSQL, facilitating the storage of data.

The choice to use PostgreSQL/PostGIS as the SRDBMS used for building my spatial relational database was based on the following considerations (Urbano & Cagnacci, 2014):

- both are free and open source;
- PostgreSQL is an advanced and widely used database system and offers many features useful for animal movement data management;
- PostGIS is currently one of the most, if not the most, advanced spatial database extensions available, and its development is quickly progressing;
- PostGIS includes support for raster data, a dedicated geography spatial data type, topology and networks, and has a huge library of spatial functions;
- there is a wide, active and very supportive community for both PostgreSQL and PostGIS;
- there is very good documentation for both PostgreSQL and PostGIS (manuals, tutorials, books, wiki, blogs);
- PostgreSQL and PostGIS widely implement standards that make them highly interoperable with numerous other tools for data management, analysis, visualization, and dissemination.

PostgreSQL/PostGIS allowed to store, query and manipulate spatial data (GPS locations and environmental data) using the Structured Query Language (SQL). R is the most important open source programming language and software environment for statistical computing and graphics used in research, and can also manage spatial data. The R statistical environment was integrated into the PostgreSQL platform, either connecting the database with R, or embedding the same tools in the database through PostgreSQL Pl/R extension. QGIS is the suggested GIS interface because it has many specific tools for managing and visualizing PostGIS data. Moreover, it is powerful and completely open source software, which offers all the functions needed to deal with spatial data.

2.2. Storing tracking and environmental data in the spatial database

The research project used information collected from several data sources (see below for details), and integrated them in the spatial database (Figure 2-1). In this database, I managed the different data sets in a unique framework, defining spatial and non-spatial relationships in order to optimize the organization of information and the handling and analysis of data. The outputs of data handling and processing were either stored back in the database or used in analyses that were more complex.

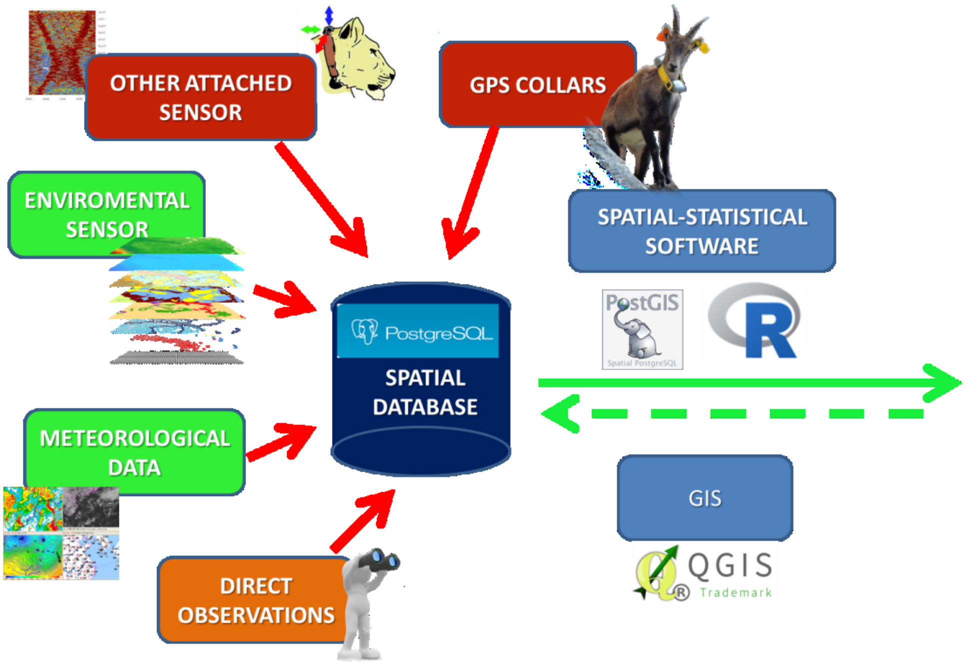

Figure 2-1 Implemented scheme of management and analysis of data derived from several sources. All information was integrated into the central spatial database; from here it was possible to manipulate, visualize and analyze the data. The output was stored back in the spatial database.

The raw data from the collars (see below) as well as the information on animals and environment (described below) were inserted within the SRDBMS. First, I integrated location data for each collar with the information on the corresponding animal. For this reason, a system of related tables (Figure 2-2) was built to guarantee a quick access to information, data integrity, and consistency, and to reduce data redundancy. Then I integrated the animal locations with the spatial information on the climatic and environmental factors, such as altitude used, slope, temperature, land cover, vegetation productivity. Each GPS position was intersected with raster or vector environmental layers stored in the spatial database, consistently with their changes in space and time. Descriptive parameters that can be used to characterize the spatial animals' behavior, such as step length, difference in altitude, the turning angle and the speed between two consecutive points and distance from relevant areas (such as refuge areas) were computed for each step of each individual trajectory. Finally, each location was associated with the information on animal status, geometry of trajectories and environmental and climatic variables. This was essential for exploring the animals’ behavior and understanding the ecological relationships with environmental features in their spatial and temporal dynamics.

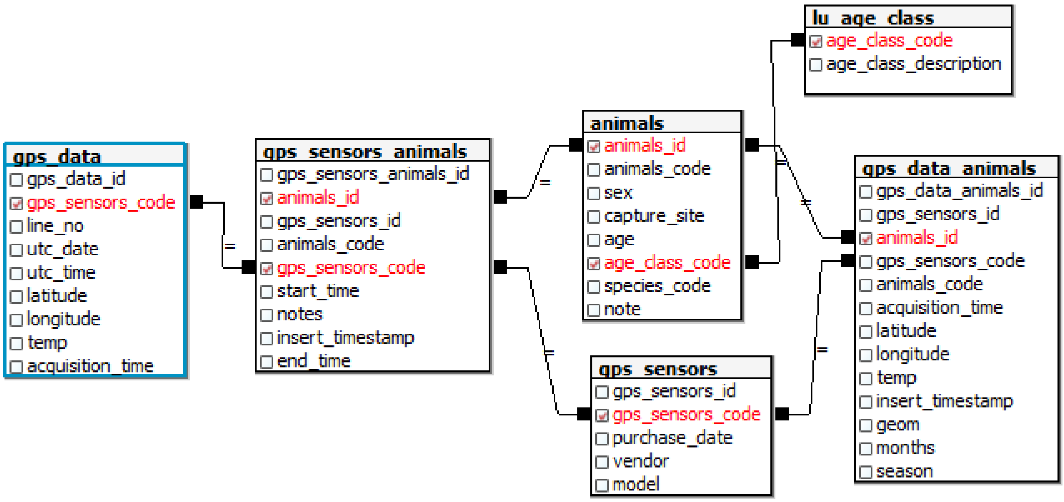

Figure 2-2 The figure shows pgAdmin GUI interface to create queries, where the relations between different objects, stored in the database, are shown. The black line identifies the links between tables connected by foreign keys.

2.2.1. Data Collection

Animal and sensor data

From September 2010 to October 2016, twenty-two female ibex were captured by tele-anaesthesia with veterinary assistance in compliance with current Italian laws. Capture and handling protocols were approved by ISPRA (*Istituto Superiore per la Protezione e la Ricerca Ambientale, ref. n. 9097-9501/2012*). Capture teams were composed by the assisting veterinarian, the personnel with the equipment for marking the captured animals, and expert personnel of “Corpo Forestale dello Stato-Comando Regionale Veneto” and “Corpo di Polizia Provinciale di Belluno” who were in charge of approaching and darting the animals. Capture and handling procedures were similar to those described by Brivio *et al.* 2015, which have a very low impact on this species. At capture, age was estimated from the horns annuli and the veterinarian examined the animals for health status. Only females 2 or more years old, and in good health status from external inspection, were captured and marked.

Each animal was equipped with GPS-GSM collars (GPS PRO Light collar, Vectronic Aerospace GmbH©), with the following sensors or mechanisms:

- animal positioning (GPS);
- activity sensor (2-axis);
- mortality sensor;
- temperature sensor;
- VHF transmitter;
- Drop Off mechanism.

All data, except activity (stored in the collar, see below), were remotely transferred to the server located at the Department of Agronomy, Food, Natural Resources and Environment of the University of Padova, using Global System for Mobile Communications (GSM), making possible nearly real-time monitoring of the animals.

Each animal was monitored for one year, e.g. 52 weeks, after capture. Drop-off was set at 54 weeks to get the time to locate the animals after the 52 weeks period before the collar‘s drop off. Dropped-off collars were retrieved either by locating and following the individuals on the day of scheduled drop-off to pick up collars when they dropped, or by locating dropped collars via homing-in with VHF tracking. In this way, 19 collars were retrieved. The other 8 were in inaccessible spots (rocky cliffs) and could not be retrieved. Some collars (n = 3) stopped transmitting data early after application, and an animal died after a few months. The GPS collars were set to attempt one location every hour, and were equipped with a two-axes activity sensor, scheduled to store the acceleration data at 5 minutes intervals. The activity data were downloaded from the collars retrieved after drop-off. During late June to early September, field work was conducted to observe the marked individuals in order to assess reproductive status. I considered to be lactating females those females that were seen breastfeeding at least once during the summer. As far as possible, attempts were made to replicate the observations on all collared females during the summer to confirm the absence of the kid. Other methods to identify pregnancy before births were methodologically or logistically unfeasible. Spring capture for eco-scanning females were considered highly dangerous for survival, also given the extreme topography, and not approvable by welfare protocols. The collection of fresh feces after deposition by marked individuals, initially considered, resulted practically unfeasible in winter and until late spring because most of the area used by female ibex was impossible or too risky to access by human in presence of snow.

In addition, intensive behavioral observations were conducted on seven marked females to collect observational data on active and non-active behaviors that were used to validate the definition of active and passive behaviors from the activity sensors (see Chapter 3 Supplementary material).

Environmental data

Environmental and climatic variables were obtained from different sources and inserted into the SRDBMS (Figure 2-1). I defined the study area as the minimum convex polygon of all points ($65km^2$) (see Chapter 1). Environmental variables were calculated within this area.

I obtained daily and hourly average temperatures from three different weather stations ("Malga Ciapela", "Falcade" and "Monti Alti di Ornella") managed by A.R.P.A.V. (Agenzia Regionale Prevenzione Ambientale del Veneto), located respectively at about 4, 6.5 and 7.3 km from the centroid of study area, and from 1,145 to 2,250 m a.s.l.. I inserted in SRDBMS the time of sunrise and sunset obtained from ephemerides for the whole period of the study and computed the day length as difference between sunrise and sunset hours, at the minute resolution. Climatic data and daylength were thus obtained at the spatial scale of study area, and were associated to each location based on date, and hour when relevant. I computed the daylength as difference between sunrise and sunset hours, at the minute resolution, obtained from ephemerides.

The environmental data were conversely stored at the temporal scale allowed by their acquisition (see below) and at the spatial scale of each location. This was obtained by overlapping the different layers.

I extracted altitude and slope from a regional digital elevation model (resolution: 5m; https://www.regione.veneto.it/web/ambiente-e-territorio/ctr; http://www.territorio.provincia.tn.it). Altitude was used to estimate the real distance between two consecutive points (3D step length).

I used a 1:5.000 vector land-cover map with high resolution (0.5 ha) obtained by editing the forest cover maps of Veneto Region and province of Trento (www.regione.veneto.it/web/agricoltura-e-foreste/carta-forestale-regionale) using a orthophoto of the study area as reference (Scillitani *et al.*, 2012, 2013). I reclassified land-cover in relation to the analytical purposes, into five habitat types: "forest" (which included coniferous and mixed forest, and shrubs, representing areas with tree/shrub cover at different density), "grassland", (which included Alpine pastures and natural grasslands, representing grassland areas either with less than 30% tree/shrub cover or 30% of rock), “scree”, representing areas of broken rock fragments with very little vegetation, “grassland mixed with rock” (defined by grassland interspersed with rocks and scree, covering at least 30%), and “rocks” (defined by rocks with no or very little vegetation). The high detail of the vector map allowed an accurate description of these habitats, as in the example shown in Figure 2-3.

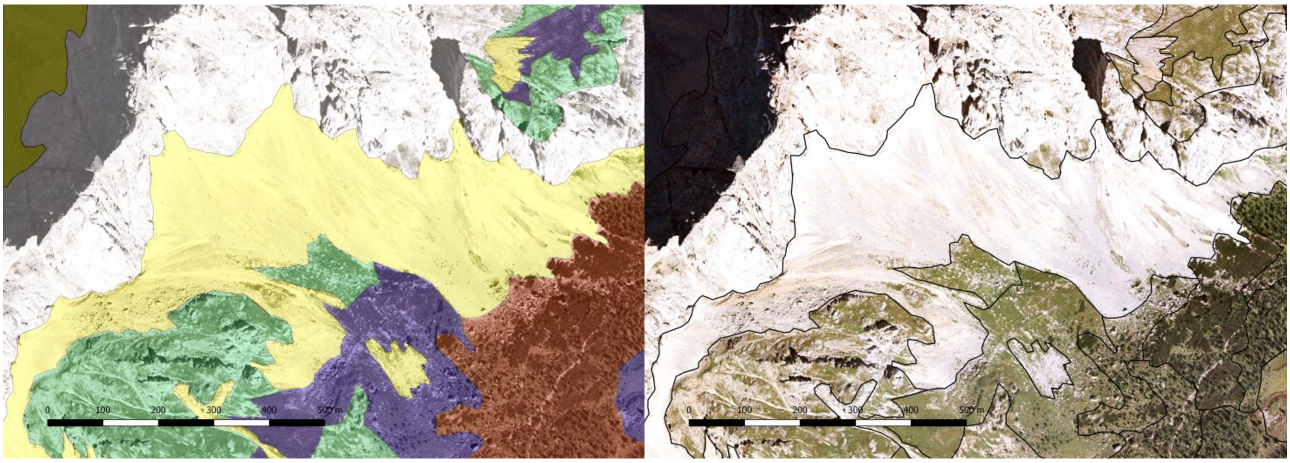

Figure 2-3. The figure shows an example of land-cover classification in a portion of the study area. Left panel: polygons of habitat types considered (“forest” in red; “scree” in yellow, “grassland mixed with rock” in green, “rock” in white and “grassland” in blue). Right panel: orthophoto of the same area overlapped with the borderline of habitat types.

I calculated from MODIS the NDVI values (250x250m spatial resolution) smoothed at 7-days intervals and corrected for contamination and atmospheric variability (Klisch & Atzberger, 2016). I determined NDVI used by individual females by spatial join between the weekly average of individual locations and weekly NDVI raster. Moreover, I determined NDVI of the study area by averaging the weekly NDVI raster clipped by the study area, defined as the minimum convex polygon of all GPS locations of all individuals. I used NDVI as an index of vegetation abundance and productivity (Pettorelli *et al.*, 2006; Hebblewhite *et al.*, 2008). Raster calculator function in PostGIS allowed me to calculate also the ΔNDVI, as the difference of NDVI values between two consecutive weeks (for more details see the Chapter 3).

Table 2-1 Variables used in this work, their scale and temporal resolution, their screening process and the corresponding derived variables.

Variable	Temporal scale resolution	Spatial scale resolution	Screening	Derived variables
GPS locations	hourly	Individual	Outliers detection	-Distance from habitat features -speed – turning angles
Activity (two-axis accelerometers)	5 minute	Individual	Identification of activity/inactivity threshold	-Total hourly and weekly active time -Active and inactive behaviors[1]
temperature	hourly daily	Study area	---	-temperature classes[1]
NDVI	weekly	250x250m	---	-ΔNDVI1
Slope	---	5x5m	from DEM	-Refuge area[2]
Altitude	---	5x5m	from DEM	-Refuge area2
Habitat type	---	0.5ha	land-cover map, editing on orthophoto and forest map	--Refuge area2
sunrise and sunset time	minute	---	---	daylength

2.2.2. Data screening: detection and management of outliers

Tracking data can potentially be affected by a large set of errors in different steps of data acquisition and processing (Urbano & Cagnacci, 2014), but whatever the source and type of errors, they have to be taken into account. Data quality assessment was, therefore, a key step in the management of GPS locations.

It is possible that a failure of transmission hardware or lack of transmission due to network conditions result into loss of scheduled locations. Assessing the fix acquisition rate (acquired as respect to scheduled locations) is important to ensure that temporal and spatial analyses are not biased since the loss of locations does not occur randomly across habitats (e.g., Frair *et al.*, 2010; Párraga Aguado *et al.*, 2017). In addition, acquired locations are affected by two sources of error. First, each location is inevitably subjected to a certain degree of inaccuracy (Frair *et al.*, 2004; Horne *et al.*, 2007; Nielson *et al.*, 2009). No screening for location accuracy was possible, because it requires stationary collars tests, but I considered a previous study (Párraga Aguado *et al.*, 2017), carried out in the same study area, which found that the median location error from stationary collars was lower than 10 m, after correcting for outliers (see below). This very good accuracy was most likely favored by the open habitats preferred by ibex and is suitable for the movement and

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[1] for details see Chapter 3 Supplemental materials

[2] for details see Chapter 4

habitat use analyses at the temporal and spatial scales of this study. The second source of inaccuracy is that acquired locations contain a variable proportion of largely inaccurate locations (outliers). Inclusion of outliers can introduce systematic biases and substantially affect analyses. (Bjørneraas *et al.*, 2010). While in some cases these positions are evident, often it is not possible to clearly identify locations as outliers because although they are suspicious (e.g. long distances covered by animals in a short time or repeated extreme values) they might still be correct, leaving a margin of uncertainty. Defining an outlier's identification protocol is therefore important for limiting subjectivity in identifying the error and making the procedure repeatable in a standardized way (Urbano & Cagnacci, 2014). I used a number of subsequent steps to identify outliers, according to the general approach to t proposed by Bjørneraas *et al.*, (2010) and Urbano & Cagnacci, (2014), see below for details. For each scheduled location, I assigned a code (missing/received; accepted/outlier) according to the methods briefly described below. This way no information was lost and using queries only the correct locations were analyzed. In addition, data screening was also conducted in order to avoid other sources of error during data acquisition and processing (misclassifications, etc.), that were identified with subsequent steps (Urbano & Cagnacci, 2014):

1. I estimated the amount of missing records (no information has been received from the sensor, although it was planned by the acquisition schedule). Missing locations were 7% of scheduled locations in spring-summer and 12% in winter. Moreover, I identified all records with missing coordinates, probably due to bad GPS coverage or a GPS failure. These location acquisition rates are very good, especially considering those obtained in other large herbivore species (see Párraga Aguado *et al.*, 2017 for a discussion). Since in this study detailed analyses on movement and habitat use were conducted in summer, I assume that the very small proportion of scheduled locations lost did not introduce any bias (Frair *et al.*, 2010).
2. I identified duplicate records, with the same acquisition time.

3. I identified all records erroneously attributed to an animal because of inexact deployment information (e.g. due to an imprecise definition of the deployment time range of the sensor on the animal). For each animal I stored the start and end time of monitoring, and on this information I defined the correct time range. Moreover, according with Brivio *et al.*, (2015) all locations during the two days post-capture were excluded to avoid the disturbing effect of immobilization on ibex behavior.

4. I identified all records located outside the study area, defined as the minimum concave polygon of all points stored during the study period (excluding outliers).

5. I identified all records located in impossible habitats (like on glacier, villages or lakes).

6. I identified all records that imply impossible movements (e.g. very long displacements, requiring movement at a speed impossible for the species). I implemented the algorithm suggested by Bjørneraas *et al.*, (2010) that considers simultaneous fulfillment of thresholds defined for step length (Δ =500m), speed (limit was set as 200m/s) and turning angle ($\theta = -0.96$), fixed for consecutive locations. These thresholds were defined through the analysis of the trajectories of all animals.

7. The last step was a visual exploration to check the correctness of the assignment of outliers. I removed additional points corresponding to improbable movements of animals.

After the screening of raw data (n = 217918) I removed 11% outliers (n = 23691), to obtain the final database (n = 194227).

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3. Summer movement and activity patterns in female Alpine ibex: a case for temperature stress compensation? [3]

3.1. Introduction

Climate warming is shifting both distribution ranges (Walther *et al.*, 2002; Walther, 2004; Parmesan, 2006) and phenology of physiological processes (Chmielewski & Rtzer, 2002; Root *et al.*, 2003; Gaillard *et al.*, 2013) of plants and animals. As a consequence, relative abundances of species within communities (Wipf *et al.*, 2006; Putten *et al.*, 2010), and behavior of individuals in those communities (Kearney *et al.*, 2009; Walther, 2010; Huey *et al.*, 2012; Stuble *et al.*, 2013), are largely affected. In Alpine environments, these effects can be accentuated, for the strong environmental and climatic gradients associated with extreme topography and altitudinal variation (Ernakovich *et al.*, 2014). Increased temperatures can alter plant altitudinal distribution range (Parolo & Rossi, 2008; Rammig *et al.*, 2010), as well as vegetation productivity and phenology, especially with anticipated green up and senescence (Wipf *et al.*, 2009; Ernakovich *et al.*, 2014). Since large herbivores are dependent on primary productivity, a mismatch between the rapid variation in environmental constraints and the evolution of mechanisms of adaptation can be observed (Gaillard *et al.*, 2013; Plard *et al.*, 2014), especially for those specialized to extreme environments (Pettorelli *et al.*, 2007; Post & Forchhammer, 2008). Species living in extreme conditions have developed physiological (e.g., Arnold *et al.*, 2006, 2004; Heldmaier *et al.*, 2004) and behavioral (Nicholson *et al.*, 1997; Arnold *et al.*, 2006; Rice, 2008) mechanisms to cope with climatic constraints and heterogeneity in resource availability. Since adaptation of behavioral responses can be faster than physiological ones, they can potentially buffer climate change impacts

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on resource acquisition (Cagnacci *et al.*, 2011; Peters *et al.*, 2017), and thus be particularly relevant in the context of conservation actions (Allred *et al.*, 2013; Sunday *et al.*, 2014).

Many mountain ungulates exhibit seasonal movements, that generally consists in altitudinal shifts to enhance access to high-quality food while trading off for predation risk (Festa-Bianchet, 1988; Hebblewhite & Merrill, 2009; Bischof *et al.*, 2012). The forage-maturation hypothesis (FMH) states that herbivores migrate along a phenological gradient of plant development in order to maximize energy intake. Specifically, the FMH predicts that adaptive spring movements prolong the access to high-quality forage in summer ranges compared to plant maturation in winter ranges (Fryxell & Sinclair, 1988; Hebblewhite *et al.*, 2008). In addition to space use, ungulates optimize forage acquisition by adjusting feeding behavior, i.e. time spent feeding (Bergman *et al.*, 2001).

Both activity and movement patterns are responses to different resource needs and physiological constraints, at multiple spatio-temporal scales. In particular, temperature gradient is a major limiting factor for species evolved in Alpine environments, both in winter and summer (Grignolio *et al.*, 2004; Aublet *et al.*, 2009; Signer *et al.*, 2011). To buffer environmental temperature fluctuations, animals may need to rely on behavioral thermoregulation to keep within tolerated thermal margins, and avoid for example heat stress (Signer *et al.*, 2010), by reducing activity, or by selecting specific habitats under extreme conditions. Cover habitats typically offer a more stable temperature range than open areas, and are often selected as thermal shelter by large herbivores (roe deer: Mysterud & Østbye, 1996; moose: van Beest *et al.*, 2012; Melin *et al.*, 2014; McCann *et al.*, 2016; white-tailed deer: Demarchi & Bunnell, 1993). Mountain ungulates are known to use the altitudinal thermic gradient to compensate for temperature fluctuations. For example, high altitude areas in summer can be functionally compared to cover habitats for protection from heat stress in chamois (*Rupicapra rupicapra*) (Mason *et al.*, 2014a) and Alpine ibex (Aublet *et al.*, 2009). However, best habitats for thermal protection may not be optimal for food acquisition, so that thermal shelter-food trade-offs are common in ungulates, by selecting habitats at different spatio-temporal scales (Mysterud & Østbye, 1999; Dussault *et al.*, 2005; Hebblewhite & Merrill, 2009; van Beest *et al.*, 2012), or by adjusting activity budgets to maximize energy intake (Aublet *et al.*, 2009; Bourgoin *et al.*, 2011). Under climate change, this adaptation may induce trophic or behavioral mismatch, for example by excessively depressing foraging activity or by forcing animals to select sub-optimal forage habitats (moose: van Beest & Milner, 2013; chamois: Mason *et al.*, 2014; see also: Galanthay & Flaxman, 2012). For example, physiological studies reported heat-sensitivity of Alpine ibex, evidencing a comfort environmental temperature range in summer fur (Signer *et al.*, 2011), and decreased horn growth rate for males at increasing temperatures (Giacometti *et al.*, 2002). Observational studies on male Alpine ibex assessed the link between temperature, altitudinal patterns of space use, and forage activity (Aublet *et al.*, 2009; Mason *et al.*, 2017). This work investigates the behavioral responses of female Alpine ibex to the variation of resource availability and temperature fluctuations at different spatio-temporal scales (annual/seasonal, daily/hourly) by means of high-frequency GPS locations and accelerometer data throughout the year and the 24 hours cycle.

