UNIVERSITÀ
DEGLI STUDI
DI PADOVA

DIPARTIMENTO DI AGRONOMIA ANIMALI ALIMENTI
RISORSE NATURALI E AMBIENTE (DAFNAE)

GPS TRACKING IN HIGH MOUNTAIN LANDSCAPES: INSIGHTS INTO THE MOVEMENT ECOLOGY OF FEMALE ALPINE IBEX (*Capra ibex ibex* L. 1758).

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INDIRIZZO: SCIENZE ANIMALI
CICLO XXVII

Direttore della Scuola: Ch. ma Prof.ssa Viviana Corich

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A mi padre,

mi ejemplo, guìa y determinación.

A mi madre y hermanas, con infinita gratitud.

CONTENTS

ABSTRACT

The three studies reported in this thesis have been conducted on the Alpine ibex population of the Marmolada-Monzoni, in the north-eastearn Italian Alps. A summary for each study is given below.

Chapter I: Land morphology, season and individual activity influence GPS fix acquisition rates and location error in an alpine ungulate.

The use of GPS technologies in wildlife research has greatly increased the opportunities for addressing ecological issues that affect ultimately the conservation of the species. However, in order to formulate accurate and unbiased conclusions in studies of movement ecology with GPS-tracking systems, it is necessary to understand the sources of potential bias and error associated with this technology, under specific environmental conditions and taking into account the behavioural patterns of the species monitored. In chapter I, I first present the results of a field trial with stationary collars scheduled to attempt a location fix every 30 min during 24 hours cycles. The collars were positioned in 64 locations throughout the study area in order to sample different land cover categories and topographic conditions. GPS collars performances were influenced mainly by available sky view. When sky view was higher than 70%, acquired as respect to scheduled locations were close to 100%, and location accuracy was within 10 m for 75% of acquired locations. When sky view was below 70 %, the proportion of acquired locations dropped to 75% and location error increased to within 20 m for 75% of locations acquired. I then examined a database of more than 90.000 attempted locations from 11 GPS-tagged females of Alpine ibex to assess the temporal trends in fix acquisition rate, and how it was influenced by habitat features of daily areas used, by individual activity, and by climate and weather variables. I found that fix acquisition rate was very good and scarcely variable in summer, but could drop to less than 85% during the coldest months and at night in winter. Fix acquisition rate was strongly and positively influenced by individual activity and declined, especially in winter, in periods of adverse weather and lower than average temperatures. Most probably female ibex, when inactive and seeking for shelter, use microhabitats providing cover that obstructs the satellites signal, so reducing

fix acquisition rate. I concluded that, although with an adequate screening procedure for identifying outliers the accuracy of locations received from different habitat conditions may remain good, the acquired locations underestimate the use of habitats providing shelter and the periods of adverse weather. In general, the results underline the importance of combining stationary tests with tests on free-ranging animals when assessing GPS bias and accuracy in field conditions.

Chapter II: Determinants of home range size across spatio-temporal scales in a high mountain ungulate.

The high seasonality of Alpine habitats might have strong effects on the spatial strategies of large herbivores. In the second chapter, I obtained a database of 672 estimates of weekly home ranges (232 in summer and 440 in winter) and 160 estimates of monthly home ranges (64 in summer and 96 in winter) from 15 female ibexes, and analysed it to describe intra-annual patterns of spatial use and to asses how it was influenced by climate, food resources and individual conditions. I used the k-LoCoH method to calculate the areas used at two spatial scales: the home range (HR; calculated on 95% of locations) and the core area (CA, calculated on 50% of the locations). At all temporal and spatial scales, the areas used by females were very small in deep winter, progressively increased until a peak in mid-summer, and then dropped again. This pattern was very marked, with a 15-20-fold increase in size from the winter minimum to the summer maximum. The HR and CA size was positively correlated with daylight, but was more synchronized with indexes of climate and vegetation phenology, as absolute temperature and average NDVI of the study area. After having defined biologically meaningful seasons with a clustering approach based on step distances and habitat features associated with locations, I then analysed, within seasons and correcting for temporal trends, the effects of the stochastic variability of climatic and weather conditions and of food resources on the size of ranges used. I found that, in winter, HRs and CAs at all temporal scales decreased strongly when snow was deeper, or precipitations more abundant, while in summer they decreased with increasing food resources (indexed by the average NDVI value or proportion of vegetation in the HRs or CAs). Also slope, which I used as an index of refuge areas from predators but also of snow accumulation, had a marked negative effect on the size of areas used. In contrast, individual conditions, as age class and reproductive status, did not influence with consistent patterns the spatial behaviour of females. These results highlight the peculiar strategy of spatial use of female ibex, which appear to be extremely energy conservative in winter and aimed at optimizing the use of food resources in summer. The understanding of factors driving spatial behaviour of female ibex is fundamental to conserve key wintering areas and habitats, and to predict how future climate changes might impact on the species.

Chapter III: Validation of a non-invasive technique for estimating diet quality in an alpine ungulate.

In seasonal environments, the behavioural patterns of large herbivores are shaped by the availability of forage resources, which affect the individual performance and reproduction success. Faecal nitrogen (FN) and Faecal Neutral Detergent Fibre (FNDF) have been proposed as indicators of diet quality in wildlife species. In the study reported in chapter III, I aimed at evaluating the use of faecal N, and secondarily of faceal NDF, to describe patterns of diet quality in Alpine ibex. Since chemical analyses are costly and time consuming, I also verificed whether NIRS estimates of faecal N might provide results as accurate as those of chemical analyses. From late June to November, I collected fresh samples of female and male ibex faeces, which were analyzed for FN and FNDF using Chemical analysis and three different NIRS instruments with variable wavelength ranges and approach (reflectance or transmittance). In order to verify possible relationships, I also associated to each sample the NDVI index of greenness of a surrounding buffer area. NIRS analyses gave good predictions for N, and only slightly lower for NDF, provided that the instrument used operated over a wide spectral range and in reflectance. Faecal N decreased, and FNDF increased, with Julian date, suggesting a reduction in diet quality thorugh summer and autumn. Females tended to have higher FN and lower FNDF contents than males, suggesting the ability to select a diet of better quality. These patterns were best described by data from chemical analyses, but were closely approximated by those from the best

NIRS method. The NDVI of the buffer area surrounding faecal samples did not influence indexes of diet quality. I concluded that FN estimated with NIRS techniques could be a useful tool for studying patterns of diet quality in Alpine ibex. The declining FN and increasing FNDF values from summer to autumn suggest that ibex do not have the ability to contrast, with alternative food sources or with increasing selectivity, the decline in vegetation quality. This emphasizes the importance of energy-saving strategies during the winter, and of exploiting the short availability of good food resources in spring.

RIASSUNTO

Questa tesi riporta I risultati di tre studi condotti sulla colonia di stambecco alpino dei gruppi "Marmolada-Monzoni". Una sintesi per ciascuno studio è riportata di seguito.

Contributo I: Morfologia del suolo, stagione e attività individuale influenzano la probabilità di acquisizione e l'errore associato alle localizzazioni con sistema GPS in un ungulato alpino.

L'applicazione della tecnologia "GPS-tracking" nella ricerca sulla fauna selvatica ha offerto nuove, ampie opportunità per affrontare questioni ecologiche che riguardano in definitiva la conservazione delle specie. Tuttavia, per sfruttare a pieno le potenzialità della tecnologia e formulare conclusioni corrette, è necessario approfondire le conoscenze sulle cause di errore in essa implicite, nelle specifiche condizioni ambientali e con le specie su cui si opera. Nel primo capitolo, ho studiato come le peculiarità dell'ambiente alpino e il comportamento di femmine di stambecco influiscano sulla probabilità di acquisizione delle localizzazioni e sulla loro accuratezza. Ho prima condotto una prova sul campo, utilizzando collari programmati a tentare una localizzazione (fix) ogni 30 minuti durante cicli di 24 ore, e posizionati in 64 punti, di cui era stata determinata la posizione con un errore di 2.0 (ds = 2.8) m, scelti in modo da rappresentare le diverse condizioni di cielo visibile e di vegetazione (bosco o area aperta) dell'area occupata dalle femmine di stambecco oggetto del mio studio.

Le prestazioni dei collari sono state influenzate soprattutto dalla percentuale di cielo visibile (skyview). Con skyview superiori al 70%, le localizzazioni acquisite sono state prossime al 100% di quelle attese, e l'errore di localizzazione si è mantenuto entro i 10 m per il 75% di esse. Con skyview minori di tale soglia, tuttavia, le localizzazioni acuisite sono scese al 75% di quelle attese e l'errore è aumentato fino a 20 m, sempre per il 75% delle localizzazioni. Ho poi analizzato un database di oltre 85.000 localizzazioni tentate, su 11 femmine munite di collare GPS durante un periodo di tre anni, al fine di individuare l'effetto delle caratteristiche ambientali dell'area usata giornalmente, del livello di attività degli animali (misurato dai sensori di movimento dei collari), e della variabilità climatica e

meteorologica sulla probabilità di acquisizione delle localizzazioni attese. In estate, tale probabilità è rimasta molto buona (intorno al 95%) durante tutti i mesi e nell'arco di tutta la giornata. In inverno, invece, è diminuita fino a meno dell'85% nei mesi più freddi e nelle ore notturne. L'attività degli animali ha influenzato positivamente la probabilità di acquisizione delle localizzazioni, che è stata invece penalizzata dalle giornate con precipitazioni e da temperature inferiori alla media del periodo, soprattutto d'inverno. L'effetto positivo dell'attività si spiega molto probabilmente con il fatto che gli animali, quando sono attivi per spostarsi o per alimentarsi, tendono a frequentare aree aperte, mentre quando sono inattivi, sia di notte che di giorno se cercano rifugio dalle intemperie, tendono a frequentare aree riparate dove la skyview diminuisce. In conclusione, sebbene con un adeguato screening per eliminare gli outliers dalle localizzazioni ricevute sia possibile assicurare una buona accuratezza dei fix provenienti da habitat diversi, le localizzazioni ricevute sottostimano l'uso di habitat che forniscono riparo e i periodi climaticamente sfavorevoli. In generale, inoltre, i risultati di questo contributo sottolineano l'importanza di abbinare alle prove con collari statici anche l'analisi di database provenienti dagli animali oggetto di studio, al fine di individuare meglio i fattori che influiscono sulle prestazioni della tecnologia.

Contributo II: Fattori determinanti le variazioni dell'home range a diverse scale spazio-tamporali in un ungulato Alpino

L'elevata stagionalità degli ambienti alpini può incidere fortemente sulle strategie di uso dello spazio da parte dei grandi erbivori che le abitano. Nel secondo contributo ho prodotto e utilizzato un database di 672 home range settimanali (232 in estate and 440 in inverno) e uno di 160 home range mensili (64 in estate e 96 in inverno), derivante dal monitoraggio con collari GPS di 15 femmine di stambecco alpino nell'arco di tre anni, per individuare i pattern di variazione intra-annuale delle aree usate individualmente e per verificare come le variabili climatiche, gli indici di disponibilità alimentare, e fattori individuali agissero su tali pattern. Ho utilizzato, per il calcolo delle aree usate, il metodo k-LoCoH con due scale spaziali: l'home range (HR, calcolato sul 95% delle localizzazioni) e la core area

(CA, calcolata sul 50% delle localizzazioni). Con tutte le scale temporali e spaziali, le aree usate dalle femmine sono risultate molto ridotte in inverno, per aumentare poi progressivamente fino a un picco in estate, e diminuire poi nuovamente. Questo andamento si è rivelato molto marcato, con un aumento fino a 15-20 volte di dimensione degli HR e delle CA passando dal minimo invernale al massimo estivo. L'area degli HR e delle CA è risultata così correlata positivamente con il fotoperiodo, ma le sue variazioni si sono sincronizzate maggiormente con l'andamento della temperatura e dell'indice NDVI medio dell'area di studio. Successivamente, dopo aver individuato stagioni biologicamente sensate sulla base di una cluster analisi della "step distance" e delle variabili ambientali associate alle localizzazioni, ho analizzato HR e CA, entro stagione e correggendo per il trend temporale, al fine di verificare gli efetti della varibilità stocastica degli indici climatici, degli indici di abbondanza trofica, e delle caratteristiche individuali degli animali. Le aree di HR a CA sono risultate negativamente influenzate dalla variabilità del manto nevoso o dall'abbondanza delle precipitazioni in inverno, e dalla disponibilità alimentare individuale (indicizzata dall'NDVI medio o dalla prevalenza di vegetazione su rocce e ghiaioni entro HR e CA). Anche la pendenza, che può indicare la disponibilità di zone di rifugio, ha influito negativamente sull'area di HR e CA. Invece, i fattori individuali, cioè la classe di età e lo stato di lattazione o meno, non hanno influito in misura apprezzabile sul comportamento spaziale. Questi risultati sottolineano la peculiarità delle strategie di uso dello spazio da parte delle femmine di stambecco alpino, che appaiono estremamente conservative nei riguardi dei dispendi energetici d'inverno e improntate a ottimizzare l'uso delle risorse alimentari, anche con rilevanti spostamenti, durante l'estate. La comprensione dei fattori che determinano tali strategie è di fondamentale importanza per la conservazione di aree e habitat chiave e per prevedere come la specie possa reagire al loro modificarsi, ad esempio in seguito al cambiamento climatico.

Contributo III: Validazione di una tecnica non invasiva per la stima indiretta della qualità della dieta in un ungulato alpino

Uno dei principali fattori che determinano i modelli di comportamento dei grandi erbivori è il variare stagionale della disponibilità di risorse alimentari, soprattutto in ambienti estremi come quelli frequentati dallo stambecco alpino. I contenuti fecali di azoto (FN) e, in minor misura, di NDF (FNDF) sono stati suggeriti come indicatori della qualità della dieta negli erbivori selvatici. Lo studio considerato dal terzo contributo ha valutato l'uso di questi indicatori per descrivere i pattern di qualità della dieta di stambecchi maschi e femmine dall'inizio dell'estate all'autunno. Dato che le analisi chimiche sono onerose in termini di costi e tempo richiesto, lo studio ha anche verificato in che misura i dati provenienti da strumenti NIRS diversi per ampiezza della gamma spettrale e per principio (riflettanza o assorbanza) potessero sostituire quelli dell'analisi chimica. Da giugno avanzato fino a novembre ho raccolto campioni freschi di feci di stambecchi maschi e femmine, su tutta l'area occupata dalla colonia. I campioni sono stati poi analizzati per N e NDF con metodo chimico tradizionale e con NIRS. Le predizioni NIRS sono risultate soddisfacenti, soprattutto per l'N, solo con lo strumento caratterizzato da ampia banda (350-1050 nm) e basato sulla riflettanza. I valori di FN sono diminuiti con il crescere della data giuliana, e quelli di FNDF sono aumentati, suggerendo un progressivo peggioramento della qualità della dieta ingerita da entrambi i sessi. Le femmine hanno tuttavia tendenzialmente mostrato valori di FN superiori e di FNDF inferiori a quelli dei maschi. Anche se questi andamenti sono stati descritti nella maniera più puntuale dai dati dell'analisi chimica, i dati prodotti dallo strumento NIRS rivelatosi più affidabile hanno prodotto patterns molto simili. Al fine di evidenziare eventuali correlazioni, ciascun campione fecale era stato caratterizzato anche con il valore medio dell'indice NDVI di un'area buffer circostante la sua localizzazione. Tuttavia, nessuna relazione è stata trovata tra indici di qualità della dieta e NDVI. In conclusione, i risultati ottenuti dimostrano che adeguate tecnologie NIRS possono sostituire le analisi chimiche per la stima dell'N e dell'NDF fecali. I patterns osservati per questi indicatori suggeriscono che, anche se le femmine sembrano capaci di selezionare una dieta migliore di quella dei maschi, entrambi i sessi sperimentano nel corso dell’estate e dell’autunno un declino progressivo della qualità della dieta ingerita. Questo risultato sottolinea l’importanza delle strategie di riduzione dei dispendi energetici messe in atto dalla specie in inverno, sia di quelle intese a massimizzare l’uso delle risorse trofiche messe in atto durante la primavera.

GENERAL INTRODUCTION

1. The ecology of movement: a brief coming into the wildlife tracking systems

Ecology is the study of the processes resulting in the observed distribution and abundance patterns of organisms across the landscape. These patterns reflect individual movement decisions, resulting in population-level mechanisms that drive the ecosystems. Therefore, determining the factors that influence such decisions is a critical step. The rich variety of movement modes seen among microorganisms, plants, and animals has fascinated mankind since time immemorial. The general framework introduced by Nathan et al. (2008) asserts that four basic components are needed to describe the mechanisms underlying movement of all kinds: the organism's internal state, which defines its intrinsic motivation to move; the motion and navigation capacities representing, respectively, the organism's basic ability to move and affect where and when to move; and the broad range of external factors affecting movement.

As a consequence, the ecology of movement has emerged as a new interdisciplinary approach during the last decades in order to achieve new insights into ecological questions still unsolved (i.e. Johnson et al. 1992, Giuggioli and Bartumeus 2010, Singh and Ericsson 2014). One of the fundamental issues for the ecology of movement is to understand the causes, mechanisms, patterns, and consequences of animal movements across a broad range of temporal and spatial scales. For example, energetic and seasonal constraints are important factors determining life-history traits of species populations (McLoughlin et al. 2000, Ferguson 2002) that lead to movement functional responses which may vary from long migratory movement to hibernation processes.

In the mid-1960s, new developments in wildlife tracking technologies offered new opportunities to study animal movements with the use of Very High Frequency (VHF) transmission collars (Mech 1967, Simmons 1968). After capturing the animal and attaching the VHF transmitter and identification tags, field operators were needed to acquire the VHF transmissions via a hand-held antenna during the study period. The location of the transmitter was usually determined by acquiring the transmissions from three (or more) different locations to triangulate the location of the device, and hence, the location of the monitored individuals. Several advantages, such as relatively low cost, long life and reasonable accuracy for most purposes encouraged the use of VHF transmitters, which became the most widespread methodology in wildlife studies (Fancy and Whitten 1991, Amstrup and Durner 1995, Tchamba et al. 1995, Bradshaw et al. 1997, Hilderbrand et al. 1999). However, the use of VHF transmitters has also significant limitations. This methodology combines intensive monitoring effort in the field with scarce location accuracy, and may be strongly restricted by weather, daylight hours, terrain accessibility and topographic conditions. Furthermore, it is difficult or impossible to monitor large-scale migratory animals or to obtain high frequency data about animal movements and activities (Coulombe et al. 2006).

About 40 years ago, a revolution in radio-tracking techniques started when the United States Department of Defense developed a Global Positioning System (GPS), primarily to provide 24-hour, complete global satellite coverage for military purposes. At the beginning there was an intentional error incorporated into GPS signals for reasons of national security, called "Selective Availability" (SA). However, by taking it into account several studies began to apply GPS-tracking technologies to wildlife research, analyzing the effect of SA on location accuracy and searching for techniques to narrow potential errors (Moen et al 1997, Adrados et al. 2002). Finally, in May 2000 the SA policy was abandoned by U.S. Authorities, allowing standard wildlife GPS units to obtain the approximate accuracy of differentially-corrected units under SA (Dussault et al. 2001).

GPS tracking is based on a radio receiver (rather than a transmitter) attached to an animal. The receiver picks up signals from constellations of orbiting satellites working in conjunction with a network of ground stations and uses an attached computer to calculate and store the animal's locations within a scheduled frequency (Tomkiewicz et al. 2010). Depending on the communication system, some GPS devices are linked to an Argos Platform Transmitter Terminal (PTT) that allows the researchers to download the animal locations via satellite Argos System; others transmit the data directly to a Ground Station at the user's office via Short Message Service (SMS) using the Global System for Mobile Communications (GSM); and still others send the data periodically to biologists who must be in the field to receive them via Handheld Terminal (Mech and Barber 2002). All GPS devices have also an on-board memory that allows to retrieve the data after the activation of a drop off mechanism, and a standard VHF radio beacon that can be used to locate animals with conventional direction-finding techniques. Despite of some limitations in comparison to the previous VHF monitoring systems, such us high costs and thus low sample sizes, or battery restrictions in the weight and the duration of operating life, the main advantages of GPS devices have been underlined by several authors (Rodgers et al. 1994, 1996; Hebblewhite and Haydon 2010; Morales et al. 2010). There is no other wildlife research technique that comes close to approximating their many benefits (Cagnacci et al. 2010).

All the same, the spatial and temporal scales at which the ecology of movement of free-ranging animals can be studied using GPS-tracking are constrained by the amount of bias in locations acquisition and by the level of accuracy of acquired locations (Dussault et al. 1999, Frair et al. 2010). Many studies have addressed these problems in different species (*Alces alces*: Rempel et al. 1995, Moen et al. 1996, Rodgers et al. 1996, Dussault et al. 1999; *Odocoileus virginianus*: Merrill et al. 1998, Bowman et al. 2000; *Canis lupus*: Merrill et al. 1998; Merrill and Mech 2000, Merrill 2002), environmental conditions and landscapes (Rumble and Lindzey 2001, D'Eon et al. 2002, Heard et al. 2008), underlying the importance of vegetation cover and terrain morphology on GPS bias and accuracy. Fewer studies have also demonstrated how the performance of GPS devices on free-ranging animals is influenced by the species behaviour in relation with seasonal, climatic and habitat conditions (Graves and Waller 2006, Cargnelutti et al. 2007). In general, researchers have now the ability to test the performance of their GPS devices in their specific study areas, and, although missing data and location inaccuracy are still problems requiring data imputation or weighting to account for differential detectability in various habitat types and species characteristics (Frair et al. 2004, 2010; Horne et al

2007; Nielson et al. 2009), a multitude of studies throughout the world using GPS data with a wide variety of species and new enhancements in statistical approaches (Fieberg et al. 2010) have achieved uncovered insights into animal ecology (for a review, see Cagnacci et al. 2010, Tomkiewicz et al. 2010). The availability of high frequency location data across a broad range of spatial and temporal scales has revealed how the life-history traits of a species is a functional response to its ability to adapt to different environmental conditions, and how such variations may influence individual performance and population dynamics (Gaillard et al. 2010, Morales et al. 2010).

2. The peculiarity of high mountain areas.

In general, the use that animals make of a particular habitat reflects a combination of different variables, such as predation risk (Mysterud et al. 1999), food availability (Bremset Hansen et al. 2009), interspecific competition (Bartos et al. 2002) or human disturbance (Herrero et al. 1996). In temperate climates, high mountain landscapes are among the harshest environments, and the strong seasonality of climatic conditions and resources availability has shaped particular adaptations of the species. The effect of forage productivity and accessibility has been recognized as the most real proxy to animal distribution and dynamics in herbivore populations (Wiegand et al. 2008, Bremset Hansen et al. 2009, Hamel et al. 2009, Cagnacci et al. 2011, Bischof et al. 2012), and temperature, precipitation or snow depth have been often examined as determinants of their spatial behaviour (Rumble et al. 2001, Biggs et al. 2001, Dussault et al. 2005), which ultimately may influence the population dynamics of the species (Jacobson et al. 2004, Månsson et al. 2007, Aublet et al. 2009). Therefore, one of the biggest challenges in wildlife research is to understand how the species have evolved their survival strategies, including the spatial adaptations to such conditions (Telfer and Kelsall 1984, Vuren and Armitage 1991, Morrison et al. 2009).

When food is scarce or spatially distributed in discrete patches, as in areas with mild winter, animals may respond with an increase in home ranges (Börger et al. 2006b, Morellet et al. 2013). Also the snow depth may have a strong influence on the spatial behaviour of animals. For instance, roe deer living in mountain regions show a facultative and opportunistic migratory behaviour to avoid deep snow in winter (Ramanzin et al. 2007, Cagnacci et al. 2011), and use smaller areas in summer at higher altitudes and larger areas at low altitudes during winter (Mysterud 1999, Lamberti et al. 2001, Rossi et al. 2003). However, another response to deep snow, in alternative with seasonal migrations, might be a reduction of the home range, in order to limit costs and risks associated with movement within an energy saving strategy (Parrini et al. 2003; Scillitani et al. 2012). This might be also linked to specific physiological adaptations. Signer and Arnold (2011) suggested that Alpine ibex survival during winter depends substantially on a metabolic reduction of endogenous heat production combined with the search for exogenous heat and the reduction of movements to those necessary for reaching the nearest emerging sunny spot. Daylight is the cue for seasonal physiological changes in animals living in temperate climates, and also a modulator factor of the photosynthetic activity of plants (Lawlor 1995) and thus of the vegetation phenology. Various studies have demonstrated that daylight is therefore also related to intra-annual patterns of movement at different spatial and temporal scales (Bradshaw and Holzapfel 2007; D'Eon et al. 2005, Rivrud et al. 2010, van Beest et al. 2011). In temperate climates, however, it is necessary to account also for the interaction between daylight and other parameters such temperature or precipitation when seeking for explanatory variables of animals behavior (Morellet et al. 2013). Annual cycles of temperature and precipitation may not be synchronised with daylight, and influence plant productivity, thermoregulatory response, costs and benefits of movements for animals (Rivrud et al. 2010, Minder 2012), and hence seasonal patterns of spatial behaviour. Again, this might be particularly evident in high mountain areas.

The selection of specific habitat features according to seasonal conditions is evident in herbivores populations. At high elevations, were rocky cliffs and steep terrains are the prevalent features, animals may tend to enlarge their home ranges during the vegetation growing season in order to increase their access to vegetation patches and hence their forage intakes (Grignolio et al. 2004, Scillitani et al. 2012). On the contrary, ungulates living at lower altitudes may select for mature forests, which allow them to reduce their summer movements since the availability of nutritional resources is not a constraint (Lamberti et al. 2006, Saïd et al. 2009). The behavioural adaptations of the species living in mountain environments might be also influenced by age and reproductive conditions, which might lead to specific spatial patterns, such the closeness to escape terrains, or the increase in feeding rates, as has been widely reported in several studies (Ferguson 2002, Boschi and Nievergelt 2003, Saïd et al. 2005, Hamel and Côté 2007). The protection of kids, the energetic requirements of lactation or the social status may induce the animals towards particular behavioural tactics with different priorities according with the habitats dynamics and interactions.

Also the selection of specific habitat features depending on seasonal periods is evident in herbivores populations, which may differ as a result of a trade-off between the metabolic requirements of the species and their spatial strategies within heterogeneous landscapes. At high mountain altitudes, were rocky cliffs and steep terrains are the prevalent features, the species tend to enlarge their home ranges during the growing season in order to increase their access to vegetation patches and then their foraging intakes (Grignolio et al. 2004, Scillitani et al. 2012). On the contrary, ungulates living at lower altitudes may select for matured forests which allow them to reduce their summer movements since the availability of nutritional resources is not a constraint (Lamberti et al. 2006, Saïd et al. 2009). Last but not least, to understand the behavioural adaptations of the species in mountain environments is crucial to have also a thorough knowledge about the effect of age and reproduction stages, leading to specific spatial patterns, such the closeness to escape terrains or the increase in feeding rates, as has been widely reported in several studies (Ferguson 2002, Boschi and Nievergelt 2003, Saïd et al. 2005, Hamel and Côté 2007). The protection of the kids, the energetic requirements of lactation or the social status may induce the animals towards the formulation of particular behavioural tactics from different priorities according with the ecosystem dynamics and landscape interactions.

3. Why the Alpine ibex?

The Caprinae subfamily includes the most adapted bovids to mountainous habitats, which may tolerate extreme temperatures and rugged terrains (Festa-Bianchet and Côté 2007, Aublet et al. 2009). These species appear to be also highly sensitive to both human disturbance and harvest (Hamr 1988), and may be one of the ungulate groups likely at risk from the effects of climate change (Colchero et al. 2009, Turunen et al. 2009, Mason et al. 2014).

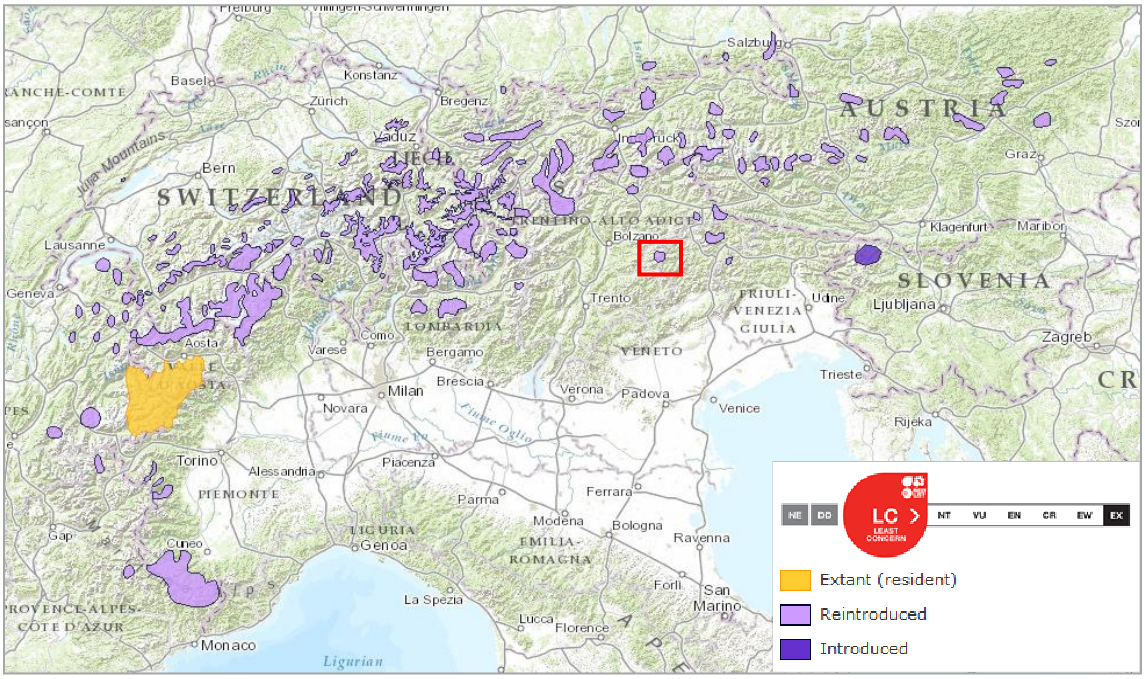

Figure 1. Geographic range of Capra ibex over the Alpine Arc. Extracted from IUCN (International Union for Conservation of Nature) Red List of Threatened Species. Version 2014.3 (http://www.iucnredlist.org). The red square indicates the location of the Marmolada-Monzoni massif.

The Alpine ibex is a highly sexually dimorphic species of the Caprinae subfamily adapted to face the most extreme environmental conditions. By setting in motion specific thermoregulatory strategies and activity patterns (Signer and Arnold 2011), the individuals are able to survive through the longest, coldest and snowiest winters in temperate climates. In addition, the species is a capital breeder (Toïgo et al. 2002) able to display its mating season from late autumn to early winter despite the inclement weather conditions, the movement restrictions by the snow depth and the scarce forage availability (Parrini et al. 2003). And, interestingly, among the large herbivores the ibex is also characterized by a particular high survival rate for yearlings of both sexes, which has been attribute to differences into interespecific growth rates, and a very high senescence rates up to 13 years linked to its hierarchical structure (Toïgo et al. 2007). Consequently, new insights into the ibex behaviour render the species to be a theoretical model to understand general strategies of other high mountain ungulates. The Alpine ibex was historically distributed throughout the Alps and neighbouring territories, but was progressively extirpated from most of its range due to over-hunting and poaching in the pursuit of its trophy, its meat, or the healing and miraculous properties that were attributed to its blood, horns or even to its droppings (Stüwe and Nievergelt 1991, Mustoni et al. 2002, Fiore and Tagliacozzo 2006). At the beginning of the 19th century only one small population of around 100 individuals survived in the north-western Italian Alps (Figure 1). In 1922 this area was transformed into the first national park in Italy, the Gran Paradiso National Park, and the resident ibex population increased rapidly in number.

Thereafter, reintroduction programs started in Switzerland, and, due to their successfully results, continued over the entire Alpine area. Currently the Alpine ibex, thanks also to hunting restrictions and natural processes of colonization, has re-occupied a great part of its original range (Gauthier and Villaret 1990, Stuewe and Nievergelt 1991) According to the Italian Institute for Environmental Protection and Research (ISPRA), the population size is approximately 47.000 individuals, which are distributed, although unevenly, throughout all the Alpine states (France, Italy, Switzerland, Austria, Germany and Slovenia). The species is classified as a “Least Concern” category by the IUCN (Temple and Terry 2007).

Across the Italian Alps, the Alpine ibex has an estimated population size of about 15.600 individuals (ISPRA, 2013), but there is a problem beyond the total number of individuals. Although the species has recovered steadily over the years to its present total populations size, its distribution is still extremely fragmented (Dupre et al. 2001, Pedrotti et al. 2007, Carnevali et al. 2009), especially in the eastern Alps. Here it is possible to identify almost half of the 53 total colonies described in Italy (Carnevali et al. 2009), with small the population sizes, often lower than 100-150 individuals, and no, or very limited, connectivity. The average densities calculated with respect to the area occupied by the colonies vary between a minimum of 2.9 individuals/km^2 in the eastern Alps to 3.2 individuals/ km^2 and 3.8 individuals/km^2 in the Western and Central Alps respectively. The risks of small and isolated populations constitute a critical issue for their conservation since environmental, demographic or genetic stochasticity may increase the probability of extinction (Soulé 1987). An environmental catastrophe, an animal disease, loss of genetic variation, inbreeding processes, or the combination of such factors may interact with the growth rates of the population raising the likelihood of its collapse (Soulé 1980; Frankel and Soulé 1981, Keller et al. 2002). Therefore, the ibex populations across the eastern Alps may not be considered as safe. One of the main risks to the Alpine ibex is the low population size within each colony and the scarce genetic variability (Randi et al. 1990). Recently, in the Eastern Italian Alps the species has also experienced the effects of a parasitic infection by the scabies mite *(Sarcoptes scabiei)*, which has led to a steep decline in some isolated populations, such as the colony of the Marmolada massif (Rossi et al. 2006, 2007). Also the theoretical impact of climate change on alpine ecosystems may be suggested as a threath for the survival of the species (Grøtan et al. 2008, Grabherr et al. 2010, Mysterud and Austrheim 2014). Therefore, from a conservation point of view, the knowledge of how the interaction between the animal behaviour and their environment influence the dynamics of such small and isolated ibex populations should represent one of the main purposes to establish an effective management of the Alpine ibex.

4. The study area

4.1 A separate history: results of an ongoing effort of conservation

With the translocation of 5 females and 5 males from the Gran Paradiso National Park in 1978 and 1979, a small colony of alpine ibex was established in the Marmolada-Monzoni, the highest massif of the mountain range of the Dolomites, in the Eastern Italian Alps (Figure 1). During the two subsequent decades, the population size of the neo-colony increased progressively up to more than 450 individuals in 2002, with an estimated growth rate (λ) of 1.24, close to the maximum rate of increase for the species (Loison et al. 2002). However, in the snowy winter of 2003/2004, the population was strongly reduced in number due to an epizootic of scabies mites (Monaco et al. 2005b). Less than a half of the individuals in the population survived, also due to an active project for sanitary treatment (Rossi et al. 2006). This was followed in 2006 and 2007 by a restocking project (Scillitani et al. 2012, 2013). Currently, the data provided by the annual counts suggest that the population experiments a slight although progressive increase in the number of individuals (Figure 2), with an estimated growth rate (λ) of 1.05.

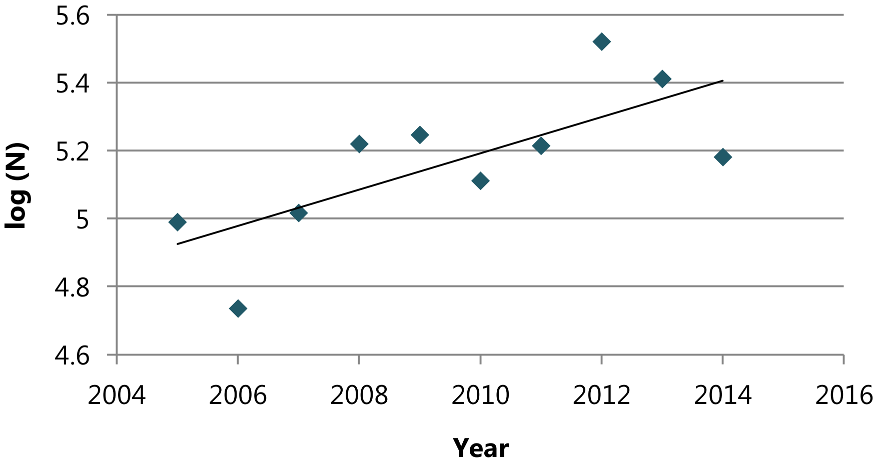

Figure 2. Trend of the population of Marmolada-Monzoni after the collapse of the colony in 2004.

During the last years, a total of 179 individuals has been captured, tagged and monitored using ear tags and/or different telemetry systems (Figure 3), producing the firsts results on the status of the colony, on the survival of males and females and a comparison of spatial and social behaviour and habitat selection of translocated and "resident" males (Scillitani et al. 2012, 2013). The use of GPS-GSM collars began in 2010 when 10 adult females were captured and fitted with the new tracking technology. At the present, 22 females have been satellite-monitored, 15 of which will be considered in my thesis.

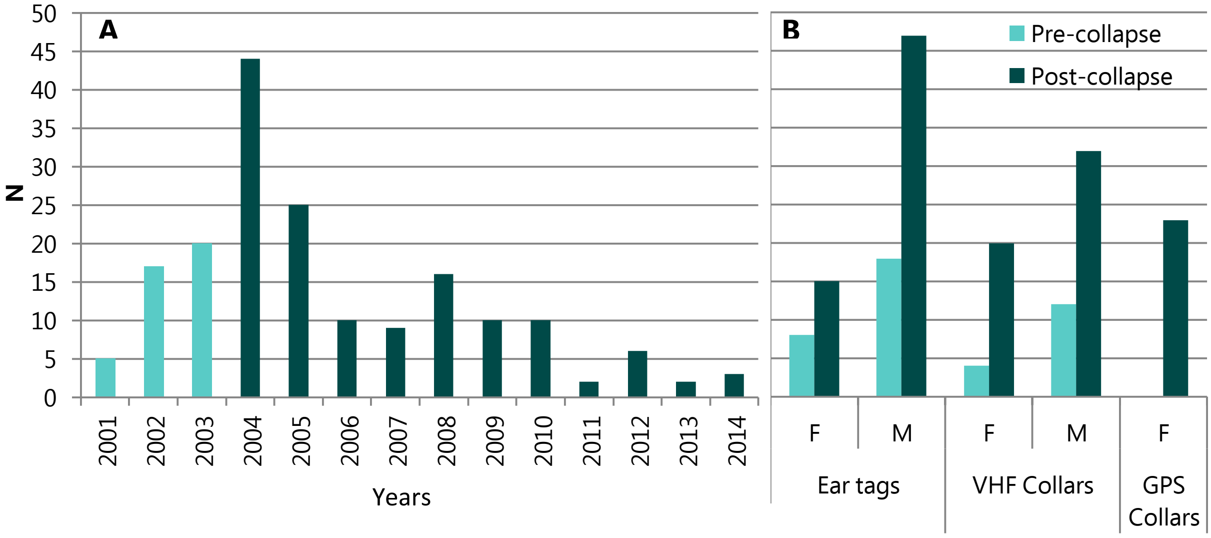

Figure 3. Number of tagged individuals in the ibex population of the Marmolada-Monzoni during the last 13 years, before and after the collapse of the colony due to the scabies epizootic (A) and with different marking and telemetry systems (B).

4.2 The environment of the Marmolada-Monzoni

The mountain group of the Marmolada-Monzoni extends over an area of about 150 km^2 and is composed by several summits reaching more than 2.500m a.s.l. of altitude. The area is characterized by two main topographic landscapes (Figure 4). The north-western boundaries are represented by gentle slopes and open valleys. On this part lies the glacier of the Marmolada, covering around 2% of the study area (Duprè et al. 2001). This side of the study area is heavily exploited during the winter season for snow sports. On the opposite, the south side is characterized by a high rugged complexity. Here we find the highest peaks: Punta Penia and Punta Rocca, at 3.343m a.s.l. and 3.309 m a.s.l. of altitude respectively. Steep rocky cliffs (Figure 6) up to 1,000 m, and narrow valleys shape the land morphology. In this side the touristic pressure is mostly constant throughout the summer, when activities such as hiking or climbing take place, and very scarce during winter. The temperature of the study area may ranged in average between -20°C in winter to 18°C in summer, and the average annual precipitation rarely exceeds the 100 mm, which means a slightly milder climate compared to other areas in the western ibex populations (Bon et al. 2001, Parrini et al. 2003).

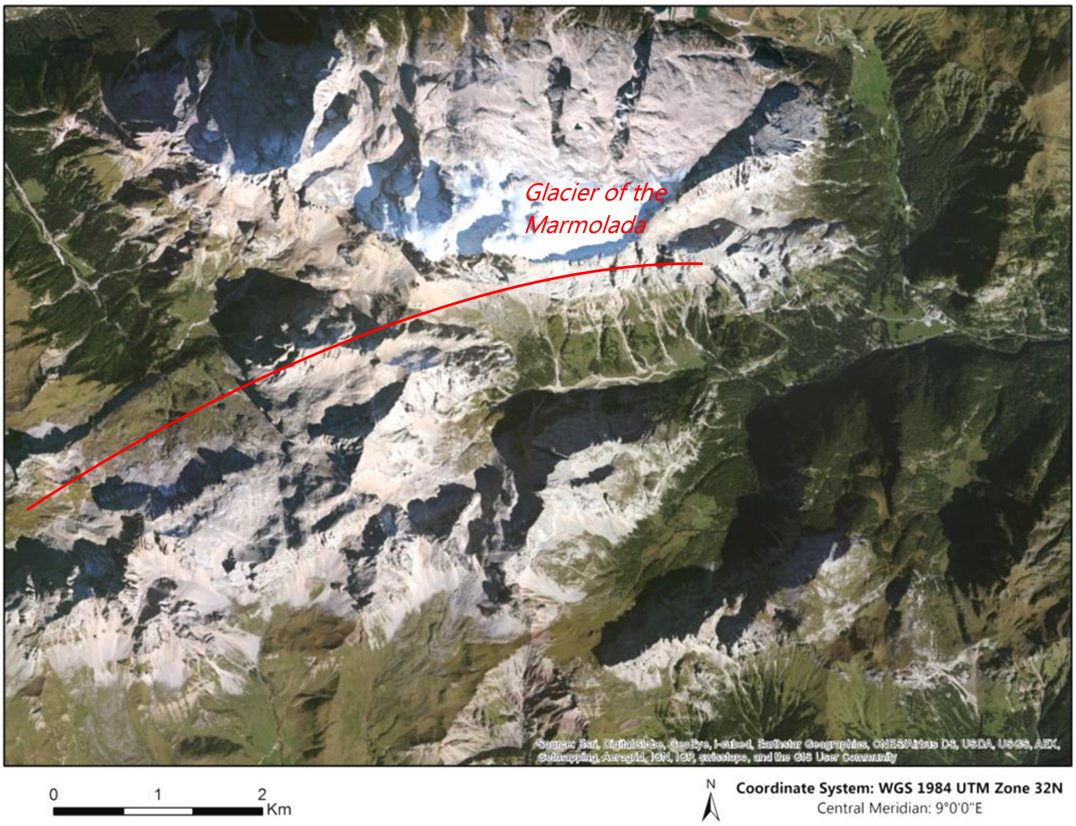

Figure 4. A general view of the study area. Separated by the red line: to the north-western the glacier of the Marmolada and open valleys, to the south-eastern side the rugged complexity of the several summits and deep valleys.

The vegetation is highly stratified following the altitudinal layers (see Scillitani et al. 2012). Up to 1,900m a.s.l. predominates a mixed woodland composed mainly by beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*), Norway spruce (*Picea abies*) and larch (*Larix decidua*). Above the forest line, vegetation is represented by alpine grasslands and shrubs as mountain pine (*Pinus mugus*) or willows (Salix spp.). Other herbaceous species shape the last pastures before the upper slopes of screes and rocks.

The alpine chamois is the only ungulate able to share certain areas with the alpine ibex, but other species are present at lower altitudes, such as the roe deer, the red deer (*Cervus elaphus*) and the mouflon (*Ovis gmelini musimon*). The risk of predation for ibex is negligible since the large predators were wiped in the study area by centuries of hunting and persecution. Only occasional events may occur for the presence of golden eagles (*Aquila chrysaetos*) that may remove offspring ibex.

Figure 5. A young male of Alpine ibex. On the background a typical rocky landscape occupied especially by females of the species in the study area. (Foto: Maria Parraga).

In particular, the ibex population in the study shows the typical seasonal pattern of the species (Tosi and Pedrotti 2003), shifting from the highest rocky and open areas during summer (Figure 5) to lowest elevations during the cold season when the snow depth may reach more than 2m in the study area. Furthermore, winter home ranges are considerable smaller than summer ones, and especially for males, they prefer to move following the altitudinal gradient within the same mountainsides rather than travel long distances to the summer areas (Scillitani et al. 2012). The core area of seasonal home ranges differs also between sex in location and habitat selection: while males show a strong site fidelity occupying predominantly open grasslands over the year, females tend to use safety areas near to rocky cliffs, probably as an antipredatory strategy (Grignolio et al. 2007), and to occupy different areas, both on location and surface, through the seasonal periods (Scillitani et al. 2012).

5. Motivations, aims and structure of the thesis

As I suggested above, the Alpine ibex is an ideal model species to characterize the animals adaptations to the strongly seasonality of mountain habitats, including the possible effects of a global climate change on alpine ecosystems. It has been an important target species for sanitary studies and studies on ecological responses of reintroduced populations, behavioural patterns of space use or population dynamics (Villaret and Bon 1995, Mayer et al. 1997, Toïgo et al. 1999, Grignolio et al. 2004, Scillitani et al. 2012, Mignatti et al. 2012). Most of the findings derive from the native population in the Gran Paradiso National Park (Figure 3), or from ibex populations in the French and Swiss Alps. The Western and Central Alps, in which these study areas are located, differ in land morphology and vegetation composition from the Eastern Alps and the Marmolada-Monzoni groups. In addition, the ibex colony of the Marmolada-Monzoni has had a very particular history due to the rapid population growth, followed by the epidemic crash and the slow recovery afterwards. This fact, added to the restricted capacity of dispersion of the species (Gauthier and Villaret 1990) and the almost complete isolation of the population, makes it a strategic example for studying the survival strategies of the Alpine ibex.

The powerful opportunities of new telemetry systems have led to a widespread application of GPS devices (Douglas-Hamilton 1998, Andersen et al. 2008, Jarolímek et al. 2014), with a broad variety of species and habitat types. Among wild herbivores, a great number of studies have assessed the relationship between the animals and their habitats: roe deer (*Capreolus capreolus*: Rossi et al. 2003, Cagnacci et al. 2011, Morellet et al. 2013, Saïd et al. 2009, Saïd et al. 2005, Börger et al. 2006a, 2006b); mule deer (*Odocoileus hemonus*: D'Eon and Serrouya 2005, Nielson et al. 2009, Long et al. 2009, Lendrum et al. 2014); elk (*Cervus elaphus*: Poole and Mowat 2005, Hebblewhite et al. 2008, Dalziel et al. 2008, Fryxel et al. 2008, Smallidge et al. 2010, Bischof et al. 2012); moose (*Alces alces:* van Beest et al. 2011, 2012). However, in particular for the Caprinae subfamily, the studies that have explored ecological issues in mountain landscapes have focused on few species (Tibetan antelope *Pantholops hodgsonii*: Leslie and Schaller 2008; Oribi *Ourebia ourebi*: Arcese et al. 1995; Bighorn sheep *Ovis Canadensis*: Martin et al. 2013; Blue sheep *Pseudois nayaur*: Oli 1996; Barbary sheep *Ammotragus lervia*: Cassinello and Alados 1996; Mountain goat *Oreamnos americanus*: Côté and Festa-Bianchet 2001; Iberian wild goat *Capra pyrenaica*: Perez et al. 2002; Alpine ibex *Capra ibex*: Marreros et al. 2012). In all the studies reviewed on Alpine ibex, the analysed data came from direct observations of tagged individuals, population counts, telemetric systems for metabolic measurements, or triangulation techniques using VHF collars. I did not find studies using high frequency data from individuals monitored with GPS collars, and I consider that it is strongly necessary to apply this powerful method to improve the knowledge of this peculiar species. Highlighting the spatial behaviour of this ibex population with more accurate data and at different spatial and temporal scales may also provide essential information for the management and conservation of other colonies across the eastern Alps.