Alpine ibex distribution range typically encompasses altitudes between 1600 and 3200 m a.s.l. (Pedrotti *et al.*, 2009), the highest altitudinal extremes of all Alpine ungulates, although some populations have been successfully reintroduced at low elevation in extremely rocky areas. They are capital breeders (Toïgo *et al.*, 2002), i.e., they accumulate body fat throughout summer to face mating at the beginning of the winter season, and to overwinter (Toïgo *et al.*, 2002; Signer *et al.*, 2011). The metabolic rate and locomotor activity are very low in winter but rise strongly in summer (Signer *et al.*, 2011). Females have only a short period to regain body reserves before engaging into parturition, that implies enhanced nutritional requirements due to lactation and kids raising (Toïgo *et al.*, 2006). It is known that both male and female ibex occupy higher altitudes in summer than in winter (Parrini *et al.*, 2003; Grignolio *et al.*, 2004). Moreover, seasonal (Mason *et al.*, 2017) and daily (Aublet *et al.*, 2009) altitudinal shifts have been recorded in male ibex, and related to temperature fluctuations. Temperature also correlated with activity patterns, in particular, during the hottest days of summer, and the hottest part of the day, male ibex dedicated proportionally less time to foraging, under the thermal-food trade-off. However, no apparent compensatory mechanisms were detected during daylight, so that nocturnal compensation was hypothesized (Aublet *et al.*, 2009; Mason *et al.*, 2017). Also, areas at high altitudes reached by ibex under heat pressure were shown to provide forage habitat of inferior productivity with respect to other areas of the spatial range of the populations (Mason *et al.* 2017). In general, the effects of summer abiotic and biotic constraints have been less studied on females that are also exposed to the costs of reproduction (births, lactation, kids' protection), in presence of a strong sexual segregation (Villaret *et al.*, 1997; Ruckstuhl & Neuhaus, 2002; Grignolio *et al.*, 2007). We addressed this knowledge gaps by analyzing movement behavior along with daily activity pattern *and* total budget in female ibex, in dependence on daily mean temperature. Moreover, we assessed how daily movement and activity patterns provided accessibility to resources by estimating the hourly relative selection of habitat types. We further investigated the adaptive value of seasonal altitudinal shifts by evaluating the seasonal trend of both activity and altitude in dependence on temperature, vegetation productivity (Normalised Differential Vegetation Index, NDVI) and its relative change throughout season (*green up*).

On these premises, we hypothesized that female ibex seasonal activity patterns and altitudinal movement followed the vegetation-growing season (**H1**). We expected that trends of activity and altitudinal movements would follow a strong seasonal pattern (**H1.1a, H1.1b**) and that the temporal variation of vegetation productivity (NDVI) or temperature would explain these patterns (**H1.2a**, **H1.2b**) better than seasonality per se (i.e., week: null hypothesis **H1.2**). Moreover, to understand whether female ibex optimize resource acquisition during summer, we verified whether summer movements allowed accessibility to areas with delayed vegetation growth with respect to winter locations (**H1.3**).

Further, we hypothesized that at the daily scale female ibex activity patterns and movement allowed access to resources, while compensating for temperature stress, in summer (**H2**). First, we expected that the activity of female ibex showed a daily pattern responding to temperature (i.e., lowest activity in the hottest hours, Aublet *et al.*, 2009), while responding also to behavioral needs (i.e., access/utilization of forage; **H2.1a**). Second, we expected that, if there was a behavioral compensation in foraging activity for temperature stress, the total daily activity budget would remain constant, for example by foraging at night (**H2.2**). Third, we expected that female ibex in summer would show daily altitudinal shifts, and that this would depend on daily temperature (**H2.1b**). Finally, because of the thermal shelter-food trade-off, we predicted that the relative probability of use of forage habitat types in summer varied amid the daily movement and activity patterns of female ibex (**H2.3**).

3.2. **Methods**

3.2.1. Study area

The study area is situated in the Marmolada massif group, in the Eastern Italian Alps (Dolomites - 46°26’ 13” N, 11°51’ 54” E). Land topography is characterized by high elevation, narrow valleys with steep slopes, delimited by rocky ridges and mountain peaks that can rise above 3000 m a.s.l.. Vegetation follows an altitudinal gradient. Above 1600 m a.s.l. it is mostly forest of Norway spruce (*Picea abies*) and larch (*Larix decidua*). Above the tree line (1900 m a.s.l.) vegetation is mainly represented by scrubs (*Pinus mugus, Rhododendrum hirsutum, Salix sp.* and *Alnus viridis*) and Alpine grasslands. At higher altitudes (over 2100 m a.s.l.) steep slopes of scree and rocky cliffs progressively prevail over grasslands. The climate is typically Alpine with a mean annual temperature of 4.2°C (DS±7.4) and average monthly temperatures varying from about 0°C (DS±5) in winter to about 11°C (DS±4) in summer. Total yearly precipitation is approximately 1400mm, and snow cover in the area used by ibex may last from late October-November to late May-early June (source: Regional Agency for Environmental Prevention of Veneto, A.R.P.A.V.).

The local ibex colony (Scillitani *et al.*, 2012) ranges over approximately 65 km^2, and spans an altitudinal range from 1700 to 2.900 m a.s.l.. Other large herbivores present in the area are roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and Alpine chamois (*Rupicapra rupicapra*), the only species that can overlap its range with that of ibex. From late June to mid-September part of the more productive grasslands, located at the gentler slopes, is grazed by domestic cattle, with no spatial overlap with ibex.

The study area is visited by hikers mostly in July-August. From 15 September to 31 January selective hunting by stalking is allowed on chamois, roe deer, and red deer. No large predators occurred in the area before and during the study period. The only potential predator on ibex was the golden eagle (*Aquila chrysaetos*).

3.2.2. Movement and activity data

From September 2010 to October 2015, we captured by tele-anesthesia twenty-one female ibex (2 or more years old at capture) and equipped them with GPS-GSM collars (GPS PRO Light collar, Vectronic Aerospace GmbH). Animals were captured with veterinary assistance in compliance with current Italian laws. Capture and handling protocols were approved by the National Agency for Environmental Protection and Research (Istituto Superiore per la Protezione e la Ricerca Ambientale, ISPRA; ref. n. 9097-9501/2012).

GPS collars were set to attempt one location every hour, and to drop-off after 54 weeks. Missing locations were 7.6% of scheduled locations in spring-summer and 11.6% in winter. The median location error estimated from stationary collars was lower than 10 m (Párraga Aguado *et al.*, 2017). We identified outlying locations using the approach suggested by Bjørneraas *et al.*, (2010) and Urbano & Cagnacci, (2014), which pinpoints locations causing abnormal deviations of step angles and distances within individual trajectories. After removing 12% outliers we obtained a database of 148,365 locations for 21 individuals.

The collars were equipped with a two-axes activity sensor, scheduled to store the acceleration data at 5 minutes intervals. We classified each interval as 'active' or 'inactive' based on a threshold identified from the bimodal distribution of the activity signal, as suggested by Gervasi *et al.* (2006), and validated this classification with observational data (see supplementary material **Appendix 1**). We visually observed that females spent about 18% of active time walking and 82% feeding (representing respectively 7% and 32% of the total observation time). The same result has been found for male ibex in the Gran Paradiso National Park, where during the daytime the activity of feeding was predominant on movements (Mason *et al.*, 2017). Therefore, we assumed that active time could be used as a good proxy of foraging activity. We used activity data from fifteen females, since activity data could be downloaded only by dropped-off collars, and we were unable to retrieve six of them. We calculated the minutes spent in activity by female ibex for each hour (hereinafter called hourly active time; n=63257 hours in the spring-summer period) and day (hereinafter called daily active time, n=5156 days for the whole year; we excluded the days with incomplete sampling, i.e. less than 24 hours).

GPS and activity data were stored and managed in a PostgreSQL DB with PostGIS extension (Strobl, 2008).

3.2.3. Environmental data

We obtained daily and hourly average temperatures from the closest (7.5 km from the center of study area) and highest (2,250 m a.s.l.) available weather station, managed by A.R.P.A.V. (Agenzia Regionale Prevenzione Ambientale del Veneto). We also summarized temperature values as follows: we calculated weekly average temperature as the average of daily values, and a categorical variable "daily spring-summer temperature class" by classifying daily average temperatures as "low" (≤ 3.80°C), "intermediate" (>3.80°C and <10.2°C) and "high"(≥ 10.2°C), which corresponded respectively to the lowest, the two intermediate and the highest quartiles of all temperature values in spring-summer. We computed the daylength as difference between sunrise and sunset hours, at the minute resolution, obtained from ephemerides. We extracted altitude from a regional digital elevation model (resolution: 5m; https://www.regione.veneto.it/web/ambiente-e-territorio/ctr; http://www.territorio.provincia.tn.it). We estimate the average altitude used by female ibex for each hour (n=73821 hours) and day (n=3838 days). We used a 1:5.000 vector land-cover map (resolution: 0.5ha) by refining the forest cover maps of Veneto Region and province of Trento (www.regione.veneto.it/web/agricoltura-e-foreste/carta-forestale-regionale) using an orthophoto of the study area (Scillitani *et al.*, 2012, 2013). Specifically, we classified land-cover data into five habitat types: "forest" (which included coniferous and mixed forest, and shrubs), "grassland", (which included Alpine pastures and natural grasslands), "scree", "mix grass and rocks" (defined by grassland interspersed with rocks and scree), and "rocks" (defined by bare rocks). Finally, we calculated the NDVI values (MODIS, NASA, USA; 250x250m spatial resolution) smoothed at 7-

days intervals and corrected for contamination and atmospheric variability (Klisch & Atzberger, 2016). We determined NDVI for individual trajectories by spatial join between the weekly average of individual locations and weekly NDVI raster. We determined NDVI for the study area by averaging the weekly NDVI raster clipped by the study area, defined as the minimum convex polygon of all GPS locations of all individuals. We used NDVI as an index of vegetation abundance and productivity (Pettorelli *et al.*, 2006; Hebblewhite *et al.*, 2008).

3.2.4. Statistical analysis

To describe temporal patterns, we used Julian dates for days and we numbered weeks starting from the 21st December to ensure consistency with the daylight cycle.

We defined seasons with a biologically meaningful classification of Julian weeks based on habitat and movement features of female ibex locations (**Appendix 2**). In particular, spring started in mid-April and ended in May (17th – 23rd weeks) and summer season ended at the beginning of October (24th – 42ndweeks). Hereafter, this period is cumulatively defined as "spring-summer".

We analysed data in R (R Core Team, 2016) using the package mgcv (Wood, 2016) to fit generalised additive mixed models, and the 'nlme' package (Pinheiro *et al.*, 2017) to fit linear mixed effects models. In all models, we fitted the individual animal as a random intercept.

Annual/Seasonal Scale

To assess the seasonality of activity patterns of female ibex (**H1.1a**), we modelled the individual daily active time (in minutes; definition of active/non active: see paragraph 'Movement and activity data' and **Appendix 1**) by fitting Generalised Additive Mixed Models with a normal distribution of errors. We compared models with different linear and non-linear temporal components by means of AIC (week as a fixed factor or as cyclic cubic regression spline smooth; year as a random or fixed factor; Table 3-1 for the set of models). We repeated the same analysis to assess the seasonality of altitudinal movements (**H1.1b**), by modelling the individual daily average of location altitude.

Moreover, we measured the percentage of the overall temporal pattern (P_{TP}) of daily active time (**H1.2a**) and daily average altitude (**H1.2b**) accounted for by weekly NDVI and weekly temperature by means of the ANODEV procedure (Skalski *et al.* 1993). In particular, we computed three generalized additive models: the null model (simplest model "S"), the regression spline smooth of the weekly NDVI and weekly average temperature of the study area, respectively (intermediate model "I"), and the observational week as a factor (most complex model "C"; see Table S. 3-5). We computed P_{TP} as:

$$P_{TP} = 1 - \frac{(LI-LC)}{(LS-LC)}$$

where LI is the loglikelihood of the intermediate model, LS of the simplest model and LC of the most complex model. We repeated the same comparison both for the whole year and for the summer season only.

To understand whether summer movements allowed accessibility to areas with delayed vegetation growth (H1.3), we computed temporal ΔNDVI as difference of NDVI values between two consecutive weeks. Practically, for each week we built a raster as standardized difference of spatially joined raster layers of that week, and the previous one:

$$\Delta NDVI = \frac{NDVIt_2 - NDVIt_1}{NDVIt_1}$$

Positive ΔNDVI values indicated growth and maturation of the vegetation (i.e., increase in the productivity), whereas negative ΔNDVI values corresponded to a decrease in vegetation productivity, e.g. because of senescence (Hamel *et al.*, 2009; Bischof *et al.*, 2012). Then, we compared the temporal pattern of ΔNDVI in the locations used by individual female ibex during the spring-summer period with that of the locations used by individual female ibex during the last 4 weeks of winter (H1.3). In other words, we compared ΔNDVI pattern of the actual locations used by individual ibex, with the temporal ΔNDVI pattern that individual ibex would have experienced if they stayed in the late winter locations during the sample period. To do so, we built a binomial variable Summer_loc, indicating whether the response variable referred to ibex locations actually used (“1”), or locations they would have used if they had stayed in the late winter area (“0”). We fitted a generalized additive model to ΔNDVI, with the cyclic cubic regression spline smooth of the week and the binomial variable Summer_loc as fixed factor. To evaluate the change in ΔNDVI used by females from winter to spring-summer, we analyzed the period starting from the 10th Julian week.

Daily/Hourly Scale

To assess the daily activity pattern of female ibex in spring-summer (**H2.1a**), we modelled the individual hourly total active time (in minutes) by fitting Generalized Additive Mixed Models with a normal distribution of errors. We compared models with different linear and non-linear temporal components by means of AIC (hour, hourly temperature, and temperature class as fixed effects and cyclic cubic regression spline smooths; Table 3-4 for the set of models). We also included in all models the linear effect of daylength to correct for the intra-seasonal variability that occurred in spring-summer (Krop-Benesch *et al.*, 2013; Ensing *et al.*, 2014; Bonnot *et al.*, 2016). We repeated the same analysis to assess the daily patterns of altitudinal movements (**H2.1b**), by modelling the individual hourly location altitude.

To assess whether female ibex maintained a constant daily activity budget across temperature classes (**H2.2**), we fitted a linear mixed-effects model with normal error distribution (R package lme4, Bates *et al.*, 2016) to the daily active time with the temperature class as linear effect, and tested the significance of differences in daily active time between temperature classes.

We evaluated the relative probability of use of forage habitat types throughout spring-summer (**H2.3)** by fitting hourly Resource Selection Functions (RSF, Boyce *et al.* 1999) to individual female ibex locations as follows. For each used location, we matched 10 available locations at a distance randomly extracted from the empirical distribution of the hourly step length for all locations of all individuals, and at a random absolute angle. We excluded the days with less of 20 locations per day. The step lengths were extremely short (Figure S. 3-5), causing a clustered distribution of available points very close to the point used. For this reason and in relation to the error associated with the point, we added 20m at each random step randomly extracted from the empirical distribution. We then fitted a RSF using a conditional logistic model for each hour of the day, where the used locations ('1s') were matched to all available locations for that animal the same day ('0s'). This way, we produced estimates of the relative probability of hourly habitat use with respect to the daily trajectories of female ibex. We fitted a two-steps conditional logistics to estimate population parameters accounting for individual-level variability (R package TwoStepCLogit, Craiu *et al.*, 2011, 2016).

3.3. Results

3.3.1. Annual/Seasonal Scale

The temporal component in the daily active time was better fitted as a regression spline smooth than as a linear effect thus indicating a strong annual pattern **(H1.1a)**. Furthermore, the regression spline smooth of the week with years as a random factor, significantly improved the goodness of fit of the model (Table 3-1; Adjusted R^2=44%). In particular, daily active time of female ibex increased very fast at the beginning of the growing season, reaching a first peak in spring at the 17th week, and a second in summer at the 35th week, to then slowly decrease until the 45th week, when it dropped again to winter levels (Figure **3-1**A). The low around the 25th week likely corresponds to births.

Similarly, female ibex showed a clear seasonal altitudinal shift **(H1.1b),** as indicated by the fit of a regression spline smooth of the week with years as random factor to the average daily altitude used (Adjusted R^2=62%; Table 3-1). The altitudinal shift towards higher altitudes was delayed with respect to the increase of daily active time, as it started at the first peak of daily active time, and progressed ing with a lower rate, noticeably overlapping the increase of NDVI of the study area (average altitude peak: 30th week); the shift towards lower altitudes, instead, paralleled the decrease of daily active time at the end of summer (Figure **3-1**B).

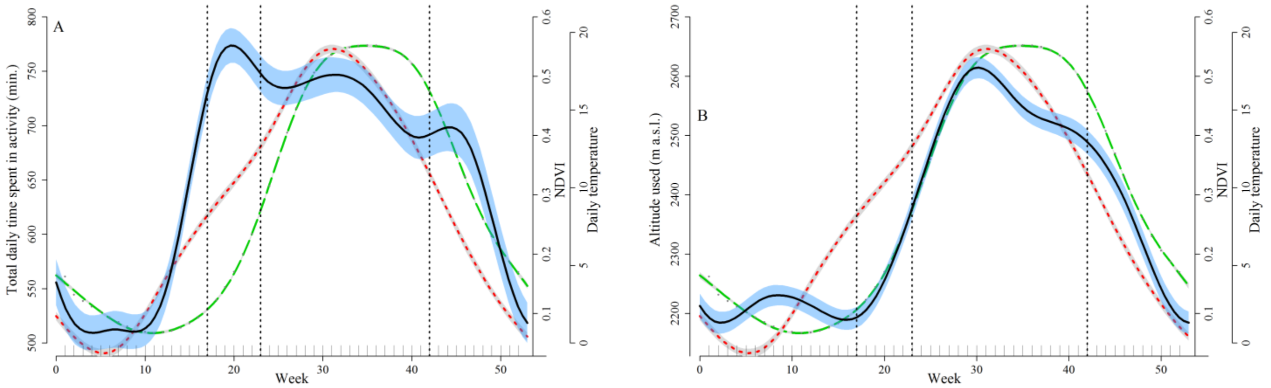

Figure 3-1 Panel A: Annual pattern of daily active time of 15 female ibex, monitored in the Marmolada massif from 2010 to 2015, fitted as the regression spline smooth of the week (best model for the temporal component of the activity pattern). Panel B: Annual pattern of daily average altitude used by 21 female ibex, monitored in the Marmolada massif from 2010 to 2015, fitted as the regression spline smooth of the week (best model for the temporal component of the daily average altitude use). The confidence bands (shaded areas) are calculated using the 95% confidence intervals. In both panels, we overlapped the annual patterns of NDVI of the study area (dashed green line) and of the daily average of temperature (dotted red line). The dashed vertical lines delimit spring (17th – 23rd week) and summer seasons (24th – 42ndweek).

Table 3-1 Model selection of candidate general additive mixed models and linear mixed effects models analysing daily active time of 15 female ibex and daily average altitude used by 21 female ibex, monitored in the Marmolada massif from 2010 to 2015.

Variables						Daily active time			Altitude used		
Individual (random)	Week (linear)	Week (spline)	Year (random)	Week*year (linear)	Year (linear)	df	ΔAIC	Model weight	df	ΔAIC	Model weight
X		X	X			27	0.0	0.5	33	0.0	0.5
X		X			X	27	0.0	0.5	33	0.1	0.5
X				X		23	166.8	0.0	29	23.7	0.0
X	X		X			25	1140.4	0.0	31	2901.7	0.0
X	X					20	1492.1	0.0	26	3742.6	0.0
X			X			19	2287.7	0.0	22	4596.5	0.0
X						16	2547.4	0.0	25	5227.8	0.0

The percentage of the overall temporal pattern of daily active time accounted for by vegetation productivity and temperature (**H1.2a**) was respectively 66% (weekly NDVI) and 82% (weekly average temperature) for the annual pattern and 41% and 26% during spring-summer (Table 3-2). When using the same approach for altitudinal patterns (**H1.2b**), NDVI and temperature explained respectively 89% and 76% of the overall temporal variation of daily average altitude used at the annual scale, and 89% and 76% during spring-summer (Table 3-2). Therefore, variation of altitude responded more to NDVI and temperature than variation of active time in spring-summer, whereas active time was especially influenced by temperature at the annual scale (Figure **3-1**).

Table 3-2 Relative importance of environmental factors (weekly NDVI and average temperature of the study area) to explain the probability of being active and the altitudinal use by female ibex, analyzed at annual scale and subsetting data for spring-summer only.

	Time scale	Weekly NDVI R^2	Weekly average temperature R^2
Daily active time	annual	0.659	0.818
	spring-summer	0.408	0.260
Daily average of altitude used	annual	0.890	0.760
	spring-summer	0.892	0.765

Weekly ΔNDVI pattern was best explained by the regression spline smooth of the week, and the variable Summer_loc, indicating that summer locations actually used by ibex had a greater positive ΔNDVI than if they had not moved from later winter locations (Table 3-3 and for parameter estimates see Table S. 3-4). When plotting ΔNDVI by the spline smooth of the week in interaction with Summer_loc (Figure 3-2a; extrapolated to the whole year), the ΔNDVI remained positive between the 10th and the 32nd-34th weeks. Between the 17th and the 32nd week, the weekly increment of NDVI was higher for locations actually used by ibex than for those used in late winter. This period exactly corresponded to the seasonal altitudinal shift of ibex (Figure 3-1b), indicating that by moving upwards, ibex obtained access to areas with better rate of vegetation growth than if they had not shifted altitudinally and had remained in lower winter quarters (H1.3). In Figure 3-2b, this pattern is explained by the comparison of absolute NDVI of used locations, broken down by habitat types, and the average NDVI of the study area: in spring, the used categories had generally higher absolute NDVI values (presence of snow in summer quarters). In summer, the used categories had generally lower absolute NDVI values than the average study area (with the exception of forest-shrubs and grassland), but with a delayed maturation pattern (e.g., mixed grass and rock, scree). The peak in the increment of productivity of used locations (17th-20th week, Figure 3-2a) corresponded to the peak in seasonal activity of ibex (Figure 3-1a). After the 32nd week, ΔNDVI fluctuated around 0 (Figure 3-2a), that corresponded to a plateaux in the altitudinal use (Figure 3-1b). The increment in productivity turned clearly negative around the 42nd week (Figure 3-2a), when ibex also started to reverse the altitudinal shift towards lower quarters (Figure 3-1b).

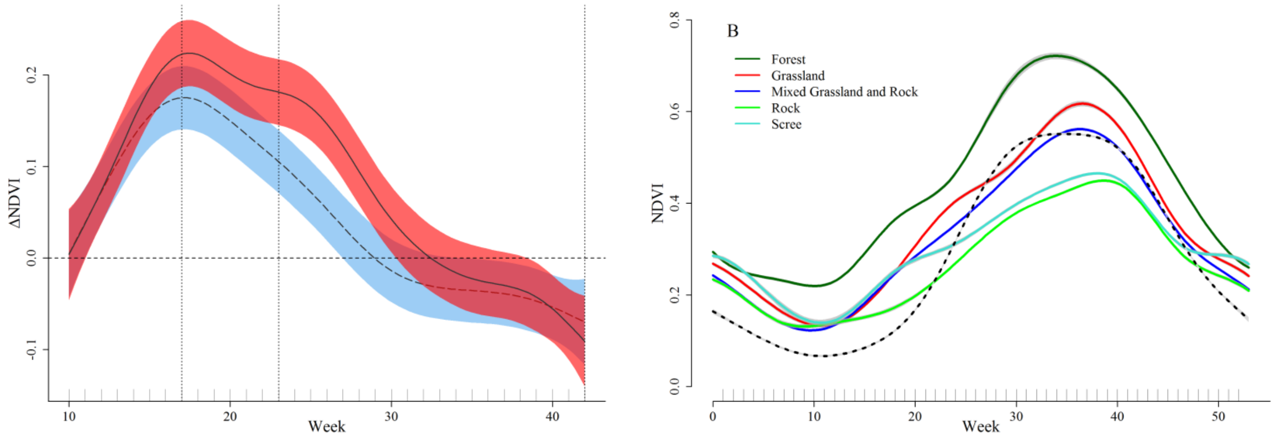

Figure 3-2 Panel A: Spring-summer ΔNDVI pattern of weekly average locations actually used by 21 female ibex, monitored in the Marmolada massif from 2010 to 2015, fitted as the regression spline smooth of the week (solid line), compared with the ΔNDVI pattern of the locations used by the females in the last 4 weeks of winter (dashed line). The confidence bands (shaded areas) are calculated using 95% confidence intervals (for parameter estimates of the best model). Panel B: annual weekly NDVI pattern of locations used by ibex plotted for the whole year, classified by land cover types, along with the average weekly NDVI pattern of the study area (dotted line). The dashed vertical lines delimit spring (17th – 23rd week) and summer seasons (24th – 42ndweek).

Table 3-3 Model selection of the best candidate models to explain pattern of ΔNDVI of used altitudinal locations ("1s") with respect to late winter locations ("0s") of 21 female ibex monitored in the Marmolada massif (2010-2015) (for parameter estimates of the best model see Table S. 3-4)

Individual (random)	Week (linear)	Week (cubic spline)	Week*summer_loc (cubic spline)	Summer_loc	Week*summer_loc (linear)	df	ΔAIC	Model weight
X			X	X		30	0.0	1.0
X		X		X		25	8.8	0.0
X			X			29	26.1	0.0
X		X				24	34.4	0.0
X	X			X		17	271.2	0.0
X					X	18	272.4	0.0
X	X					16	291.3	0.0
X				X		14	548.6	0.0
X						13	564.3	0.0

3.3.2. Daily/Hourly Scale

The temporal component of hourly active time during spring-summer was better fitted as a the cyclic cubic regression spline smooth of the hour in interaction with temperature class (Table 3-4; Adjusted $R^{2=}$ 34%, for parameter estimates see Table S. 3-6), thus indicating a strong daily pattern of activity and a degree of variability according to the temperature range, especially between the hottest days and the others **(H2.1a)**.

Specifically, the pattern of hourly active time was bimodal, with the first peak in the early morning and the second in late afternoon or evening, and a period of lower activity in between. The timing of the second activity peak and the average value of the hourly active time in the central hours of the day strongly varied according to the average daily temperature class. In hot days, the hourly active time in the central part of the day was much lower than in cooler days; moreover, the second peak was delayed and the activity prolonged in the early night hours, indicating a nocturnal compensatory behavior with respect to daylight hours in the hot days (Figure 3-3a). Indeed, the total daily active time (i.e., sum of hourly active time across days) was slightly higher in the hottest days (**H2.2;** highest T class: total daily active time = 12.34 (± SD 1.7) hours; intermediate T class: 11.92 (± SD 2.3); lowest T class: 11.94 (± SD 2.4); differences between lower classes and highest T class: $p<0.001$, see Table S. 3-5). For visualization purposes, we also plotted hourly active time against temperature as a continuous variable: the hourly active time increased steadily to a maximum at 15°Cm to then drop at very low rates (Figure 3-3b).

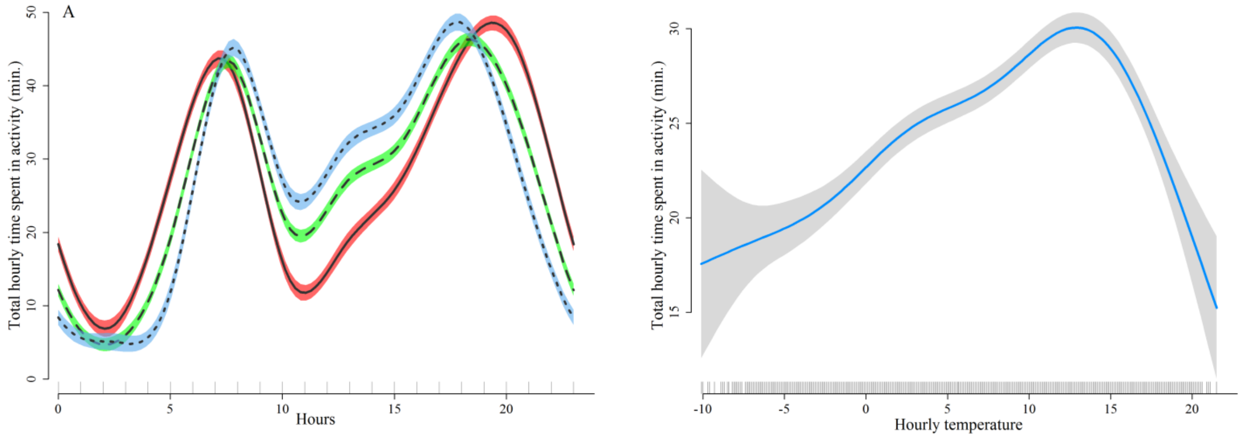

Figure 3-3 Panel A: spring-summer daily pattern of the hourly active time (min.) of 15 female ibex, monitored in the Marmolada massif from 2010 to 2015, fitted as the regression spline smooth of the hour (local time) in interaction with the average daily temperature class (high: ≥10.0°C, solid red line; intermediate: >3.70 °C and < 10.0°C, dashed green line; low: <=3.70°C, dotted blue line; best model). Panel B: spring-summer hourly active time fitted as the regression spline smooth of the hourly temperature expressed as a continuous variable, for the same sample size. Confidence bands (shaded areas) are calculated using the 95% confidence intervals.

Table 3-4 Model selection of the best candidate models to explain the daily pattern of the hourly active time of 15 radio-collared adult female ibex in the Marmolada massif (2010–2015).

Individual (random)	day length (linear)	Hours*Tclass (cubic spline)	Tclass (linear)	Hours (cubic spline)	T (spline)	T (linear)	Hours (linear)	df	ΔAIC	Model weight
X	X	X	X					42	0.0	1.0
X	X				X			33	1669	0.0
X	X					X		25	2148	0.0
X	X			X				24	2149	0.0
X	X						X	17	18225	0.0
X	X				X			25	21923	0.0
X	X					X		17	22164	0.0
X	X							16	22601	0.0

The temporal component of the hourly altitude used by female ibex during spring-summer was best modelled by the regression spline smooths of the hour and of the hourly temperature, and showed a steady, almost linear increase with T (**H 2.1b**; Table 3-5 and Figure 3-4a; Adjusted R^2= 41.8%). Thus, the altitudinal gain must have been greater in the hottest part of the day. For visualization purposes, we modelled the hourly altitude used against the regression spline smooth and linear component of the hour: indeed a clear daily altitudinal shift was observed, with the night time spent at the lowest altitudes, a steep increase after dawn that peaked around mid-morning, and a slower return during the day (Figure 3-4b; see Figure S. 3-6 for the same plot for all months, including winter ones).

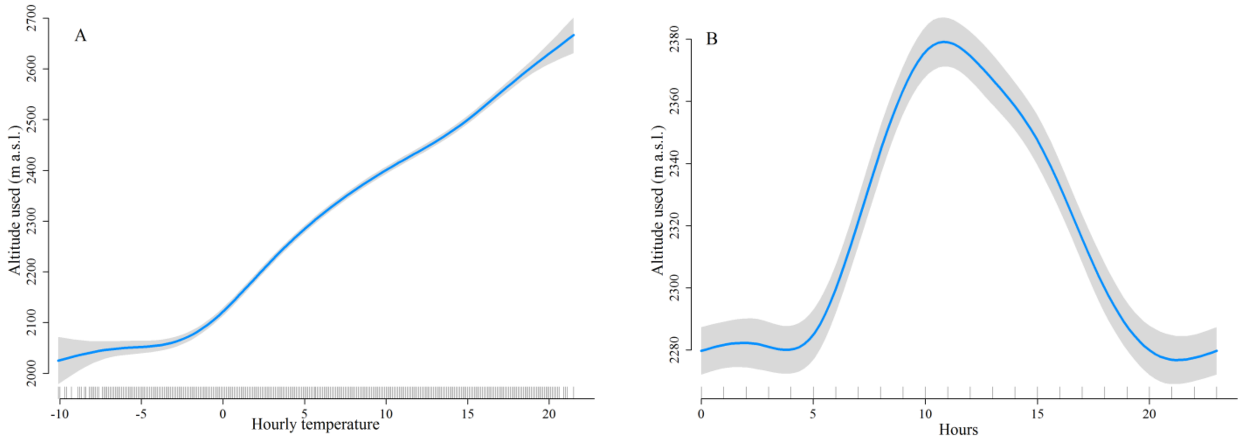

Figure 3-4 Panel A: spring-summer altitude used by 21 female ibex, monitored in the Marmolada massif from 2010 to 2015, fitted as the regression spline smooth of the hourly temperature (best model: see Table 3-5). Panel B: spring-summer daily pattern of altitude fitted as the regression spline smooth of the hour, for the same sample size. Confidence bands (shaded areas) are calculated using the 95% confidence intervals.

Table 3-5 Model selection of the best candidate models to explain the daily pattern of the hourly altitude used by 21 radio-collared adult female ibex in the Marmolada massif (2010–2015).

Individual (random)	daylength (linear)	Hours*Tclass (cubic spline)	Tclass (linear)	Hours (cubic spline)	T (spline)	T (linear)	Hours (linear)	df	ΔAIC	Model weight
X	X			X	X			37	0.0	1.0
X	X			X		X		30	461	0.0
X	X				X			30	1227	0.0
X	X					X		23	1709	0.0
X	X	X	X					44	2666	0.0
X	X			X				29	22593	0.0
X	X							22	24699	0.0
X	X						X	23	24699	0.0

The Resource Selection Analysis showed a distinct daily pattern of the coefficients of relative probability of use of land-cover types in spring-summer, that reflected the daily activity patterns and altitude used (Figure 3-5; see also Figure 3-3 and Figure 3-4). Rocky habitats (rock, scree: Figure 3-5) were positively selected with respect to forest-shrubs only in daylight. Grassland habitats (grassland, grasslands mixed with rock: Figure 3-5) were positively selected with respect to forest-shrubs amidst the two peaks of the probability of being active, hence in the central part of the day, but also in late evening-early night. The relative probability of use of mix-grass rock was not different from forest during night-time, whereas all other categories were negatively selected.

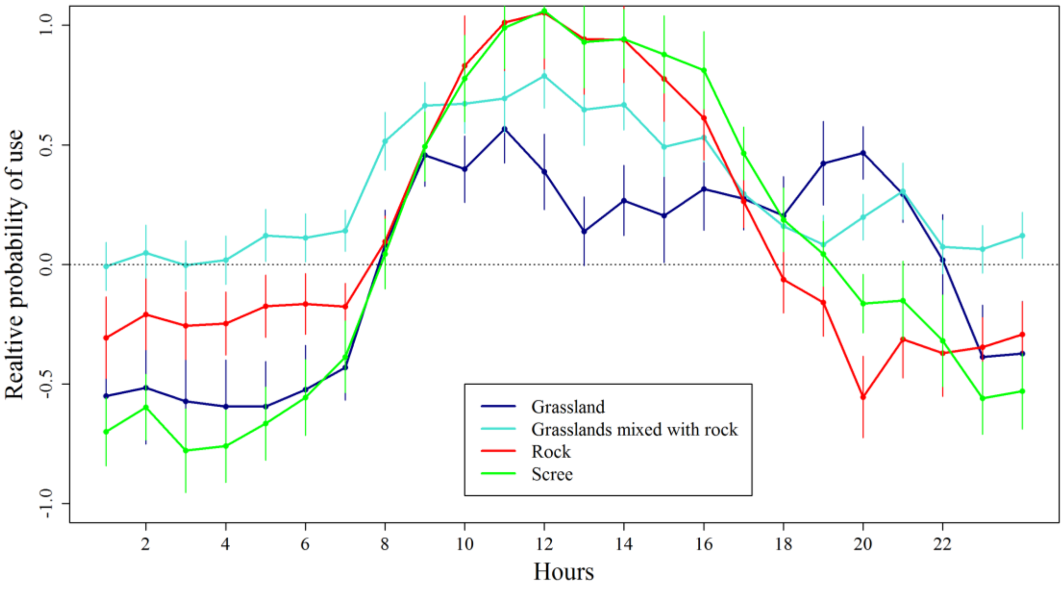

Figure 3-5 Plot of the coefficients of relative probability of use of land-cover types by 21 female ibex in spring-summer, monitored in the Marmolada massif from 2010 to 2015, as estimated by hourly Resource Selection Functions. Used locations refer to each hour, and are conditionally matched to all available locations of the same day. The coefficients are referred to forest-shrubs as reference category.

3.4. **Discussion**

In this study, we showed that female ibex responded to climatic factors and forage availability at different temporal scales (Parrini *et al.*, 2003; Rivrud *et al.*, 2010). At the annual scale, they responded to vegetation productivity and phenology with an altitudinal shift that started in spring and peaked in summer. This way, they first followed the vegetation green-up, to then access habitats where vegetation had a lower absolute productivity than lower quarters, but a less-steep senescence too. This suggests that the altitudinal shift of ibex is part of a resource acquisition tactic in potential accordance with the forage maturation hypothesis (Fryxell, 1991; Hebblewhite *et al.*, 2008; Bischof *et al.*, 2012), for the first time here reported in ibex. Moreover, in spring-summer, at the daily scale, female ibex also reacted to thermal stress by varying activity and altitude throughout the day. Moreover, they showed behavioral plasticity in relation with daily mean temperature, by modifying daily activity rhythms in order to forage during the hours when thermoregulation costs were lower. This way, they were able to keep the total daily foraging time constant across widely different daily mean temperatures, such as those observed in the study area (from -6.9°C to +17.7 °C), a result we firstly show in a temperature-sensitive mountain ungulate, thanks to high resolution, remotely logged activity data. Moreover, female showed a daily pattern of relative probability of use of land-cover types in response to altitudinal shifts, preferring ‘forage’ habitats during high activity hours and refuge areas during resting hours. Hence, female ibex maximized both thermal cover and resource acquisition, because they moved across food-rich habitats when shifting between low altitude bed-sites and high altitude cool areas (see Mitchell & Lima, 2002 and van Beest *et al.*, 2013). Below, we discuss these patterns and then their implications in a perspective of changing climate.

Female ibex showed very low activity in deep winter, to then increase it sharply in late winter and spring. We expected this pattern because Alpine ibex have evolved a physiological reduction of metabolic rate and consequently of activity to reduce energy expenditure at low temperatures (Arnold *et al.*, 2004; Signer *et al.*, 2011). Similar trends, although less marked, have been reported for other wild ungulates living in areas with harsh winters (e.g.: Beier & McCullough, 1990a; Loe *et al.*, 2007). However, the change in activity that we observed was very rapid, with a 60% increase in total daily active time occurring within few weeks in late winter. The ANODEV analysis indicated that at the annual scale the total daily active time was influenced by both temperature and NDVI. Rising temperatures likely triggered a physiological increase in metabolic rate and activity (Signer *et al.*, 2011), which can be advantageous if the animals find, at low locomotion cost, new forage. Indeed, activity peaked already before the female ibex started to shift to higher elevations, and while they were maintaining very small weekly home ranges (Párraga *et al.* unpublished data). This suggests that they were exploiting the vegetation regrowth at low elevations, without the need, or the convenience, to modify space use. Indeed, in this early period of high activity at low elevation, the NDVI increased between successive weeks at an incremental rate. This interpretation is also consistent with the observations of Villaret *et al.*, (1997) and Parrini *et al.*, (2003) that in spring ibex used low altitude grasslands more than other habitats. When NDVI weekly incremental rate started to decrease, ibex initiated the seasonal altitudinal migration. Consequently, the annual pattern of altitude use by female ibex was more synchronous with that of NDVI than with that of temperature (almost overlapped trend), as suggested by the ANODEV. Hence, our results suggest that the spring-summer altitudinal migration allowed the female ibex to exploit the altitudinal gradient in vegetation productivity. During this period, they experienced NDVI values increasing at a higher rate than what they would have experienced in winter quarters, although with lower absolute values. When the average NDVI reached a plateau and then started to decrease, the female ibex stopped the altitudinal migration and used habitats with a delayed NDVI peak and senescence (i.e. grasslands mixed with rocks and scree). Because of the ability to optimize the *increment* in NDVI values (as opposed to *absolute* NDVI values, Mason *et al.*, 2017), we suggest that female ibex obtained a higher vegetation quality by migrating at higher altitudes, and compensated for the decreased relative vegetation abundance and the increased spatial fragmentation of vegetation patches by modifying space use. Párraga *et al.* (unpublished data) found that weekly home range size of female ibex in this population increased markedly during spring and summer, and was negatively correlated with the average NDVI of areas used.

Our results are in agreement with research on other ungulates (mainly deer, e.g., Albon & Langvatn, 1992, and African antelopes, e.g., Fryxell & Sinclair, 1988), that predicts that the animals migrate along a phenological gradient of plant development in order to maximize energy intake. The interplay between absolute productivity, and rate of incremental productivity, are also potentially in accordance with the Forage Maturation Hypothesis that suggests an optimized energy intake for intermediate forage biomass (Fryxell, 1991; Hebblewhite *et al.*, 2008). However, the use of sparsely vegetated habitats at the end of the vegetation growth season and of the altitudinal migration may indicate a seasonal plasticity in optimizing quantity, and quality, also in consideration of their capital breeding strategy (Toïgo *et al.*, 2002). Schweiger *et al.*, (2015) verified that ibex foraged in areas where plant biomass was lower, but of higher nutritional value, than where red deer or Alpine chamois foraged. In agreement with this, Aublet *et al.*, (2009) found that the nitrogen content of Alpine grasslands increased, while biomass and fibre content decreased, along an altitudinal gradient and over the summer. Further research on biomass, diversity and quality of plant species utilized in these extreme environments could clarify such variability.

Other studies on large herbivores indicate that seasonal movements enhance access to high quality food in trade-off with predation risk (Festa-Bianchet, 1988; Hebblewhite & Merrill, 2009; Bischof *et al.*, 2012). In this analysis we did not include perception of predation risk (Bonnot *et al.*, 2016), but it should be interesting to understand how this affects the use of space (see Chapter 4). Other factors (e.g., tourism effect: Lovari *et al.*, 2007; presence of domestic animals (Mason *et al.*, 2014b)) were not included in our analysis because these variables were not quantified, or because they were perceived of secondary importance for the population under study (tourists restrained to trails; domestic animals managed at lower elevation; Semenzato P., pers. comm.).

The seasonal variation in activity rhythms and the altitudinal migration are tactics to optimize resources acquisition during spring-summer. In summer, high temperature can be an important limiting factor for wild ruminants in warm and arid areas (e.g., Maloney *et al.*, 2005; Bourgoin *et al.*, 2008, 2011; Marchand *et al.*, 2015), but also at northern latitudes (e.g.: van Beest *et al.*, 2012; Melin *et al.*, 2014; Street *et al.*, 2015) or in mountainous areas, where temperature has remarkable daily variations (e.g.: Aublet *et al.*, 2009; Mason *et al.*, 2014). Under thermal stress, different species of ungulates reduce activity rhythms and select for thermal cover habitats (Bourgoin *et al.*, 2011; van Beest *et al.*, 2012; Allred *et al.*, 2013; Street *et al.*, 2015). Activity patterns and habitat selection are indeed highly flexible behaviors that can be adjusted to variations in resource availability and energetic costs or external constraints. In particular, daily altitudinal migration and adjustments of the activity budgets are thermoregulation tactics of mountain ungulates (Rice, 2008; Aublet *et al.*, 2009; van Beest & Milner, 2013; Mason *et al.*, 2014b). Moreover, Signer *et al.*, (2011) suggested that physiological adaptations to extreme winter weather (e.g. fur, heart rate, …) make ibex highly sensitive to high temperature in summer, and predicted a collapse of activity with ambient temperatures exceeding 16°C. Aublet *et al.*,(2009) found that male Alpine ibex showed heat discomfort in temperatures above 15–20°C. In agreement with these results, we found an asymmetric effect of hourly temperature on hourly active time, which peaked at about 14°C, and dropped drastically at temperatures higher than this threshold.

The daily pattern of hourly active time of the female ibex during spring-summer was similar to that extrapolated for August by Signer et al (2011). We found a reduction of activity in the central and hottest hours of the day that was compensated by an activity increase in early morning and late night, especially in warmer days. This way, females were able to keep a constant daily activity budget, and hence foraging time, across a wide range of average daily temperatures, in summer. This explains also why temperature had little relation with daily active time for the summer season (see ANODEV analysis). Therefore, at the daily scale, female ibex showed behavioral plasticity to trade-off between foraging and thermoregulation needs, a result so far unclear, e.g. for male ibex (Aublet *et al.*, 2009; Mason *et al.*, 2017). Elk compensated for the decrease in diurnal activity time by increasing nocturnal feeding (Merrill, 1991). Our results showed a complex interdependence between activity rhythms, and movement behavior in a temperature-sensitive mountain ungulate adapted to environments with sparse and patchy resources. In this case, the compensation for total forage activity in trade-off with heat stress was accompanied daily migration. Indeed, throughout spring and summer, average altitude of hourly locations increased linearly with hourly temperature, so that highest elevations were used in the central hours of the day. This is in agreement with what found on males, and other alpine species (male ibex: Aublet *et al.*, 2009; Alpine chamois: Mason *et al.*, 2014), and supports the hypothesis that the daily altitude migration is a tactic to reduce thermal stress.

Our results supported the temperature-sensitivity hypothesis for this mountain species, and the thermoregulatory role for daily activity patterns and altitudinal shifts. However, this came with a cost, since female ibex moved to potentially sub-optimal habitats with low plant biomass in the hottest part of the day, especially in more-than-average hot days. Our direct observations indicated that female ibex exploited the altitudinal movement phases to feed, thus optimizing the transition from night resting areas to day thermal-cover areas by foraging- as reflected in activity patterns. In support to this, the resource selection analysis showed a clear relationship between the relative probability of use of land-cover types and daily activity patterns and altitude use.

Climate warming can dually affect heat-sensitive large herbivores: directly, by the effect of temperature increase on thermonetruality and thermoregulation effectiveness and costs, or indirectly, via spatio-temporal variation of resource availability, including phenology. Alpine ungulate are well adapted to winter low temperatures, but poorly to high summer temperatures.

Energetic costs increase dramatically when an individual is outside its thermo-neutral zone (Boyles *et al.*, 2011). In this work, we support that behavioral plasticity may provide resilience to the environmental pressure associated with current climate change (Boyles *et al.*, 2011). Changes in activity and movement patterns and resource selection are responses to avoid thermal stress and maintain the fitness of individuals (van Beest & Milner, 2013), by balancing the trade-off between the need for temperature control and forage acquisition. However, an excessive increase in temperature, i.e. beyond the limits in which these mechanisms evolved, can decrease fitness. In Alpine chamois the temperature increment recorded under climate change reduced forage activity (Mason *et al.*, 2014b), with negative consequences on body conditions (Mason *et al.*, 2014a). One important finding of our study was that female ibex were able to modify daily patterns of activity to keep the total activity budget constant. It would be important to understand whether this mechanism would still be efficient in the forecasted temperature increase scenarios. Excessive summer temperatures could force females to prolong the use of sub-optimal habitats beyond the possibility for a compensation. This could be worsened by the expected upward shift of the plant communities due to climate warming (Walther *et al.*, 2005; Dirnböck *et al.*, 2011), which might reduce the area of suitable habitats for ibex. Conversely, habitats may become richer in nutrients also at high elevation. Hence, further research also in other Alpine ibex colonies should be undertaken, in order to improve our ability to forecast this species resilience to temperature and forage variability

Spring phenology is another recorded effect of climate warming in ungulates (Pettorelli *et al.*, 2007; van Beest & Milner, 2013). In the Alpine context, the balance between temperature increase and vegetation productivity is thin. Winter snow accumulation and snowmelt determines the timing of spring vegetation onset. The increase in the altitudinal threshold for snow cover accumulation and the higher late winter-spring temperatures, as predicted in a context of climate change, may generate a rapid snowmelt, with earlier and more prolonged vegetation growth seasons (Ernakovich *et al.*, 2014). Nevertheless, in Alpine regions, photoperiod limits plant productivity, limiting the extent to which the growing season can lengthen (Keller & Körner, 2003; Ernakovich *et al.*, 2014). Moreover, an early snowmelt may also alter plant water availability (Marty *et al.*, 2017), on which alpine plants depend for growth (Jonas *et al.*, 2008), so that an earlier plant senescence could be expected (Ernakovich *et al.*, 2014). These changes might lead to an earlier, but also shorter period of availability of high-quality forage. Acceleration of plant productivity (or vegetation maturation) during green-up can have profound effects on the energy balance during late gestation and lactation, causing a mismatch between the peak of resource availability and demand, with direct consequences on growth, body mass and survival of kids in mountain ungulates (Pettorelli *et al.*, 2007; Rughetti & Festa-Bianchet, 2012; Mason *et al.*, 2014a). In a capital breeder, like ibex (Toïgo *et al.*, 2002), spring is fundamental to recover body mass and, in females, to face the high energetic requirements of parturition and lactation. The rapid post-winter rise of activity that we found in female ibex supports the crucial role of this period for the annual energy budget. Hence, the consequences of spring anticipation should be further assessed in Alpine ibex, as a model species for climate change effects in the Alpine range.

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3.7. Supplementary Material

Appendix 1: Validation of activity behavior classification

We verified the possibility to use the signal of activity sensors of the GPS collars to discriminate between behavioral categories of female ibex behaviors. The GPS collars used in this study (GPS PRO light, Vectronic Aerospace GmbH) were equipped with a dual-axis activity sensor, scheduled to store the average of acceleration data (x,y; range 0-255) at five-minute intervals. We used the method proposed by Gervasi et al. (2006) to discriminate between "inactive" and "active" behaviors. This method relies on the bimodal frequency distribution of the activity signal and defines the separation point between "inactive" and "active" intervals as the lowest activity value between the two modes of the distribution. Using the frequency distribution of the summed x+y signals (range: 0-510) collected from fifteen free-ranging ibex females from 2010 to 2015, we identified such separation point at a summed activity signal of 45 (Figure S. 3-1). Based on this, we classified as 'inactive' all intervals having a summed activity signal < 45, and as 'active' those with an activity signal ≥ 45. Other studies have identified the threshold to discriminate 'inactive' and 'active' behavior between 30 and 50 (sum x + y) (Gervasi *et al.*, 2006; Löttker *et al.*, 2009).

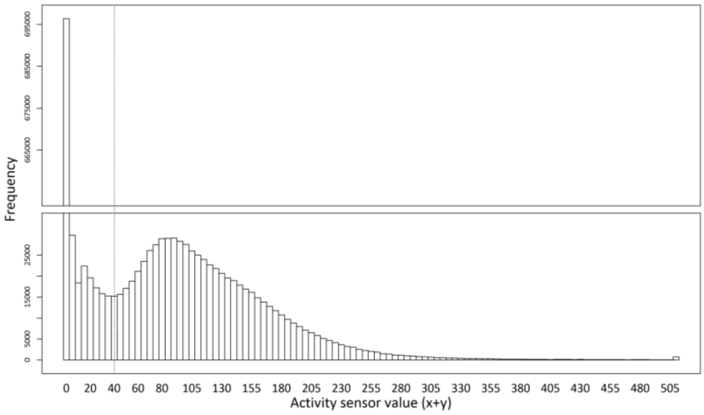

Figure S. 3-1 Frequency distribution of the activity signal (sum x+y) from the dual-axis activity sensors of 16 radio-collared female ibex, monitored in the Marmolada massif (2010-2015). The dotted line defines the threshold value of 45 used to discriminate active and inactive behaviors of animals.

We validated the threshold used to discriminate between 'active' and 'inactive' behaviors based on the activity sensor through direct observations of behavioral categories conducted on seven radio-collared free-ranging female ibex. We observed the radio-collared animals for a total of 79 hours (corresponding to 798 five-minute intervals), from July to September of 2013 and 2015, between 6:00 and 20:00 local time. With the aid of a digital clock with 1 second resolution, synchronized on GPS time, we recorded the time spent into 'feeding' (bouts of feeding: biting, chewing and swallowing, interrupted by relocation movements between clusters of plants (Owen-Smith *et al.*, 2010); 'walking' (with a clear directionality, including active interactions between individuals); 'standing' (standing in rumination or vigilance without leg movements); and 'resting' (lying asleep or ruminating). We observed that females spend most of the time resting (54.25%) and feeding (32.43%). We switched to a new behavior if it lasted more than 10 seconds. Then, for each five-minute interval, we summed the seconds spent in each behavior. We classified the five-minute intervals of observations using two behavioral categories: 'active' and 'inactive'. Feeding and walking were categorized as 'active' behaviors, while standing and resting as 'inactive' behaviors. We classified observed intervals as 'active' when the active behaviors accounted for ≥ 50% of the observed time (≥ 150 seconds of the five-minute interval) and as 'inactive' otherwise. We then compared the classification of intervals based on the signal threshold with the ground truth based on visual observation. The signal threshold based on activity sensor classified correctly 85.5% of 'inactive' intervals and 92.1% of 'active' intervals (Table S. 3-1).