Thereby, the aims of this thesis were as follows.

Chapter I. Due to the high topographic complexity of the study area, I investigated on the factors that might determine the performance of GPS-GSM collars, in terms of fix acquisition rates and accuracy. Many studies have already examined such factors under various environmental features, reaching a general agreement on the importance of canopy cover, sky view and individual activity as the main variables to be taken into account before drawing results from GPS data (Biggs et al. 2001, Wells et al. 2011, Webb et al. 2013). However, I found that no studies have so far addressed the effects of such factors on Alpine ibex in its extreme landscapes. Hence, I decided to analyze how differences in the percentage of visible sky, the season, the habitat types, the weather and the species activity patterns may affect the probability of receiving a location and the quality of the received data. I used both tests with fixed collars and data collected on free-ranging ibexes, in order to understand how inherent limitations in the methodology may induce biased conclusions. These insights are both necessary for addressing the subsequent analyses of spatial behaviour and, in general, useful for other similar studies in mountain habitats.

Chapter II. Having evaluated the methodological limitations associated with the use of GPS technologies in high mountain areas, I then investigated into the general strategies of space use of female Alpine ibex, by analyzing home range patterns at weekly and monthly scales. My aim was to understand how extrinsic and intrinsic factors might determine patterns of individual space use. To do this, I considered also two different spatial scales, examining both the home ranges and the core areas. I focused the analysis first on intra-annual temporal patterns, and then, after having defined biologically meaningful seasons, I looked within season for the effects of variables indexeing climate and weather, food and shelter resources, and individual status. This chapter provides the most detailed approach into the home range patterns of the species so far available to my knowledge.

Chapter III. To complement the results of chapter III, and in view of the intrinsic difficulties in sampling and assessing vegetation and food resources in high mountain habitats, I aimed here to develop a rapid method for estimating variations in diet quality, and tested its ability to evaluate biological trends. I collected fresh faecal samples from observed groups of animals across the overall population range, and then examined them for N and NDF contents using reference chemical methods and different Near-Infrared Spectroscopy (NIR) instruments. I compared prediction accuracies and tested how different methods were able to identify temporal patterns of diet quality from summer through autumn, and differences between males and females. Moreover, I explored the relationship between the vegetation phenology, expressed as NDVI, and the seasonal trends in N and NDF faecal content. The results of this chapter provide additional knowledge on the applicability of a rapid, non-invasive technique for indexing diet quality, and on how the species might respond to seasonal variations in foode resources and energetic requirements.

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CHAPTER 1

LAND MORPHOLOGY, SEASON AND INDIVIDUAL ACTIVITY INFLUENCE GPS FIX ACQUISITION RATES AND LOCATION ERROR IN AN ALPINE UNGULATE

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INTRODUCTION

During the last decades, the technologies applied to wildlife studies have experienced most significant advances. Following the use of conventional very high-frequency (VHF) triangulation techniques, the new Global Position System (GPS) radiotelemetry has greatly increased the possibility to analyze use of habitats, behavior and activity patterns for free-ranging animals over a broad range of temporal and spatial scales (Fuller et al. 2005, Cooke et al. 2004, Handcock et al. 2009).

However, limitations of GPS technologies remain under study because of two main types of error. The first is the variable ability of GPS transmitters to acquire an animal location (Fix Acquisition Rate, FAR). Missing data do not occur randomly, but depend on several factors such us topography (D'Eon et al. 2002), canopy cover (Moen et al. 1996, Rumble and Lindzey 1997, Heard et al. 2008), vegetation characteristics (Janeau et al. 2004, Hansen and Riggs 2008), or animal activity (Graves and Waller 2006, Cargnelutti et al. 2007). Missed locations can influence the estimates of resources used by animals, generating biased conclusions for habitats where fix success is limited. This bias effect depends on the proportion of data lost, the frequency of use of biased habitat types by individuals, and the spatial association among habitat types (Rettie and McLoughlin 1999). The second source of error is the location inaccuracy (Location Error, LE), which is the difference between the estimated position and the true position. A GPS device must simultaneously receive signals from at least 3 satellites to calculate a location, and the total number of satellites used determines whether a two-dimensional (at least 3 satellites) or a three-dimensional (more than 3 satellites) position is obtained. These two categories are conventionally identified with the 2D or 3D navigation (NAV) classification. The number of visible satellites, and therefore positional accuracy, can be affected by physical obstructions between the GPS device and available satellites orbiting the earth. Several studies (Adrados et al. 2002, Lewis et al. 2007, Sager-Fradkin et al. 2007) have addressed location accuracy focusing on fix quality (2D or 3D and an associated index of satellite geometry based on a dilution of precision (DOP)). These studies outlined the effects of rugged topography and vegetation cover (Dussault et al. 1999, Gamo et al. 2000, D'Eon et al. 2002, DeCesare et al. 2005), as well as that of collar orientation (Girard et al. 2002, D'Eon and Delparte 2005, Jiang et al. 2008) on location accuracy. However, unequivocal quantitative methods of screening GPS radio-telemetry data are currently unavailable, and failing to account for location inaccuracy can lead to a misclassification of resource selection and to an incorrect interpretation of results (Nielson et al. 2009).

Fix acquisition rates and GPS accuracy are frequently studied using stationary tests with fixed collars positioned in different habitat types, for a given periods of time, and with pre-determined temporal intervals. These tests are useful to model FAR and location Error (LE) under different environmental conditions, can be replicated across a range of spatial and temporal variation, and are readily comparable among study sites and time periods (Cagnacci et al. 2010). However, GPS errors are also related to unknown factors that may be linked to the interaction between the behaviour of free-ranging animals and the features of the habitats that they use (D'Eon 2003). For instance, comparisons of the results from fixed GPS collars at known locations with the results from collars fitted to free-ranging animals suggest that fixed collars overestimate FAR (Zweifel-Schielly and Suter 2007, Denis et al 2010, Guthrie et al. 2011, Wells et al. 2011), especially at short fix intervals (Cain et al. 2005). In fact, GPS collars performance depends also on types of behavior, such as walking or standing, or lying, and on meteorological conditions, which are expected to be related to habitat selection (Edenius 1996, Heard et al. 2008, Bourgoin et al. 2009, Webb et al. 2013).

Most of the studies aiming to identify sources of bias and inaccuracy of GPS tracking devices have been conducted on gentle mountain or forested landscapes, where missing data or location errors occur mainly due to canopy closure or collar orientation (Gamo and Rumble 2000, Janeau et al. 2004, Jiang et al. 2008, Williams et al. 2012). More work is needed to understand and quantify the factors affecting GPS performance in high mountain landscapes, where topographic complexity and terrain ruggedness can lead to lower FAR, higher proportions of 2D fixes, and higher LE than in lowlands (Zweifel-Schielly and Suter 2007), and where the high seasonality in climate and food resources may exert important effects on animals behaviour and selection of habitat features.

The Alpine ibex (*Capra ibex* L. 1758) is a large ungulate living at high elevations in the European Alps, where the marked spatio-temporal heterogeneity of food resources and climatic conditions shape the survival strategies of species (Pepin et al. 1996). According to Grignolio et al. (2003) and Scillitani et al. (2012), adult males select high elevation grasslands instead of rocks and stone ravines, while females prefer suboptimal but safer habitats, such as cliffs and rocky slopes, especially during the parturition or weaning period (Villaret et al. 1997, Grignolio et al. 2007), probably because of antipredator strategies or human disturbance. In contrast with other species living at lower elevations (Danilkin and Hewison 1996, Rossi et al. 2003, Morellet et al. 2013), ibexes make little use of forest habitats, except possibly during winter. In this season, in addition, they adopt a very conservative strategy, selecting small, favourable areas and strongly reducing activity and movements (Signer et al. 2011). Therefore, the habitat conditions experienced by ibex, and their intra-annual cycles of activity, differ markedly from those of other mammals living in less extreme climates. Habitat selection, and what animals do in the habitats selected, may have an important effect on the number of visible satellites from which collars may receive signals, and hence on FAR and LE.

The main objective of this study was to understand the factors affecting FAR and LE in the habitats used by female Alpine ibex. For this purpose, we used both field trials with fixed collars, in order to identify how habitat features influence both FAR and LE, and results from free-ranging animals, in order to understand how the intensity of activity and the habitats used, in interaction with climate conditions, influenced FAR. We expected that in Alpine habitats with a high complex topography FAR and LE were influenced especially by the proportion of visible sky, but wanted also to verify the effect of forest canopy. We aimed also at assessing whether FAR from collars fitted to free-ranging animals showed a seasonal pattern, and whether this pattern was influenced by individual activity, habitats used, and climatic conditions.

MATERIALS AND METHODS

Study area

The study area (see Scillitani et al. 2011) comprises 5.027 Ha and is located in the Italian eastern Alps, covering the Marmolada massif (46°25′13″ N, 11°51′54″), the highest mountain group in the Dolomites. Topography is highly variable, with altitude ranging from 750 m a.s.l. in the valleys to 3,434 m a.s.l. of the highest point, Punta Penia. To the north lies the Glacier of the Marmolada, but it covers less than 2% of the total area (Dupre et al. 2001). Northern sides are characterized by gentler slopes than the southern sides, where deep valleys and vertical rock cliffs, up to 1,000 m in height, are present.

The vegetation is clearly stratified. Under the large vertical cliffs at the highest elevations steeps of scree, sparse patches of alpine grasslands and isolated shrubs predominate. When the elevation and slopes begin to decrease, alpine grasslands interspersed with isolated rocks may offer the conditions necessary for the subsequent growth of species such as *Rhododendron ferruginuem*, *Vaccinium myrtillus* and *Vaccinium gaultherioides*. Then starts the arboreal stratum, dominated by European larch (*Larix decidua*) and Norway spruce (*Picea abies*).

Land cover, morphology and environmental variables

We used a land cover map of the study area based on a high resolution digital orthofoto (1x1m, WGS84/UTM32) (Scillitani et al. 2012, 2013) to classify land cover into "forest" (> 30% tree cover) and "open", using using the GIS software ArcMap® 10.1 (Esri Inc., Redlands, USA). Land morphology features were obtained from a Digital Elevation Model with 5 m resolution (Unità di Progetto per il SIT e la cartografia 2006, *http://idt.regione.veneto.it/app/metacatalog/,* Regione Veneto). We used the Spatial Analyst for ArcMap® to create a map of elevation and slope of the study area, and Terrain Analysis algorithms for SAGA Systems 2.0.8© (Free Software Foundation Inc., Boston, USA) to obtain maps of the percentage of visible sky as a Sky View factor (D'Eon et al. 2002, Frair et al. 2004, Sager-Fradkin 2007).

Climatic data were obtained from two meteorological stations within 11 km from the study area (one at 2,250 m a.s.l and the other at 2,032 m a.s.l). We recorded daily precipitation (mm), average temperature (°C) and snow depth to the ground (cm).

Stationary tests

Data collection

We used four Vectronic GPS Plus collars (Vectronic Aerospace© GmbH, Germany) scheduled to attempt to record a position every ½ hour. Collars were placed at approximately 40-60 cm from ground in 64 sites representing the different land cover and skyview conditions throughout the study area, and allowed to record positions for at least 24 hours. The total number of resulting attempted fixes was 3.176. We recorded the *true position* as the centroid of 20 positions recorded in every test-site by a portable GPS receiver (Garmin eTrex® 10 with high-sensitivity, WAAS-enable and HotFix® satellite prediction), reaching an estimated accuracy of 2.0 ± 2.8 m. Data from GPS collars were downloaded using a Link Manager connection and processed using a specific software (GPS Plus Collar Manager© 3.11.3, Vectronic Aerospace GmbH). We classified each scheduled attempt as successful if it resulted in the acquisition of location coordinates and unsuccessful otherwise. We calculated LE as the Euclidean distance in meters between each acquired position and the true position. We grouped the scheduled times of acquisition into day-periods, i.e. "night" (from 10 pm to 2 am), "deep night" (from 3 am to 6 am), "morning" (from 7 am to 10 am), "midday" (from 11 am to 2 pm), "afternoon" (from 3 pm to 6 pm), "evening" (from 7 pm to 9 pm). We associated to each attempted location the corresponding day period, number of satellites available, obtained using Occupation Planning 1.0© (Topcon

Positioning Systems, Inc. California, USA), and the sky view (%), the slope (degrees) and the land cover category (forest or open) of the corresponding true position. In addition, received fixes were associated with the NAV classification of fixes quality (2D or 3D) and the number of satellites used to acquire the location.

Data Analysis.

We first examined possible multi-collinearity or nesting of effects between explanatory variables. Sky view and slope were highly correlated (n =3.174; r = 0.98; P<0.001) and virtually interchangeable in the analysis, therefore we decided to use the first one. We categorized sky view values into 5 classes: 100-90%; 89-80%; 79-70%; 69-60%; <60%. The number of satellites available (range: 4-11) was nested within day periods ("night": 9.3 ± 1.5; "deep night": 7.4 ± 1.2; "morning": 6.4 ± 0.9; "midday": 6.6 ± 1.5; "afternoon": 6.8 ± 1.3; "evening": 9.0 ± 1.0). Therefore we tested number of satellites and day period alternatively in the models. Since the frequency of 4 and 11 satellites available was very low, we pooled them with the 5 satellites and 10 satellites classes. The number of satellites used (note that it is a different variable than satellites available) was obviously nested within the NAV classification. We decided to use NAV because the number of satellites is not included in GSM-transmitted locations, which might be the only data source when dropped-off collars are not recovered.

We tested the factors influencing the probability of an attempted location to be successful through general linear mixed-models (GLMM) with a binomial error distribution using the "GLIMMIX" procedure in SAS 9.2® (SAS Institute, 2009). We compared different models, which included the collar as random factor, to account for repeated measures with the same collar, and sky view class, land cover category, day period or class number of available satellites, as fixed effects. We started from the most complex model and sequentially excluded non-significant effects. We selected the most parsimonious model based on the AIC value (Bozdogan 1987).

Distances of acquired fixes from true positions followed a highly skewed distribution, with most acquired positions lying at short distances and few acquired positions lying at long distances. Since our aim was to simulate the error associated with the positions acquired from animals, we needed to exclude as outliers only the distances that would be recognized as outliers also in the processing of databases from the animals monitoring (see below). Any approach based on the distances distribution would have excluded distances too short to be recognizable as outliers in the animal databases. Therefore, we used a cut-off threshold of 270 m. This threshold comprised 95% of the distances between subsequent animals locations that were not excluded as outliers in the animals database (see below), with longer distances being mostly steps of linear movement paths. Therefore, the actual probability of accepting a location with an error greater than 270 m is in fact extremely low. We log-transformed distance values (m) as log(distance+1) to obtain a normal distribution and then analysed them with linear mixed models (PROC MIXED, SAS 9.2®; SAS Institute, 2009) which included the collar as random factor, and sky view class, land cover category, NAV, day period or, in alternative, class number of available satellites as fixed effects. We selected the most parsimonious model based on the AIC value (Bozdogan 1987). When difference in AIC between two competing model was < 2, we chose the simplest one.

Tests on free-ranging female ibexes

Data collection.

We used GPS locations collected from September 2010 to October 2013 from 11 Alpine ibex females (estimated age ranged from 2 to 12 years). Animals were captured with veterinary assistance in compliance with current Italian laws, using a tele-injection of xylazine (Rompun©, Bayer, Leverkusen, Germany; Gauthier 1993). All captured individuals were aged from horn annuli growth, examined for health status, and equipped with GPS-GSM Plus collars (Vectronic Aerospace© GmbH, Germany).

Collars were scheduled to attempt to record an animal location every 1 hour during 54 weeks. Each attempted location was classified as successful or unsuccessful as above described, and associated with the average of the X and Y activity values obtained from the GPS motion sensors of the collars during the 5 minutes immediately preceding and following the scheduled acquisition time, the day period (as above described), the month, and the season (summer: June-November; winter: December-May). Seasons were defined using a clustering approach of average daily elevation, activity index, step distance and land cover categories proportions associated with individual locations (see chapter II for details). Since we did not have hourly values of temperature, precipitation and snow depth, each attempted location within a single day was classified with the average temperature, precipitation, and snow depth of the day. Similarly, since we did not have the true position of locations attempted, we used the features of the area used daily to index habitat features. We shaped the daily individual minimum convex polygons (for days with more than 10 successful locations, accounting for 0.99 of individual days) and associated to each daily polygon a sky view and a slope index. For this purpose, we grouped pixels for 10% intervals in sky view or slope, scored them (1,2…) starting from flat slope and 100% sky view, and expressed the index as $\Sigma(S_i*P_i)$, where S_i is the score of interval class i, and P_i is its proportion in the polygon area. In addition, we categorized each polygon with the percentage of land cover categories (forest or open areas). Each location within one single day was classified with the features of the corresponding polygon.

Data analysis.

We obtained a database with a total of 90,585 attempted GPS locations, during 4,975 individual days. The outliers in the database were detected following the screening method for GPS data proposed by BjØrneraas et al. 2010. We expressed the daily snow depth and average temperature as deviations from the weekly average during the study period. In order to compare the relative effects of sky view, slope and temperature, we standardized them by subtracting the sample means and dividing by the sample standard deviations (Schielzeth 2010). Since activity index, proportion of forest and precipitation followed a highly skewed distribution, we categorized them into classes. Activity and forest were classified as “low” when their proportions were lower than the 25th percentile threshold, as ”average” when they were comprised between the 25th and the 75th percentiles, and ”high” when they were higher than the 75th percentile. Precipitations were classified as “absent” or “present”. Slope and sky view were negatively correlated (summer: n = 45.537, r = -0.499, P<0.001; winter: n = 45,048, r = -0.669, P<0.001), and we used them alternatively in the different models.

We used generalized linear mixed-models (GLMM) with a binomial error distribution (”GLIMMIX” procedure, SAS 9.2©) to analyze FAR and fix quality (NAV). We compared different models, which included the animal and the year as random factors, and month, day period, land cover category, activity class, and precipitation as fixed effects, and sky view in alternative with slope and temperature as covariate fixed effects. We started from the most complex model and sequentially excluded non-significant effects. We selected the most parsimonious model based on the AIC value. (Bozdogan 1987). When difference in AIC between two competing model was < 2, we chose the simplest one.

RESULTS

Stationary collars

We recorded 2.905 fixes from 3.176 fixes attempted, corresponding to an average FAR of 0.91. Using the screening method for outliers, we removed 164 fixes.

Model selection for FAR gave support for two most parsimonious models (ΔAIC <2), which excluded land cover and included sky view class and day period or class of available satellites (appendix table 1). The small ΔAIC between the model with day period and the one with available satellites is understandable, since the number of satellites is nested within day period. We chose to present the results of the model with available satellites, because this is the determinant of variations between day periods, and in this way we maintained the consistency with the results of the subsequent analyses (see below). The effect of sky view class was much stronger than that of available satellites (table 1). The proportion of acquired over scheduled locations was 0.98-0.99 for the sky view classes wider than 70% (figure 1), and dropped to 0.74-0.75 for those narrower, while it decreased slightly from 0.96 for the 10-11 satellites class to 0.91 for the 4-5 satellites class. The random effect of collar was much smaller than those of fixed factor (table 1).

The most parsimonious model for the analysis of NAV included the effects of the sky view class and the class of available satellites (Appendix table I). Land cover was never significant and day period, although highly significant, showed a lower explanatory power than the class of satellites available, and was not included in the most parsimonious model. The probability of an acquired location to be 2D instead than 3D was more influenced than FAR by both sky view and number of satellites (table 1). The proportion of 3D acquired locations ranged between 0.92-0.94 for the sky view classes wider than 70% (figure 2), and dropped to 0.84 and 0.70 for the 60-70% and < 60% sky view classes. When number of satellites available decreased from 10-11 to 4-5, the proportion of 3D acquired locations decreased from 92% to 86%. Again, the random effect of collar was much smaller than those of fixed factor (table 1).

The selection of mixed models for log-transformed accuracy indicated as the most parsimonious model the one including the effects of sky view class, land cover, and, as expected, NAV (Appendix table I). Location error was similar for the 80-90% and 90-100% sky view classes, but then progressively increased with decreasing sky view, and was larger for the forest than the open land cover class and for 2D than 3D locations (table 1). Since our data had a highly skewed distribution, and producing least square means of log-transformed values does not give an immediate picture of patterns, we provide in figure 3 the distribution of LE for the 10th, 25th, 75th and 90th percentiles. In the sky view range between 70 and 100%, the 75th percentiles were close to 10 m, and the 90th percentiles to 15-20 m. For lower sky view classes, LE increased remarkably, with the 75th percentiles rising to 18 and 21m, and the 90th percentile to 32 and 72m. Location points in forest had a LE of 20 m within the 75th percentile and of 32 m within the 90th percentile, while those in open had a LE of 11 m within the 75th percentile of of 20 m within the 90th percentile. Regarding NAV, 2D locations had an LE of 20 m within the 75th percentile and of 94 m within the 90th percentile, while 3D locations had an LE of 10 m within the 75th percentile and of 37 m within the 90th percentile.

Tests on free-ranging female ibexes

We acquired 85.993 fixes from 11 GPS collars fitted on Alpine ibex females, which represent an average individual FAR of 0.91(SD=0.04), with a range across all individuals from 0.82 to 0.98. We detected 3.809 fixes as outliers and the proportion of locations classified as 3D after data screening was 89%.

The selection of models for FAR in summer (appendix table 2) indicated as the most parsimonious model the one including the effects of month, day period, slope, activity, precipitation and temperature, and excluding land cover and slope. In winter, the selected model included month, day period, land cover, sky view, precipitation, and temperature, and excluded slope and snow depth. The differences between months were smaller in summer (table 2 and Figure 4). Observed FAR ranged between 93 and 96% from June to November, and from 85% during December-February to a maximum of 95% during April-May. Also the differences between day periods were small in summer, while there was a clear circadian pattern during winter (table 2 and figure 5), when the observed FAR dropped to values of 89-82% from the evening through the night to rise to 91-93% from morning to afternoon. In both seasons, the probability of missing an attempted location decreased strongly when the activity index increased and in days without precipitations, but the absence of precipitations was much more influential in winter (table 2). The proportion of forest had only a minor, although significant, effect in increasing the probability of unsuccessful locations in winter. This probability increased in summer with slope and decreased in winter with sky view, which is consistent with the negative correlation between the two variables (table 2). However, the effect of sky view in winter was comparatively less marked than that of slope in summer. Finally, higher temperatures decreased the probability of missing a location both in summer than in winter, although with a stronger effect in this latter season (table 2).

Model selection for NAV indicated the same model as the most parsimonious in summer and in winter (Appendix table 2). This model included the effects of month, day period, sky view, activity, precipitation and temperature, and excluded those of land cover, slope and, in winter, the snow depth. During summer, 2D fixes were higher in June and July, reaching 12% of the total received locations, and decreased slowly afterwards to 8% in October. Then, 2D fixes increased to a maximum value of 16% in December, before a new progressive decrease from January to May (table 3 and figure 6). Day period had a stronger influence in winter, when 3D fixes increased in morning and midday, while the differences during summer were much less marked (table 3 and figure7). Proportion of 3D fixes increased with increasing sky view and activity index in both seasons (table 3), and also when precipitations were absent and temperatures higher, especially during the winter season.