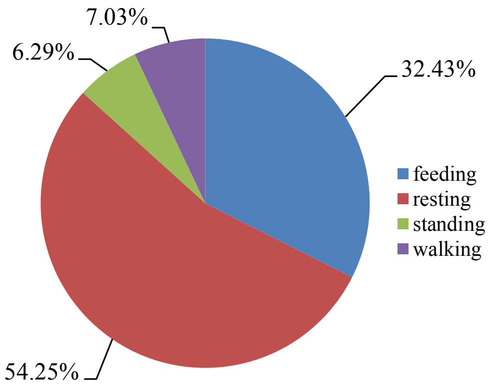

Figure S. 3-2 Proportion of time (in second) spent in the different behaviors recorded by direct observations of seven radio-collared free-ranging female ibex, monitored between 6:00 and 20:00 local time, for a total of 79 hours, from July to September of 2013 and 2015 in the Marmolada massif.

Table S. 3-1 Correspondence between the collar-based (GPS PRO Light, Vectronic Aerospace GmbH) and the observation-based classifications into "inactive" or "active" of 948 intervals of 5 minutes recorded on seven radio-collared free-ranging female ibex monitored in the Marmolada massif between July and September in 2013 and 2015.

Observed activity	**Sensor collar-based activity**	
	Inactive	**Active**
Inactive	85.5%	7.9%
Active	14.5%	92.1%

Our results are consistent with previous studies on dual-axis activity sensors. In these studies, correspondence between observed and sensor-measured classification of activity ranged from 76% to 93% (moose *Alces alces:* Moen et al. 1996; red deer *Cervus elaphus*: Adrados et al. 2003, and Lottker et al. 2009; bear *Ursus arct*os: Gervasi et al. 2006).

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Appendix 2: Identification of ibex behavioral seasons

Alpine areas are characterized by extreme seasonality with climate and food resources following patterns of temporal variation that poorly match with astronomic seasons or arbitrarily pre-defined periods. In order to identify biologically relevant seasons for Alpine ibex females in the study area, we used a clustering approach to define periods with homogenous habitats use and movement features of the animals, following a procedure derived from Basille et al., (2013).

We used 87.795 hourly GPS location data collected from September 2010 to October 2014 on 12 Alpine ibex females. We assigned each location to the Julian date, starting from 21st December. To derive habitat data, we extracted altitude and slope (°) from a regional digital elevation model (resolution: 5x5m; https://www.regione.veneto.it/web/ambiente-e-territorio/ctr; http://www.territorio.provincia.tn.it) and land cover from a 1:5.000 vector land-cover map . For our purposes we re-reclassified land-cover data into "forest-shrubs" (which included coniferous and mixed forest, and shrubs), "grassland", (which included Alpine natural grasslands and pastures), and "scree plus rocks" (which included scree and bare rocks). We associated each location with the corresponding elevation, slope, and land use category. We calculated for each location an activity index as the average of the XY activity values from the accelerometers embedded into the GPS collars in the 10 minutes immediately preceding and following the scheduled time for the location. Finally, we calculated speed (m/h) between subsequent hourly locations. We then calculated for each Julian date and across all individuals the average values of elevation, slope, activity index and speed, and the frequency of each land use category. We used a hierarchical cluster analysis of these variables (proc cluster, method = Ward; SAS© 9.3, SAS Institute, Cary NC) to group Julian dates into homogeneous periods.

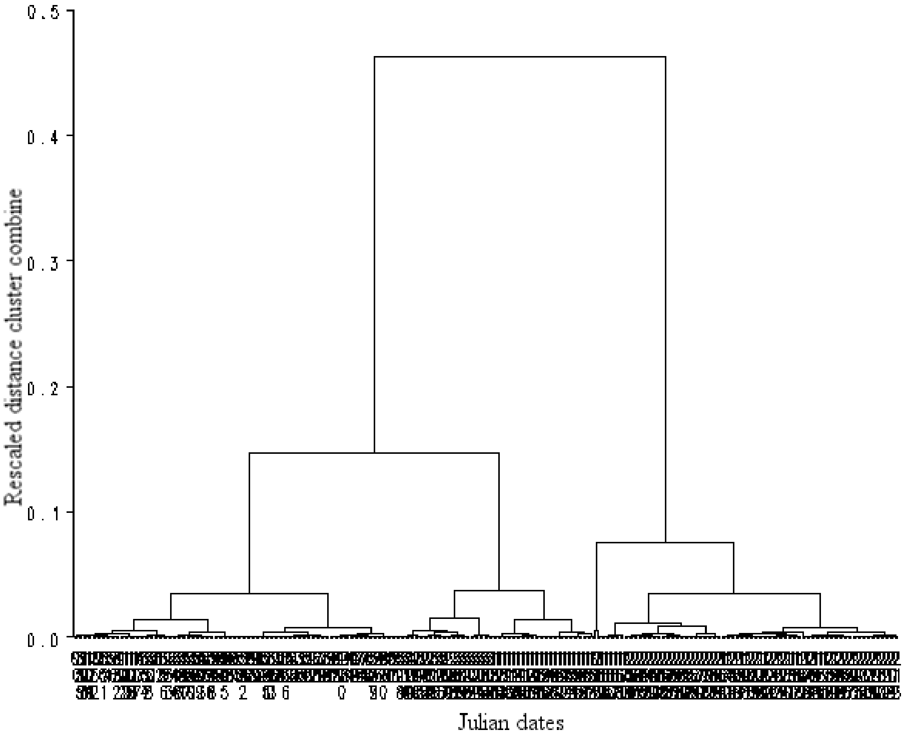

Figure S. 3-3 Dendrogram of the clustering procedure to group Julian dates according to habitat and movement features associated with hourly GPS locations from the female Alpine ibex in the Marmolada Massif.

The results supported the presence of three clusters (Figure S. 3-3). One cluster corresponded to a prolonged winter season, a second cluster to a shorter summer season, and the third cluster to two very short periods (approximately 30-40 days) corresponding to a transition from winter to summer (named "spring") and from summer to winter (named "fall") (Figure S. 3-4).

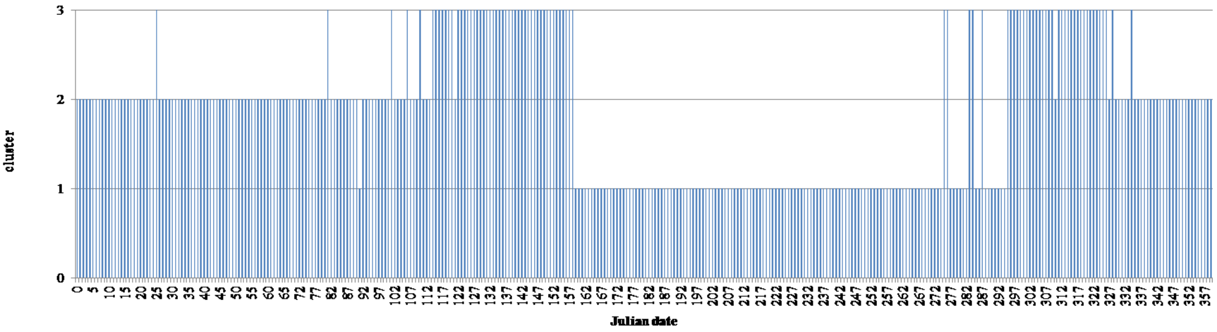

Figure S. 3-4 Assignment of Julian dates (0 = December 21st) to clusters 1 ("summer"), 2 ("winter") and 3 (winter-summer and summer-winter transitions, named respectively "spring" and "autumn")

The winter cluster was characterized, in comparison with the summer cluster, by lower elevations and higher slopes, a similar use of grasslands, a much higher use of forest-shrubs and a much lower use of screes and rocks, and by clearly lower speed and activity index values (Figure S. 3-3). The transition cluster showed intermediate values between the other two clusters for elevation, slope, and forest, a much higher use of grasslands, a use of screes and rocks similar to winter, a speed index similar to that of winter, but an activity value similar to that of summer (Figure S. 3-3).

Table S. 3-2 Average habitat and movement features of the three clusters identified. The Transition cluster is split into the winter to summer transition (spring) and the summer to winter transition (fall).

	Winter		Summer		Transition	
	Mean	SD	Mean	SD	Mean	SD
Elevation (m)	2067	51	2379	69	2150	77
Slope (°)	48.6	1.6	44.5	1.8	45.0	2.1
Grasslands (%)	10.5	4.3	7.8	4.3	21.3	5.7
Forest (%)	33.6	10.6	6.0	4.4	22.2	9.8
Screes + rocks (%)	54.7	11.1	85.3	7.6	55.3	10.1
Activity index	17.4	3.3	35.5	7.4	30.0	7.9
Speed index (m/h)	56.2	60.9	125.4	62.8	70.8	22.3

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Table S. 3-3 Generalized additive mixed models used in the ANODEV procedure for daily active time and average altitude (y): the null model (simplest model "LS"), the regression spline smooth of the weekly NDVI and weekly temperature, respectively (intermediate model "LI"), and the observational week as a factor (most complex model "LC").

Model	
LS	y ~ s(individual, bs = "re") + 1
LI temp	y ~ s(individual, bs = "re") + s(weekly temperature)
LI ndvi	y ~ s(individual, bs = "re") + s(NDVI study area)
LC	y ~ s(individual, bs = "re") + as.factor(week)

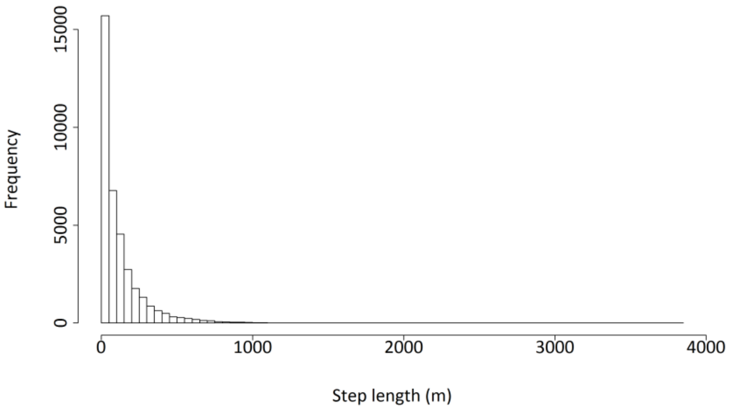

Figure S. 3-5 Empirical distribution of step lengths (distance between two consecutive points) in spring summer of 21 radio-collared adult female ibex monitored in the Marmolada massif (Italy) 2010–2015.

Table S. 3-4 Coefficients of the best model fitting pattern of ΔNDVI of used spring-summer locations with respect to late winter locations (response used'1'/winter'0') of 21 female ibex in the Marmolada massif (2010-2015). Response (R^2adj=0.39)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	0.08	0.009	8.7	<0.001
Summer_loc	0.03	0. 007	5.3	<0.001

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value
s(individual)	14.69	18.00	4.28	<0.001
s(week): Summer_loc (0)	5.85	6.98	40.6	<0.001
s(week): Summer_loc (1)	7.21	8.23	51.07	<0.001

Table S. 3-5 Coefficients of the linear mixed-effects model fitting the total daily active time of 15 female ibex against three classes of daily average temperature [Model : total daily active time ~ T avg. class, random = individual]

	Value	Std.Error	df	t-value	p-value
Intercept	12.43	0.20	2371	51.69	<0.001
T avg. class intermediate	-0.46	0.12	2371	-4.56	<0.001
T avg. class lower	-0.47	0.11	2371	-4.01	<0.001

Table S. 3-6 Coefficients of the best model fitting the daily pattern of the hourly active time of 15 adult female ibex in the Marmolada massif (2010–2015).

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	19.921	1.0817	18.416	<0.001
T class intermediate	-0.586	0.197	-2.977	0.003
T class lower	-0.598	0.228	-2.622	0.008
Daylight	0.801	0.063	0.063	<0.001

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value
s(individual)	13.702	14	51.27	<0.001
s(hours): T class higher	7.964	8	835.89	<0.001
s(hours): T class intermediate	7.987	8	1588.82	<0.001
s(hours): T class lower	7.986	8	1064.23	<0.001

Table S. 3-7 Coefficients of the best candidate models to explain the daily pattern of the hourly altitude used by 21 radio-collared adult female ibex in the Marmolada massif (2010–2015).

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	2218.186	20.662	107.357	<0.001
daylight	3.664	0.547	6.696	<0.001

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value
s(individual)	19.955	20.000	1103.6	<0.001
s(hours)	6.516	8.000	161.1	<0.001
s(T hourly)	7.790	8.534	3099.1	<0.001

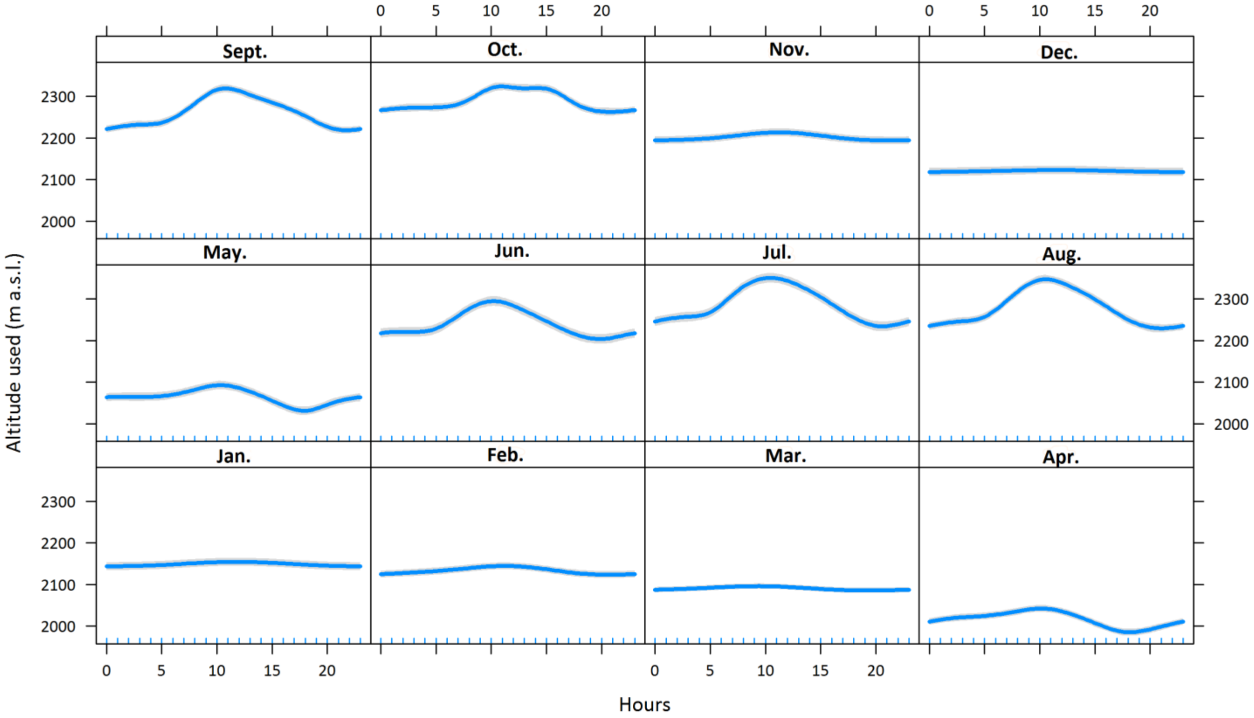

Figure S. 3-6 Monthly variation of daily pattern of altitude used by 21 female ibex, monitored on Marmolada massif from 2010 to 2015, fitted as the regression spline smooth of the week nested by years, the individuals as random factor.

4. Better safe than sorry: anti-predatory response of female ibex under multiple environmental and life-history constraints. [4]

4.1. Introduction

Predation represents a major selective force for animal populations, with direct consequences on their dynamics and evolution (Lima & Dill, 1990). In a predator-prey system, the preys' behavior co-evolves with predators in order to minimize the risk of predation and to maximize survival and reproductive success. Preys respond to predation risk by, e.g., changing morphology (Tollrian & Harvell, 1999), physiology (Rovero *et al.*, 1999; Creel *et al.*, 2007) and behaviors (Lima & Dill, 1990; Lima, 1998; Creel *et al.*, 2005; Hebblewhite *et al.*, 2005). Unlike the former responses, anti-predatory behaviors are more flexible to variations in predation risk, because they may change not only over evolutionary times (co-evolutionary process), but especially at ecological times (i.e., an animal's lifetime, or less), and among individuals. Moreover, at the individual level, behavioral tactics can help to face variations in predation risk on a seasonal, daily, or even a minute by minute basis (Lima & Dill, 1990), and take different forms: vigilance (Toïgo, 1999; Childress & Lung, 2003; Creel *et al.*, 2014), retreat to safe habitats (Kotler *et al.*, 1991; Sih, 1997), grouping/herding (Blumstein & Daniel, 2005; Creel *et al.*, 2014), and movement and activity patterns (Sih & McCarthy, 2002; Creel *et al.*, 2005; Fortin *et al.*, 2005; Hebblewhite *et al.*, 2005).

Large herbivores are long-lived species with high parental investment and generally sexual dimorphism, so that the perception of predation risk, and hence the strength of responses, is affected by life-history traits, including sex, body mass, and parental investment (Main *et al.*, 1996; Ruckstuhl & Neuhaus, 2002). Females with dependent offspring, in particular, should adopt

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behavioral tactics to lower predation risk more than non-reproducing females, for the higher vulnerability, and the fitness cost due to offspring loss. This, in some instances, leads to spatial segregation between females with and without offspring (Ruckstuhl & Neuhaus, 2002). In gregarious species, differences in anti-predatory response can emerge at a finer temporal scale, such as the use of specific habitat features. For example, mouflon females (*Ovis orientalis musimon*) selected closed habitats during lactation in contrast with non-lactating females, that selected open habitats richer in forage (Bon *et al.*, 1995; Ciuti *et al.*, 2009).

Reproductive females are also constrained by other factors than predation risk, such as increased energy demand due to lactation (Loudon, 1985), and limited mobility of offspring, in case of ‘followers’ species (Ralls *et al.*, 1986; Grignolio *et al.*, 2004; Ciuti *et al.*, 2006; Ramanzin *et al.* unpublished data). Hence, reproductive females have to respond to environmental factors common to all individuals, as forage availability and climatic constraints, as well as to specific needs linked to reproduction. In this paper, we considered an ungulate species adapted to extreme environments, the Alpine ibex (*Capra ibex*), to study the effect of female anti-predatory response in presence of steep environmental and climatic gradients, at different temporal scales. Several studies on anti-predatory behaviors of high mountain ungulates have identified steep rocks as elective refuge areas (e.g., Grignolio *et al.*, 2007a; Festa-Bianchet & Côté, 2008) and the use of these areas by females with kids as an anti-predatory tactic (Bergerud *et al.*, 1984; Fox *et al.*, 1992; Festa-Bianchet & Côté, 2008). As a proxy for environmental variation, we considered seasonal and daily altitudinal use, since previous studies have shown that female ibex perform seasonal and daily altitudinal shifts, and that this behavior is a trade-off between thermoregulation needs and trophic resource acquisition (Chapter 3; for male ibex: Aublet *et al.*, 2009; Mason *et al.*, 2017).

Alpine ibex is a gregarious species, where individuals within the colony show associated space use and movement responses (Toïgo, 1999). This is particularly evident for nurseries, where reproductive and non-reproductive females (i.e., with and without kids), and young individuals aggregate. The occurrence of movements linked with anti-predatory behavior shall therefore be assessed within this framework. Previous studies on Alpine ibex have analyzed the spatial behavior of female ibex via direct observations during daytime, at broad temporal scale, whilst the persistence of anti-predatory behavior at the daily scale, comparing daytime and nighttime behaviors, has not been addressed yet, to our knowledge. Hence, we analyzed movement behavior in order to gain insights into the temporal scale at which anti-predatory behavior of female ibex emerge.

To assess the occurrence of anti-predatory behavior in presence of other environmental and reproductive constraints, we assessed the use and distance from refuge areas and the use of altitude, in lactating and non-lactating females during different periods of the reproductive cycle, and between daytime and nighttime. If the perceived risk of kid predation was an important factor affecting the movement behavior of females, we expected different patterns for the use of refuge areas (H1), but not for the use of the altitudinal range (H2), between the two groups of females. In particular, we expected that distance from refuge areas differed between lactating and non-lactating females, but only in presence of kids (i.e., after births) (P 1.1), with lactating females staying inside or closer to refuge areas for quick escapes with kids in case of risk. We expected this difference between reproductive status' responses to be maintained both during daytime and nighttime periods, under a constant perceived risk of kid predation. Alternatively, time of the day would affect use of and distance from refuge areas, in case of lower perception of risk, or prevalence of other constraints, during either daytime or nighttime (P 1.2). For thermoregulation and trophic resource acquisition needs, female ibex are expected to vary their altitudinal use amongst seasonal periods (seasonal altitudinal shift), regardless of their reproductive status, given the highly gregarious behavior of ibex. Alternatively, if females with kids were affected more than females without kids by the same constraints, a difference should be observed, but only after births (P 2.1). In response to thermal stress (daily altitudinal shift: Semenzato *et al.*, unpublished; Aublet *et al.*, 2009), female ibex are expected to vary their altitudinal use between day and night differently among seasonal periods, but independently of their reproductive status. Alternatively, specific requirements of their kids, such as high sensitivity to high temperatures, and/or less efficient locomotion capacities (Grignolio *et al.*, 2007b), would force lactating females to adapt their daily variation in altitude use differently from females without kids (P 2.2).

4.2. Methods

4.2.1. Ibex population, study area and environmental covariates

The study area consisted of four Alpine valleys in the Marmolada massif group, in the Eastern Italian Alps (Dolomites - 46°26’ 13” N, 11°51’ 54” E). The massif group extends over about 150 km² and is composed by several summits ranging between 1200 and 3343 m a.s.l., with extreme topography characterized by very steep cliffs and screes (Scillitani *et al.*, 2013; 5x5 m Digital Elevation Model, DEM). With such landscape features, vegetation follows a strong altitudinal gradient, with mixed and conifer woodlands at the lowest elevations, and alpine meadows and shrubs above the timberline (1900 m a.s.l.). Based on a substantial body of literature on wild goats (e.g., Grignolio *et al.*, 2007a; Festa-Bianchet & Côté, 2008; see also Introduction), and our personal observations, we identified refuge areas with steep rocks, i.e. rocky areas at ≥ 45° slope. We used this threshold as reported for Asiatic ibex *(Capra ibex sibirica*) (Fox *et al.*, 1992) and Cantabrian chamois (*Rupicapra pyrenaica parva*) (Pérez-Barbería & Nores, 1994). We used GIS to combine land cover (Scillitani *et al.*, 2013) and DEM (https://www.regione.veneto.it/web/ambiente-e-territorio/ctr; http://www.territorio.provincia.tn.it), and to create a new vector layer of refuge polygons (minimum polygon size = 1000 m^2).

The Alpine ibex colony (latest official population estimate: about 300 individuals, block count census, Province of Belluno Wildlife Office) was founded in 1978 from the source population of the species in Gran Paradiso National Park, Western Alps. The ibex are free to range in the entire area, given the very low human impact and absence of roads. Tourists visit the area mainly in summer, with a peak of attendance from mid-July to mid-August that however is largely restricted to few hiking trails following the valley bottoms.

Other ungulates present in the study area included roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) from the lowest altitudes to the valley bottoms at about 2200 m a.s.l.; alpine chamois (*Rupicapra rupicapra*) throughout the altitudinal range; and domestic ungulates, although only cows overlapped the lower end of ibex range in summer. No large mammal predators were recorded in the area at the time of the study, hence golden eagle (*Aquila chrysaetos*) and red fox (*Vulpes vulpes*) were the only potential predators resident in the area. The hunting season by stalking on roe and red deer, and chamois spanned from August to November, whilst Alpine ibex is a fully protected species under the Bern Convention (www.coe.int/en/web/bern-convention), EU Habitats and Species Directive (92/43/CEE), and is protected under national legislation.

The temperature of the study area during the study period ranged, in average, between 0°C (SD±5) in winter to 11°C (SD±4) in summer, and the total yearly precipitation was approximately 1400 mm (local weather stations, Province of Belluno meteorological service). The wintertime precipitation is mostly in the form of snow from October-November to April-May, but the snow cover at highest altitudes lasts longer.

4.2.2. Data collection & preparation

From 2010 to 2016, we captured 22 female ibex by tele-anaesthesia (>2 years old at capture) and equipped them with GPS-GSM collars with dual-axis activity sensor (GPS PRO Light collar, Vectronic Aerospace GmbH). Animals were captured with veterinary assistance in compliance with current Italian laws, and capture and handling protocols were approved by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale, ref. n. 9097-9501/2012).

We set GPS collars to attempt one location every hour, and to drop-off after 54 weeks. We removed 11% GPS outliers following Bjørneraas *et al.*, (2010) and Urbano and Cagnacci, (2014), and subsetted the data to reproductive period only (see criteria below). In the analysis and interpretation of the results we assumed a median location error lower than 10 m, as estimated from stationary collars in the same area (Párraga Aguado *et al.*, 2017). Of the 22 monitored females, we identified 11 with kids (lactating) and 11 without kids (non-lactating) from direct observations during the summer period (from July to the beginning of September). Specifically, we considered to be lactating females those seen breastfeeding at least once during summer; observations were replicated throughout summer to confirm the presence of the kid. The reproductive status observed during lactation was retrospectively assigned to early reproduction periods (i.e., before births). Hence, false negatives cannot be completely excluded for the pregnancy period. Other methods to identify pregnancy before births were methodologically or logistically unfeasible. Spring captures to eco-scan females were considered highly dangerous for survival, also given the extreme topography, and not approvable by welfare protocols. The collection of fresh feces after deposition by marked individuals, initially considered, resulted exposed to a high error of individual identification because of gregarious behavior, and homogeneous, largely rocky terrain, with little points of reference at the microscale.