DISCUSSION

The advantages of using GPS technology have been well demonstrated (see Cagnacci et al. 2010 for a review). However, the effectiveness of this powerful technology depends on the ability of users to identify the limitations associated with its practical application. These limitations arise from two main sources: the pattern of activity of the species under consideration and the topographical and vegetation conditions in which they live (Bourgoin et al. 2009, Tomkiewicz et al. 2010, Williams et al.

2012). In this study, using stationary tests we identified the factors influencing location accuracy and fix acquisition rate, and then, using data from free-ranging animals, demonstrated how these factors interact with climate and individuals activity patterns in determining fix acquisition rate.

Stationary tests indicated a strong effect of visible sky and a lower effect of available satellites on FAR (Girard et al 2002, Cain et al. 2005, Sager-Fradkin et al. 2007, Hebblewhite et al. 2007, Jiang et al. 2008, Bourgoin et al. 2009) and on quality of received locations (Girard et al. 2002, Hansen and Riggs 2006, Lewis et al. 2007) as indicated by the NAV 2D/3D coding (Biggs et al. 2001, DeCesare et al. 2005, Glasby and Yarnell 2013). This tendency for the quality of locations received to decrease with FAR is important, since it indicates that the availability of good quality locations decreases more than proportionally than FAR. For instance, with sky views higher than 70%, we had a FAR of approximately 0.95 and a proportion of 3D fixes of approximately 0.95, which means a proportion of good quality received fixes of about 0.9 of those scheduled. With sky views lower than 70%, FAR and proportion of 3D fixes dropped to values below 80%, which means a proportion of good quality received fixes of about 0.5-0.6 of those scheduled.

We found, as expected, that LE might range from few meters in unobstructed terrains up to kilometres under high-obstructed conditions (Villepique et al. 2008). These results are consistent with other studies that included sky view in their analyses (D'Eon et al. 2002, Hansen and Riggs 2006, Lewis et al. 2007, Jiang et al. 2008, Bourgoin et al. 2009). The negative effect of forest cover on LE was also expected (Deckert and Bolstad 1996, Gamo et al. 2000, Cargnelutti et al. 2007, Lewis et al. 2007, Hansen and Riggs 2008, Jiang et al. 2008, Williams et al. 2012), as obviously that of NAV (Janeau et al. 2004, Lewis et al. 2007, Jiang et al. 2008; D'Eon and Delparte 2005). However, in our study the loss of accuracy with decreasing sky view or with the other factors was due much more to an increase in the proportion of highly inaccurate locations than to an increase in the mean error of locations. This means that, if proper approaches are used to screen the acquired locations for outliers, the general accuracy of the edited dataset can be good. Using data from our stationary tests, with a very conservative approach to avoid an excessive exclusion of data as outliers, we had LE below 10 m for 50% of the locations, and 20 m for 75% of them. Thus, our test with fixed collars suggests that the main limitation of GPS data, when collars are in high-obstructed areas, is not the accuracy of locations but the bias in probability of acquiring them and of rejecting them as outliers. Therefore, although accuracy might be comparable in edited datasets for locations originating from areas with different sky view, the areas with higher obstruction would be underestimated. How much this limitation might affect the results obtained and their interpretation depends on the proportion of high-obstructed areas as respect to open areas, but also on the selection exerted by animals. The proportion of surface with skyview lower than 70%, in the total range of the female ibexes, was less than 30%, but still remarkable. Assessing the selection exerted by animals was obviously impossible, but the results of the tests with the data on free-ranging females provided interesting indications.

The effects found for variables indexing physical obstruction, as sky view and/or slope, confirmed as expected the trends indicated by stationary tests. Forest cover had only a minor effect on FAR during winter, when use of this land cover is appreciable (see chapter 2.). More interestingly, we found clear intra-annual and daily patterns in the probability of acquiring a location, and in the quality (2D/3D) of acquired locations. In general, FAR and proportion of 3D locations were high, and varied little between months and daily periods, during summer. In contrast, they were lower and varied more between months and daily periods during winter, being lowest in the central months of winter and at nightime. The reason behind these patterns is, we believe, an interaction between the activity level of individuals and climatic and habitat features. The FAR and proportion of 3D fixes increased greatly with the activity index of animals. Ibex females are more active during summer than in winter, especially at night, because of the highly energy saving strategy (Signer et al., 2011) that limits movement with snow and in cold periods (see chapter II). When animals are active they move for feeding and spend more the time in open areas with high sky visibility (Bourgoin et al. 2009), and the antenna orientation is pointed to the sky, which has a positive effect on fix acquisition and quality

(D'Eon and Delparte 2005, Heard et al. 2008, Jian et al. 2008). In other studies and species, the intensity of activity has either improved (White-tailed deer *Odocoileus virginianus*: Bowman et al. 2000; Grizzly bear *Ursus arctos*: Graves and Waller 2006; Mediterranean mouflon *Ovis gmelini musimon*: Bourgoin et al. 2009) or reduced fix acquisition rates (Moose *Alces alces*: Moen et al. 2001), depending on whether the habitats used during activity periods had a lower or higher obstruction to satellites. Similarly, differences between seasons are also related to the features of the habitats selected, and may explain why lower FAR in winter were found by Wells et al. (2011) with mountain goats (*Oreamnos americanus*), and higher by Rumble et al. (2001) and Biggs et al. (2001) with elk (*Cervus elaphus*).

Even after considering monthly and daily trends, we found that climatic variables had a significant effect on FAR and fix quality. We expected that in winter the stochastic variation in snow depth had an important influence. However, snow was not retained by the selected winter models. This might appear surprising, since snow has an important effect on animals' mobility and strongly limits the home range sizes of our females (see chapter II). However, the snow data that we had available did not reflect the snow actually experienced by individual females, being instead an index of temporal differences in snow abundance. Therefore, the variability of our snow data could match with the variability of home range data estimated at weekly or monthly scales, but not with that of FAR collected at the hourly scale. In this regard, precipitations were more explanatory, with a negative effect on fix acquisition rate and quality. During snowfalls female ibexes most probably strongly reduced activity and took shelter under rock cliffs or in forest, where the obstruction generated by rocks or the multipath effect (i.e. reflections of satellites signals before reaching the GPS) may limit the percentage of visible sky (Bourgoin et al. 2009). Also temperature stochastic variability had also an influence on FAR, which increased when temperatures were higher than the average. Higher temperatures may influence snow melting, vegetation phenology, and thermoregulatory needs of animals, in this way influencing the selection of more open areas. In summer, we expected that climatic variables had a lower importance than in winter. In fact, although tendencies were similar, the influences of precipitation, and especially temperature, were smaller in the warmer season. Rumble et al. (2001) and Biggs et al. (2001) in elk (*Cervus elaphus*), and Moen et al. (1996b) and Dussault et al. (1999) in moose (*Alces alces*) found that warmer temperatures reduced FAR. The difference with our results probably reflects different thermoregulatory responses by the species. While ungulates during the hottest periods at low elevations tend to move into forested areas seeking for shade, Alpine ibex move at higher altitudes (Wiersema 1984, Grignolio et al. 2004), even on the top of the rocky cliffs, as suggested by our field observations, where there is minimal or no topographic obstruction between the collars and the roving satellites.

In general, our FAR were higher than those obtained from free-ranging animals in forested or agricultural landscapes (Edenius 1996, Janeau et al. 2004). In fact, we found a strong variability of fix acquisition rates from animals data between studies with different species, ranging from around 50 to 100% (elk: Biggs et al. 2001, Zweifel-Schielly and Surter 2007; mountain goat: Wells et al. 2011; mule deer *Odocoileus hemionus*: Webb et al. 2013). Since fix success is a combination of no-random effects of habitat features and animals behaviour (Nielson et al. 2009), it is important that researchers understand how these interactions may influence their results and conclusions. In our study area, we may conclude that indications of habitats used and estimates of home range sizes, even at short time intervals (for instance daily scales), should be little biased by the probability of acquiring locations and by their accuracy, which remain constantly high. However, in winter FAR can drop significantly in the coldest months, at night, and during periods of inclement weather. This may bias estimates of home range sizes at short time intervals and evaluations of habitat selection, because locations originating from habitats where animals stay inactive and take shelter are underestimated.

Table 1. Parameter estimates (least-square estimates and standard errors) and test statistics from the selected GLMMIX models analysing fix acquisition rate (probability of a scheduled location to be unsuccessful) and navigation (probability of an acquired location to be 2D), and from the selected GLMM model analysing location accuracy (Log (m)) in stationary collars tests.

	l.s. estimate	SE	T	P
Fix acquisition rate				
Intercept	-4.638	0.393	-11.80	<0.01
Random effect collar	0.283	0.218		
Sky view:				
<60 *vs* 90-100	2.935	0.2449	11.98	<0.001
60-70 *vs* 90-100	3.003	0.2395	12.54	<0.001
70-80 *vs* 90-100	-0.434	0.6214	-0.70	0.4854
80-90 *vs* 90-100	-0.331	0.3522	-0.94	0.3477
Satellites available				
4-5 *vs* 10-11	0.7003	0.2853	2.45	<0.05
6 *vs* 10-11	0.9319	0.2376	3.92	<0.001
7 *vs* 10-11	0.7114	0.2529	2.81	<0.01
8 *vs* 10-11	0.3800	0.2690	1.41	0.158
9 *vs* 10-11	0.4134	0.2970	1.39	0.164
Navigation				
Intercept	-4.186	0.316	-13.24	<0.001
Random effect collar	0.056	0.053		
Sky view:				
<60 *vs* 90-100	2.1067	0.1801	11.70	<0.001
60-70 *vs* 90-100	0.6777	0.2139	3.17	<0.01
70-80 *vs* 90-100	-0.07495	0.2884	-0.26	0.795
80-90 *vs* 90-100	0.1496	0.1819	0.82	0.411
Satellites available				
4-5 *vs* 10-11	1.9492	0.3244	6.01	<0.001
6 *vs* 10-11	2.1538	0.2903	7.42	<0.001
7 *vs* 10-11	1.6005	0.3064	5.22	<0.001
8 *vs* 10-11	1.0232	0.3200	3.20	<0.01
9 *vs* 10-11	0.8665	0.3511	2.47	0.136
Location accuracy				
Intercept	2.254	0078	28.76	<0.001
Sky view:				
<60 *vs* 90-100	0.675	0.066	10.30	<0.001
60-70 *vs* 90-100	0.595	0.062	9.53	<0.001
70-80 *vs* 90-100	0.155	0.060	2.58	<0.01
80-90 *vs* 90-100	-0.024	0.044	-0.55	0.584
Open *vs* forest	-0.431	0.046	-9.27	<0.001
2D *vs* 3D	0.608	0.066	9.22	<0.001

Table 2. Parameter estimates (least-square estimates and standard errors) and test statistics from the selected GLMMIX models analysing fix acquisition rate (probability of a scheduled location to be unsuccessful). Night: 23 pm-02 am; Deep night: 03 am-06 am; Morning: 07 am-10 am; Midday: 11 am-14 pm; Afternoon: 15 pm-18 pm; Evening: 19 pm-22 pm.

		l.s. estimate	SE	T	P
Summer	Random effect individual	0.169	0.077		
	Random effect year	0.034	0.315		
	Intercept	-2.467	0.1783	-13.81	<0.01
	Month:				
	June *vs* November	0.470	0.112	4.21	<0.001
	July *vs* November	0.718	0.111	6.47	<0.001
	August *vs* November	0.268	0.107	2.50	<0.05
	September *vs* November	0.284	0.096	2.97	<0.01
	October *vs* November	-0.116	0.080	-1.44	0.151
	Day period				
	Deep Night *vs* Night	0.001	0.075	0.01	0.989
	Morning *vs* Night	0.167	0.074	2.96	<0.05
	Midday *vs* Night	0.305	0.072	4.23	<0.001
	Afternoon *vs* Night	-0.098	0.089	-1.08	0.274
	Evening *vs* Night	-0.067	0.073	-0.09	0.923
	Sky view	--	--	--	--
	Slope	0.316	0.025	12.59	<0.001
	Activity				
	Average *vs* low	-0.775	0.049	-15.91	<0.001
	High *vs* low	-2.476	0.096	-25.69	<0.001
	Precipitation				
	no *vs* yes	-0.532	0.052	-10.14	<0.001
	Temperature	-0.155	0.030	-5.23	<0.001
Winter	Random effect individual	0.642	0.288		
	Random effect year	0.041	0.040		
	Intercept	-1.039	0.289	13.59	0.173
	Month:				
	January *vs* December	0.116	0.209	0.55	0.579
	February *vs* December	-0.106	0.210	-0.51	0.613
	March *vs* December	-0.433	0.209	-2.06	0.039
	April *vs* December	-1.484	0.215	-6.90	<0.001
	May *vs* November	-1.221	0.214	-5.70	<0.001
	Day period				
	Deep Night *vs* Night	-0.205	0.050	-4.13	<0.001
	Morning *vs* Night	-1.103	0.069	-15.97	<0.001
	Midday *vs* Night	-1.688	0.089	-19.00	<0.001
	Afternoon *vs* Night	-0.952	0.069	-13.87	<0.001
	Evening *vs* Night	-0.112	0.049	-4.13	<0.001
	Forest proportion				
	Average *vs* low	0.125	0.047	2.65	<0.01
	High *vs* low	0.078	0.061	1.27	0.204
	Sky view	-0.040	0.018	-2.22	<0.05
	Slope	--	--	--	--
	Activity				
	Average *vs* low	-0.682	0.041	-16.78	<0.001
	High *vs* low	-2.371	0.131	-18.09	<0.001
	Precipitation				
	no *vs* yes	-0.336	0.039	-8.73	<0.001
	Temperature	-0.286	0.018	-15.67	<0.001

Table 3: Parameter estimates (least-square estimates and standard errors) and test statistics from the selected GLMMIX models analysing navigation (probability of an acquired location to be 2D) in ibex tests. Night: 23 pm-02 am; Deep night: 03 am-06 am; Morning: 07 am-10 am; Midday: 11 am-14 pm; Afternoon: 15 pm-18 pm; Evening: 19 pm-22 pm.

		l.s. estimate	SE	T	P
Summer	Random effect individual	0.376	0.183		
	Random effect year	0.037	0.052		
	Intercept	-2.356	0.226	-10.41	<0.01
	Month:				
	June *vs* November	0.444	0.092	4.85	<0.001
	July *vs* November	0.464	0.091	5.08	<0.001
	August *vs* November	0.346	0.082	4.24	<0.001
	September *vs* November	0.232	0.079	2.92	<0.01
	October *vs* November	0.055	0.065	0.84	0.399
	Day period				
	Deep Night *vs* Night	0.253	0.058	4.33	<0.001
	Morning *vs* Night	0.356	0.057	6.14	<0.001
	Midday *vs* Night	0.311	0.058	5.32	<0.001
	Afternoon *vs* Night	0.153	0.063	2.43	<0.05
	Evening *vs* Night	-0.059	0.061	-0.97	0.331
	Sky view	-0.282	0.022	-12.57	<0.001
	Slope	--	--	--	--
	Activity				
	Average *vs* low	-0.321	0.041	-7.88	<0.001
	High *vs* low	-0.769	0.048	-16.01	<0.001
	Precipitation				
	no *vs* yes	-0.285	0.037	-7.73	<0.001
	Temperature	-0.095	0.021	-4.42	<0.001
Winter	Random effect individual	0.556	0.246		
	Random effect year	0.008	0.011		
	Intercept	-1.094	0.240	-4.55	0.138
	Month:				
	January *vs* December	0.073	0.106	0.69	0.493
	February *vs* December	0.003	0.107	0.03	0.979
	March *vs* December	-0.392	0.107	-3.68	<0.001
	April *vs* December	-0.708	0.108	-6.58	<0.001
	May *vs* November	-0.601	0.108	-5.57	<0.001
	Day period				
	Deep Night *vs* Night	-0.141	0.052	-2.69	<0.01
	Morning *vs* Night	-0.937	0.064	-14.58	<0.001
	Midday *vs* Night	-1.025	0.067	-15.38	<0.001
	Afternoon *vs* Night	-0.219	0.058	-3.81	<0.001
	Evening *vs* Night	0.159	0.050	3.16	<0.01
	Forest proportion				
	Average *vs* low	--	--	--	--
	High *vs* low	--	--	--	--
	Sky view	-0.122	0.017	-7.07	<0.001
	Slope	--	--	--	--
	Activity				
	Average *vs* low	-0.579	0.039	-14.09	<0.001
	High *vs* low	-0.812	0.058	-14.09	<0.001
	Precipitation				
	no *vs* yes	-0.343	0.036	-9.57	<0.01
	Temperature	-0.191	0.017	-10.91	<0.001

Appendix table I. Model selection for fix acquisition rate (FAR), navigation and accuracy (LE) in stationary collars.

	Model	Sky view	Land cover	Satellites available	Day period	Navigation	AIC	Δ AIC
FAR	1	<0.001	0.460	<0.01	--	--	1360.0	2.7
	2	<0.001	0.447	--	<0.01	--	1358.8	1.5
	3	**<0.001**	**--**	**<0.001**	**--**	**--**	**1358.6**	**1.3**
	4	**<0.001**	**--**	**--**	**<0.01**	**--**	**1357.3**	**0**
Navigation	**1**	**<0.001**	**0.117**	**<0.001**	**--**	**--**	**1700.7**	**0**
	2	<0.001	0.099	--	<0.001	--	1743.3	42.6
	3	**<0.001**	**--**	**<0.001**		**--**	**1701.2**	**0.5**
	4	<0.001	--	--	<0.001	--	1744.1	43.4
LE	1	<0.001	<0.001	0.207	--	<0.001	6351.0	5.7
	2	<0.001	<0.001	--	0.455	<0.001	6362.0	16.7
	3	**<0.001**	**<0.001**	**--**	**--**	**<0.001**	**6345.3**	**0**

Appendix table II. Model selection for fix acquisition rate (FAR) and Navigation in the test with free-ranging ibex

			Month	Day period	Land cover	Sky view	Slope	Activity	precipitation	Temperature	Snow	AIC	ΔAIC
FAR	Summer	1	<0.001	<0.001	0.442	<0.001	--	<0.001	<0.001	<0.001	--	15793.63	42.03
		2	<0.001	<0.001	0.867	--	<0.001	<0.001	<0.001	<0.001	--	15755.30	3.7
		3	<0.001	<0.001	--	<0.001	--	<0.001	<0.001	<0.001	--	15791.25	39.65
		4	**<0.001**	**<0.001**	**--**	**--**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**--**	**15751.60**	**0**
	Winter	1	<0.001	<0.001	<0.05	<0.05	--	<0.001	<0.001	<0.001	0.129	22026.11	0
		2	<0.001	<0.001	<0.05	--	0.225	<0.001	<0.001	<0.001	0.179	22030.30	4.19
		3	**<0.001**	**<0.001**	**<0.05**	**<0.05**	**--**	**<0.001**	**<0.001**	**<0.001**	**--**	**22026.42**	**0.31**
		4	<0.001	<0.001	<0.05	--	0.2648	<0.001	<0.001	<0.001	--	22030.10	3.99
		5	<0.001	<0.001	<0.05	--	--	<0.001	<0.001	<0.001		22029.30	3.19
		6	<0.001	<0.001	--	<0.05	--	<0.001	<0.001	<0.001	--	22029.64	3.53
		7	<0.001	<0.001	--	--	--	<0.001	<0.001	<0.001		22032.62	6.51
Navigation	Summer	1	<0.001	<0.001	0.170	<0.001	--	<0.001	<0.001	<0.001	--	25502.00	0.44
		2	<0.001	<0.001	0.112	--	<0.001	<0.001	<0.001	<0.001	--	25567.44	65.88
		3	**<0.001**	**<0.001**	**--**	**<0.001**	**--**	**<0.001**	**<0.001**	**<0.001**	**--**	**25501.56**	**0**
		4	<0.001	<0.001	--	--	<0.001	<0.001	<0.001	<0.001	--	25567.70	66.14
	Winter	1	<0.001	<0.001	0.060	<0.001	--	<0.001	<0.001	<0.001	0.370	25353.89	0
		2	<0.001	<0.001	0.067	--	<0.05	<0.001	<0.001	<0.001	0.098	25396.51	42.62
		3	<0.001	<0.001	0.061	<0.001	--	<0.001	<0.001	<0.001	--	25532.69	178.8
		4	<0.001	<0.001	0.069	--	<0.05	<0.001	<0.001	<0.001		25397.27	43.38
		5	**<0.001**	**<0.001**	**--**	**<0.001**	**--**	**<0.001**	**<0.001**	**<0.001**	**--**	**25354.29**	**0.4**
		6	<0.001	<0.001	--	--	<0.05	<0.001	<0.001	<0.001	--	25398.63	44.74

Figure 1: proportion of acquired over scheduled locations for the different sky view and available satellites classes. Values are means of location points within classes. Vertical bars indicate SD.

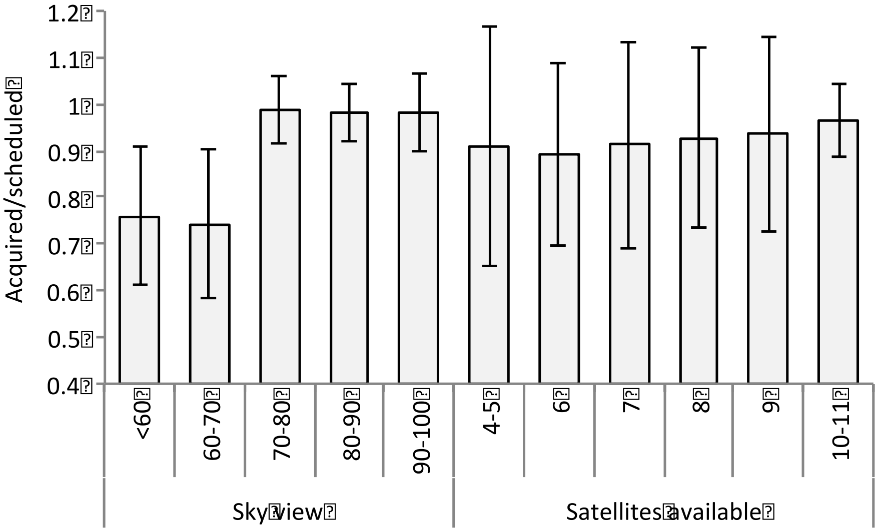


Figure 2: proportion of locations over acquired locations for the different sky view and available satellites classes. Values are means of location points within classes. Vertical bars indicate SD.

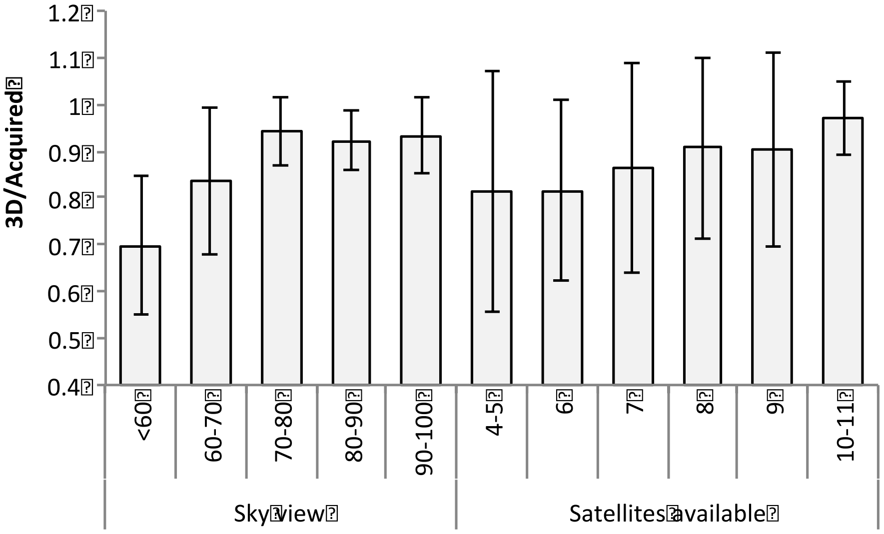


Figure 3: Accuracy (distance from true location, m) within different sky view classes and land use and navigation categories. Box plots comprise the 25th and 75th quintiles, while vertical bars indicate the 10th and the 90th quintiles.

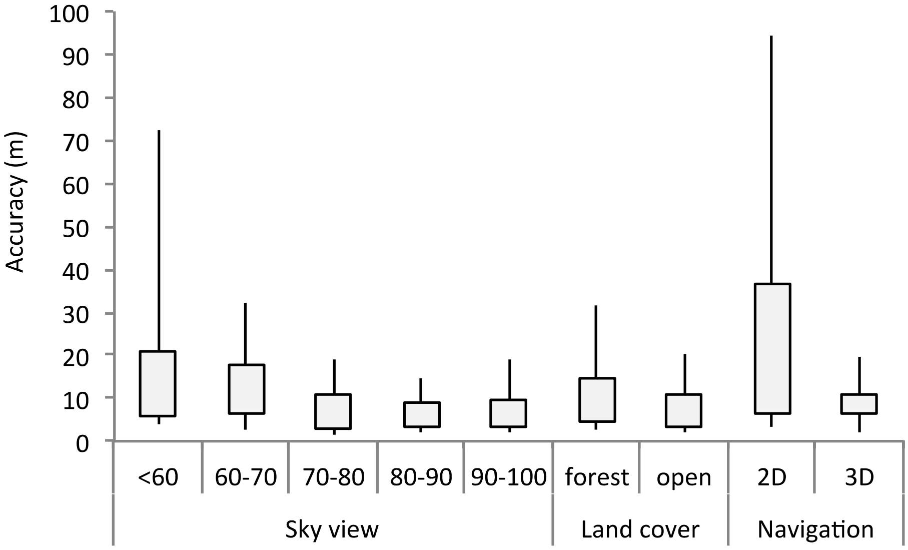


Figure 4: proportion of acquired over scheduled locations in the various seasons and months with ibex tests. Values are means of individual female ibex. Vertical bars represent SD.

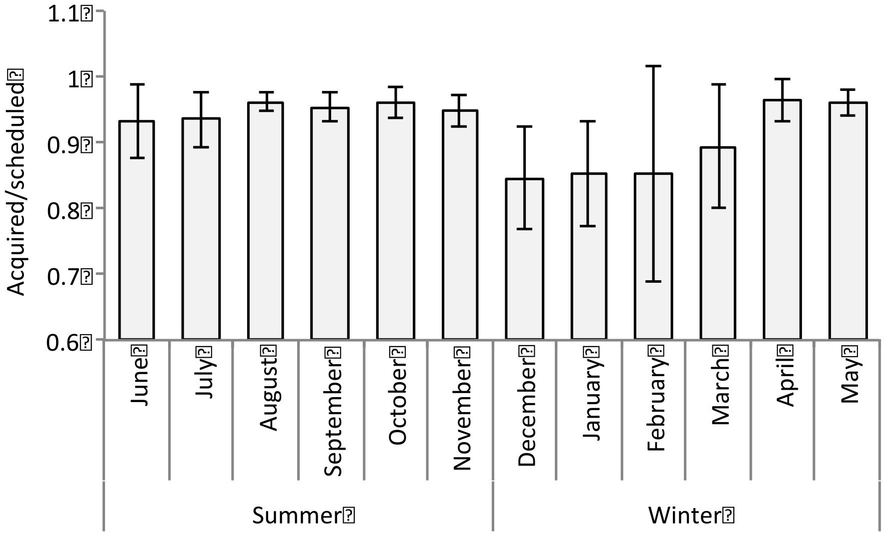


Figure 5: proportion of acquired over scheduled locations in the various seasons and day periods with ibex tests. Values are means of individual female ibex. Vertical bars represent SD. Night: 23 pm-02 am; Deep night: 03 am-06 am; Morning: 07 am-10 am; Midday: 11 am-14 pm; Afternoon: 15 pm-18 pm; Evening: 19 pm-22 pm.

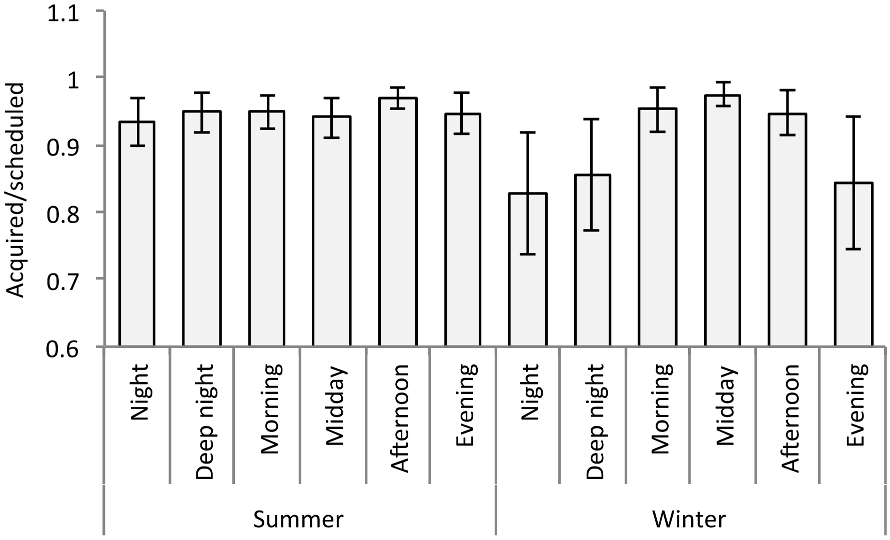


Figure 6: proportion of 3D over acquired locations in the various seasons and months with ibex tests. Values are means of individual female ibex. Vertical bars represent SD.

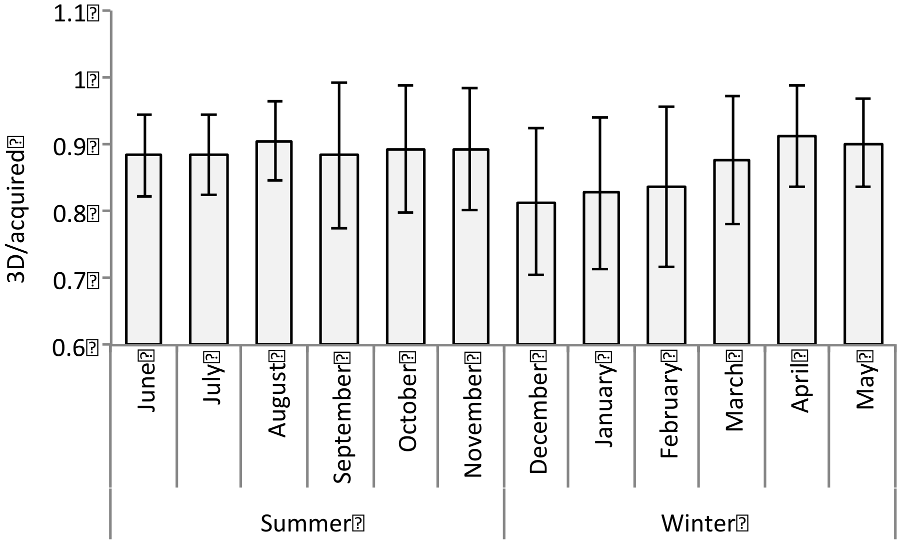
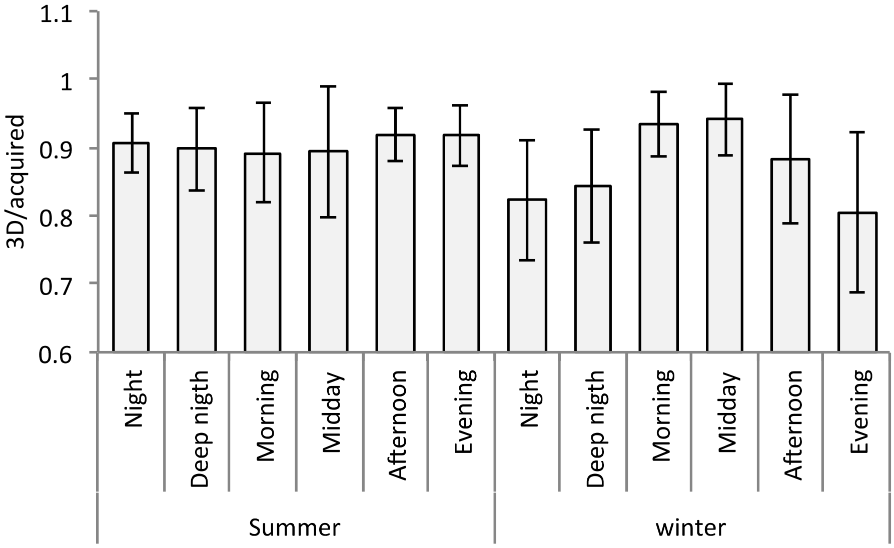


Figure 7: proportion of 3D over acquired locations in the various seasons and day periods with ibex tests. Values are means of individual female ibex. Vertical bars represent SD. Night: 23 pm-02 am; Deep night: 03 am-06 am; Morning: 07 am-10 am; Midday: 11 am-14 pm; Afternoon: 15 pm-18 pm; Evening: 19 pm-22 pm.



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CHAPTER 2

DETERMINANTS OF HOME RANGE SIZE ACROSS SPATIO-TEMPORAL SCALES IN A HIGH MOUNTAIN UNGULATE

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INTRODUCTION

Patterns of space use by animals reflect their responses to habitats and climate variations (Johnson et al. 1992, Morales et al. 2004, Fieberg et al. 2010, Tomkiewicz et al. 2010), and may influence individual performance and population dynamics (Gaillard et al. 2010, Morales et al. 2010, Spencer 2012). A concept widely used to describe animal space use is the home range (HR), which defines the areas used with different intensities and frequencies by an individual in search of food, shelter and mates (Börger, Dalziel and Fryxell 2008). The HR concept has greatly evolved during the last decades (Burt 1943, Powell 2000, Gaillard et al. 2010, Kie et al. 2010, Powell and Mitchell, 2012), especially after the advent of GPS tracking technologies that allow to describe movement at very detailed spatio-temporal scales (Börger et al. 2008; Kie et al. 2010, Benhamou and Riotte-Lambert 2012). However, in principle the size of a HR reflects how an individual is able to satisfy its needs in relation to the available resources. Therefore, understanding why HR size varies among and within species has received and continues to receive widespread consideration in ecology research (see reviews in Börger, Dalziel and Fryxell 2008; Kie et al. 2010; Moorcroft, 2012, Potts and Lewis 2014). Among terrestrial mammal species, body mass, being an index of the energy needs and movement capability of animals, is the main determinant of HR size, with type of food playing a significant but lower role (McNab, 1963; Harestad and Bunnell, 1979, Tucker et al., 2014). Within species, the HR size of large herbivores may be affected by several factors, such as population density (Vincent et al. 1995, Kjellander et al. 2004), forage availability (Bremset Hansen et al. 2009, Owen-Smith et al. 2010), human disturbance (Creel et al. 2002, Manor and Saltz 2003), climatic conditions (Jacobson et al. 2004, Floris et al. 2012), or individual status (Green 1992, Dahle and Swenson 2003, Said et al. 2005). However, studies attempting to examine in a single analysis the range of extrinsic and intrinsic factors affecting HR size are very few (see van Beest et al. 2011 for moose *Alces alces* and Borger et al. 2006 and Morellet et al. 2013 for roe deer *Capreolus capreolus*). These studies suggested that, in temperate regions, the HR size of large herbivores follows predictable intra-annual patterns in response to seasonality of climatic conditions and food resources, with an additional variation introduced by stochastic or local variability in climate, vegetation dynamics, individual conditions and reproductive status. The effects of extrinsic and intrinsic factors varied for the different temporal and spatial scales at which HR were investigated, indicating that mechanism determining HR size are scale-dependent.

High mountain areas are characterized by extreme seasonality, both in climate and food resources, which may have strong effects on survival (Rughetti et al., 2011, Pettorelli et al., 2007), reproduction (Apollonio et al., 2012) and population dynamics (Jacobson et al., 2004). Large herbivores living in these areas have evolved specific life-history strategies (ToÏgo et al., 2007) and physiological adaptations to optimize the energy annual balance (Rughetti and Festa-Bianchet, 2011, Corlatti et al., 2013), in order to survive through long, harsh winters (Signer et al., 2011). However, how the constraints of extreme seasonality shape the patterns of HR size of large herbivores living in high mountain areas is still poorly understood. A few studies, based on VHF tracking techniques on Alpine chamois (*Rupicapra rupicapra)* and Alpine ibex (*Capra ibex)* suggest that HR size should increase in summer as respect to winter, and that snow cover, trophic resources, mating behaviour of males or reproductive condition of females may also have an influence (Parrini et al. 2001; Grignolio et al. 2003; Parrini et al. 2003; Grignolio et al. 2005, 2007; Scillitani et al. 2012). However, no study has yet examined in a single analysis and with detailed GPS data how seasonality and other extrinsic and intrinsic factors influence HR size. Here, we used a database of high-frequency GPS locations of 15 female Alpine ibex during three years to first identify temporal patterns of HR size and then to assess the variation due to food resources (indexed by land cover categories and NDVI), weather and climate variability (snow depth, precipitations, temperature), land morphology (indexed by slope), and individual conditions (age and reproductive status). Since HR size variations are scale-dependent (van Beest et al. 2011, Borger et al. 2006, Morellet et al. 2013), we investigated them at different temporal (monthly and weekly) and spatial (HR and core area) scales.

In particular, we hypothesized that:

H1. Due to the extreme seasonality of high mountain areas, HR should follow an intra-annual pattern at all temporal and spatial scales, and particularly that (H1a) HR size should decrease during autumn and winter, and increase during spring and summer (Gross et al. 2002, van Beest 2011), due to the strong limitations to movement imposed by deep snow (Rossi et al. 2003, Grignolio et al. 2003) and the marked energy-saving behaviour of Alpine ibex in winter (Signer et al. 2011). Since daylight is directly related with the predictability of climate and resource availability, we expected (H1b) that HR size was positively correlated with photoperiod, in contrast to the negative correlation found in other species inhabiting lower altitudes with milder winter and higher forage availabilities (Borger et al. 2006, Saïd et al. 2005, Morellet et al. 2013), and that (H1c) cyclic intra-annual trends in climate (indexed by average daily temperature) and forage availability (indexed by NDVI of study area, Hamel et al. 2009) might exert further influence on HR size patterns.

H2 We expected that spatiotemporal stochastic variations in climate and food resources had a strong influence on HR size (van Beest et al. 2011; Saïd et al. 2005, 2009). In particular, we predicted that in winter (H2a) HR size decreased with increase in snow depth (Grignolio et al. 2003) and in periods of high precipitations (H2b) and low temperatures (H2c), due to reduced mobility and energy saving behaviour of ibex in such conditions (Grøtan et al. 2007, Signer and Arnold 2008). In summer (H2d), we expected low or no effects of precipitations or temperature, although high temperatures might induce a greater mobility in search of cooler areas. According to the energy needs theory, we predicted that (H2e) HR size should decrease with increase in food resources (Aublet and Festa-Bianchet 2009, Owen-Smith et al. 2010), which we indexed with the proportion of vegetation as respect to bare ground (Scillitani et al., 2012), but also with NDVI (Bremset Hansen et al. 2009, Mueller et al. 2011).

H3. Steep slopes are the predominant landscape feature in the study area and the habitat preferred by ibex when searching for shelter during the weaning period, for refuge to warm temperatures in summer and for shallower snow patches during winter (Gross et al. 2002, Grignolio et al. 2004). Therefore we predicted that (H3a) HR sizes may decrease when increase in the degree of the occupied slopes (Scillitani et al. 2012).

H4. The individual age and reproductive status may influence the space use by females in different ways. We expected that young females might show (H4a) larger HR than older females due to social and spatial instability, as suggested by Grignolio et al. (2004). Females with offspring have been found to have either larger (Cederlund and Sand 1994, Saïd et al. 2005) or smaller (van Beest et al. 2011) HR than barren females. In response to the reduced mobility hypothesis, we expected (H4b) that non-lactating females had larger HR than lactating females (Grignolio et al. 2007). However, given the gregariousness of Alpine ibex females, we also predicted (H4c) that the effects of reproductive status were much less marked than those found in non-gregarious species (van Beest 2011).

MATERIAL AND METHODS

Study area

The Marmolada massif is the highest mountain group in the Dolomites area and is located in the eastern Italian Alps (see Scillitani et al. 2012 for details). It is characterized by a complex topography with several summits around 3.000 m a .s.l. It is possible to identify two main boundaries corresponding to different landscapes: the north-western, which is composed by gentle slopes and open valleys, and the south-eastern side, where vertical rock walls up to 1.000 m of height, high ruggedness, and deep valleys shape the environment. The vegetation in the areas used by ibex (from 1.491 m to 3.261 m in elevation) is clearly stratified, from isolated shrubs and alpine grasslands at higher altitudes to alpine forests dominated by species of the genus *Larix* at the lowest one,.

Animals and tracking

GPS locations were collected from September 2010 to October 2013 from 15 females of Alpine ibex (estimated age ranged from 2 to 12 years). Animals were captured during the summer seasons, from July to early October, with veterinary assistance in compliance with current Italian laws, using a tele-injection of xylazine (Rompun©, Bayer, Leverkusen, Germany). All captured individuals were aged from horn annuli growth and examined for general health condition. Reproduction status was assessed from udder morphology and presence of milk, and confirmed by visual observations of mother-kid associations in the period immediately following the release, and in the following summers of monitoring. The individuals were marked with colored and numbered ear tags and equipped with GPS-GSM Plus collars (Vectronic Aerospace GmbH). Collars were scheduled to attempt to record an animal location every 1 hour during 54 weeks. Data were received on a GSM Ground Station and downloaded and processed using a specific software (GPS Plus Collar Manager© 3.11.3, Vectronic Aerospace GmbH).

Data editing and calculation of Home Range sizes

We identified largely erroneous positions as "outliers" data with the screening method developed by Bjørneraas et al, (2010), using PgAdmin tool for PostgreSQL© 1.16.0 (http://www.pgadmin.org). After removing the outliers, we then calculated individual home ranges at a weekly and a monthly temporal scale, setting the starting date at the 21st of December. We used a local convex hull (LoCoH) non parametric kernel method for constructing the home range polygons, using the adehabitat package for R (R Development Core Team 2008) as developed by Calenge (2006). Particularly, we used the k-LoCoH approach which constructs the convex hull associated with each GPS location and its *k*-1 nearest neighbors ($k=\sqrt{n}$, where n is the number of points for the corresponding individual and annual week), representing the frequently used areas by the resulting union of hulls in x% isopleths (Getz and Wilmers 2004, Getz et al. 2007). This method is appropriate when working with species living in areas of complex topography, since it takes into account physiographical boundaries, such lakes or rocky outcrops, which are not used by the animals. We estimated weekly and monthly home ranges at two different spatial scales: using the 95% isopleths (hereafter called HR) and the 50% isopleths, (hereafter called core areas, CA). We excluded weeks with less than 4 days and/or less than 72 locations, and months with less than 350 locations. We associated to each retained HR and CA the variables described below.

Variables description

Seasons.

We used a clustering approach (Kaufman and Rousseeuw 2009) to identify biological seasons based on movement and habitat descriptors associated with locations. The results are detailed in "Supplementary material I". Based on these results, we classified as "summer" the weeks from 22 to 40, and the months from 6 to 10, and as "winter" the weeks from 41 to 52 and from 1 to 21, and the months from 11 to 12 and from 1 to 5.

Individual variables.

Age class of the females was classified into "subadult" (≤ 3 years old) or "adult" (> 3 years old); we set the date of age change at June 1st. Reproductive status was defined as "lactating " or "non-lactating" respectively. We used this classification only for summer HR and CA, since this season covered the parturition and weaning periods.

Climatic variables and daylight.

Climatic data were obtained from two meteorological stations, "Monti Alti di Ornella" located at 4.5 km from the Marmolada massif e "Passo Valles" located at 11.3 km (altitude: 2.250 m a.s.l and 2.032 m a.s.l respectively). We recorded daily snow depth to the ground (cm), total daily precipitation (mm) and average daily temperature (°C). The variables were expressed both as absolute values and as residuals from the average trend during the study period, to index stochastic variability. Note that these variables express only approximately the conditions experienced by ibex, but record the temporal trends and stochastic variations. Daylight was calculated based on the geographic coordinates of the study area and Julian date. All variables were standardized as z-scores.

Land cover and morphology.

We used a land cover map of the study area based on a high resolution digital orthofoto (1x1m, WGS84/UTM32) (Scillitani et al., 2012; Scillitani et al., 2013) to reclassify with ArcGIS® 10.1 (Esri Inc., Redlands, USA) 11 different vegetation covers into 2 prevalent types: "vegetation", combining grasslands, shrubs and forest, and "scree and rocks", using. We used a high resolution (5x5m) Digital Elevation Model (Regione del Veneto, Unità di Progetto per il SIT e la cartografia, 2006. *http://idt.regione.veneto.it/app/metacatalog/*) to create the slope layer of the study area. Slope values were then grouped into 9 intervals of 10 per cent units. Once overlapped with the polygons of the HRs and CAs, each interval class was assigned a unit score (1,2,…10), starting from the lowest class, and a slope index was calculated as $\Sigma(S_i{*}P_i)$, where S_i is the score of interval class i, and P_i is its proportion in the polygon (HR or CA) area.

NDVI index of vegetation greenness.

We used remotely sensed data from MODIS (Moderate Resolution Imaging Spectroradiometer, NASA TERRA satellites) that provides the NDVI satellite imagery with high temporal (16-day compositing periods) and spatial resolution (250x250m) (Huete et al. 2002). To reduce the temporal resolution we resampled the images into 7-days intervals by calculating the mean value of each pixel between two successive images using ArcGis 10.1 (ESRI®). Total NDVI images were 165, with a weekly temporal resolution from September 2010 to mid-October 2013. We calculated the average value of the weekly and monthly NDVI at three spatial scales: within the entire study area, and within the polygons (HR or CA) areas.

Statistical analysis

We log-transformed HR and CA size values, and excluded as outliers the values lying outside the mean ± 3 SD. We had 672 HR weekly estimates (232 in summer and 440 in winter), 680 weekly CA estimates (233 in summer and 445 in winter), and 160 monthly HR and CA estimates (64 in summer and 96 in winter).

Temporal trends of HR and CA.

The analyses were conducted in R (Development Core Team 2008), using the mgcv and nlme packages. We first tested for intra-annual patterns of variation of HR and CA size with generalized additive mixed models (mgcv package, Wood 2001) models, using the week or the month, depending on the temporal scale of analysis, as fixed covariate factors, and the individual as random factors. In order to test the effects of daylight, NDVI and temperature (absolute) on intra-annual patterns, we used two approaches: first, we verified whether the addition of these variables as linear terms improved the fit of the general additive mixed models with week, using a likelihood ratio test; second, we tested the linear relationship between HR and CA size and daylight, NDVI, and temperature using mixed linear models (nlme package, Pinheiro et al. 2011), with individual as random factor.

Effects of individual, climatic and habitat variables on HR and CA size.

In order to assess the effects of individual, climatic and habitat factors, we analysed HR and CA size within summer and winter with linear mixed models at the two temporal scales, using individual as random factor. Fixed categorical factors used were age class, reproductive status (summer only) and prevalent land cover class, while fixed covariate factors were daylight, absolute temperature, NDVI of study area, NDVI of the polygons (summer only), slope index, snow stochastic variation (winter only), temperature stochastic variation, and precipitation stochastic variation. We started from the most complex model and then removed sequentially all factors, starting from those non-significant in order to reach the most parsimonious model (Caswell, 1988). Model selection was based on the Akaike's Information Criterion index (AICc) (Zuur et al. 2009); when two models differed less than 2 in AIC value, we selected the simpler one. We tested in alternative the covariate variables with a correlation higher than 0.45 (see appendix tables I, II, III, IV).