We defined 5 periods of 4 weeks, using the birth period as reference (usually observed in June: Grignolio *et al.*, 2007a; specifically: 24th May to 20th June, see below), a four-week period before ('Pregnancy' from 26th April to 23th May: i.e., the late pregnancy period characterized by high energetic demand, Loudon, 1985), and three four-weeks period after ('Early Lactation' from 21st June to 18th July: new-born kids are closely dependent on the mother; 'Lactation' from 19th July to 15th August: high energetic demand for lactation, but more mobile kids; "Late lactation", from 16th August to 11th September: weaning has started and kids are more agile and independent). The timing of births was confirmed in our study by the temporal pattern of the weekly average activity, as suggested by (Long *et al.*, 2009): the sharpest spring decrease of activity in reproductive females (but not in non-reproductive females) corresponded to the week starting with 24th of May (Semenzato *et al*. unpublished data).

To disentangle the anti-predator response from other potentially confounding effects (food and protection trade-off, e.g. Hebblewhite & Merrill, 2009), we limited our analysis to periods of inactivity, both in the day and at night, as derived from activity sensors (Chapter 3). Specifically, for each animal, we selected two GPS locations per day at 0:00 pm (GMT+1) to characterize the nighttime anti-predator behavior and 12:00 am to characterize the daytime anti-predator behavior. We chose only two locations to remove the effect of pseudo-replication. If locations at these hours were missing, we used the following (1pm and 1am, respectively) or the previous location (11pm and 11am, respectively). To address our hypotheses, we estimated the minimum Euclidean distance of the locations from the closest refuge area, and annotated the elevation, using the aforementioned geographic layers. The final database consisted of 5,152 locations for 22 females.

As a preliminary screening, and to verify the independence of our addressed hypotheses, we verified the relation between the two response variables in the study area, defined as the minimum concave polygon of all points (44 km^2). Specifically, we first calculated the Pearson correlation coefficient between altitude and distance from refuge areas for the used location. Then, we performed 10,000 extractions of 5000 random points at the same altitudes as those used by female ibex and random distances from refuge areas, and computed the Pearson correlation coefficient for all 10.000 correlation.

4.2.3. Statistical analysis

To assess H1 (use of/distance from refuge areas), we considered distance from the refuge areas equal to zero (‘0’) or greater than zero (‘1’) as the binomial variable to analyze the probability to be outside the refuge areas. We used Generalized Linear Mixed Models (GLMM, with a logit link function) to investigate the probability to be outside the refuge areas using female reproductive status (2-level factor: with versus without kids), periods (5-level factor: pregnancy, birth, early lactation, lactation, late lactation) and time of the day (2-level factor: night versus day) as fixed factors, with the individual identity as a random factor to control for repeated observations per individual. For locations outside the refuge areas only, we used Generalized Linear Mixed Models (with a gamma distribution of errors) to investigate the distance from refuge areas in dependence on female reproductive status, periods and time of the day, with the individual identity as a random factor.

We used Linear Mixed-Effects Models (with a Gaussian distribution of errors) to investigate the altitude use (H2) in dependence on female reproductive status, periods and time of the day, with the individual identity as a random factor to control for repeated observations per individual.

In all cases, we considered the three-way interaction between female reproductive status, periods and time of the day as the full model that includes all hypotheses, and their alternatives. We identified 19 models derived from the full model to express the specific predictions (Table S. 4-1). We used the Akaike's Information Criterion (AIC; Burnham and Anderson, 1998) to select the most parsimonious model. In case of several models within a ΔAIC range of 2, we selected the model with fewest number of parameters (K) (Arnold, 2010). All generalized linear mixed models were fitted using the function 'glmer', whereas linear mixed-effects models were fitted using the function 'lmer', both in the library 'lme4' (Bates *et al.*, 2015) implemented in R software (R Core Team, 2016).

We selected the approach to analyse separately the probability to be outside the refuge areas and the distance from the refuge areas, as the interpretation of results is more intuitive. However, to ascertain the validity of the results based on the two sets of GLMM models, we also used a hurdle model (Cragg, 1971) which includes a hurdle between the zero and nonzero outcomes. Hurdle models consist of two parts. The first part uses a binomial distribution to model the use versus no-use of refuge areas. The second part is a count model with a Gamma distribution to handle nonzero distance from the refuge areas. We used the Bayesian Regression Models with hurdle-gamma distribution to investigate the distance from the refuge areas (including zero value), considering the same 19 models used in the previous approaches (see Table S. 4-2), with the individual identity as a random factor to control for repeated observations per individual. These hurdle models were fitted with the function ‘brm’ in the library ‘brms’ (Bürkner, 2017), implemented in R software. To select the best model, we used the Leave-one-out cross-validation (LOO; Vehtari *et al.*, 2017) based on the posterior likelihood using the function ‘loo’ in the library ‘brms’ and retained the model with the lowest LOO.

To evaluate if female ibex used altitude and distance from refuge area independently, or in relation with their availability, we compared the correlation coefficients of the used set of altitude and use of/distance from refuge areas with the set of correlations of the random set of points chosen in the study area (for details see Figure S. 4-4).

4.3. Results

We found very similar results considering separate models, to handle the probability to be outside the refuge areas and the distance from the refuge areas, or hurdle models (Table S. 4-7, Figure S. 4-3); thus, we only present results using separate models in the following.

Concerning the probability to be outside the refuge areas, the model with the highest support included the two-way interaction between period and reproductive status and the two-way interaction between period and time of the day (Table S. 4-3). Concerning the distance from the refuge areas, the model with the highest support included the two-way interaction between period and reproductive status and the time of the day as a main effect (Table 4-1, Table S. 4-4). Female ibex showed strong seasonal variations in the probability to be outside the refuge areas and the distance from the refuge areas, decreasing sharply from pregnancy to early lactation, and then increasing again slightly in lactation and late lactation (see Figure 4-1, Figure 4-2, and Table 4-1 for parameter estimates). Then females used more the refuge areas and stayed closest to the refuge areas during lactating periods than during the pregnancy period, and this pattern was more pronounced for lactating females than non-lactating females. Indeed, lactating females had lower probabilities to be outside the refuge areas (**P1.1**; Early lactation: 0.69±0.03 versus 0.76±0.03, lactation: 0.68±0.03 versus 0.74±0.03; late lactation: 0.79±0.03 versus 0.84±0.02, for lactating and non-lactating females respectively) and maintained lower distances from the refuge areas than non-lactating females, but only after birth, and especially when kids were more independent (**P1.1**; Early lactation: 56±6 m versus 72±7 m; lactation: 59±6 m versus 96±10 m; late lactation: 83±9 m versus 119±12 m, for lactating and non-lactating females respectively).

The two-way interaction between time of day and reproductive status has no support (Table S. 4-4 and Table S. 4-5) to model the probability to be outside the refuge areas and the distance from the refuge areas. However, the two-way interaction between period and time of the day was included in the most parsimonious model of the probability to be outside the refuge areas: female ibex had higher probability to be outside the refuge areas during nighttime than during daytime (0.69±0.03 versus 0.76±0.02, during daytime and nighttime respectively during early lactation for example), regardless of the reproductive status, but these probabilities changed among periods (Figure S. 4-1). In contrast, for the distance from the refuge areas, the most parsimonious model included the time of the day as a main effect, without a two-way interaction with periods: female ibex were farther from the refuge areas during nighttime than during daytime, regardless of their reproductive status (**P1.2,** 93.6±6.06 versus 108.0±7.01 m, during daytime and nighttime respectively; Figure S. 4-2). In other words, lactating and non-lactating females shifted away from the refuge areas at night in a similar proportion, so that the relative distance from the refuge areas did not differ between these groups of females.

Concerning the altitude used, the model with the highest support included the three-way interaction between period, reproductive status and time of the day (Table 4-1, Table S. 4-5). Female ibex showed strong seasonal variations in altitude used (Figure 4-3), as well as a daily pattern of altitudinal shift, with a peak in early lactation/lactation periods (daily altitude of lactating female and non-lactating 2481±33 versus 2429±32 m a.s.l. respectively, during early lactation), and higher altitudes used during daylight (Table 4-1, Figure 4-3). Both these effects depended on reproductive status: starting from early lactation, lactating females shifted daily less than the non-lactating ones, thus remaining at higher altitudes at night (Figure 4-3; the effect during lactation period was only marginally significant, but in the same direction).

The comparison between observed values and the distribution of correlations (altitude vs distance from the refuge areas) along with the distribution of average of distance from refuge areas, demonstrated that female ibex performed a strong selection of distance to refuge areas, which was less influenced by altitude than what expected by random locations. Moreover, that this distance was significantly lower than that of random locations. (for details see Appendix 1 and Figure S. 4-4).

Table 4-1 Parameter estimates of the retained models analyzing probability to be outside of refuge areas, distance from refuge areas, and of altitude used. The corresponding models selection results are given in tables S.3, S.4 and S.5) RS: reproductive status (2 levels); T: time (2 levels); P: periods (5 levels).

	probability to be outside of refuge areas				distance from refuge areas				altitude used			
	Estimate	Std. Error	t.value	p-value	Estimate	Std. Error	t.value	p-value	Estimate	Std. Error	t.value	p-value
(Intercept)	2.16	0.20	10.97	0.00	5.13	0.10	52.3	0.00	2101.6	32.09	65.48	0.00
RS	0.41	0.25	1.61	0.11	0.02	0.14	0.16	0.87	7.27	45.39	0.16	0.87
T: night	0.02	0.20	0.11	0.91	0.15	0.03	4.48	0.00	-62.69	14.86	-4.21	0.00
P: birth	-0.79	0.21	-3.77	0.00	-0.51	0.07	-7.38	0.00	199.56	14.96	13.34	0.00
P: early lactation	-1.20	0.20	-5.90	0.00	-0.93	0.07	-13.31	0.00	327.40	15.01	21.82	0.00
P: lactation	-1.13	0.21	-5.43	0.00	-0.64	0.07	-8.75	0.00	340.36	15.66	21.73	0.00
P: late lactation	-0.91	0.22	-4.10	0.00	-0.42	0.07	-5.66	0.00	264.78	16.28	16.27	0.00
RS:T night	---	---	---	---	---	---	---	---	-13.38	21.06	-0.64	0.53
RS: P birth	-0.38	0.26	-1.49	0.14	0.16	0.10	1.61	0.11	-10.46	21.28	-0.49	0.62
RS: P early lactation	-0.77	0.25	-3.09	0.00	-0.28	0.10	-2.65	0.01	45.46	21.69	2.10	0.04
RS: P lactation	-0.70	0.25	-2.76	0.01	-0.51	0.11	-4.71	0.00	27.57	22.54	1.22	0.22
RS: P late lactation	-0.79	0.28	-2.86	0.00	-0.39	0.11	-3.5	0.00	12.51	23.88	0.52	0.60
T night : P birth	0.14	0.25	0.54	0.59	---	---	---	---	-9.95	21.23	-0.47	0.64
T night : P early lactation	0.36	0.25	1.45	0.15	---	---	---	---	-72.28	21.20	-3.41	0.00
T night : P lactation	-0.02	0.25	-0.07	0.94	---	---	---	---	-63.28	21.98	-2.88	0.00
T night : P late lactation	0.83	0.27	3.03	0.00	---	---	---	---	-63.21	22.82	-2.77	0.01
RS:Tnight : P birth	---	---	---	---	---	---	---	---	10.06	30.28	0.34	0.74
RS:T night : P early lactation	---	---	---	---	---	---	---	---	57.84	30.58	1.89	0.06
RS:T night : P lactation	---	---	---	---	---	---	---	---	44.59	31.74	1.41	0.16
RS:T night : P late lactation	---	---	---	---	---	---	---	---	66.47	33.28	1.99	0.05

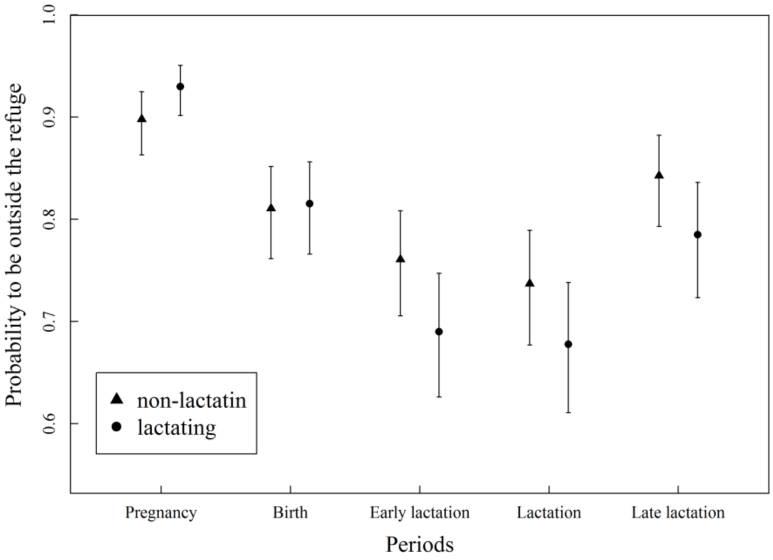

Figure 4-1 Predicted probability to be outside of refuge areas over five reproductive periods for 11 lactating and 11 non-lactating female ibex, monitored in the Marmolada massif from 2010 to 2016, according to the retained model (Table S. 4-3). Error bars show 95% confidence intervals.

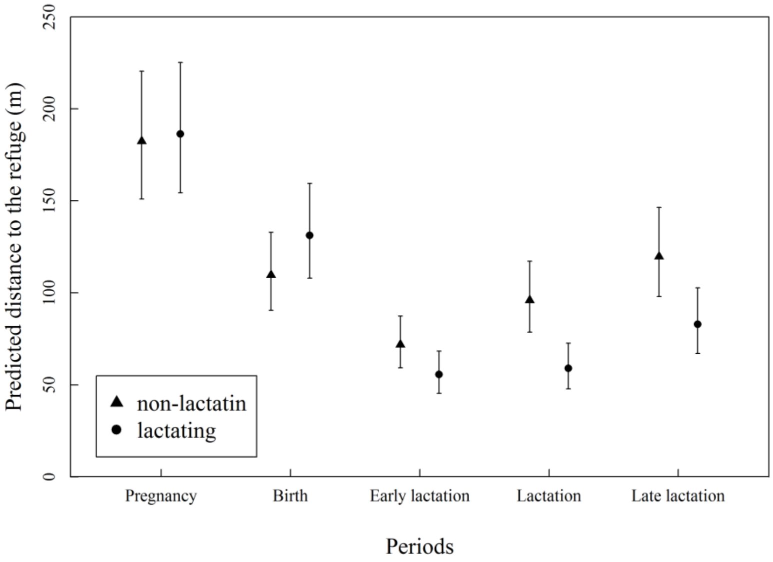

Figure 4-2 Predicted distance from refuge areas over five reproductive periods for 11 lactating 11 non-lactating female ibex, monitored in the Marmolada massif from 2010 to 2016, according to the retained model (Table S. 4-4). Error bars show 95% confidence intervals.

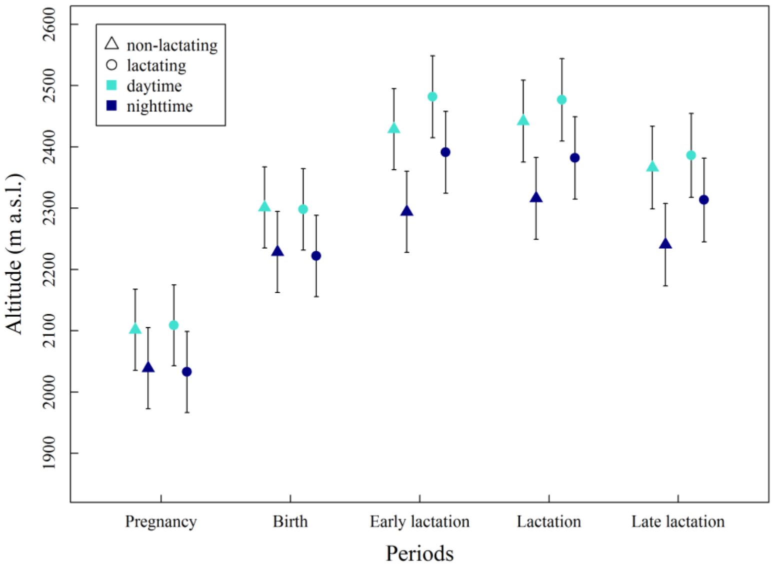

Figure 4-3 Predicted altitude used over the five reproductive periods by 11 lactating and 11 non-lactating female ibex, monitored in the Marmolada massif from 2010 to 2016, according to the retained model (Table S. 4-5). Error bars show 95% confidence intervals.

4.4. **Discussion**

In mammal species with high parental investment, the increase in energy demand and the offspring's predation risk shape the behavioral responses of females with young at heel, thus affecting the trade-off between survival and resource acquisition (Bongi *et al.*, 2008; Hebblewhite & Merrill, 2009). These behaviors must also allow females to cope with other environmental constraints, as the increase in temperature, which is an important limiting factor for females during the summer. Our results showed that females with kids adjusted their space use, responding at the same time to kids presence and to environmental constraints.

The presence of anti-predatory behavior in female ibex has been described in previous studies considering vigilance behavior, group size (Toïgo, 1999; Brivio *et al.*, 2014), and distance from refuge areas (Villaret *et al.*, 1997; Grignolio *et al.*, 2007a, 2007b). In this study, we considered the use of refuge areas and the distance from them along with other environmental constraints, common to all females, to evaluate the anti-predatory responses as part of a more complex trade-off between resource acquisition, thermoregulation needs, and kids' protection.

Our results showed a pronounced anti-predator behavior in lactating females, highlighting a different spatial use as respect to that of non-lactating females, with an increased probability to be inside refuge areas and, when outside, to be closer to them, starting from early lactation and continuing through the reproductive season. The same pattern was observed in other Alpine ibex populations (Villaret & Bon, 1995; Grignolio *et al.*, 2007a, 2007b) and in other ungulate species (e.g. Bon *et al.*, 1995; Barten *et al.*, 2001; Ciuti *et al.*, 2009), with lactating females selecting more protected habitats than non-lactating females during parturition and lactation, but not before births. Unlike these studies, we did not observe anti-predatory behavior during the birth period. This unexpected result might be due to the duration of the birth period defined by us (four weeks) that might have included part of late pregnancy, in this way possibly confounding the results. Otherwise, we cannot exclude the possibility that some of the females classified as non-lactating were pregnant, but lost the kid soon after the birth, determining a bias in the results. Indeed, in ungulates, according to Gaillard *et al.*, (2000), fecundity of prime-age females is generally high with high probability to be pregnant, but with kid survival rates dependent of environmental factors or female body condition.

While at the seasonal scale reproductive status affected the use and the distance from refuge areas, at the daily scale there were no differences between lactating and non-lactating females. All female ibex had a higher probability to be inside and closer to refuge areas during daytime than during nighttime. Our results did not, therefore, demonstrate an evident anti-predatory behavior by lactating females at the daily scale. The reasons for this can be many. It is possible that anti-predatory behaviors alternative to distance and use of refuge areas were predominant. For instance, Toïgo, (1999) reported that during daytime lactating females were more vigilant than non-lactating females. Moreover, the scale at which limiting factors (such as predation risk) occur defines also the scale of the response (Anderson *et al.*, 2005; Mayor *et al.*, 2009), depending on the relative importance of such limiting factors (Rettie & Messier, 2000). This means that, in relation to the scale of analysis and its importance in comparison with other constraints, the anti-predatory behavior may be more or less visible. It might not be a priori excluded, therefore, that the daily pattern in the use of refuge areas that we observed was actually related due to the presence of other, more important constraints acting at the daily scale on the spatial use of female ibex, as thermoregulation and consequently altitudinal shifts (see chapter 3). However, we found also that female ibex selected for shorter distances from refuge areas independently of altitudes used, which therefore do not appear to have influenced use and proximity to refuge areas. Furthermore, in our study area, the prolonged absence of large-mammal-predators and hunting activity on ibex may have led to the loss of a daily variation of anti-predatory behavior show instead in other ungulate species in presence of predator (e.g., Fortin *et al.* 2015). Finally, the non-evidence of anti-predatory behavior at the daily scale may be related to the temporal characterization of responses. Several studies showed how the behavioral response to predation risk may be not only chronic, with a systematic selection of safer habitat types, but also acute under the threat of predators appearing in the immediate surroundings (Valeix *et al.*, 2009; Basille *et al.*, 2015). In this second case, the behavioral response does not follow a spatio-temporal pattern: an acute response is unpredictable and becomes evident only at a high temporal resolution, with synchronized monitoring of prey and predators. Our hourly data may not have allowed us to record round-trip movements from refuge areas in response to unexpected risk stimuli.

Our study has therefore shown that female ibex exhibited an anti-predator behavior at the seasonal scale in a free-large-mammal-predator area (Chapron *et al.*, 2014), with golden eagle and red fox as the only potential predators present. The 'Ghost of predators past' hypothesis (Peckarsky & Penton, 1988; Byers, 1997) was used to explain the persistence of anti-predator behaviors in Alpine ibex in free-large-mammal-predator and free-ibex-hunting areas, in Italian Alps (Villaret *et al.*, 1997; Aublet *et al.*, 2009). We are not aware of assessments of red fox predation rate on ibex, whereas golden eagles' predation rate on several species of mountain caprinae is considered to be very low, and restricted to a short period after birth (e.g. Grignolio, Rossi, Bassano, *et al.* 2007; Festa-Bianchet and Côté 2008; Hamel and Côté 2009). Despite this, an active maternal defensive behavior was observed in our study area, (similar to the one observed in other alpine ungulates, such as chamois Bertolino 2003, mountain goats Hamel & Côté, 2009 and iberian ibex Viana *et al.* 2018) with alarm calls in herds and flights to nearby cliffs in response to eagles' presence, but also to paragliders and helicopters flying at low altitudes (Semenzato P., personal communication). On the other hand, the presence of this diurnal predator in the study area did not determine a daily variation of space use linked to an anti-predatory behavior. It is possible that the behavioral response was of an acute type without significant effect on the variation in daily use of refuge areas.

Parallel to the need for kids' protection, female ibex must maintain thermal balance and fulfill energy needs. In Chapter 3 we demonstrated that during spring and summer female ibex performed an altitudinal shift, responding to the increase in temperature and to altitudinal gradient of vegetation growth. Moreover, they performed a daily altitudinal shift as a trade-off between thermoregulation needs and feeding habitats distribution (Chapter 3). In the present work we found that, at both scales of analysis, these altitudinal shifts were affected by reproductive status: females with kids stayed at higher altitudes than bare females. In particular, in early lactation and lactation females with kids reduced the daily altitudinal shifts, maintaining higher altitudes than non-lactating female both at daytime and nighttime. This reduction of altitudinal movements was in accordance with the observed reduction of home range size by female ibex with kids compared to bare females during the reproductive period (Grignolio, Rossi, Bertolotto, *et al.* 2007; Viana *et al.* 2018; Ramanzin unpublished). These difference in altitudinal displacements was probably affected by the limited kids' locomotion capacity (Grignolio, Rossi, Bertolotto, *et al.* 2007; Viana *et al.* 2018), and by the need to reduce exposure to predation risk which can increase when moving between different areas (Neuhaus & Ruckstuhl, 2002). Moreover, reducing daily altitudinal shifts may reduce the energy costs that these movements entail (Aublet *et al.*, 2009; Biancardi & Minetti, 2017) favoring the energy balance of lactating females and their kids. However, females must move also in response to thermoregulation needs. Therefore, lactating female ibex used a range of altitudes that contemporarily allowed them to compensate for thermoregulation needs and to remain close to refuge areas, fulfilling the kids' specific needs (such as protection and low mobility).

Our results confirmed the spatial segregation observed by Ruckstuhl and Neuhaus (2002) in female ibex with different reproductive status, which occurs, according to the authors, due to differences in level of risk of predation (reproductive strategy hypothesis) and/or differences in forage selection (forage selection hypotheses, see also Main 2008 and Viana *et al.* 2018 for other ibex species).

In this study, we found a different spatial use between lactating and non-lactating female, due to a trade-off, implemented in particular at daily scale, between protection of kids, thermoregulation, and feeding by lactating females.

This work thus demonstrated the presence of an anti-predatory behavior in female ibex, which through the variation of spatial behavior allows realizing a trade-off between different needs related to the life-history of individuals. The marked difference of spatial behavior between lactating and non-lactating females evidenced the presence of individual behavioral plasticity mediated by reproductive effort. To better understand the evolutionary relevance of these responses, future studies should address the individual variability within each reproductive category (that here we have accounted for with random effects), and the fitness consequences on medium-term survival and growth of kids. Moreover, future studies should investigate whether possible constraints on foraging associated with proximity to escape terrain impacts on the fitness of individual and kids (e.g. investigating body condition of females, such as variations in summer mass gain between lactating and non-lactating females). The understanding of the persistence of anti-predator behavior and of the trade-off between resource acquisition and safety is particularly important in a context of changing resources availability (e.g., Parolo & Rossi, 2008; Rammig *et al.*, 2010) and recolonization by large-mammal-predators (Chapron *et al.*, 2014). The possibility and the capacity to responding to rapid changes in the environment will have to be considered in conservation and reintroduction actions.

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4.6. Supplementary Material

Table S. 4-1 Number of individuals considered in the analysis for each week and period.