RESULTS

Weekly home ranges and core areas

Weekly HR size was extremely variable (mean = 21.1 ha; SD = 27.3) as well as that of CA (mean = 2.0 ha; SD = 3.1). Both were larger in summer (HR: mean = 37.8 ha, SD = 32.9, CA: mean = 4.3 ha, SD = 4.1) than in winter (HR = 10.2 ha, SD = 14.4; CA: mean = 0.7 ha, SD = 0.9).

Temporal trends.

The general linear additive mixed models with week as a covariate indicated that there was a strong intra-annual pattern for both HRs and CAs, with an increase during late winter and spring, a peak in summer and a decline afterwards (Figure 1). However, weekly HRs peaked earlier and had much less pronounced variations than weekly CAs. The addition of daylight, NDVI of study area and absolute temperature (see figure 2 for their intra-annual trends) as linear covariates to the general additive mixed models with week did not improve the fit of the models for HRs, as indicated by the likelihood ratio test (daylight: $P = 0.115$; NDVI: $P = 0.497$; temperature: $P = 0.227$). The addition of NDVI ($P < 0.001$) and temperature ($P < 0.001$), but not that of daylight ($P = 0.514$) improved the fit of general mixed linear models for CAs. When tested singularly in mixed linear models, all the three variables were highly significantly related to HR and CA size, but the most explicative was daylight for HRs (daylight model: AIC = 2333.2, Δ AIC = 0; NDVI model: AIC = 2335.6, Δ AIC = 2.4; Temperature model: AIC = 2339.4, Δ AIC = 6.2) and temperature, close to NDVI, for CAs (daylight model: AIC = 2325.9, Δ AIC = 165.9; NDVI model: AIC = 2167.8, Δ AIC = 6.8; Temperature model: AIC = 2160.0, Δ AIC = 0).

Effects of individual, climatic and habitat variables.

The results of the selection of mixed linear models are given in Appendix table V for summer HR and CA, and in Appendix table VI for winter HR and CA. In both seasons, the most parsimonious models for both spatial scales did not include reproductive status, prevalent land cover, temperature stochastic variation, and precipitations stochastic variations. In summer, age class was retained only in the HR model. Among the temporal and climatic variables, daylight and NDVI of study area were retained in both HR and CA models, while absolute temperature (tested in alternative with NDVI of study area) was excluded. The NDVI of polygon (HR or CA) was retained in the most parsimonious HR model, but not in that of CA. Slope was retained by selected models for both HR and CA. In winter, daylight (in alternative with NDVI of study area) and snow stochastic variation were retained by both the most parsimonious models for HR and CA, slope was retained by the best HR model, and temperature by the best CA models. The solutions for the fixed effects selected in the most parsimonious models are given in table 1. Subadult females had smaller HR sizes than adult females in summer only (Table 1). Daylight, NDVI of study area, and absolute temperature, when selected, had always a positive effect on HR and CA size, while NDVI of the polygon, slope, and snow (stochastic) had a negative effect.

Monthly home ranges and core areas

Also monthly HR and CA size was highly variable (HR: mean = 60.4 ha; SD = 67.6; CA: mean =6.7 ha; SD = 8.5) and were accordingly larger in summer (HR: mean = 119.5 ha, SD = 74.7; CA: mean = 14.0 ha, SD = 10.2) than in winter (HR: mean = 28.6 ha, SD = 34.0; CA: mean = 2.8 ha, SD = 3.6).

Temporal trends.

Also at the monthly scale HRs and CAs showed a strong intra-annual pattern (figure 1), which was more synchronous between spatial scales than that of weekly estimates. For both HRs and CAs, the fit of the general additive mixed models improved with the inclusion of temperature (likelihood ratio test: $P < 0.001$), but not with inclusion of daylight and NDVI of study area (likelihood ratio test for HR models: $P = 0.23$ and $P = 0.43$; likelihood ratio test for CA models: $P = 0.48$ and $P = 0.39$). Mixed linear models indicated that temperature was more related than NDVI and Daylight to the patterns of monthly HR (temperature model: AIC = 387.61, Δ AIC = 0; NDVI model: AIC = 446.94, Δ AIC = 59.3; Daylight model: AIC = 452.56, Δ AIC = 64.9) and monthly CA (temperature model: AIC = 466.70, Δ AIC = 0; NDVI model: AIC = 525.87, Δ AIC = 59.2; Daylight model: AIC = 532.91, Δ AIC = 66.2).

Effects of individual, climatic and habitat variables.

The results of model selection are given in Appendix table VII for summer and Appendix table VIII for winter. In summer, the most parsimonious models retained the effects of daylight, prevalent land cover, and slope for both HR and CA. In winter, the selected models retained the effects of absolute temperature (in alternative with daylight and NDVI of study area) for HR and CA, plus slope and snow stochastic variation for HR and precipitation stochastic variation for CA. For CA only, also the effect of age class was retained. The solutions for the fixed effects included in the selected models are shown in table 2. Absolute temperature had a positive effect on HR or CA size, while "vegetation", in comparison with "scree and rocks", slope and precipitation stochastic variability had a negative effect. Subadult females in winter had larger CAs than adult females.

DISCUSSION

In general, the size of HRs and CAs that we found in this population of alpine ibex are smaller than those of other ibex populations (Grignolio et al. 2003, 2004) or species (Iberian ibex *Capra pyrenaica*: Escòs and Alados, 1992), although this could be due to differences in the applied method to construct the HRs and in the tracking methodology. In fact, to our knowledge this is the first description of spatial behavior of female Alpine ibex obtained from high frequency GPS data, which allowed us to investigate the patterns in spce use at detailed temporal (weekly and monthly) and spatial scales. This enabled us to identify a very marked and peculiar intra-annual pattern in HR and CA size, and to assess that spatial movements of female ibex are influenced mainly by the yearly cycling of climatic conditions and food resources, and much less by individual factors. In the following, we will discuss our findings according to the hypotheses formulated.

In accord with our expectation (H1a), HR and CA sizes, at both the weekly and monthly scales, showed the smallest values in winter, to increase progressively during spring until the peak in summer, before decreasing through autumn to the winter ranges. Large herbivores living in temperate climates may tend to decrease the HR size in summer and increase them in winter, in responses to variations of food abundance and spatial distribution (Danilkin 1996, Rossi et al. 2003, Börger et al. 2006, Morellet et al. 2013), but may also show the opposite strategy where winters are harsh and with deep snow cover, so that the costs of increasing movements are higher than the benefits that might derive from the scarce food available (Gross et al. 2002, van Beest et al. 2011, Rivrud, et al. 2010). This is clearly the strategy of female ibex in our study area, which is consistent with the previous results reported using VHF tracking systems in other populations (Grignolio et al. 2004, 2007). What is striking in our results, however, is the magnitude of the change in HR and CA size during the year, which is greater than that observed in other studies comparing intra-annual or seasonal patterns for other species (Börger et al. 2006, van Beest et al. 2011; Morellet et al. 2013). In this study, for both the weekly and monthly HRs there was a 15/20-fold increase from the winter minimum to the summer maximum. This indicates how strong can be the effect of seasonality in the extreme climate conditions experience by ibex, which might be typical also for other mountain ungulates (Côté and Festa-Bianchet 2003). In fact, although daylight was positively correlated with HR and CA size, as expected (H1b), the fit of the models describing intra-annual patterns generally improved when absolute temperature and NDVI were included. Daylight regulates physiological cycles in animals, thus inducing also a change in metabolic activity and energy expenditure (Signer et al. 2011), which may result in different movement patterns. However, our results indicate that in the Alpine ibex the fluctuations of climatic constraints and food availability, which are not completely synchronized with daylight as indexed by the temperature and NDVI cycles of our study area, are determinant in modulating the patterns of space use (prediction H1c).

Females started to move after the winter period when the snow started melting and the vegetation re-growth began, as suggested by the increase in temperatures and NDVI of the study area, leading to an increase in the size of areas used until mid summer. Late spring and summer are crucial periods for ibex females after a long winter in order to recover body mass and to face the high energetic requirements of parturition, lactation and maternal requirements. As suggested by Pettorelli et al. (2007) and by Hamel and Côté (2007), the quality of vegetation in alpine ecosystems reaches the maximum during mid-summer and then declines, which is consistent with the pattern of NDVI that we found in our study area. The increase of HRs and CAs while the overall quality of the vegetation in the study area was also increasing may suggest a selective-seeking behaviour of females, i.e., females tend to expand their ranges in order to include the maximum availability of patches with specific clusters of plants in early phenologic stages. For instance, Dalziel et al. (2008) used a network approach to demonstrate how individual elk (*Cervus elaphus canadensis*) based their movements on visits to preferred habitat patches, which were connected by rapid jumps, enlarging consequently their home ranges. In addition, during the transition period after winter until mid summer, females shifted towards higher elevations (see supplementary material), likely following the altitudinal cline in vegetation phenology (Johnson et al. 1968, Shank 1985, Albon and Langvatn 1992, Pettorelli et al. 2007). At higher altitudes, the vegetation patches become smaller and fragmented by larger areas of scree and rocks, which would require the use of wider ranges. Females started to reduce the size of their ranges when vegetation quality started declining. In late summer, the metabolic needs might be lower than in the preceding months, because females have recovered their body condition and the lactation period is close to the end. Therefore, with the declining quality of vegetation and the reduced individual requirements, they might start the shift towards the marked energy saving strategy used in the following winter. They also shift to lower elevations, which allow them to benefit from grasslands more than in summer (Supplementary material).

When we analysed the variation of weekly and monthly HRs and CAs in winter, we found that snow stochastic variation negatively influenced the individual areas used at both spatio-temporal scales (as expected from H2a), with the only exception of monthly core areas (for which there was however a negative effect of precipitation, see below). The ibex is a well adapted ungulate to climate variability (Toïgo et al. 2007), although the snow depth may limit its ability to move, which leads to a reduction in their spatial movements due to the strong energy expenditure (Rossi et al. 2003; Grignolio et al. 2003, 2004). We expected that stochastic precipitation (H2b) and temperature (H2c) influenced ranges sizes in winter, although we found partial support only for precipitation, which reduced monthly CAs in in winter, possibly as a result of a heat-saving strategy (Rivrud et al. 2010, Van Beest et al. 2011). However, in most statistical analyses we had to test snow, precipitation and temperature in alternative, because they were correlated. The effects we found for precipitation and temperature were significant and in line with what predicted, but the selected models were those including snow, which seems hence to be a more powerful variable. To disentangle the effects of these factors, we would have needed individual data of snow depth, temperature and precipitation, which are almost impossible to obtain in the habitats used by ibex. In summer we found no effects of precipitation (H2d) on space use at all spatial and temporal scales. In this season, precipitations are less frequent and abundant than in winter, and absolute temperature is high enough to avoid risks of excessive heat dispersal by animals during rain events. On the contrary, during summer spatial behaviour of high mountain ungulates and hence the ibex might be influenced by the search of higher or shaded areas to avoid excessive heat (Mason et al. 2014), but we found no effect of stochastic temperature. However, we did not have access to the temperature directly experienced by ibexes, and therefore our result do not exclude an effect of this variable, although it suggests that it should be low in comparison with the temporal trends and those of other habitat factors. The effects of the indexes of food resources (mean NDVI value or proportion of vegetation land cover inside the HR/CAs) on reducing the size of weekly HR and monthly HR and CA were on the contrary remarkable, supporting our prediction (H2e) based on the nutritional hypothesis (Peek et al. 2002) and as found in other species (Svalbard reindeer *Rangifer tarandus platyrhynchus*: Hansen et al. 2009; mule deer *Odocoileus hemionus*: Relyea et al. 2000; roe deer Capreolus capreolus: Saïd et al. 2009).

In synthesis, we found that, after correcting for temporal trends, the variation in HR and CA size was more influenced by climatic variables in winter and by variables indexing food resources only in summer. This result is in accord with our interpretation of factors driving the intra-annual cycle, as above discussed. In highly seasonal environments, the weather conditions have a strong influence in the behavioural traits of the species, determining whether and why to move in order to balance their energetic demands (Nathan et al. 2008). The Alpine ibex is one of the most adapted ungulates to the cold and long winters that characterize the high alpine landscapes, and its survival strategies have been approached in several studies (Aublet et al. 2009; Signer et al. 2011). Our findings confirm that climate parameters may have a strong effect on the spatial behaviour of large herbivores (Börger et al. 2006, Aublet et al. 2009, Bourgoin et al. 2011, van Beest et al. 2012), especially at fine spatio-temporal scales (Loe et al. 2007, van Beest et al. 2011).

Habitats used by Alpine ibex are characterized by rugged terrains and steep slopes, that make the ibex one of the ungulates with greater skill and agility to move in rocky environments (Geist 1987, Tosi and Pedrotti 2003). The selection of steep habitat features has been attributed to several reasons in mountain species, from refuge to warmth or human disturbance (Dussault et al. 2005, Zweifel-Schielly et al. 2009), to exploitation of snow-free patches during winter (Rideout and Hoffman 1975, Gross et al. 2002), or to protection of offspring during the weaning period, a widespread behaviour among ungulates (Festa-Bianchet 1988, Boschi and Nievergelt 2003, Grignolio et al. 2007). Our results confirm our prediction (H3): as expected, we observed that females reduced the size of the areas used with increasing slope, at all spatial and temporal scales both in summer and winter seasons, except only for the CA during winter. On the other hand, CAs in winter were very small, and ibexes appeared to use also forest areas, where slope is less important as shelter habitats (see Supplementary material). Our results are consistent with the spatial behaviour of males within the same population, described by Scillitani et al. (2012).

We found significant but contrasting effects of the age class on space use, with subadult females having smaller HR sizes than adults at the weekly scale in summer, but larger CA sizes at the monthly scale in winter. The result for summer is in contrast with our expectations (H4a) and with the results reported for the resident ibex population in the Gran Paradiso National Park (Grignolio et al. 2004). Dominance or social interactions between females (Hamel and Côté 2007), that are still unexplored for the Alpine ibex, might perhaps explain this difference with the colony in the Gran Paradiso National, characterized by higher population densities (Jacobson et al. 2004). However, our findings were due to very few individuals in the subadult age class, and we think that they should be taken with great caution.

Reproductive status had no effects on space use, in contrast with our expectation (H4b). In this case, the lack of effects was very clear and consistent across spatial and temporal scales, and the lactating and non-lactating classes were equilibrated in number of individuals/seasons. Females with kids might increase their ranges in response to anti-predatory behaviour (White and Berger 2001) and higher costs of lactation (Parker et al. 1990, Robbins 1993, Zimmerman et al. 2006, Main 2008). Such response during the stages of pregnancy and weaning has been reported in ibex (Grignolio et al. 2003, 2005) and other mountain species (Iberian ibex *Capra pyrenaica*: Escòs and Alados, 1992; Alpine chamois *Rupicapra rupicapra*: Boschi and Nievergelt 2003). In support to our result, we may consider that females ibex have a gregarious behaviour (Gross et al. 1995), as other Caprinae species (Asiatic ibex *Capra ibex sibirica*: Fox et al. 1992; Iberian ibex: Granados et al. 2001), whith groups composed by both barren and lactating females. Lactating females might compensate the higher costs by dedicating more time to grazing (Neuhaus and Ruckstuhl 2002), or even increasing digestive efficiency (Zimmerman et al. 2006, Monteith et al. 2014). In any case, although we believe that the effects of individual status should be further investigated with a larger individual sample, our results support the prediction (H4c) that such effects are in female ibexes much less pronounced than in females of other, non-gregarious species.

Table 1. Solutions of the fixed effects retained by the most parsimonious linear mixed models in summer and winter at a weekly scale.

	HR					CA				
Summer	l.s. estimate	SE	DF	t	P	l.s. estimate	SE	DF	t	P
Intercept	3.429	0.237	214	14.482	<0.001	0.850	0.104	218	8.164	<0.001
Subadult *vs* Adult	-1.602	0.372	214	-4.311	<0.001	--	--	--	--	--
Daylight	0.275	0.068	214	4.047	<0.001	0.310	0.077	218	4.007	<0.001
NDVI Study area	0.273	0.078	214	3.513	<0.001	0.561	0.079	218	7.148	<0.001
NDVI polygon	-0.316	0.090	214	-3.514	<0.001	--	--	--	--	--
Slope	-0.432	0.082	214	-5.250	<0.001	-0.267	0.080	218	-3.307	<0.01
Winter										
Intercept	1.612	0.085	423	18.95	<0.001	-1.213	0.103	429	-11.77	<0.001
Daylight	0.485	0.051	423	9.56	<0.001	0.459	0.050	429	9.18	<0.001
Temperature	--	--	--	--	--	0.530	0.053	429	10.03	<0.001
Slope	-0.336	0.065	423	-5.18	<0.001	--	--	--	--	--
Snow (stochastic)	-0.372	0.054	423	-6.93	<0.001	-0.406	0.058	429	-7.03	<0.001

Table 2. Solutions of the fixed effects retained by most parsimonious linear mixed models in summer and winter seasons at a monthly scale

	HR					CA				
Summer	l.s. estimate	SE	DF	t	P	l.s. estimate	SE	DF	t	P
Intercept	4.174	0.111	48	37.57	<0.001	2.076	0.114	48	18.234	<0.001
Daylight	0.312	0.093	48	3.36	<0.01	0.239	0.106	48	2.25	<0.05
Vegetation *vs* Scree-rocks	-0.841	0.373	48	-2.25	<0.05	-1.195	0.339	48	-3.528	<0.001
Slope	-0.385	0.097	48	<0.001	<0.01	-0.368	0.0768	48	-4.80	<0.001
Winter										
Intercept	3.400	0.090	79	37.75	<0.001	0.894	0.134	79	6.673	<0.001
Subadult *vs* Adult	--	--	--	--	--	0.610	0.248	79	2.455	<0.05
Temperature (absolute)	0.153	0.174	79	8.758	<0.001	0.251	0.018	79	13.88	<0.001
Slope	-0.321	0.074	79	-4.349	<0.001	--	--	--	--	--
Snow (stochastic)	-0.189	0.067	79	-2.842	<0.01	--	--	--	--	--
Precipitations (stochastic)	--	--	--	--	--	-0.247	0.079	79	-3.132	<0.01

Figure 1: smoothing splines of week and month on weekly and monthly HR and CA.

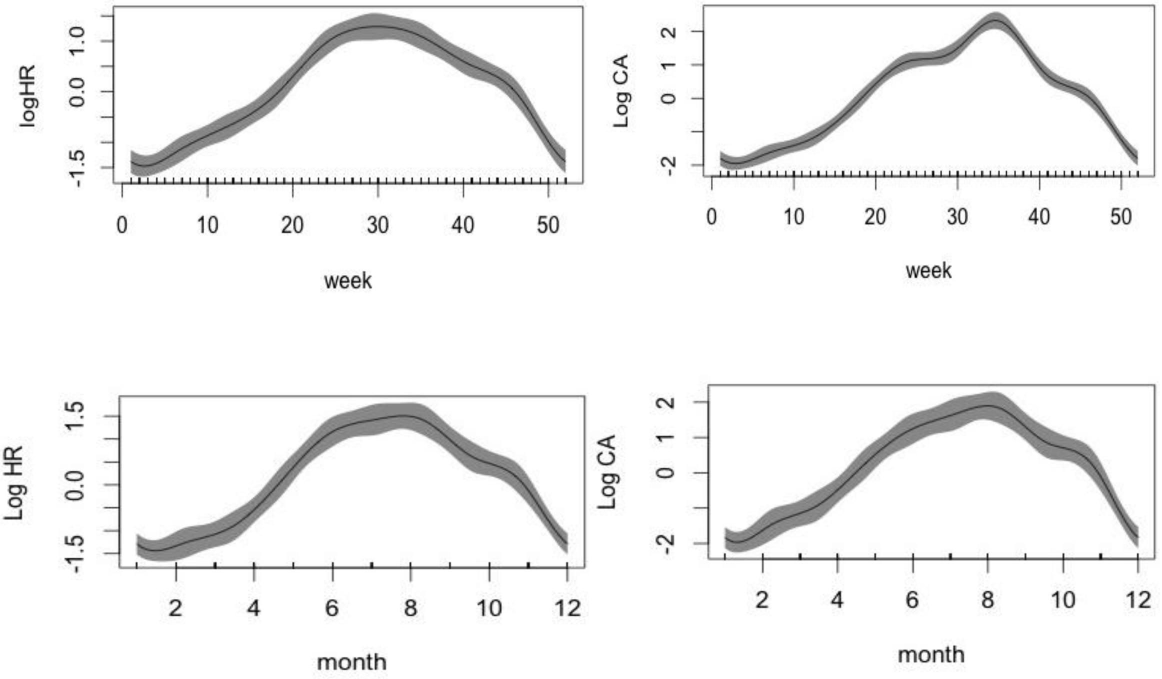
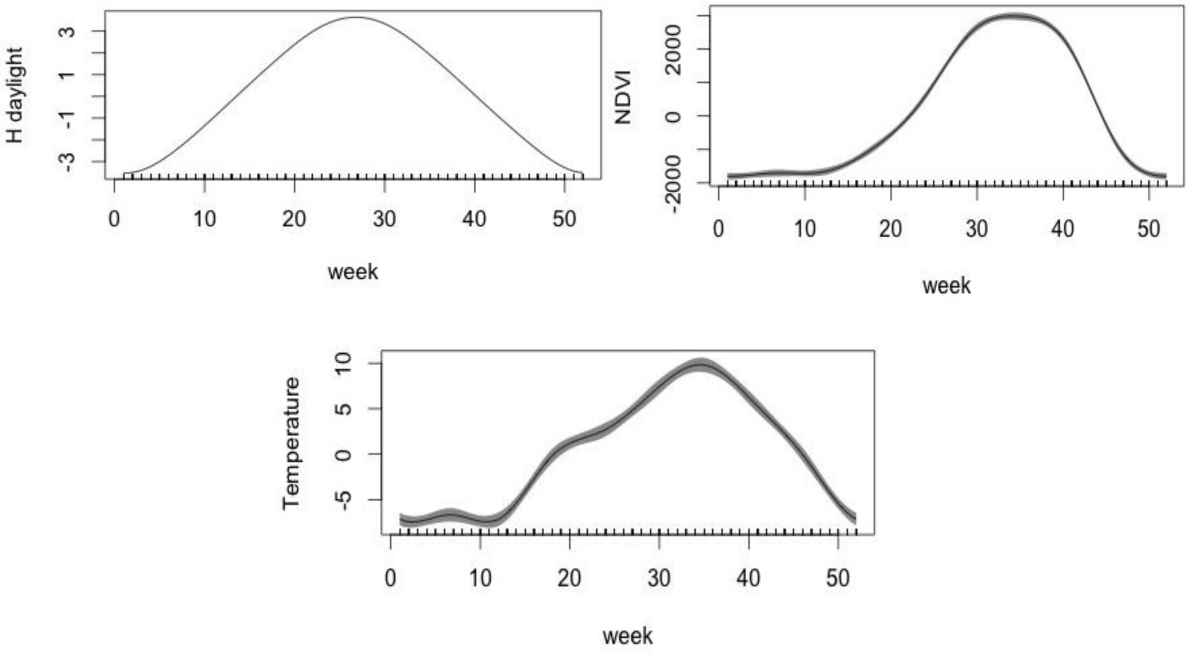


Figure 2: smoothing spline of week on daylight, NDVI of study area, and temperature (absolute)



Appendix table I: correlations between covariate variables in summer at a weekly temporal scale.

	Daylight	Temperature (absolute)	Temperature (stochastic)	Precipitation (stochastic)	Slope	NDVI Study area	NDVI polygon
Daylight		-0.056	-0.011	-0.013	0.097	-0.160	-0.165
Temperature (absolute)			**0.682**	-0.093	-0.100	0.620	0.170
Temperature (stochastic)				-0.165	0.061	0.182	0.023
Precipitation (stochastic)					-0.019	0.170	0.183
Slope						-0.212	-0.047
NDVI Study area							0.407

Appendix table II: correlations between covariate variables in winter at a weekly temporal scale

	Daylight	Temperature (absloute)	Slope	Snow depth (stochastic)	Temperarture (stochastic)	Precipitation (Stochastic)	NDVI Study area
Daylight		0.054	-0.166	-0.028	-0.025	0.007	**0.473**
Temperature (absolute)			0.023	-0.171	-0.029	0.074	-0.005
Slope				0.085	0.021	0.060	-0.307
Snow (stochastic)					**-0.460**	**0.455**	-0.308
Temperature (stochastic)						-0.322	0.177
Precipitation (stochastic)							-0.066

Appendix table III: correlations between covariate variables in summer at a monthly temporal scale.

	Daylight	Temperature	NDVI study area	Temprerature (stochastic)	Precipitaton (stochastic)	Slope
Daylight		0.014	-0.327	-0.010	-0.001	-0.081
Temperature (absolute)			**0.801**	**0.603**	-0.054	-0.110
NDVI study area				0.319	0.065	-0.048
NDVI polygon				0.234	0.196	-0.273
Temperature (stochastic)					-0.153	0.029
Precipitation (stochastic)						-0.002

Appendix table IV: correlations between covariate variables in winter at a monthly temporal scale

	Daylight	Temperature (absolute)	NDVI study area	Temperature (stochtic)	Precipitation (stochastic)	Snow	Slope
Daylight		**0.500**	0.230	-0.245	-0.036	-0.068	-0.180
Temperature (absolute)			**0.680**	0.321	-0.100	-0.334	**-0.425**
NDVI study area				0.203	-0.089	-0.356	**-0.458**
Temperature (stochastic)					-0.178	**-0.456**	-0.090
Precipitation (stochastic)						0.615	0.099
Snow (stochastic)							0.119

Appendix table V: model selection for summer weekly HR and CA

		Kid	Age Class	Daylight absolute	NDVI Study area	Temperature absolute	Prevalent Land Cover	NDVI HR	slope	Temperature stochastic	Precipitation stochastic	AIC	Δ AIC
Home range	1	X	X	X	X	--	X	X	X	X	X	725.21	14.54
	2	X	X	X	--	X	X	X	X	--	X	726.51	15.84
	3	X	X	X	X	--	X	X	X	--	X	720.07	9.4
	4	--	X	X	X	--	X	X	X	--	--	713.19	2.52
	5	**--**	**X**	**X**	**X**		**--**	**X**	**X**	**--**	**--**	**710.67**	**0**
	6	--	--	X	X		--	X	X	--	--	720.86	10.19
	7	--	--	X	X		--	X	--	--	--	735.34	24.67
	8	--	--	X	X		--	--	--	--	--	746.74	36.07
	9	--	--	X	--		--	--	--	--	--	750.93	40.26
	Null											759.77	49.1
Core area	1	X	X	X	X	--	X	X	X	X	X	783.56	18.65
	2	X	X	X	--	X	X	X	X	--	X	792.67	27.76
	3	X	X	X	X	--	X	X	X	--	X	779.31	14.4
	4	X	X	X	X	--	X	--	X	--	X	774.58	9.67
	5	X	--	X	X	--	X	--	X	--	X	771.94	7.03
	6	X	--	X	X		--	--	X	--	X	768.90	3.99
	7	--	--	X	X	--	--	--	X	--	X	766.16	1.25
	8	**--**	**--**	**X**	**X**		**--**	**--**	**X**	**--**	**--**	**764.91**	**0**
	9	--	--	X	X		--	--	--	--	--	770.37	5.46
	10	--	--	X	--		--	--	--	--	--	816.59	46.22
	Null	--	--	X	--		--	--	--	--	--	818.05	53.14

Appendix table VI: model selection for winter weekly HR and CA

		Ag class	Prevalent Land Cover	Daylight absolute	Temperature absollute	NDVI Study area	slope	Snow stochastic	Temperature stochastic	Precipitation stochastic	AIC	Δ AIC
Home range	1	X	X	X	X	--	X	X	--	--	1331.71	5.03
	2	X	X	--	X	X	X	X	X	--	1368.03	41.35
	3	X	--	X	X	--	X	X	--	--	1329.84	3.16
	4	--	--	X	--	--	X	X	--	--	1330.76	4.08
	5	**--**	**--**	**X**	**--**	**--**	**X**	**X**	**--**	**--**	**1326.68**	**0**
	6	--	--	X	--	--	X	--	X	--	1368.33	41.65
	7	--	--	X	--	--	X	--	--	X	1370.16	43.48
	8	--	--	X	--	--	X	--	--	--	1366.30	39.62
	9	--	--	X	--	--	--	--	--	--	1391.46	64.78
	Null	--	--	--		--	--	--	--	--	1476.69	150.01
Core area	1	X	X	X	X	--	X	X	--	--	1263.11	6.24
	2	X	X	--	X	X	X	X	--	--	1281.45	24.58
	3	X	--	X	X	--	X	X	--	--	1259.82	2.95
	4	--	--	X	X	--	X	X	--	--	1259.21	2.34
	5	**--**	**--**	**X**	**X**	**--**	**--**	**X**	**--**	**--**	**1256.87**	**0**
	6	--	--	X	X	--	--	--	X	--	1271.12	14.25
	7	--	--	X	X	--	--	--	--	X	1301.22	44.35
	8	--	--	X	X	--	--	--	--	--	1297.96	41.09
	9	--	--	X	--	--	--	--	--	--	1416.84	159.97
	Null	--	--	--	--	--	--	--	--	--	1557.18	300.31

Appendix table VII: model selection for monthly HR and CA in summer

		KId	Age Class	Daylight	Prevalent land cover	Slope	Absolute temperature	NDVI study area	NDVI polygon	Temperature stochastic	Precipitation stochastic	AIC	Δ AIC
Home ranges	1	X	X	X	X	X	X	--	--	--	X	121.97	12.23
	2	X	X	X	X	X	--	X	--	--	X	121.53	11.79
	3	X	X	X	X	X	--	--	X	--	X	121.27	11.53
	4	X	X	X	X	X	--	--	--	X	X	123.68	13.94
	5	--	X	X	X	X	X	--	--	--	X	117.91	8.17
	6	--	--	X	X	X	X	--	--	--	X	115.54	5.8
	7	--	--	X	X	X	X	--	--	--	--	112.94	3.2
	8	**--**	**--**	X	X	X	--	X	--	--	--	112.86	3.12
	9	--	--	X	X	X	--	--	X	--	--	112.79	3.05
	10	**--**	**--**	**X**	**X**	**X**	**--**	**--**	**--**	**--**	**--**	**109.74**	**0**
	11	--	--	X	X	--	--	--	--	--	--	118.33	8.59
	12	--	--	X	--	--	--	--	--	--	--	121.98	12.24
	Null	--	--	--	--	--	--	--	--	--	--	129.36	19.62
Core areas	1	X	X	X	X	X	X	--	--	--	X	141.64	14.84
	2	X	X	X	X	X	--	X	--	--	X	139.19	12.39
	3	X	X	X	X	X	--	--	X	--	X	140.66	13.86
	4	X	X	X	X	X	--	--	--	X	X	143.84	17.04
	5	--	X	X	X	X	--	X	--	--	X	135.22	8.42
	6	--	--	X	X	X	--	X	--	--	X	131.59	4.79
	7	--	--	X	X	X	--	X	--	--	--	126.95	-0.15
	10	**--**	**--**	**X**	**X**	**X**	**--**	**--**	**--**	**--**	**--**	**126.80**	**0**
	11	--	--	X	X	--	--	--	--	--	--	141.29	14.49
	12	--	--	X	--	--	--	--	--	--	--	145.61	18.81
	Null	--	--	--	--	--	--	--	--	--	--	146.28	19.48

Appendix table VIII: model selection for monthy HR and CA in winter

		Age Class	Daylight	Prevalent land cover	Absolute temperature	NDVI study area	Slope	Snow stochastic	Temperatue stochstic	Precipitations stochstic	AIC	Δ AIC
Home range	1	X	X	X	--	--	X	X	--	--	211.91	26.58
	2	X	--	X	X	--	X	X	--	--	189.58	4.25
	3	X	--	X	--	X	X	X	--	--	222.23	36.9
	4	X	--	X	X	--	X	--	X	--	226.53	41.2
	5	X	--	X	X	--	X	--	--	X	225.97	40.64
	6	--	--	X	X	--	X	X	**--**	**--**	189.02	3.69
	7	**--**	**--**	**--**	**X**	**--**	**X**	**X**	**--**	**--**	**185.33**	**0**
	8	--	--	--	X	--	X	--	--	--	187.39	2.06
	9	--	--	--	X	--	--	--	--	--	197.70	12.37
	Null	--	--	--	--	--	--	--	--	--	276.40	91.07
Core area	1	X	X	X	--	--	X	X	--	--	272.15	50.11
	2	X	--	X	X	--	X	X	--	--	230.12	8.08
	3	X	--	X	--	X	X	X	--	--	283.64	61.6
	4	X	--	X	X	--	X	--	X	--	235.65	13.61
	5	X	--	X	X	--	X	--	--	X	228.03	5.99
	6	X	--	--	X	--	X	--	--	X	224.13	**2.09**
	7	**X**	**--**	**--**	**X**	**--**	**--**	**--**	**--**	**X**	**222.04**	0
	8	--	--	--	X	--	--	--	--	X	224.33	2.29
	9	--	--	--	X	--	--	--	--	--	228.57	6.53
	Null	--	--	--	--	--	--	--	--	--	318.16	96.12

Supplementary material: Identification of biological seasons

We used data from 12 females for a total of 87.795 hourly locations. We associated each location with the corresponding elevation (m), slope (°), prevalent land use category (forest, grasslands, scree+rocks), activity index (calculated as the average of the XY activity values from the accelerometer embedded to the GPS collar in the 10 minutes immediately preceding and following the scheduled time for the location), and distance (m) from the previous location (distance was calculated only between fixes separated by 1 h).

We then calculated for each Julian date the average values of elevation, slope, activity index and distance, and the frequency of each land use category (across individuals and years). Julian dates were then grouped into "seasons" using a clustering procedure (proc cluster, SAS© 9.2)

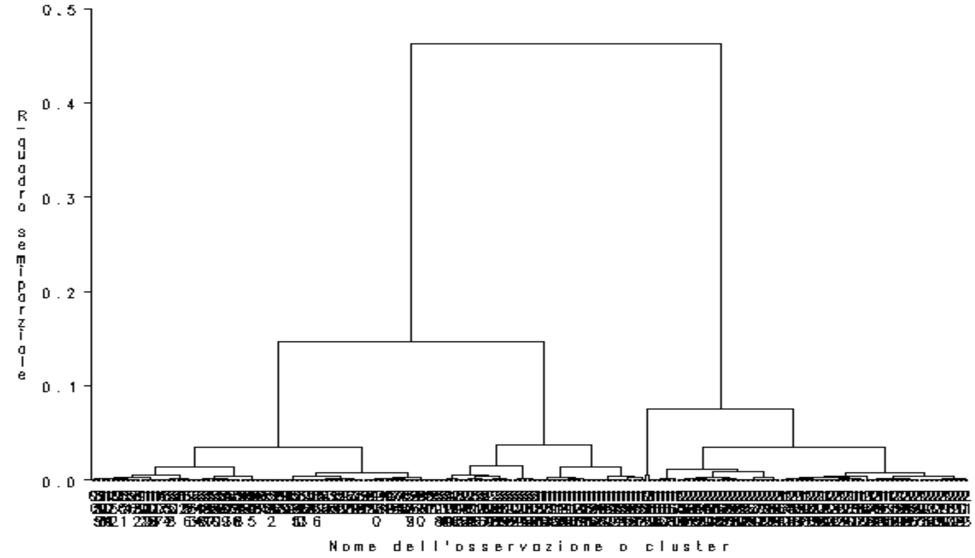


Figure A1: Results from the clustering procedure to identify the experienced seasons of the female ibex in the Marmolada Massif.

The results supported the presence of two or three clusters (Figure A1). With two clusters, Julian dates were divided into a prolonged winter of around 225 days and a short summer lasting around 140 days (Figure A2).

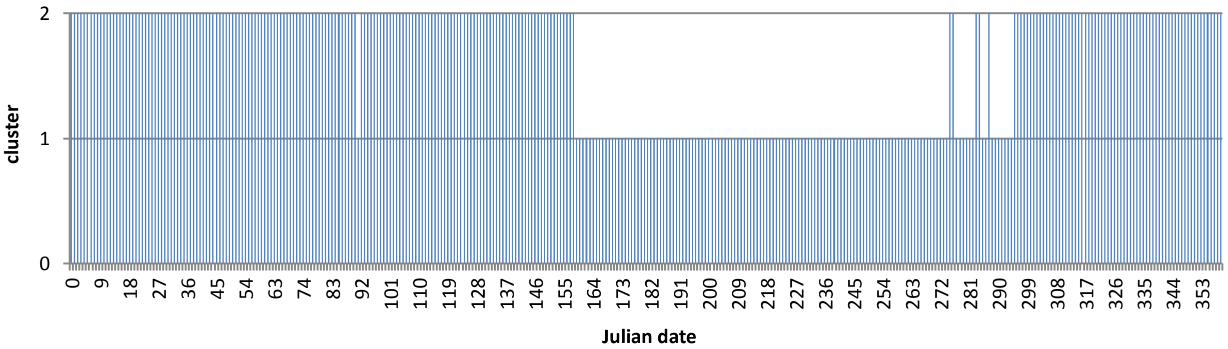


Figure A2. Assignment of Julian dates (0 = December 21st) to clusters 1 (summer) or 2 (winter).

As respect to summer, winter was characterized by lower elevations, smaller use of scree and rocks, higher use of grasslands and forest, lower activity and speed index values (Table A1). Only slope did not differ between clusters.

	Winter		Summer	
	Mean	SD	Mean	SD
Elevation (m)	2097	74	2380	68
Slope (°)	47.3	2.5	44.5	1.8
Grasslands (%)	14.3	7.0	7.7	4.3
Forest (%)	29.5	11.6	5.9	4.3
Screes + rocks (%)	55.0	10.7	85.5	7.5
Activity index	21.9	8.0	35.6	7.2
Speed index (m/h)	61.5	51.0	125.7	62.9

Table A1. Profiles of the two clusters (mean ± SD) for the considered variables.

With three clusters, 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 autumn) (Figure A3).

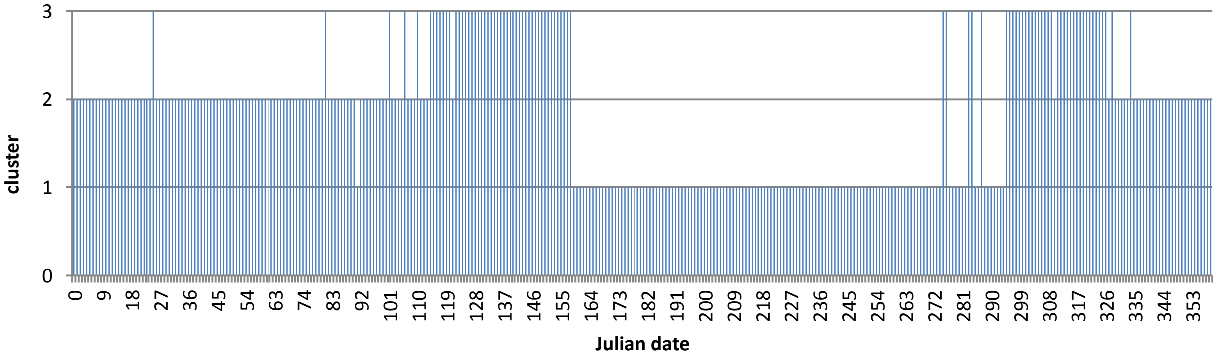


Figure A3. Assignment of Julian dates (0 = December 21st) to clusters 1 (summer), 2 (winter) and 3 (winter-summer and summer-winter transition

In the case of three clusters, the winter cluster was characterized, as respect to the summer cluster, by lower elevations and higher slopes, a similar use of grasslands, a much higher use of forest and a much lower use of screes and rocks, and by clearly lower speed and activity index values (Table A2). 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 (Table A2)

	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

Table 2. Profiles of the three clusters (mean ± SD) for the considered variables

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CHAPTER 3

VALIDATION OF A NON-INVASIVE TECHNIQUE FOR ESTIMATING DIET QUALITY IN AN ALPINE UNGULATE

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INTRODUCTION

Improving the knowledge of foraging strategies of herbivore species is a fundamental basis to understand the individual performance and reproduction success, which in turn drive the populations dynamics (Hernandez and Laundrè 2005, Cebrian et al. 2008). Hence, spatiotemporal variation of forage quality is an essential indicator for behavioural patterns in ungulate species living in free-predation systems. However, developing a useful tool for determining diet quality is not a simple matter, especially in high mountain environments where sampling plant species at a broad spatial scale is difficult and may not reflect the real composition of animal diet.

Faecal material from wild ruminants encompasses undigested material, such as in particular lignin, suberin, cutin and proteins, plus secondary metabolic excretions and microbial cells (Robbins 1983). Sampling faeces is possible over large temporal and spatial scales without human intervention on animal welfare. Therefore, assessing diet quality of free-ranging animals from faecal analysis has become a widespread technique in wildlife research (Wrench et al. 1997, Homolka and Heroldovà 2001, Showers et al. 2006, Verheyden et al. 2011). In particular, faecal nitrogen (FN) represents an indicator of the relationship between diet properties and vegetation characteristics, due to its correlation with plant digestibility and with dietary proteins (Holechek et al. 1982). After the ingestion of the plants, ruminants are capable to metabolize endogenous and exogenous sources of N through the fermentative action of anaerobic microbes located in the rumen (Van Soest 1994), and the subsequent digestive processes lead to a proportional quantity of metabolic N excreted with the faeces (Wehausen 1995). Higher quality and quantity of forage intakes increase fermentation rates (Berteaux et al. 1998) and microbial activity (Hanley 1982), which ultimately turns into high levels of FN (Schwarm et al. 2009). Although it has been demonstrated that the relation between FN and dietary N may be affected by the presence of tannins in the plants consumed, the problem appears stronger for browsers and mixed feeders than for grazers (Wofford et al. 1985, Robbins et al. 1987). Other faecal constituents such as neutral detergent fibre (NDF), acid detergent fibre (ADF) or ash (AIA) are indexes of low digestibility compounds normally negatively correlated with protein, and might help to predict nutritional status of ruminants, but they seem to have a role more for integrating N results than as single indicators (Wofford 1985).

Chemical analysis implies high labour and laboratory costs and requires samples destruction. Therefore, other indirect methods have been developed and improved over the last years to identify chemical compound in organic matrices. Near infrared spectroscopy (NIRS) consists in the projection of a known quantity of NIR light onto organic substances and the recording of the reflectance or transmittance values obtained from such substances, which depend on the characteristics and richness of chemical bonds. Calibration equations can be obtained relating the spectral properties of a large and diverse set of samples to the results obtained by a reference laboratory method (Stuth et al. 2003). Then, NIRS can be used to routinely estimate chemical compounds, and has been recognized since 1970s as an optimal resource to reduce,labour, sample processing and costs inputs in the assessments of diets in livestock using faecal samples (see Roberts et al. 2004 for a review). Lyons and Stuth (1992) were the pioneers in the application of NIRS technology to predict diet quality in free-ranging animals. Due to the differences on diet selectivity and digestive physiology, one faecal NIRS equation may not be applicable from one species to another, and hence the validation of calibration models is an essential step to predict accurate conclusions of diet quality (Leite and Stuth 1995).

Studies on several wild ungulate species also recognized that fluctuations in FN estimated using fecal NIRS analysis follow the seasonal variation of the quality of vegetation (bighorn sheep *Ovis canadensis*: Blanchard et al 2003; moose *Alces alces*: Leslie et al. 1989; black-tailed deer *Odocoileus hemionus columbianus*: Leslie and Starkey 1985, 1987; Red deer *Cervus elaphus*: Kamler and Homolka 2005; roe deer *Capreolus capreolus*: Kamler and Homolka 2005 and Verheyden et al. 2011). To identify the relationship between FN and plant phenology, or quality of diets, researchers have commonly used plant samples collections or feeding trials that require remarkable effort, time and high costs (Verheyden et al.2011, Showers et al 2006). The Normalized Difference Vegetation Index (NDVI; Tucker

1986) is a remotely global index of vegetation productivity measured from the red/near-infrared ratio of growing vegetation reflectance in the electromagnetic spectrum (Jackson and Huete 1991), and represents an attractive opportunity to monitor vegetation quality and quantity dynamics without the need of analysing vegetation characteristics directly from field-collected samples. In addition, satellite imagery is a proxy of vegetation dynamics across wide geographic landscapes and over a long time scales, in this improving the opportunities of understanding the interactions between trophic resources and behavioural patterns of free-ranging animals. Although NDVI has been used in numerous studies across different environmental condition (see Pettorelli et al. 2005, 2011 for a review), the validation of its biological significance in terms of plant productivity or vegetation dynamics is still a work in progress (Steltzer and Welker 2006, Ryan et al. 2012, Borowik et al. 2013). However, the combination of faecal NIRS analysis for estimating diet quality and NDVI greenness indexes of vegetation may provide new insights into animal space use and selection of forage resources (Showers et al 2006, Ryan et al. 2012). Hamel et al (2009) demonstrated in two alpine ungulate populations (mountain goats *Oreamnos americanus* and bighorn sheep) that NDVI was a powerful predictor of temporal variation in the timing of spring green-up and dynamics in diet quality in alpine habitats, which has an important effect on the early access to high-quality vegetation and hence on animals life-history traits and habitat use.

In this study, we first compared two different NIRS instruments, one based on reflectance of a broad range of wavelengths, and the other based on transmittance of a narrower range of wavelengths, for the prediction of N and NDF components of male and female ibex faeces. Then we seeked insights into the dietary quality patterns during summer of male and female ibexes, and the effect of variations in NDVI on such patterns. The Alpine ibex is a large ungulate inhabiting a highly seasonal environment, characterized by severe and prolonged winters and strongly fluctuations of forage resources. According with other studies (bighorn sheep: Portier et al. 1998; mountain goats: Cotè and Festa-Bianchet 2001) spring and summer are the critical seasons for reproduction success and offspring performance in mountain ecosystems, since vegetation availability is absent or extremely limited for the rest of the year because of the snow layer. We hypothesized (H1) that both sexes experimented a progressive decrease in the availability of good quality forage resources with the advancing of summer and through autumn, as in other mountain ungulates (Kamler and Homolka 2005, Parker et al. 2005, Verheyden et al. 2011), and expected a positive effect on diet quality of NDVI greenness index for both sexes (H2). We also wanted to assess whether FN suggested a better dietary quality in females than in males (H3), as the result of higher metabolic demands and feeding selectivity (Moen 1973, Barboza and Bowyer 2000, Zimmerman et al. 2006, Main 2008), and of lower relative feed intakes and retention times in the digestive tract as respect to the larger males (Robbins 1983, Leslie and Starkey 1985, Perez-Barberia et al. 2008 van Soest 1996).

MATERIALS AND METHODS

Study area

The study area is located in the highest group of the Dolomite mountains, the Marmolada massif, in the north-eastern Italian Alps (see Scillitani et al. 2012). It is characterized by a complex topography, which divides its landscape in two main categories: the north-western sides are represented by gentle slopes and shallow valleys while the eastern and southern sides are characterized by deep corridors, steep screes and rocks walls that reach in some cases 1000 m of height. The highest point is the Punta Penia peak (3.343 m a.s.l.), which is part of a group composed by several peaks that reach more than 2.500 m a.s.l. Vegetation varies along the altitudinal strata used by ibex. At the highest altitudes (above 1.900 m), it is mainly represented by alpine grasslands composed by different herbaceous species (*Sesleria varia, Carex sempervirens, Nardus stricta, Carex firma*) and scattered shrubs as mountain pine (*Pinus mugus*), hairy alpen rose (*Rhododendrum hirsutum*), willows

(*Salix sp.*), and green alder (*Alnus viridis*). Decreasing in altitude, woodlands composed mainly by Norway spruce and larch (*Larix decidua*) predominate.