Julian week	period	n. of individuals
19	pregnancy	22
20	pregnancy	22
21	pregnancy	22
22	pregnancy	22
23	birth	22
24	birth	22
25	birth	22
26	birth	22
27	early lactation	22
28	early lactation	21
29	early lactation	21
30	early lactation	21
31	lactation	22
32	lactation	21
33	lactation	20
34	lactation	16
35	late lactation	16
36	late lactation	15
37	late lactation	15
38	late lactation	16

Table S. 4-2 List of candidate models used to fit the GLMM and LMM, respectively, to distance from refuge areas and altitude used by 22 females of Alpine ibex in the Marmolada massif during 2010-2016. RS: reproductive status (2 levels); T: time (2 levels); P: periods (5 levels).

Models	P	RS	T	P*RS	P*T	T*RS	P*T*RS
1	X						
2		X					
3			X				
4	X	X					
5		X	X				
6	X		X				
7	X	X	X				
8				X			
9					X		
10						X	
11	X					X	
12		X			X		
13			X	X			
14				X	X		
15				X		X	
16					X	X	
17				X	X	X	
18							X

Table S. 4-3 Performance and model selection of candidate GLMM models (Binomial distribution of residuals) explaining the probability to be outside refuge areas for 22 females of Alpine ibex in the Marmolada massif during 2010-2016. RS: reproductive status (2 levels); T: time (2 levels); P: periods (5 levels).

	K	AIC	ΔAIC	AICw
RS*P + P*T	16	4991.2	0	0.5
RS*P + P*T+RS*T	17	4991.9	0.7	0.3
P*T	11	4995.5	4.3	0.1
RS*P*T	21	4996.2	5.1	0.04
RS+P*T	12	4997.1	5.9	0.03
Null model	2	5206.4	215.2	0.0

Table S. 4-4 Performance and model selection of candidate GLMM models (Gamma distribution of residuals) explaining the distance from refuge areas of 22 females of Alpine ibex in the Marmolada massif during 2010-2016. RS: reproductive status (2 levels); T: time (2 levels); P: periods (5 levels).

	K	AIC	ΔAIC	AICw
RS*P + T	13	46544.2	0.0	0.6
RS*P+RS*T	14	46545.4	1.2	0.3
RS*P+P*T	17	46547.8	3.6	0.1
RS*P + P*T+RS*T	18	46549.2	5.0	0.1
RS*P*T	22	46555.8	11.5	0.0
Null model	3	47057.9	513.6	0.0

Table S. 4-5 Performance and model selection of candidate linear mixed effects models explaining altitude used by 22 females of Alpine ibex in the Marmolada massif, 2010-2016. RS: reproductive status (2 levels); T: time (2 levels); P: periods (5 levels).

	K	AIC	ΔAIC	AICw
P*RS*T	22	68219.6	0.0	1.0
T*P + P*RS+ T*RS	18	68252.4	32.8	0.0
P*RS+P*T	17	68260.3	40.9	0.0
T*RS+ P*RS	14	68287.0	67.4	0.0
T+RS*P	13	68295.6	75.9	0.0
T*RS+ P*T	14	68310.9	91.2	0.0
RS+T*P	13	68319.2	99.6	0.0
Null model	3	70593.5	2373.8	0.0

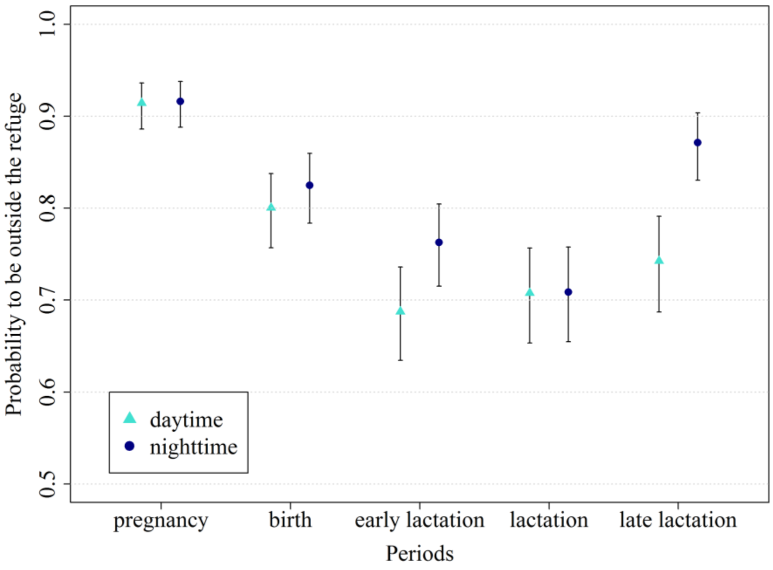

Figure S. 4-1 Predicted probability to be outside of refuge areas at daytime and nighttime during the reproductive period (from 26 April to 11 September) of 22 females of Alpine ibex, monitored in the Marmolada massif from 2010 to 2016, according to the retained model (Table S. 4-3). Error bars show 95% confidence intervals.

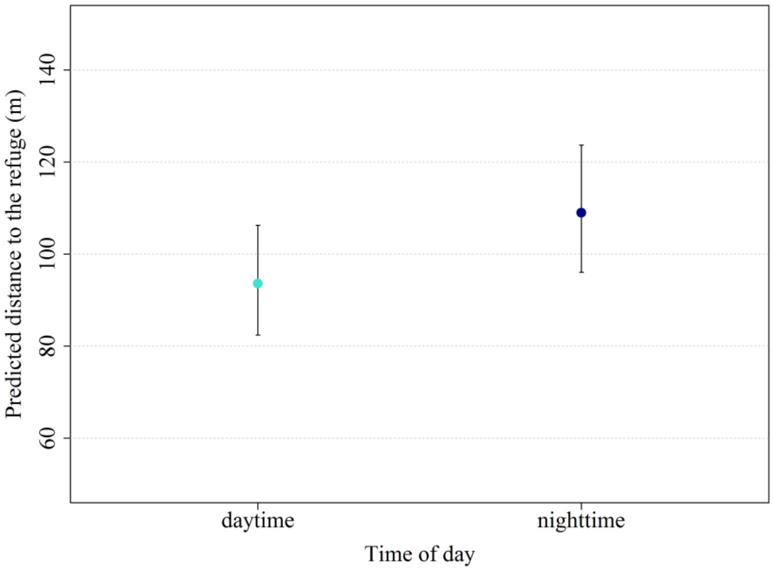

Figure S. 4-2 Predicted distance from the refuge areas at daytime and nighttime of 22 females of Alpine ibex, monitored in the Marmolada massif from 2010 to 2016, according to the retained model (Table S. 4-4). Error bars show 95% confidence intervals.

Table S. 4-6 Performance and model selection of hurdle models (Bayesian Regression Models; Family Hurdle Gamma) explaining the distance from refuge areas of 22 females of Alpine ibex in the Marmolada massif, 2010-2016 RS: reproductive status (2 levels); T: time (2 levels); P: periods (5 levels).

	Loo	Se
RS*P + T	52070.56	293.68
RS*P+RS*T	52070.99	293.68
RS*P+P*T	52073.67	293.70
RS*P + P*T+RS*T	52074.43	293.64
Null model	52573.33	294.88

Table S. 4-7 Parameter estimates from the best hurdle model (Table S. 4-6). The coefficients were obtained at the population level and the percentiles were computed by the quantile function.

	Estimate	SD	5%IC	95%IC
Intercept	5.135	0.109	4.955	5.309
Time-night	0.152	0.034	0.094	0.207
Period-birth	-0.508	0.071	-0.625	-0.392
Period-early lactation	-0.932	0.071	-1.049	-0.813
Period-lactation	-0.643	0.074	-0.762	-0.518
Period-late lactation	-0.422	0.075	-0.546	-0.297
RS	0.017	0.150	-0.226	0.263
Period-birth: RS	0.157	0.101	-0.006	0.325
Period-early lactation: RS	-0.275	0.107	-0.451	-0.100
Period-lactation: RS	-0.505	0.110	-0.684	-0.323
Period-late lactation: RS	-0.383	0.113	-0.561	-0.194

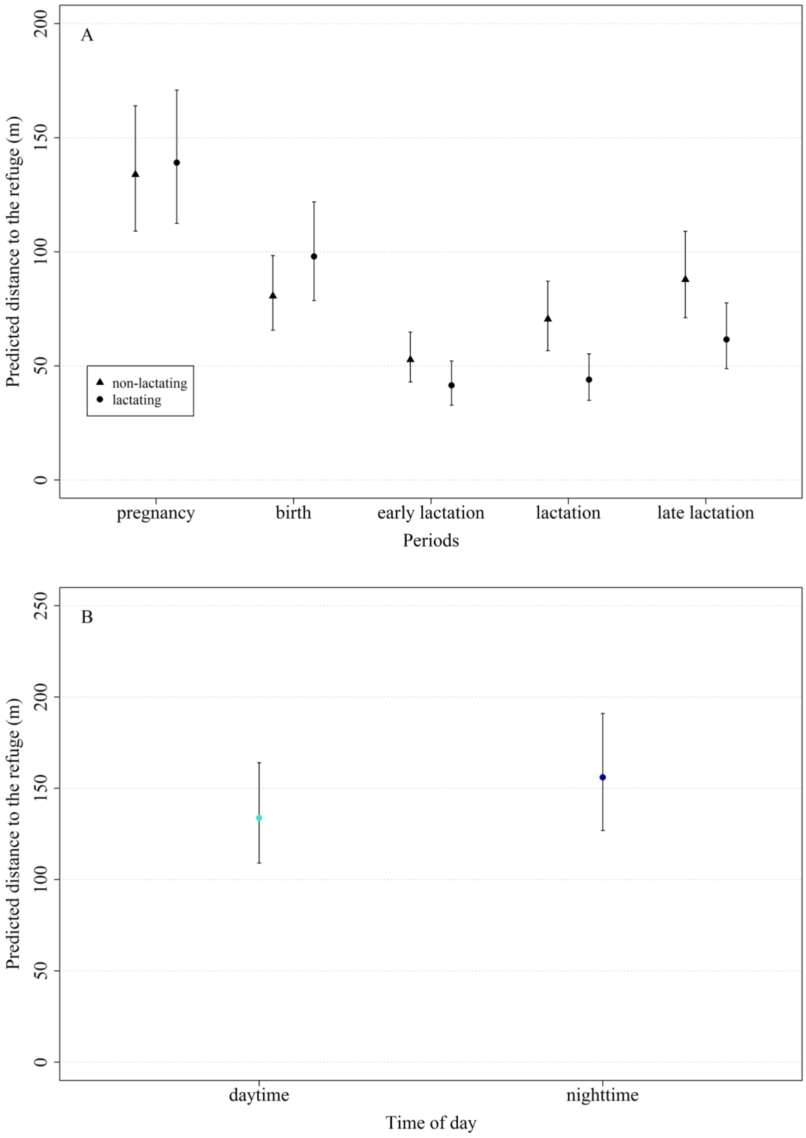

Figure S. 4-3 Predicted distance from refuge areas over the five reproductive periods (panel A) and at daytime and nighttime (panel B) for 22 females of Alpine ibex, monitored in the Marmolada massif from 2010 to 2016, according to the retained hurdle model. Error bars show 95% confidence intervals.

Appendix 1

Since we expected altitude to be negatively correlated with distance from refuge areas, because steep slopes and cliffs are more frequent at higher elevations, I wanted to verify whether the altitudinal shifts of ibex females could influence the distance from refuge areas that they used. In other words, we verified whether distance from refuge area was proportional to the availability at a given elevation, or there was instead a selection by the females. For this purpose, using the 5000 locations of female ibex we first calculated the Pearson correlation coefficient between the elevations and the corresponding distances from refuge areas, and the average of such distances. We then compared this correlation and this average with a random distribution of correlations and average distances obtained from ‘available’ points. To obtain these distributions, we replicated 10000 extractions of 5000 random points, fixing elevations to correspond with those of the locations, and calculated the correlations with refuge areas, and the average of distances, for each replicate. The Pearson correlation coefficients obtained from the extractions of random points ranged between-0.55 to -0.49, whereas the correlation estimated from locations used was -0.44 (Figure S. 4-4, Panel A). A permutation test of the correlation between distance and altitude estimated a probability of 0% that the ibex selected randomly the distance to the refuge taking into account the altitude. The mean distances from refuge areas obtained from random extractions ranged between 198 and 201 m, whereas the mean distance from the female ibex locations was of 98 m (Figure S. 4-4, Panel B). These results indicate that, although in general, there was a negative correlation between altitude and distance from refuge areas, female ibex consistently selected shorter distances irrespective of elevation.

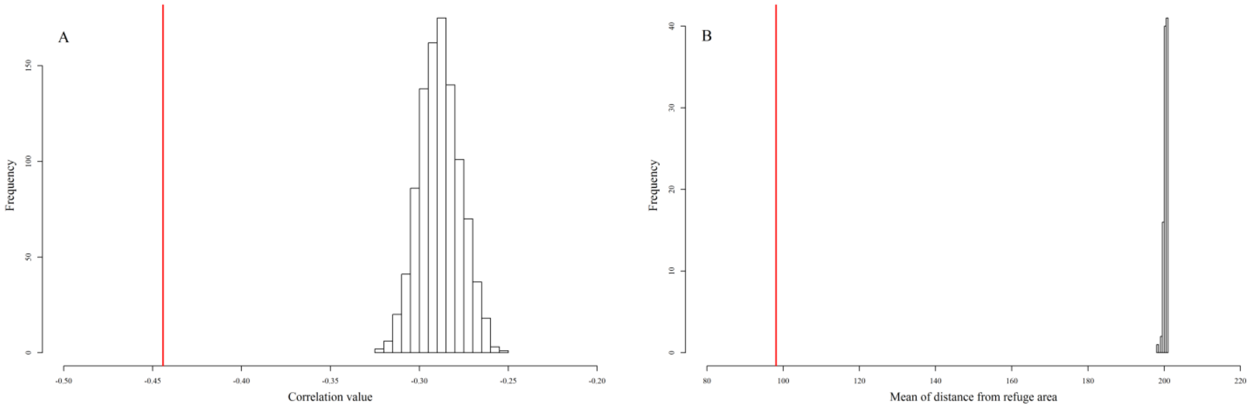

Figure S. 4-4 Panel A: Pearson correlation coefficient between elevation and distance from refuge areas obtained from the 5000 locations of female ibex (red line) and distribution of correlation coefficients obtained from 10000 replicated extractions of 5000 random points at elevations corresponding to those of female ibex locations. Panel B: average distance from refuge areas of 5000 locations of female ibex (red line) and distribution of average distances obtained from 10000 replicated extractions of 5000 random points at elevations corresponding to those of female ibex locations.

5. Feed first, forage later: spatio-temporal tactics for habitat use under life-history constraints in female Alpine ibex[5]

5.1. Introduction

Animals move through heterogeneous landscapes searching for resources and conditions available to fulfil their internal needs and ultimately to ensure survival and reproduction. In this way, they shift among different habitat types in response to variation in space and time of environmental and climatic factors, and internal physiological constraints, as well as to interactions with other species or individuals of the same species. Habitat use is thus governed by the functional role that habitat types have in responding to the needs of animals, because different habitat types offer different resources, such as forage, thermal cover, and protection from predators (Sih, 1980). A single habitat, often, does not provide a combination of all these factors to respond to all the animals' needs (Orians & Wittenberger, 1991). Therefore, animals move through habitats in a trade-off mechanism between the costs and benefits that they perceive (Lima & Dill, 1990; Mysterud & Ims, 1998). A common trade-off strategy in ungulate species is to move among different habitats in order to maximize access to forage resources while minimizing the limiting conditions imposed by climate variation and predation risk. The temporal and spatial scales of these movements vary in response to the scale at which limiting or favorable conditions occur (Rettie & Messier, 2000; Hebblewhite & Merrill, 2009; Dupke *et al.*, 2016). For instance, in many ungulate species living in temperate climates the seasonal variation in environmental conditions generated by predictable variation in climatic constraints and vegetation phenology triggers large scale seasonal migrations (Hebblewhite & Merrill, 2009; Zweifel-Schielly *et al.*, 2009; Cagnacci *et al.*, 2011). On the other

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hand, responses to immediate stimuli, such as the circadian rhythm (Ensing *et al.*, 2014), rumination cycles in herbivore species (Kamler *et al.*, 2007), weather conditions (Ewald *et al.*, 2014), or disturbance (Ciuti *et al.*, 2012; Bonnot *et al.*, 2013) generate behavioral decisions at short-term temporal and fine spatial scales, as when animals make circadian movements between high-forage exposed habitats to low-forage shelter habitats (Dussault *et al.*, 2004, 2005; Hebblewhite *et al.*, 2008; Godvik *et al.*, 2009). In addition to modifying habitat use, ungulates respond to environmental constraints and the need to optimize resource acquisition by adjusting activity budgets. For instance, females of mouflon (Bourgoin *et al.*, 2011) and Alpine ibex (Chapter 3) modified activity levels in response to temperature during summer, in the apparent attempt to optimize foraging and thermoregulation. However, different behaviors (response to different animals' needs) should be associated with use of different habitat types (e.g. access to different resources) with, in general, animals choosing safer habitats when resting than when feeding (Mysterud & Ims, 1998; Mysterud & Østbye, 1999). Therefore, describing activity patterns in different habitats may help elucidating the functional role of such habitats (Marchand *et al.*, 2015). In this regard, costs and benefits deriving from the limiting or favorable conditions associated with different habitat types vary in interaction with the animals' needs, determined by sex, age, and reproductive status (Beier & McCullough, 1990; Nikula *et al.*, 2004; Dussault *et al.*, 2005). Hence,Wemight also expect that changes in habitat use induced by different animals' needs should match with different activity patterns, reflecting the different constraints/resources trade-offs.

Lactation is the biological state when energy costs are highest for females. During the first month post-partum, energy requirements for female ungulates increase 65–215% (Robbins, 1993). Before lactation, more than 90% of the energy requirements for gestating females occurs during the last trimester, and these costs are almost 50% higher for pregnant than non-pregnant animals (e.g., Pekins *et al.* 1998). At the same time, reproducing females face a higher predation risk (Lima & Dill, 1990), and may be hindered by the offspring's sensitivity to predation and limited movement capacity. For instance, reproducing females of mouflon (Genus *Ovis*) (Bon *et al.*, 1995; Ciuti *et al.*, 2009) and fallow deer (*Dama dama*) (Ciuti *et al.*, 2006) did not show differences in habitat use as respect to non-reproducing females before parturition, but used habitats offering more cover and less forage when lactating.

In this work, we used high–frequency GPS locations to study the habitat use and activity patterns of reproducing and non-reproducing female Alpine ibex (*Capra ibex*) in summer. The Alpine ibex is a capital breeder (Toïgo *et al.*, 2002) living in extreme environments with a strong seasonal gradient in food resources. The short vegetative season, therefore, is a crucial period for females that need to restore body condition and, if reproducing, satisfy the energy needs of late pregnancy and lactation. Previous research with VHF telemetry suggested that marked differences in space and habitat use between reproducing and non-reproducing female Alpine ibex may occur essentially during birth and lactation, with lactating females reducing home range size and selecting rocky habitats more then non-lactating females (Grignolio *et al.*, 2007a, 2007b).

Specifically, we contrasted the habitat use of reproductive and non-reproductive females in relation with slope, an important topographic feature that influences the ability of ibex to find refuge from disturbance or predation risk (Villaret & Bon, 1995; Ruckstuhl & Neuhaus, 2002; Grignolio *et al.*, 2007a). In addition, we contrasted patterns of activity, a proxy for foraging behavior (see Chapter 3 supplemental material appendix 1), of reproductive and non-reproductive females in the different habitats used. During summer, female Alpine ibex make circadian altitudinal shifts (see Chapter 4), which, given the strong altitudinal gradient in habitat types distribution in Alpine environments, should involve changes in the habitats used. Therefore, we also contrasted the patterns of habitat use and of activity of reproducing and non-reproducing females throughout the 24 hours cycle.

We hypothesized that female ibex modified their use of habitat types in relation with slope (H1) and reproductive status (H2). In particular, we expected that use of all habitats should be positively related with slope, especially for reproducing females (P.1.1.). However, we expected that this relation could vary across habitats, being less marked for those offering mostly forage (P.1.2), because steeper slopes increase costs of movement (Biancardi & Minetti, 2017) and are negatively associated with biomass production (Ziliotto *et al.*, 2004). In relation to reproductive status, we expected that, because of the need to protect kids, reproducing females used scree and rock more than non-reproducing females, especially when these habitat types were associated with steep slope. Consequently, we expected that they used grasslands and grasslands mixed with rock less than non-reproducing females, especially when these habitat types were associated with gentle slopes (P.2.1). Since forest is located at lower elevations than the other habitats, and during summer females move to higher elevations (Chapter 3), we expected that use of this habitat was very low for all females (P.2.2.). In addition, since in forest risk of predation may be higher for species evolved in open habitat types (Sand *et al.*, 2005; Festa-Bianchet & Côté, 2008; Gervasi *et al.*, 2013), we also expected that forest should be used less by reproductive than non-reproductive females (P.2.3).

At the daily scale, we hypothesized that use of the different habitats varied with a circadian pattern following the daily variation of activity level as showed in Chapter 3 (H3). In particular, we expected that all females used scree and rock at steep slopes, especially during deep night and in the middle of the day when they were less active, because these habitats are more likely to provide refuge, and used grasslands and grasslands mixed with rock especially during morning and evening, when they were more active, because these habitats provide forage (P.3.1).

Moreover, we hypothesized that the females' activity patterns varied in the different habitat types in relation with the associated resource (refuge, forage) (H4). We expected that all females were less active in habitats offering refuge but little forage, and vice versa (P.4.1).

Increasing foraging time may be a tactic used by lactating females to compensate for their higher energy needs and possibly for use of sub-optimal habitats (Neuhaus & Ruckstuhl, 2002a; Hamel & Côté, 2008). With this hypothesis, we expected that reproducing females were more active than non-lactating females, especially when they were in forage-rich habitats (H5-P5.1). However, considering also the kids limitation hypothesis, we expected that lactating females could show a reduced activity shortly after births, when movement ability of kids is lowest, which they should balance with an increased activity in the following periods (P.5.2). At the daily scale (H6), we expected that lactating females should show increased activity with respect to non-lactating females during the day foraging periods, because of the need to increase foraging, but not during the night resting periods, because of the need to protect kids (P.6.1).

5.2. Materials and Methods

5.2.1. Study area

The study area is situated in the Marmolada massif group, in the Eastern Italian Alps (Dolomites - 46°26' 13" N, 11°51' 54" E). Land topography is characterized by high elevation, narrow valleys with steep slopes, delimited by rocky ridges and mountain peaks that can rise above 3000 m a.s.l. Vegetation follows a typical Alpine altitudinal gradient (Figure S. 5-1). Above 1600 m a.s.l. it is mostly forest of Norway spruce (*Picea abies*) and larch (*Larix decidua*). Above the tree line (1900-2000 m a.s.l.) vegetation is mainly represented by shrubs (*Pinus mugus, Rhododendrum hirsutum, Salix sp.* and *Alnus viridis*) that merge into Alpine grasslands, composed by different herbaceous species (mainly *Sesleria varia, Carex sempervirens, Nardus stricta, Carex firma*). Further up in elevation (2200-2300 m), screes and rock interrupt the vegetation patches, to dominate land cover above 2500-2600 m. Steep slopes of scree and rocky cliffs characterize the highest elevations. The climate is typically Alpine with a mean annual temperature of 1.7°C and average monthly temperatures varying from about 0°C (SD±5) in winter to 11°C (SD±4) to in summer. Total yearly precipitation is approximately 1400 mm, and snow cover in the area used by ibex may last from late October-November to late May-early June.

The local ibex colony ranges over approximately 65 km^2, and spans an altitudinal range from 1700 to 2900 m a.s.l.. In the summer of 2017, a minimum number of 288 individuals was counted (Vendrami S. 2017, personal communication) with the ground counts method (validated for this specie by Largo *et al.* 2008). Other large herbivores present in the area are Alpine chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), and red deer (*Cervus elaphus*). From late June to mid-September part of the more productive grasslands, located at the gentler slopes, were grazed by domestic cattle, with no spatial overlap with ibex. From September to January, selective hunting by stalking is allowed on chamois, roe deer, and red deer. No large predators occurred in the area before and during the study. Hikers visit the study area mostly in July-August. However, touristic presence is concentrated along the main paths that follow the bottoms of the valleys.

5.2.2. Habitat use and activity data

From September 2010 to October 2016, we captured by tele-anaesthesia 22 female ibex (2 or more years old at capture) and equipped them with GPS-GSM collars (GPS PRO Light collar, Vectronic Aerospace GmbH). Animals were captured with veterinary assistance in compliance with current Italian laws. Capture and handling protocols were approved by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale, ref. n. 9097-9501/2012). GPS collars were set to attempt one location every hour, and to drop-off after 54 weeks.

We removed outliers GPS locations presenting abnormal deviations of step angles and distances following the approaches suggested by Bjørneraas *et al.* (2010) and Urbano and Cagnacci (2014). After removing 11% of outliers and considering only the reproductive season, as described below, we obtained a database of 49,152 locations for 22 females. In the analysis and interpretation of the results we assumed a median location error lower than 10 m, as estimated from stationary collars in the same area (Párraga Aguado *et al.*, 2017), which we assumed was suitable for matching the habitats maps resolution and analyses of this study (Godvik *et al.*, 2009). During summer, GPS locations acquisition rate was very high (95% on average, Párraga Aguado *et al.* 2017). Therefore, we assumed that the no bias could be introduced into the assessment of habitat use by using the received locations (Frair *et al.*, 2010).

To define habitat types, we used a 1:5000 vector land-cover map (resolution: 0.5 ha) obtained by refining the forest cover maps of Veneto Region and province of Trento (www.regione.veneto.it/web/agricoltura-e-foreste/carta-forestale-regionale) and using a orthophoto of the study area (Scillitani *et al.*, 2013). Specifically, we classified land-cover data into five habitat types (for details see Chapter 2): “forest” (which included coniferous and mixed forest, and shrubs), “grassland”, (which included natural Alpine grasslands and small portions of grazed pastures), “grassland mixed with rocks” (defined by grassland interspersed with rocks and scree), “scree”, and “rocks” (defined by bare rocks). we extracted slope from a regional digital elevation model (resolution: 5x5 m; www.regione.veneto.it/web/ambiente-e-territorio/ctr; www.territorio.provincia.tn.it). The distribution of habitat types across the elevation and slope gradients is given in Figure S. 5-1 and Figure S. 5-2. Habitats are clearly stratified across elevations, with forest being concentrated at the lowest elevations, grasslands and grasslands mixed with rock at the intermediate elevations, and scree and especially rock at the highest elevations. In contrast, habitats are much more uniformly distributed across slopes, with only a slight prevalence of steeper slopes for rock and gentler slopes for grassland.

The GPS collars were equipped with a two-axes activity sensor, scheduled to store the acceleration data at 5 minutes intervals. we classified each interval as ‘active’ or ‘inactive’ based on a threshold identified from the bimodal distribution of the activity signal, as suggested by Gervasi *et al.* (2006), and validated this classification with observational data (for details, see Chapter 3 supplemental material appendix 1). The observed active behavior was composed of 18% of time spent walking and 82% of time spent foraging (for details, see Chapter 3 supplemental material appendix 1), defined by bouts of feeding (biting, chewing and swallowing) interrupted by relocation movements between clusters of plants. Movements between patches of plants did not interrupt feeding because the time taken per step was approximately equal to the time required to process (i.e. chew and swallow) a bite (Owen-Smith *et al.*, 2010). Our results were in accord with what observed on male ibex in the Gran Paradiso National Park (Mason *et al.*, 2017). Therefore, we assumed that active time could be used as a good proxy for foraging activity. we used activity data from sixteen females, since activity data could be downloaded only by dropped-off collars, and six of them were impossible to retrieve.

We observed the 22 monitored females starting from late June, as soon as the area became accessible, until beginning of September, and considered as lactating those females that were seen breastfeeding at least once during the summer. We identified 11 females with kids and 11 without kids (for details, see Chapter 2 - Data collection).

We considered as the reproductive season the period comprised between the end of April and mid August. We defined four periods of 4 weeks using a Julian week's classification starting from 21st December (see Chapter 3 supplemental material appendix 2). To define the limits of the intra-periods, we kept as reference the birth period, corresponding to the period from 24th May to 20th June (23th to 26th Julian weeks). Birth in Alpine ibex are usually observed in June (Grignolio *et al.*, 2007b) and we confirmed this period by comparing patterns of weekly average activity as suggested by Long *et al.* (2009): the spring decrease of activity in reproductive females (but not in non-reproductive females) corresponded to the week starting with 24th of May (Semenzato *et al.* unpublished data). We considered one 4 week period before the birth period ('Pregnancy' from 26th April to 23th May: late pregnancy with high energetic demand, but no kid's limitation), and two 4 weeks period after ('Lactation' from 21st June to 18th July: kids are closely dependent on the mother; high energetic demand for lactation. 'Late lactation' from 19th July to 15th August: kids are more mobile; energy expenditure for lactation starts to decrease).

5.2.3. Statistical analysis

Habitat use

To analyze the habitat use of female ibex, we used multinomial mixed logit models (Kneib *et al.*, 2011). This approach considers a categorical variable indicating the habitat type used by animals as the dependent variable, allowing a simultaneous analysis of several habitat types, and automatically taking the dependence in the selection or use processes into account (Kneib *et al.*, 2011). The relative probability of use of different habitat types may be estimated in relation to several explanatory categorical and continuous variables. Moreover, temporal variables can be introduced to describe the probability of use over time. The power of predictions of these models is greater considering individual-specific random effects to account for intra-individual correlations (Kneib *et al.*, 2011). The tools of classical frequentist statistics make it difficult to implement the model with a random effect. For this reason, we used a Bayesian method to estimate multinomial mixed models with "Markov chain Monte Carlo" (*MCMC*) methods, which allow implementing a maximum likelihood estimation of a multinomial model with random effects.

Due to temporal autocorrelation in patterns of movement of animals, with a location every one hour, our data had a strong spatiotemporal correlation. To take into account this autocorrelation, for each location we measured the observed probability for an ibex to be located in each habitat type during the five previous hours, and defined it as the explanatory variable "history". We considered an arbitrary period of five hours as a compromise between too few data to evaluate the probability of use of each habitat, and too much data to keep the circadian patterns of space use. Then, we measured for each habitat type and for each ibex separately the probability of each location to be located in each habitat type during the five previous hours. These probabilities are based on non-missing data, however, when no data were available during the five previous locations, we used a uniform distribution and considered a probability of 1/5 for an ibex to be located in each habitat type during the five previous hours. We calculated five history variables, corresponding to the five habitat types considered in this study, and retained only four of them as their probabilities sum up to one and we only need four variables to describe the full pattern.

We used generalized linear mixed models using Markov chain Monte Carlo techniques (package "MCMCglmm", Hadfield 2010) in R (R Core Team, 2016) to investigate variation in use of different habitat types (5-level categorical response) with a multinomial response, in relation with reproductive status of females (2-level factor), period (4-level factor), hours (24-level factor), slope at each location (continuous variable), and taking into account the four history variables (continuous variables). We included individual identity as a random factor on the intercept because we had repeated individual measures for habitat use. We considered slope to understand how the habitat use was influenced by the risk of predation, inasmuch as the slope is a topographical feature that characterizes the refuge areas for the ibex (see Chapter 4).

We expected that female ibex should modify their habitat use in relation with their reproductive status. Moreover, we expected that habitat use should show daily and seasonal temporal variations and that these temporal patterns would change in relation with slope and reproductive status. Therefore, we compared complex models with different combinations of three-way interactions, between reproductive status, periods, slope and hours. we then compared these models to simpler possible model combinations, but considering the model containing the variables "history" to take into account the spatio-temporal correlation in habitat use (the baseline model) as the simplest model (Table S. 5-1). We used the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002) to select the model with the most support.

Activity patterns

We defined each location as 'active' or 'inactive' based on the signal activity values averaged over the 15 minutes preceding and following acquisition time. we modeled the probability of a female to be active by fitting Linear Mixed-Effects Models ('glmer' function) with a binomial distribution of errors, using the package 'lme4' (Bates *et al.*, 2016) in R (R Core Team, 2016). In all models, we included the individual identity as a random factor. The most complex model included the three-way interaction between reproductive status, period, and habitat and the two-way interaction between hour (24 levels) and reproductive status) (Table S. 5-1). we compared this model with a set of simpler possible model combinations by means of the Akaike's Information Criterion (AIC; Burnham *et al.* 2002). In case of several models within a ΔAIC range of two, we selected the model with fewest number of parameters (K) (Arnold, 2010). Since preliminary analyses indicated that probability of being active when in forest had erratic patterns with a great residual variability, most likely because of the marginal use of this habitat, we excluded locations in forest from the final analyses.

5.3. **Results**

5.3.1. Habitat use

The model with highest support included the three-way interaction between period, reproductive status and slope and the two-way interaction between hours and reproductive status (Table S. 5-1). Habitat use, thus, varied at the seasonal scale between periods depending on slope (H1) and reproductive status (H2), and at the daily scale between hours depending on slope (H3). There was no support for an effect of reproductive status on daily variation of habitat use.

The probability of using rock (Figure 5-1) was almost nil, in all periods and for both categories of females, at flat or gentle slopes, but then increased with a strong positive relation with slope. This relation was steeper for reproducing than non-reproducing females. The probability of using scree (Figure 5-1) was less dependent on slope than that of using rock. The trend with slope was weakly positive and linear in pregnancy, but increasingly quadratic in the following periods. Therefore, scree tended to be used more at steep slopes in pregnancy and at mid slopes in the following periods. Reproductive females tended to use scree more than non-reproductive females, in all periods. The probability of using grassland mixed with rock (Figure 5-1) was, on average, negatively related with slope, but with contrasting patterns between the two categories of females: the relation was strongly negative for reproductive females, and quadratic for non-reproductive females. As a result, reproductive females used grassland mixed with rock more than non-reproductive females at flat or gentle slopes, but less at steep slopes. In addition, the probability of using grasslands (Figure 5-1) was negatively influenced by slope, being highest at flat slopes and nil for both categories of females with slopes > 60°. This probability was lower for reproducing females than for non-reproducing females, in all periods. The probability of using forest was very low in all periods, being very little influenced by slope, and was consistently lower for reproducing than non-reproducing females.

In synthesis, these results were in agreement with our prediction of a positive relation between habitat use and slope (P.1.1) only for rock, while for the other habitat types this relation was quadratic or even negative, indicating a more complex interaction between land morphology and cover than the one we had predicted (P.1.2). Our predictions concerning the low use of forest, especially by reproducing females, were instead supported (P.2.2 and P.2.3).

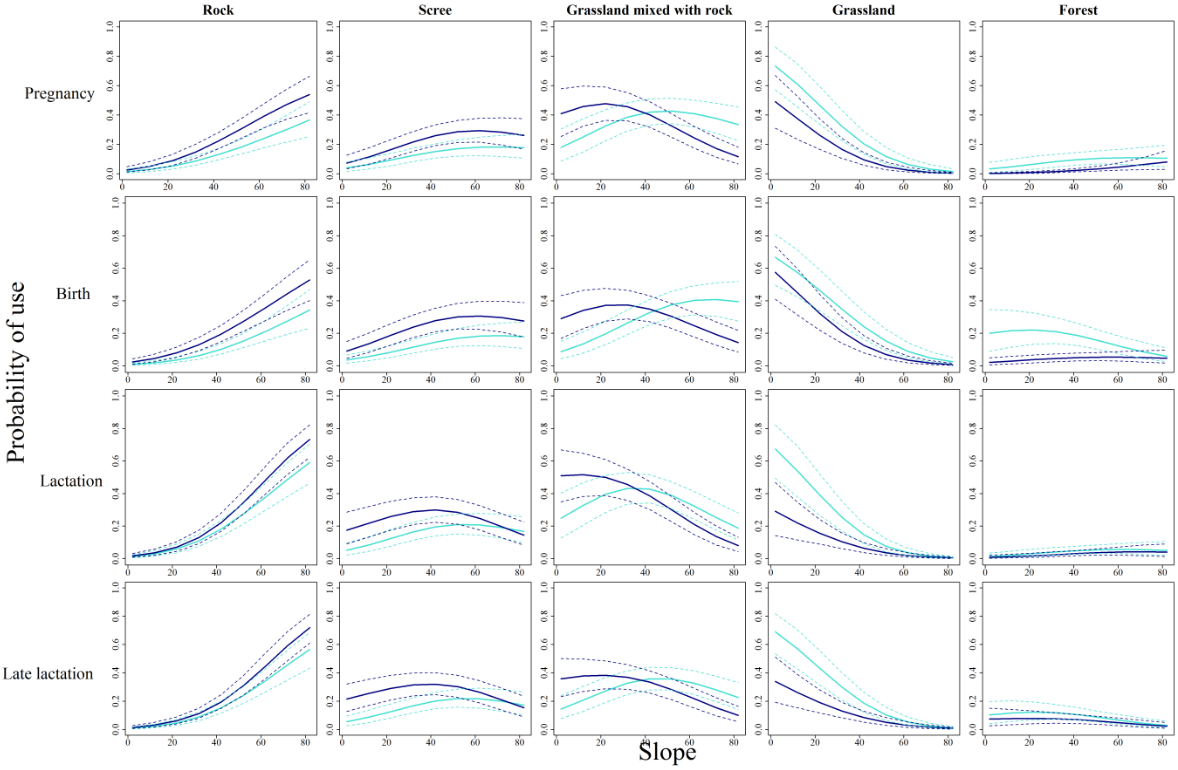

Figure 5-1 Predicted pattern of probability of using different habitat types over the reproductive period of 11 lactating and 11 non-lactating females ibex, monitored in the Marmolada massif from 2010 to 2016, fitting the best model in relation with reproductive state, period, and slope. The solid dark blue line indicates reproductive females, and the solid light blue line non-reproductive females. Dotted lines show 95% confidence intervals.

Concerning the variation of habitat use in relation with hour and slope, the probability of using rock was little influenced by time of the day at low to mid slopes (Figure 5-2). At steep slopes, probabilities of use were more diversified between hours, but without a clear temporal pattern. The probability of using scree (Figure 5-2) showed, at flat or gentle slopes, the highest values during hours of evening activity (18 and 21 hours) and the lowest values during hours of night resting (0 and 3 hours) or morning rise of activity (6 and 9 hours). No clear pattern was evident at steep slopes. The probability of using grassland mixed with rock (Figure 5-2) was little influenced by time of the day at steep slopes, when it was lowest. At flat to mid slopes, it was highest during the resting periods of deep night and the morning rise of activity, and decreased progressively from mid-day to evening. Probability of using grassland (Figure 5-2) was little influenced by slope in interaction with time of the day, except for a higher use at flat slopes during the rise of activity in the afternoon and evening (15 and 18 hours). Use of forest was very low without any remarkable influence of slope and time of the day. These results indicate that the circadian pattern of habitat use followed a more complex pattern than that predicted (P.3.1), most probably in interaction with the daily altitudinal shifts of females and the consequent variation in the availability of the different habitat types.

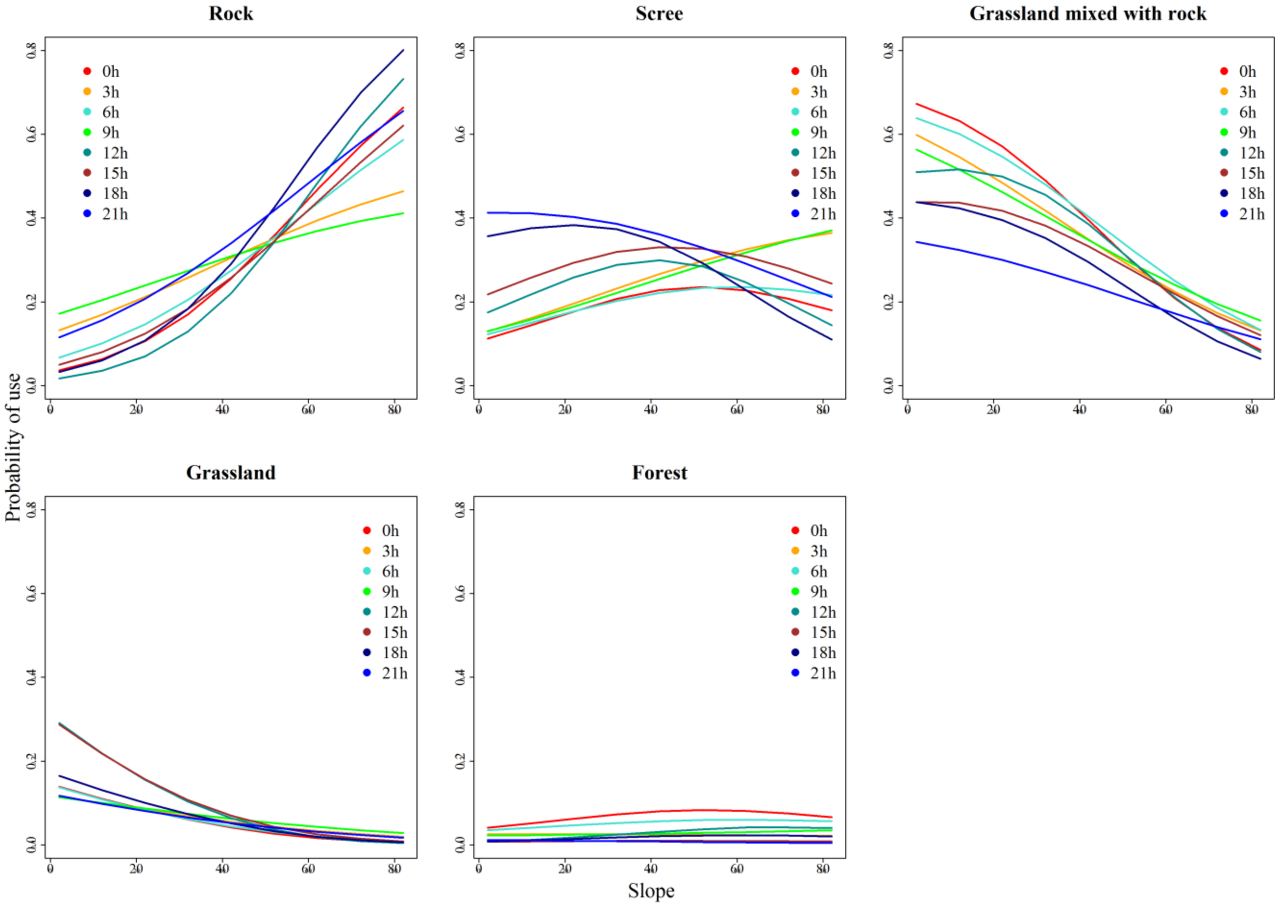

Figure 5-2 Predicted pattern of probability of using the different habitat types over the reproductive period of 22 female ibex, monitored in the Marmolada massif from 2010 to 2016, fitting the best model in relation with hour and slope. Predicted patterns are shown at 3 hours intervals to allow readability.

5.3.2. Activity patterns

The best model analyzing the probability of a female to be active included the three-way interaction between reproductive status, period and habitat, and the interaction of hours with reproductive status (Table S. 5-1 and Table S. 5-3 for model outputs). Therefore, female ibex modified activity patterns at the seasonal scale in relation with habitat used, reproductive status and period (H5), and at the daily scale between hours depending on reproductive status (H6).

Probability of all females to be active when in rock was lower than when in the other habitat types (Figure 5-3), This probability was also lower for reproducing females than non-reproducing females in birth and early lactation (Figure 5-3). Probability of all females to be active in scree (Figure 5-3) was slightly higher than in rock. This probability was only slightly lower for reproducing than for non-reproducing females in pregnancy and especially in birth, but higher in lactation. The probability of all females to be active in grassland mixed with rock (Figure 5-3) was, on average, higher than that showed in rock but similar to that showed in scree. It changed little in relation with reproductive status and across periods. Probability of all females to be active in grassland (Figure 5-3) was higher than in all the other habitats, and changed little with reproductive status and across periods and until lactation. In late lactation, it decreased. These results in general supported our hypothesis (P.4.1) that females should be more active in forage rich-habitats, but showed also a gradient from bare (rock) to totally vegetated (grasslands) habitats. Concerning reproductive status, our prediction that lactating females should be more active than non-lactating females (P.5.1) was not supported, while the prediction that lactating females reduced activity as respect to non-lactating females during birth, and increased it afterwards (P.5.2) was weakly supported, and only in habitats with little vegetation.

Finally, circadian patterns of activity (Figure 5-4) indicated that reproductive females were more active than non-reproductive females during the mid-day period of resting (P.6.1).

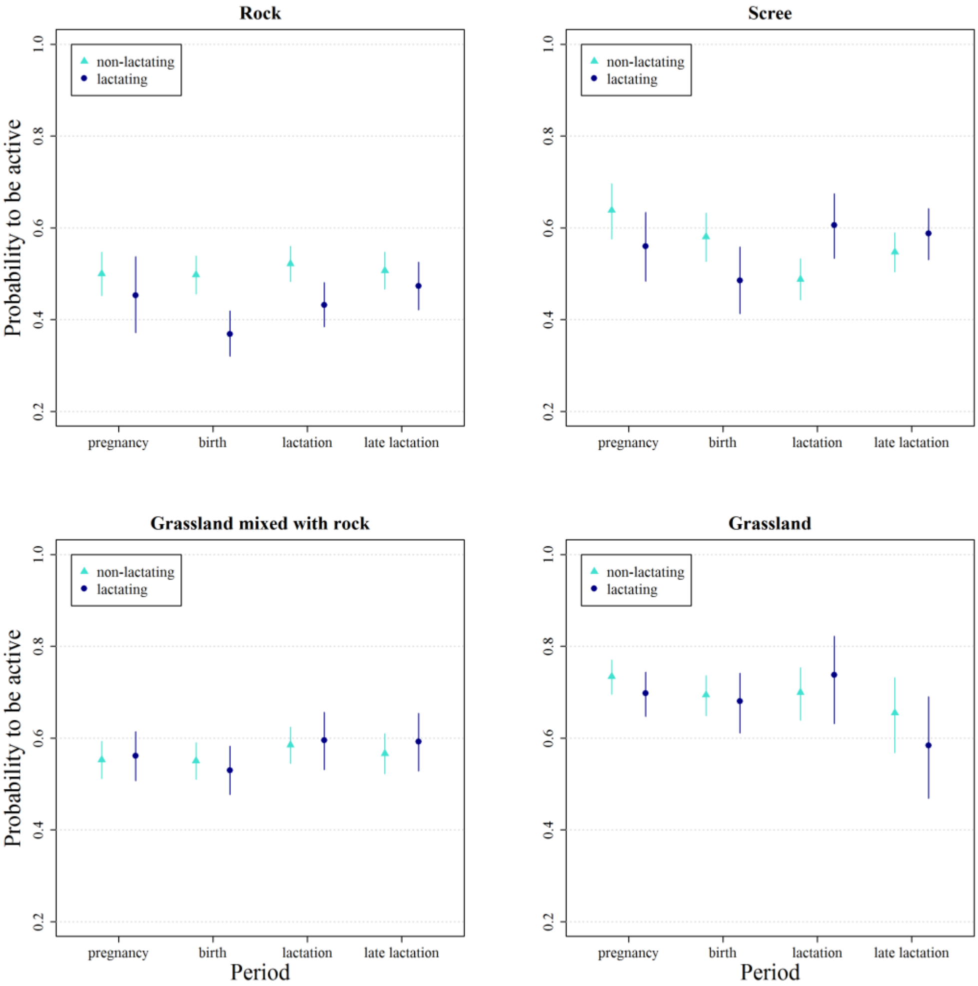

Figure 5-3: Predicted probabilities of being active over the reproductive period in different habitat types, of 11 lactating and 11 non-lactating females ibex, monitored in the Marmolada massif from 2010 to 2016, obtained fitting the best model.

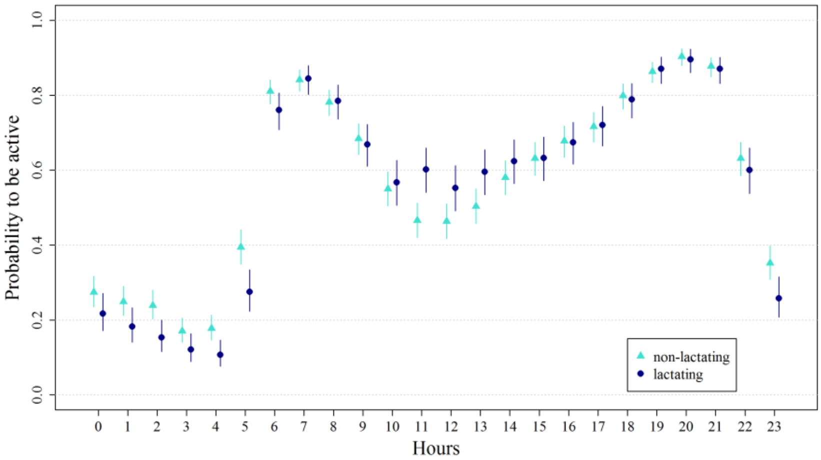

Figure 5-4 Circadian pattern of the probability of being active over the reproductive period of 11 lactating 11 non-lactating females ibex, monitored in the Marmolada massif from 2010 to 2016, obtained fitting the best model.

5.4. **Discussion**

In this study, by combining the high-resolution analysis of habitat use in dependence to slope with that of activity (foraging) patterns during summer, we found that slope and land cover interact to determine functional roles of different habitat types for female ibex that are more diversified than what suggested by previous studies (Villaret *et al.*, 1997; Grignolio *et al.*, 2007b). This approach allowed me also to observe that lactating female ibex showed behavioral plasticity to respond to the multiple constraints imposed by reproduction, and were able to adjust use of the different habitat types with activity patterns in the attempt to cope with the constraints and needs deriving from their reproductive status.

Habitat use in relation with slope and activity

Rock is a habitat with very little or no vegetation that was used by female ibex especially when it was very steep and when they were inactive. Assuming that the combination of steep slopes with low activity indicates that a habitat is used mostly for refuge and that the combination of flat or gentle slopes with high activity indicates that it is used mostly for foraging, this indicates that rock was mainly searched as a source of refuge. This was largely expected based on previous studies (e.g. Villaret and Bon 1995; Grignolio, Rossi, Bertolotto, *et al.* 2007).

The relation with slope of the probability of using scree was different than the positive one predicted. In addition, females' activity levels were remarkably higher in scree than in rock. Steep scree areas are very poor of vegetation, but presumably safer, while screes at gentle slopes are richer in vegetation but presumably riskier. Therefore, we interpret our results as an indication that screes, although poor of vegetation, were used also as a foraging habitat. During summer, at the altitudes of the study area where scree areas are concentrated (see Figure S. 5-1) the vegetation might be of better quality in comparison with that of forage-rich habitats located at lower elevations, because of a delayed senescence (see Chapter 3). In support of our interpretation, behavioral observations during summer indicated that diurnal feeding activity of females occurred for 39% in scree, and for 54% in forage – rich habitats (Ramanzin, unpublished).

Surprisingly, the probability of use of grasslands and grasslands mixed with rock decreased with slope, which clearly indicates that they were not used for refuge. In addition, probabilities of the females being active in these habitats were high. Both findings suggest that female ibex used these habitats mostly when foraging. However, patterns of use and activity differed clearly between grasslands and grasslands mixed with rock. In grasslands, the use of flat or gentle slopes was much stronger and activity levels were higher, suggesting a predominant use of this habitat for grazing. The use of grasslands and the probability of a female of being active in them decreased in lactation (mid-July to mid-August), possibly in relation with the concomitant advancing of the grass phonological stage, which is anticipated as respect to that of other habitats (see Chapter 3). In grasslands mixed with rock, activity levels were lower than those observed in grasslands, being only marginally higher than in scree. In addition, high probabilities of using flat slopes were observed both in resting periods (as deep night) and foraging periods (as morning rise of activity). These results suggest that grassland mixed with rock were used by female ibex not only for foraging, but also for resting. In this regard, the rock outcrops and cliffs that interrupt the continuity of the grassland might offer to the females quick escape when grazing or safe vantage points where to rest.

Finally, our results demonstrated that forest was a habitat with a marginal importance for female Alpine ibex during summer. In other species, forest may offer shelter from thermal stress (Demarchi & Bunnell, 1993; Mysterud & Østbye, 1999; Melin *et al.*, 2014), but the Alpine ibex search for lower temperatures by shifting to higher elevations (Aublet *et al.* 2009; Mason *et al.* 2017; see Chapter 3). In addition, forest may be a habitat where predation risk was perceived as higher by a species that has evolved in open habitats and relies on eyesight for detecting predators (Festa-Bianchet & Côté, 2008).

The habitat use and activity patterns in relation with reproductive state

Our results demonstrated that reproductive females are able to modify habitat use and patterns of activity across reproductive phases to optimize the trade-offs between the needs of protecting kids with limited movement ability and of acquiring the forage resources necessary for sustaining the increased energy requirements of lactation. Previous studies suggested that in order to protect kids lactating female ibex might be forced to use suboptimal foraging habitats (Grignolio *et al.*, 2007b; Hamel & Côté, 2007). Indeed, we found here that reproductive females used rock more, and grassland less, as respect to non-reproductive females. However, they also used grassland mixed with rock and scree more than non-reproductive females, most likely as alternative compensatory foraging habitats. Interestingly, too, reproductive females used flat or gentle slopes less than non-reproductive females in grassland but more in grassland mixed with rock. This might suggest that they searched for similar foraging conditions and possibly forage quality, but in a safer habitat. Similarly, the use of scree could provide protection, with the excellent visibility due to its homogeneous micromorphology and the proximity to rock cliffs, but also forage. This higher use of grasslands mixed with rock and scree might also be a tactic adopted by lactating female to adjust foraging needs with the lower movement ability of kids. In this respect, in Chapter 4 we showed that lactating females had less pronounced daily altitudinal shifts than non-lactating females, thus remaining at higher elevations where availability of scree and grassland mixed with rock was higher.

In relation with the kid limitation hypothesis, reproducing females showed a lower activity than non-reproducing females especially during birth and, less, during lactation, but only in rock. This might be related to the mobility of kids which is presumably limited especially in this usually steep habitat, but might also allow females to reduce energy expenditure given the high costs of moving in steep slopes (Biancardi & Minetti, 2017). Conversely, lactating females maintained activity levels similar to those of non-reproducing females in all periods in forage-rich habitats, and higher activity levels in scree during lactation. In addition, circadian patterns of activity showed that reproducing females were more active than non-reproducing females during the mid day resting period, presumably because they foraged more and rested less in a period where surveillance of kids was easier.

Our results, therefore, indicate that reproducing females were able to combine changes in habitat use and foraging activity to access forage resources while trading for protection and limited movement ability of kids. However, we had also expected that female ibex increased foraging activity during lactation, as respect to non-lactating females, to increase energy intake. Our results did not support this prediction. We interpret this as an indication that the aim of increasing energy intake is not pursued by lactating female ibex through strongly modifying patterns of foraging. However, this indication should be further explored acquiring data on the biomass and quality of vegetation, and hence of the forage value, of the different habitat types, which we did not have. Furthermore, in addition to habitat use and activity patterns, lactating females could have adopted other behavioral tactics that we could not address here. For instance, higher food intakes during foraging may be obtained by increasing bite rate (Mountain goat (*Oreamnos americanus*) Hamel and Côté 2009; bighorn sheep: Ruckstuhl *et al.* 2003; plain zebra *Equus burchelli*; (Neuhaus & Ruckstuhl, 2002b); Alpine ibex: (Neuhaus & Ruckstuhl, 2002a), and digestion efficiency might be possibly improved through longer rumination time Hamel and Côté 2008 and faster rumination chewing rate Blanchard 2005; Hamel and Côté 2009). These behaviors might allow lactating females to cope with their higher requirements even when being in different habitats, or similarly active, than non-lactating females.

5.5. References

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5.6. Supplementary Material

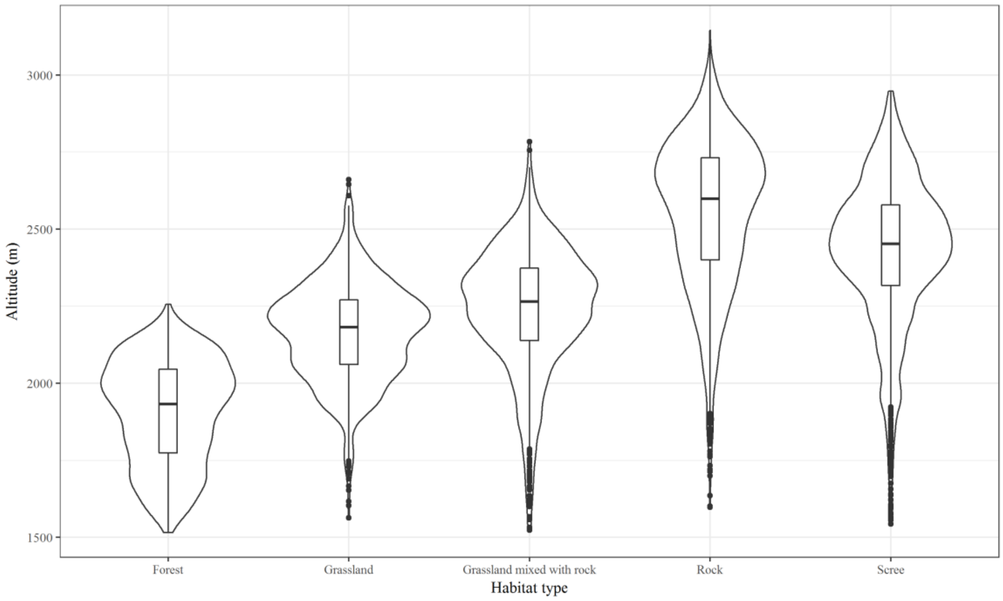

Figure S. 5-1 Altitudinal distribution of habitat types in the study area, defined as the minimum concave polygon of all location points (44km^2). I extracted from DEM and land cover layers the values of 10.000 random points and plotted the distributions.

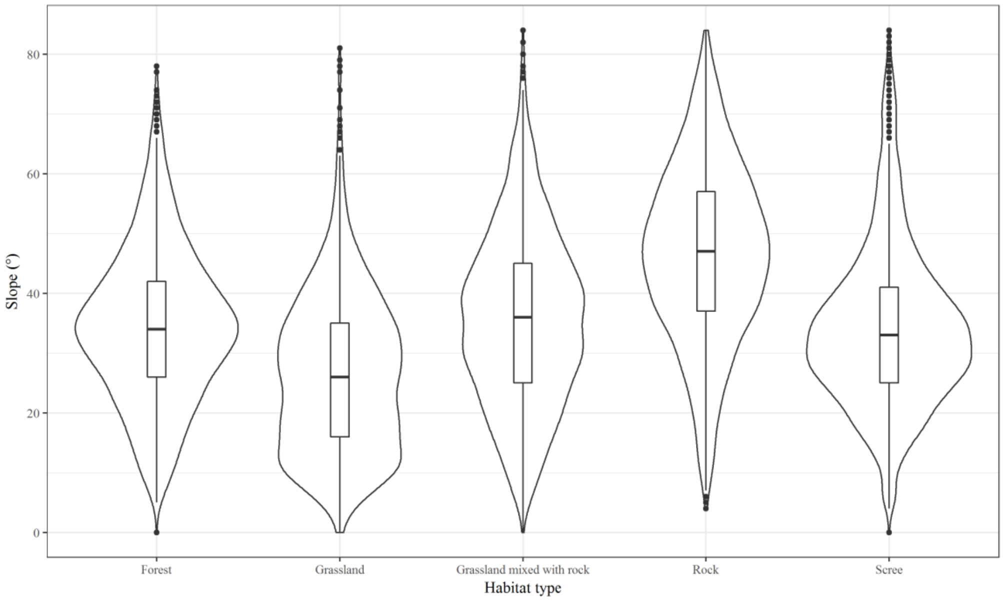

Figure S. 5-2 Slope distribution of habitat types in the study area, defined as the minimum concave polygon of all location points (44km^2). I extracted from DEM and land cover layers the values of 10.000 random points and plotted the distributions.

Table S. 5-1 Model selection of candidate multinomial mixed logit models analyzing probability of use of the different habitats. H: hours (categorical variable, 24 levels); S: slope (continuous variable); RS: reproductive status (categorical variable, 2 levels); P: period (categorical variable, 4 levels), History is a continuous variable indicating the probability that a given habitat was used in the 5 locations preceding each location. All models included the individual identity as random factor.

Candidate models	DIC	ΔDIC
H*S + S*RS*P+ history	94299.26	0.00
H*S+H*P + S*RS*P+ history	94313.02	-13.76
H + S*RS*P+ history	94330.46	-31.20
H*P+H*S+P*S+S*RS+RS*P+ history	94340.93	-41.66
H*P + S*RS*P + history	94344.75	-45.49
H*P + P*S + S*RS + RS*P+ history	94370.94	-71.68
H*RS + S*RS*P+ history	94393.01	-93.75
H*P+H*S+P*S+S*RS+RS*P+H*RS + history	94411.92	-112.66
H*RS*P + S*RS+S*P + history	94416.16	-116.90
H*RS+H*P + S*RS*P+ history	94417.64	-118.38
H*P+H*RS+P*S+S*RS+RS*P+ history	94435.41	-136.14
H*RS*S + S*RS*P+ history	94446.70	-147.44
H*RS+H*P + S*RS+S*P+ history	94489.41	-190.15
H*P*S + S*RS*P + history	94543.58	-244.32
H*RS*P + S*RS*P + history	94545.70	-246.44
H*P*S + RS*S+RS*P + history	94554.73	-255.47
H + P + S + RS + history	94574.62	-275.36
H + P + S+ history	94577.82	-278.56
H*P*S + P*RS + history	94590.13	-290.87
H*P*S + S*RS+ history	94600.42	-301.16
H*P*S + RS+ history	94643.22	-343.95
H*P*S + H*RS+ history	94711.67	-412.41
H*RS*S + H*RS*P+ history	94749.91	-450.65
H*P*S + H*RS*P+ history	94766.88	-467.62
H*P*S + H*RS*S+ history	94772.23	-472.97
P * S + history	95474.99	-1175.73
H+P*RS + history	97290.84	-2991.58
H + P+ history	97354.50	-3055.24
H+P+RS + history	97354.96	-3055.71
H*RS + P+ history	97436.67	-3137.41
P*RS+ history	98529.56	-4230.29
P+ history	98593.58	-4294.32
H+ history	98797.87	-4498.61
RS + history	100048.43	-5749.17
+ history	100050.58	-5751.32

Table S. 5-2 Model selection of candidate generalized linear mixed models analyzing the probability of a female to be active. Hab: habitat type (categorical variable, 5 levels); RS: reproductive status (categorical variable, 2 levels); P: period (categorical variable, 4 levels); Hours (24 levels). All models included the individual identity as random effect.

Candidate models	DF	AIC	Delta AIC	Model Weight
RS*P*Hab +hour* RS	79	34876.7	0.0	0.7
RS*P + RS*Hab + P*Hab +hour* RS	70	34880.0	3.3	0.1
RS*Hab + P*Hab +hour* RS	67	34890.4	13.7	0.0
RS*P + RS*Hab +hour* RS	61	34890.5	13.8	0.0
RS*Hab + P +hour* RS	58	34900.3	23.7	0.0
RS*Hab +hour* RS	55	34908.7	32.1	0.0
RS*P + P*Hab +hour* RS	67	34909.3	32.7	0.0
Hab*P +hour* RS	64	34916.6	40.0	0.0
P*Hab + RS +hour* RS	64	34916.6	40.0	0.0
RS*P + Hab +hour* RS	58	34920.0	43.4	0.0
RS+ Hab +hour* RS	55	34928.2	51.5	0.0
RS + Hab + hour*RS	52	34937.3	60.6	0.0
Hab +hour	52	34937.3	60.6	0.0
RS*P + Hab +hour	56	34943.6	67.0	0.0
RS*P + RS*Hab + P*Hab +hour	47	34948.2	71.5	0.0
RS*Hab + P*Hab +hour	44	34956.6	79.9	0.0
RS*P + RS*Hab +hour	38	34959.1	82.4	0.0
Hab*RS +P +hour	35	34967.1	90.4	0.0
Hab*P + P*RS +hour	44	34973.5	96.8	0.0
Hab*RS +hour	32	34976.9	100.2	0.0
Hab*P +hour	40	34979.5	102.8	0.0
Hab*P +RS +hour	41	34981.1	104.4	0.0
RS*P + Hab +hour	35	34985.9	109.2	0.0
P + Hab +hour	31	34992.7	116.0	0.0
RS+ Hab +hour	29	35004.8	128.1	0.0
RS*P +hour* RS	55	35318.1	441.5	0.0
P + RS +hour* RS	52	35337.0	460.3	0.0
P +hour* RS	52	35337.0	460.3	0.0
RS*P+hour	32	35372.2	495.6	0.0
P +hour	28	35390.6	513.9	0.0
P + RS +hour	29	35392.0	515.3	0.0
hour* RS	49	35407.4	530.7	0.0
hour	25	35462.7	586.0	0.0
Null	2	43217.7	8341.0	0.0

Table S. 5-3 Coefficient parameters from the best generalized linear mixed models analyzing the probability of a female to be active analyzing the probability of a female to be active. Hab: habitat type (categorical variable, 5 levels); RS: reproductive status (categorical variable, 2 levels); P: period (categorical variable, 4 levels); Hours (24 levels).

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0.29986	0.126176	-2.37656	0.017475	*
RS-Yes	-0.39351	0.20845	-1.8878	0.059053	.
P-birth	-0.19785	0.109656	-1.80432	0.07118	.
P-early lactation	-0.17172	0.143611	-1.19574	0.231798	
P-lactation	-0.37749	0.189557	-1.99145	0.046431	*
Hab-grass mixed rock	-0.80485	0.090995	-8.84497	9.16E-19	***
Hab-rock	-1.01752	0.103405	-9.84014	7.56E-23	***
Hab-scree	-0.4497	0.13755	-3.26938	0.001078	**
hours1	-0.12911	0.117085	-1.10266	0.270174	
hours2	-0.18305	0.117884	-1.55283	0.120463	
hours3	-0.60742	0.126489	-4.80211	1.57E-06	***
hours4	-0.56112	0.126227	-4.44537	8.77E-06	***
hours5	0.544546	0.109686	4.964573	6.89E-07	***
hours6	2.430338	0.117069	20.75993	9.97E-96	***
hours7	2.643073	0.120294	21.97183	5.4E-107	***
hours8	2.250936	0.113488	19.83415	1.51E-87	***
hours9	1.747221	0.108721	16.07064	4.1E-58	***
hours10	1.175695	0.106134	11.07744	1.61E-28	***
hours11	0.837363	0.106856	7.836398	4.64E-15	***
hours12	0.828739	0.107213	7.729835	1.08E-14	***
hours13	0.988097	0.106835	9.248842	2.27E-20	***
hours14	1.299509	0.107209	12.12124	8.15E-34	***
hours15	1.512638	0.108298	13.96741	2.46E-44	***
hours16	1.717287	0.109879	15.62882	4.63E-55	***
hours17	1.901046	0.110928	17.13764	7.77E-66	***
hours18	2.352756	0.117445	20.03277	2.85E-89	***
hours19	2.81872	0.12741	22.12321	1.9E-108	***
hours20	3.212866	0.138853	23.1386	1.9E-118	***
hours21	2.942407	0.13015	22.60786	3.6E-113	***
hours22	1.511461	0.109329	13.82486	1.8E-43	***
hours23	0.363569	0.111528	3.259898	0.001115	**
RS-Yes:P-birth	0.116066	0.187734	0.618246	0.536413	
RS-Yes:P-early lactation	0.369281	0.289091	1.277388	0.201465	
RS-Yes:P-lactation	-0.12084	0.30089	-0.40161	0.68797	
RS-Yes:Hab-grass mixed rock	0.215856	0.143193	1.507449	0.131696	
RS-Yes:Hab-rock	-0.00669	0.199927	-0.03346	0.973304	
RS-Yes:Hab-scree	-0.1459	0.20668	-0.70593	0.480232	
P-birth:Hab-grass mixed rock	0.187724	0.13244	1.417431	0.156357	
P-early lactation:Hab-grass mixed rock	0.302835	0.162476	1.86388	0.062339	.
P-lactation:Hab-grass mixed rock	0.432282	0.207228	2.086025	0.036976	*

P-birth:Hab-rock	0.188931	0.142662	1.324334	0.185392	
P-early lactation:Hab-rock	0.260014	0.167516	1.552175	0.12062	
P-lactation:Hab-rock	0.404985	0.2094	1.934025	0.05311	.
P-birth:Hab-scree	-0.04446	0.183749	-0.24194	0.808824	
P-early lactation:Hab-scree	-0.44405	0.195746	-2.26851	0.023298	*
P-lactation:Hab-scree	-0.00051	0.230406	-0.0022	0.998248	
RS-Yes:hours1	-0.08809	0.214048	-0.41154	0.680678	
RS-Yes:hours2	-0.24275	0.220281	-1.10199	0.270465	
RS-Yes:hours3	-0.08922	0.23478	-0.38003	0.703925	
RS-Yes:hours4	-0.28041	0.239991	-1.16841	0.242643	
RS-Yes:hours5	-0.22894	0.199199	-1.14929	0.250437	
RS-Yes:hours6	0.006856	0.200301	0.03423	0.972693	
RS-Yes:hours7	0.332187	0.210028	1.58163	0.113734	
RS-Yes:hours8	0.327629	0.198622	1.649506	0.099044	.
RS-Yes:hours9	0.238766	0.189975	1.256829	0.208816	
RS-Yes:hours10	0.377078	0.186527	2.021572	0.043221	*
RS-Yes:hours11	0.857405	0.18744	4.574288	4.78E-06	***
RS-Yes:hours12	0.66468	0.187169	3.551229	0.000383	***
RS-Yes:hours13	0.682359	0.188075	3.628132	0.000285	***
RS-Yes:hours14	0.491168	0.188556	2.604884	0.009191	**
RS-Yes:hours15	0.312482	0.189753	1.646783	0.099603	.
RS-Yes:hours16	0.293632	0.191985	1.529457	0.126151	
RS-Yes:hours17	0.329827	0.19469	1.694117	0.090243	.
RS-Yes:hours18	0.247906	0.202806	1.222379	0.221565	
RS-Yes:hours19	0.372076	0.221702	1.678267	0.093295	
RS-Yes:hours20	0.218692	0.236396	0.925111	0.354908	
RS-Yes:hours21	0.245511	0.222531	1.103269	0.26991	
RS-Yes:hours22	0.17675	0.190614	0.927268	0.353788	
RS-Yes:hours23	-0.13718	0.201241	-0.68168	0.49544	
RS-Yes:P-birth:Hab-grass mixed rock	-0.23287	0.2259	-1.03085	0.302612	
RS-Yes:P-early lactation:Hab-grass mixed rock	-0.36158	0.323426	-1.11796	0.263583	
RS-Yes:P-lactation:Hab-grass mixed rock	0.193737	0.337707	0.573684	0.566182	
RS-Yes:P-birth:Hab-rock	-0.45863	0.26705	-1.71738	0.085909	.
RS-Yes:P-early lactation:Hab-rock	-0.54336	0.341611	-1.59057	0.111706	
RS-Yes:P-lactation:Hab-rock	0.174118	0.35345	0.492624	0.622278	
RS-Yes:P-birth:Hab-scree	-0.17217	0.298431	-0.57693	0.563983	
RS-Yes:P-early lactation:Hab-scree	0.436522	0.36628	1.19177	0.233351	
RS-Yes:P-lactation:Hab-scree	0.612521	0.362921	1.687753	0.091459	.

6. **General Conclusion**

This thesis provides new knowledge on the behavioral tactics of female Alpine ibex to cope with environmental and life-history constraints during spring and summer, a critical period for a capital breeder species (Langvatn *et al.*, 1996). Moreover, this was the first attempt, to my knowledge, to describe these behavioral tactics both at the seasonal and circadian scales, including night hours. My results indicated that movement, habitat use, and foraging activity of female ibex responded to forage acquisition, thermoregulation, and predation risk, in dependence on their reproductive status.

Female ibex responded to vegetation productivity and phenology with an altitudinal shift that started in spring and peaked in summer. This way, they accessed habitats where vegetation had a lower absolute productivity but a steeper green-up. This clearly suggests that the altitudinal shift was part of a resource acquisition tactic according to the forage maturation hypothesis (Hebblewhite *et al.*, 2008; Bischof *et al.*, 2012), that this work suggests for the first time in ibex, and a goat in general.

At the same time, the summer temperature increase forced females to adopt a behavior to avoid thermal stress. My results showed that thermoregulatory behavior occurred mainly at the daily scale by means of altitudinal shifts. As females moved at higher altitude in spring-summer, they also began to perform daily altitudinal migrations, using higher altitudes in the hottest hours, when they substantially reduced the forage activity. I have also shown that this compensatory effect was not fixed, but plastic: female ibex adjusted the total daily shift to the mean daily temperature, with larger shifts to reach higher altitudes in the hottest days. While some components of these behaviors were previously recorded (Aublet *et al.*, 2009; Mason *et al.*, 2017), I have shown for the first time that the reduction in activity during hot hours was compensated with a prolonged foraging activity in early morning and evening/early night. This way, female ibex kept a constant total daily foraging time across a wide range of mean daily temperatures (see general introduction).

I have also shown for the first time the correspondence between circadian patterns of activity, altitude use, and habitat selection. Thermal-cover habitats were selected during the central, hottest hours, whereas 'forage' habitats were selected during high activity periods. Hence, female ibex maximized both thermal cover and resource acquisition, because they moved across food-rich habitats when shifting between low bed-sites and high, cool areas (see Mitchell & Lima, (2002) and van Beest *et al.*, (2013).

In mammal species with high parental investment, offspring's predation risk and physiological constraints shape the behavioral responses of females with young at heel, thus affecting the trade-off between survival, and resource acquisition (Ruckstuhl & Neuhaus, 2002). By contrasting females with and without kids, I verified this effect in ibex. The presence of anti-predator behavior in female ibex had already been described by previous studies on vigilance behavior (Toïgo, 1999; Brivio *et al.*, 2014) and use of refuge areas (Villaret *et al.*, 1997; Grignolio *et al.*, 2007a, 2007b). In this work, I have considered anti-predator responses along with other external constraints, common to all females, as part of a more complex trade-off mechanism. In this work, I have considered anti-predator responses along with other external constraints, common to all females, as part of a more complex trade-off mechanism. I demonstrated a marked anti-predatory behavior at seasonal scale. At daily scale, I showed the presence of a complex space behavior allowed lactating females to compensate for thermoregulation needs and kids specific needs. Lactating females used a range of altitudes that contemporarily allowed to reach refuge and forage areas while compensating for thermoregulation needs and kids specific needs. The marked difference in movement behavior between lactating and non-lactating females was also an evidence of individual behavioral plasticity in dependence on life-history traits. In addition, by contrasting the use of different habitats and the activity patterns of lactating and non-lactating females, I also disentangled the functional role of habitats in dependence on reproductive status. After births, lactating females used rocks more and grassland less than non lactating females. In turn, lactating females used, and foraged in, more grassland mixed with rock and scree than non-lactating females, possibly because these habitats represented the best compromise between forage acquisition and protection of kids with their low mobility.

My findings provide important knowledge for assessing the potential of ibex populations to adapt to abiotic and biotic consequences of climate change, such as temperature increase and plant phenology variability. In particular, this study helped clarify the functional role of altitudinal migration, linking it with delayed vegetation phenology of habitat temperatures at the seasonal scale, and with thermoregulation needs at the daily scale. Furthermore, I showed that, in temperature-sensitive species, the evaluation of the trade-off between predation risk and resource acquisition should also consider thermoregulation. So far, trade-offs between forage and thermoregulation were analyzed only on male ibex (Aublet *et al.*, 2009; Mason *et al.*, 2017). Here, I consider these constraints in females, which have higher reproductive investments and constraints than males in spring-summer.

Through the analysis of individual behaviors of female ibex that were all part of the same colony, I was able to identify differences in behavioral tactics at the population level, related to the life-history of individuals. My findings further suggested individual behavioral plasticity, in terms of proximate adaptive responses to the environmental heterogeneity (such as variability in temperature).

Even though I did not specifically analyze the among-individual variability of behaviors, but accounted for that (since we fitted individuals as random effect), the low variance of predicted behavioral responses suggested that female ibex showed a pronounced behavioral consistency between individuals with similar life-history traits (sex, age, and reproductive status). Such consistency strongly differs from the sheer inter-individual variability of spatio-temporal responses observed in other ungulates (e.g., roe deer; Cagnacci *et al.* 2011; Cagnacci *et al.* 2016), and could be arguably related to the gregariousness of the species. In turn, common, stereotypical responses to the same perturbation may be due to a reduced pool of behavioral types at the population level, and hence less capability to respond to climate and other human-induced changes.

For a complete understanding of the adaptive ability of female ibex to buffer environmental changes in the current distribution range, it would be necessary: 1) to better study individual plasticity within population (i.e., repeatability of behavioral types within and across individuals), and evaluate the effects of different individual behaviors on individual fitness; 2) to compare behavioral responses across colonies/populations.

The latter objective, in particular, would unfold knowledge on the actual portfolio of behavioral types of ibex under different environmental conditions, and therefore their resilience to climate change scenarios. To this end, more extensive individual-based studies with biologging devices, such as GPS based radio-telemetry and activity/physiological sensors, and a better integration of existing datasets (e.g., Europan Ibex Group; Gruppo Stambecco Italia) would of paramount importance.

6.1. References

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