Faecal samples collection and chemical analysis

A total of 154 faecal samples were collected from July to November 2013 throughout all the area occupied by the population. We located ibex groups, recorded the age-sex composition, and, when groups moved, collected fresh faecal pellets by gloved hand. Faecal samples were geo-referenced using a GPS receiver (Garmin eTrex® 10) and assigned to female or male categories according to differences in size and texture of the pellets and the position of the pellet group as respect to that of the different individuals observed. The faecal samples were refrigerated at 4° C for a maximum of 48 hours until the final storage at -20°C. Before chemical and NIRS analysis, samples were air-dried at 60 °C until constant weight and then ground. A sub sample of 154 faeces were analysed for Dry Matter (DM) (# 934.01; AOAC, 2003), Faecal Nitrogen (N) (# 976.05; AOAC, 2003), and Neutral Detergent Fibre (NDF), expressed inclusive of residual ash, which was determined (Mertens, 2002) in the neutral detergent solution using an Ankom220 Fibre Analyzer (Ankom Technology® Corporation, Macedon, NY).

NIRS Procedures

Spectral Acquisition

The spectra were collected using two instruments: LabSpec2500 (Qualityspec Pro, ASD Inc., Boulder, CO) and FoodScan (Foss Electric A/S, Hillerød, Denmark). The LabSpec2500 works in reflectance over the spectral range of 350 to 1830 nm at 1 nm interval, including the Visible and the Near Infrared radiation. Three spectra for each samples were recorded and averaged prior of the data analysis, and stored as absorbance (A=log(1/R); A is the absorbance and R the reflectance). The

FoodScan works in transmittance, scanning the region between 850 and 1050 nm with a 2 nm interval. The spectrum of each sample was the average of 16 scans and was recorded as absorbance (A=log(1/T); T is the transmittance).

Data Analysis and Chemometric Models

- *Pre editing of data, spectra and outlier detection*

All the data analysis and the chemometric models were conducted in the R environment (R Core Team 2013). On the 154 samples used for the calibrations, N and NDF values higher or lower than three standard deviations were excluded as outliers. In order to detect outliers in the spectra, the absorbance values of each wave in the spectra were centered and standardized to a null mean and a unit sample variance; next, the Mahalanobis distances were calculated and observations with a Mahalanobis distance greater than three times the standard deviation were discarded as outliers. The spectra were then analyzed across the whole interval of each instrument (350-1830 nm for the LabSpec2500, and 850-1050 nm for the FoodScan) and using the LabSpec spectra in the same range of the FoodScan (850-1050 nm), "LabSpec-FS", in order to compare the results of the two instruments in the same spectral range conditions.

- *Statistical analysis*

The model used was based on the Bayesian analysis, commonly used for genomic selection. Separate models were fitted for each of the traits, and the model used was Bayes B (Meuwissen et al., 2001). The statistical model for a generic phenotype (y_i; i=1,..., n) is described. Phenotypes were regressed on standardized spectra covariates using the linear model:

$$y_i = \beta_0 + \sum_{j=1}^{1,060} x_{ij}\beta_j + \varepsilon_i$$

where β_0 is an intercept, $\{x_{ij}\}$ are standardized FTIR spectra-derived wavelengths data ($j = 1, \ldots, 1{,}481$), β_j are the effects of each of the wavelengths and ε_i are model residuals assumed to be *iid* (independent and identically distributed) normal distribution centered at zero with variance σ_ε^2. Given the above assumption, the conditional distribution of the data given effects and variance parameters is:

$$P(\boldsymbol{y}|\boldsymbol{\theta}) = \prod_{i=1}^{n} N(\mu_i, \sigma_\varepsilon^2),$$

where $\boldsymbol{\theta}$ represents the collection of model parameters $\boldsymbol{\theta} = \{\beta_0, \boldsymbol{\beta}, \sigma_\varepsilon^2\}$, $N(\mu_i, \sigma_\varepsilon^2)$ is a normal distribution centered at $\mu_i = \beta_0 + \sum_{j=1}^{1{,}060} x_{ij}\beta_j$ and with variance σ_ε^2, and $\boldsymbol{\beta} = \{\beta_j\}$ is a vector containing the effects of the individual spectra-derived wavelengths. Specification of the Bayesian model is completed by assigning a prior distribution to the unknowns, $\boldsymbol{\theta}$. In the Bayesian model considered here, the prior density was as follows:

$$p(\boldsymbol{\theta}) = N(\beta_0|0{,}1 \times 10^5)\chi^{-2}(\sigma_\varepsilon^2|df_\varepsilon, S_\varepsilon)\left\{\prod_{j=1}^{1{,}060} p(\beta_j|\Omega)\right\}p(\Omega)$$

The intercept is assigned a normal prior with a very large variance, which amounts to treating the intercept as a "fixed" effect, the residual variance is assigned a scaled-inverse chi-square density with degree of freedom and scale parameters df_ε and S_ε, respectively, and the effects of wavelengths are assigned IID priors, $p(\beta_j|\Omega)$, indexed by a set of hyper-parameters, Ω, which are also treated as random. In Bayes B the prior density assigned to the effects is a mixture of a poit of mass at zero and a scaled-t density, that is $(\beta_j|\Omega) \overset{iid}{\sim} \pi \times t(\beta_j|df_\beta, S_\beta) + (1-\pi) \times 1(\beta_j = 0)$; this density is indexed by three hyperparameters $\{\pi, df_\beta, S_\beta\}$, therefore, a-priori, with probability π, β_j is drawn from the t-density and with probability $(1-\pi)$ $\beta_j = 0$. We set $df_\beta = 5$ and the other hyperparameters were treated as random, specifically, $S_\beta \sim Gamma(S_\beta|rate, shape)$ and $\pi \sim Beta(\pi|shape_1, shape_2)$. The above models have high-order hyperparameters (df_ε, S_ε, $df_\beta, rate, shape, shape_1, shape_2$), that were specified using built-in BGLR rules, selecting default values for this unknown and are fully explained in Pérez and de los Campos (2014). In all the Bayesian models, inferences were based on a total of 30,000 samples collected after discarding the first 10,000 samples. The described models were implemented in the BGLR package (de los Campos and Pérez-Rodriguez, 2014).

Predictive Ability

For the assessment of the predictive ability of the calibration equations, we adopted a validation technique based on a training-testing procedure, replicated 15 times. In each replica, the main data set was split into a training (TRN) and a testing (TST) subset. The training subset was used to fit the model and to develop the calibration equation for the prediction of individual traits in the testing subset as validation. For the TRN and TST partition we sampled randomly groups and assigned all samples in the selected group to the TST subset, we added groups until we had at least 20% samples in the TST subset. The remaining groups (records) were assigned to the TRN subset. The observations included in the TST set were independent from those used to build the calibration equations. The TRN-TST procedure was repeated 15 times, and this guaranteed that the records of a given group were in either the TRN or the TST subset, allowing to assess the 'across-group' predictive power of the calibration equation. To measure the prediction accuracy and to compare the calibration and validation results, we used the square of the correlation between predicted and measured traits in the TRN (R^2_{TRN}) and in the TST (R^2_{VAL}), also the squared root of the mean squared prediction error in the TST ($RMSE_{VAL}$) was calculated.

Prediction equations

Generally, the higher is the number of samples used for the calibration and the better is the accuracy. Thus, we used the entire data set (154 samples) in the calibration for the final prediction equations. This procedure does not allow to test directly the accuracy of the prediction equations using an external set of data, but an indication can be obtained with the TRN-TST procedure explained above. Therefore, we calculated the square of the correlation of calibration (R^2_{CAL}) between the predicted and the measured traits, and the squared root of the mean squared prediction error in calibration ($RMSE_{CAL}$). In addition, we tested then whether the intercept and slopes of the regressions of Chemical on each of the three NIRS methods differed from 0.

Vegetation NDVI index of greenness

We used remotely sensed data from MODIS (Moderate Resolution Imaging Spectroradiometer, NASA TERRA satellites) that provide a useful tool to monitor the photosynthetic activity of the vegetation (Justice et al., 1998). MOD13Q1 VI products have a high temporal (16-day compositing periods) and spatial (250x250 m) resolution with high quality of NDVI data (Huete et al. 2002). To reduce temporal gaps during the collecting period, the data were re-sampled to 7-days intervals: we used images from MODIS from 26 June 2013 to 17 Nov 2013 (10 satellite images) and then calculated the mean value of each pixel between two successive images using ArcGis 10.1 (ESRI®). The total number of NDVI images was 20, with a weekly temporal resolution. To assign to each faecal sample a corresponding NDVI value, we calculated, using ArcGis 10.1, a buffer around its location with a diameter varying from 150m to 350m according to the month. These buffers were aimed at approximating the daily areas used by ibex, and were calculated on the basis of GPS-GSM monitoring data (see chapter 1). In order to exclude from the buffers the areas unsuitable for ibex, we then intersected the buffers with all the GPS-GSM location dataset and eliminated the portions of each buffer where we had never received any GPS position during the monitoring period. Finally, we measured the average value of the NDVI pixels inside each clipped buffer within the corresponding week.

Statistical analysis of chemical and predicted values

We used 112 samples from females and 38 samples from males. We first tested for heterodasticity of variances between NIRS methods. For this purpose, we run mixed linear models using PROC MIXED of SAS (SAS Institute Inc., Cary, NC) on FN with the fixed factors method, category, their interaction and Julian date as covariate, and the random factor "sample id" within category. We then extracted the residuals, converted the negative into positive values, and subjected them to a Levene's test (Schultz 1985) with a GLM that included the method as a factor.

Since the Levene's test had indicated that variances between NIRS methods were heteroscedastic (N: $F_{3,588} = 15.1$, $P < 0.001$; NDF: $F_{3,588} = 52.02$; $P < 0.001$), to assess the ability of each method to identify biological patterns, we run separate mixed linear models for each method with the fixed factors category, Julian date and NDVI as covariates, and the random factor group within category. Julian date and NDVI were positively correlated, but the proportion of variability non-explained by the correlation was not remarkable ($n = 30$; $r = 0.38$; $P < 0.05$). We started with the most complex model and then removed non-significant terms. We compared models based on AICC (Bozdogan 1987).

RESULTS

NIRS Prediction ability

To assess the predictive ability with the Bayesian analysis as chemometric model, an external validation based on a training-testing procedure repeated 15 times for was used for both N and NDF The results obtained from the calibrations are reported in table 1. The best accuracies in calibration (R^2_{TRN}) for both N and NDF were obtained with Labspec. A very poor prediction accuracy was obtained with FoodScan. When Labspec spectra within the same wavelength range than Foodscan were used, prediction accuracy increased only slightly.

Prediction equation

To calculate prediction equations, the entire data set was used in the calibrations. The determination coefficient between the predicted and measured values (R^2_{CAL}), and the squared root of the mean squared prediction error ($RMSE_{CAL}$) are shown in table 2, together with the descriptive statistics of predicted and chemically analysed values.

The R^2_{CAL} and the $RMSE_{CAL}$ values for the three methods suggested that prediction equations followed the trends of the prediction accuracies in table 2. Predicted values of FN and FNDF showed similar averages for all methods, but only Labspec was able to detect a variability similar to that of chemical

The analysis of regression of N and NDF from chemical analysis on N and NDF from NIR methods is given in table 3. For N, with all the three methods neither the intercept differed significantly from 0 nor the b estimate differed significantly from 1. However, LabSpec tended to perform better than Foodscan and LabSpec-FS. For NDF, with FoodScan the intercept was significantly different from 0 and the b coefficient from 1, while for Labspec and Labspec-FS there were no significant differences. However, LabSpec performed again better than Labspec-FS.

Comparison of biological patterns

Faecal Nitrogen

The single mixed linear model analyses of FN confirmed a different ability of NIRS methods to identify biological patterns. With Chemical and LabSpec, the two competing best models (Δ AIC < 2) retained the effects of category and Julian date, while with FoodScan and LabSpec-FS the best model was clearly that including only the Julian date (Table 4). NDVI was excluded by all selected models.

To allow a better comparison of the results given by the three methods, we present in table 3 the solutions for the fixed effects of the models that included both category and Julian date. With chemical analysis data, category had a significant effect ($F_{1,33}$ = 4.31; P<0.05), with females having higher FN contents than males (Table 5). Labspec data showed a similar tendency (table 3), although only close to statistical significance ($F_{1,33}$ = 2.58; P = 0.118). Foosdcan ($F_{1,33}$ = 0.75; P = 0.392) and Labspec-FS ($F_{1,33}$ = 0.41; P = 0.528) data were clearly unable to differentiate between categories. For all methods Julian date had a significant effect on FN (Chemical: $F_{1,112}$ = 46.31, P <0.001; Labspec: $F_{1,112}$ = 46.44, P <0.001; Foodscan: $F_{1,112}$ = 15.35, P <0.001; Labspec-FS: $F_{1,112}$ = 5.37, P <0.05), with a negative trend (table 3). However, the decline of FN with increasing Julian date was much steeper for Chemical and LabSpec data than for those from the other two methods (Figure 1).

Faecal NDF

In accord with the results for FN, the best linear mixed models with Chemical and LabSpec data were those including the effects of category and Julian date, (Table 6). With FoodScan and LabSpec-FS data, the most parsimonious among competing models (Δ AICC < 2) included only Julian date. The NDVI greenness index was excluded by all the selected models.

The effect of category was almost significant ($F_{1,33}$ = 2.53, P = 0.121; Labspec: $F_{1,33}$ = 2.32, P = 0.137) with Chemical and Labspec data, with males having tendentially higher faecal NDF than females, but with the other two methods was far from statistical significance (Foodscan: $F_{1,33}$ = 0.25, P = 0.623; Labspec-FS: $F_{1,33}$ = 0.89, P = 0.352) with data from the other two methods (Table 7). All methods, with the exception of Labspec-FS, identified a positive trend of NDF with increasing Julian date (Chemical: $F_{1,\ 112}$ = 16.60, P <0.001; Labspec: $F_{1,\ 112}$ = 37.02, P <0.001; Labspec-FS: $F_{1,\ 112}$ = 0.01, P = =.918). However, only Labspec was able to produce intercept and slope values similar to those of Chemical (Figure 2).

DISCUSSION

Predictive ability of Vis-NIR and NIR instruments

The analysis of faecal N or other metabolites from free-ranging herbivores is a powerful tool to predict the quality of forage intakes and to improve knowledge on behavioural strategies of the species (Hernández and Laundré 2005, Osborn and Ginnett 2001, Moço et al. 2013, Lendrum et al. 2014), focusing mainly on the use of the near infrared (NIR) spectroscopy as a useful and non-invasive technique (Kamler and Homolka 2011, Gálvez-Cerón et al. 2013, Jean et al. 2014). A large variety of NIR instruments are commonly used for the analysis of milk, cheese and meat (Berzaghi and Riovanto 2010). The most important differences in the functional principles of NIR are the spectral range at which each instrument works and the scanning technique. The most commonly used instruments include the visible and the near infrared absorption bands, in spectral ranges varying between 350 to 2,500 nm. Scanning techniques may rely, briefly, on the recording of the transmittance through the sample or, in alternative, the reflectance by the sample surface of the NIR radiation (Aernouts et al. 2011). The choice of one or another technique depends mainly on the nature and the pre-treatments of the samples (e.g., fresh or dried, entire or minced) (De Marchi et al. 2013).

Our results indicate that the accuracy of prediction of faecal N and NDF depends more on the wavelength range than on the scanning technique of the instrument used. The LabSpec instrument, which works in reflectance from 350 to 1830 nm at 1 nm interval, produced reliable prediction equations, while the FoodScan, which is restricted at 850 to 1050 nm with a 2 nm interval, did not. When we used the Labspec spectra within 850-1050 nm, to compare scanning techniques within the same wavelength range, the accuracy of prediction increased slightly but remained unsatisfactory. In fact, in general the ability of prediction improves when spectral range is closer to infrared light (Leite and Stuth 1995, Cerón et al. 2013). FoodScan works in transmittance, which means that the result is the relation between the light that passed through the sample compared to the light that has not, and then it depends strongly on the sample thickness. This property leads to an important limitation since the available quantity of the samples is often very low when working with free-ranging herbivores. In general, accuracy of prediction with Labspec at 350-1050 nm was slightly lower than that obtained in other studies (Showers et al. 2006, Tolleson et al. 2007). One explanation is the chemometric procedure adopted, based on the Bayesian models and on the assessment of 'across-group' predictive power of our calibration equation, leading to a bit lower but more realistic results accounting for the group rather than individual patterns in gregarious species. Our predictions were also more accurate for N than for NDF, probably related to the strong C-N and N-H absorptions in the NIR region (Stuth et al. 2003, Galvez-Ceron 2013).

Biological patterns of FN and FNDF

In this study, we found a clear temporal trend and a difference between males and females in FN used to index dietary quality. These patterns were best described by chemically analysed FN, but were closely matched by Labspec predicted FN. As expected from the poor predictive ability, patterns obtained with data from Foodscan and Labspec-FS were unable to approximate the patterns described by chemical analyses or Labspec. This suggests that, especially if longer time series are used with larger sample sizes, NIRs prediction can be as accurate as chemically analysed values in identifying biologically meaningful patterns in FN. The FNDF values followed opposite patterns to those of FN, which is sensible since this component indicates the low-digestible compounds of the vegetable cell-walls, and has been observed in other studies (Jianzhang et al. 1999). However, chemically analysed FNDF values did not show the same ability as FN to pinpoint differences between males and females, and Labspec predicted values were less accurate than those of FN. Therefore, while our results encourage the use of FNDF to complement FN to index of dietary quality, they also confirm that FN is a better indicator.

As we predicted (H1), FN decreased and FNDF increased from June to November. Similar trends in diet quality have been observed in other studies (Kamler and Homolka 2005, Parker et al. 2005, Verheyden et al. 2011, Gàlvez-Ceròn et al. 2013, Moço et al. 2013). Aublet and Festa-Bianchet (2009) monitored the forage quality experimented by the alpine ibex over the warm season in the Grand Paradiso National Park, western Alps. Crude protein content of vegetation samples decreased from mid-May to September, while NDF and lignin increased, leading to a lower food digestibility and supporting our temporal trend. Strategies used by wild herbivores to maintain or improve diet quality are an increase in feeding selectivity (Hofmann and Nygren 1992, Van Soest 1996) or altitudinal shifts in search of earlier phonological stages (Mysterud et al. 2001, Walker et al. 2006). However, our results suggest that the Alpine ibex in this population is unable to contrast the decline in vegetation quality in order to maintain a high-quality diet through summer and autumn, as reported by other ungulates that can progressively supply a decrease in diet quality by feeding on alternative resources (Martinez 2002, Abbas et al. 2011, Kamler and Homolka 2011, Moço et al. 2013). We did not have faecal samples for spring and winter (access to the areas used by ibex was impossible or dangerous because of snow depth and avalanche risk) but it is most plausible to assume that diet quality remained low during winter, and could increase to the June values only after the snow melting. This pattern of food resources availability would be consistent with those of movement and activity, which in this species (Signer et al. 2011, Parraga et al. unpublished) as well as in other mountain ungulates (Clarke and Henderson 1984, Crampe et al. 2007) reach a maximum in summer and a minimum during winter, most probably in order to minimize energy expenditure (Signer et al. 2011).

Contrary to our expectations (H2) we did not find significant effects of the NDVI on FN or FNDF. Other studies in Alpine habitats have found that peaks of dietary quality and forage quality are synchronized, over long term annual series, with peaks of NDVI (Fontana et al. 2008). In our study, we used NDVI at a detailed spatial scale, i.e. the buffers approximating the areas used around the pellet groups. The lack of consistency between NDVI values and indexes of dietary quality might be due either to an inadequate description of such areas, or to the limitations of comparing absolute values of NDVI in mountain landscapes, where rocks and steep terrains with low vegetation surfaces are the predominant habitat types. Therefore, our results suggest that further investigation is needed, with a solid spatial relationship between faecal samples and NDVI, for instance by collecting samples from GPS – monitored animals, and an adequate processing of NDVI data to take into account the non-vegetated areas.

In general, the average percentage of FN content that we observed for ibexes were similar to those found in other wild ruminants (*Cervus elaphus*: Hernández and Laundrè 2004, *Rupicapra pyrenaica pyrenaica*: Galvez-Ceron et al. 2013), or slightly lower (*Sika deer*: Watanabe and Takatsuki 1993; *Roe deer*: Verheyden et al. 2011). Females had higher FN and lower FNDF values than males, supporting our hypothesis (H3) that females select a diet of a higher quality. The alpine ibex has one of the greatest differences on body mass among ungulates, with females weighting approximately half than males (Loison et al. 1999, Mysterud 2000). Throughout most of the year, they live in separate groups, and groups of adult females, yearlings and kids use different habitat patches than groups of males, although occasional overlaps are possible (Villaret et al. 1995, 1997; Scillitani et al. 2012).

Especially for high dimorphic ungulates, the spatial segregation between sexes has been explained (Bowyer 2004, Main, 2008) considering the combination of the "forage-selection hypothesis" (Beier 1987, Ruckstuhl and Nehuaus 2002, Parker 2009) and the "reproductive strategy hypothesis" (Main and Coblentz, 1996; Miquelle et al. 1992; Ruckstuhl and Nehuaus 2000, 2002). Small ruminants have a lower digestive efficiency than large ones, even within the same species, leading to differences in quality and quantity of forage sources selected (Bowyer 1984, Demment and Soest 1985), which imply different activity patterns and the selection of spatially separated areas. Large, adult males have a higher relative feed intake and a longer rumen retention time than females, and hence a higher ability to extract energy from low-quality forage (Baker and Hobbs 1987, Barbosa et al. 2009, Parker et al. 2009). In addition, males have lower relative energy requirements than females, and therefore may adopt a feeding strategy that privileges the quantity more than the quality of the diet. In fact, adult males of Alpine ibex select for grasslands (Grignolio et al. 2003, Scillitani et al. 2012) that are a constant source of vegetation, although of rapidly declining quality during summer (Aublet and Festa-Bianchet, 2009), although they may probably in part respond with changes in feeding behaviour and selectivity (Brivio et al. 2014). Females of Alpine ibex need to maintain an annual complex energy balance between winter survival, pregnancy and lactation (Parker et al. 1990). In their alpine environments, they must maximize the benefits of the brief period in which vegetation is accessible, and at the same time they must select rocky or high elevation habitats offering refuge to protect kids from predators (Festa-Bianchet 1988, Barten et al. 2001, Poole et al. 2007, Ruckstuhl and Neuhaus 2002, Grignolio et al. 2007). Despite such strategy to ensure the offspring survival may mean less access to vegetation biomass, by shifting in elevation females maximize the intake of the first high quality forage in areas where the snow is melted in the late spring (Moen et al. 2008), and may keep a selective behaviour through summer, as suggested by our results. Lactating females might be also able to increase the N absorption by remodeling their gastrointestinal tract, which a consequent reduction of FN (Jenks et al. 1994, Zimmerman et al. 2006, Monteith et al. 2014). Although in this study we could not identify samples from lactating or non-lactating females, this further supports the suggestion that, having higher FN concentrations, females selected a higher dietary quality than males. Neuhaus and Rucksthul (2002) reported also that female ibexes with or without kids spent more time feeding than males, in addition to selecting better diets. We suggest that during summer female ibexes select in general for high forage quality rather than abundance since they need to face the extreme conditions of the upcoming cold season. Average N and energy intakes may decline drastically during winter, as observed for other species (*Rangifer tarandus*: Parker et al. 2005), and may be a critical determinant not only for individual survival, but also for the energetic costs of a potential pregnancy (Martin et al. 1997). In ruminants, maternal N reserves may dictate the foetal development during the winter season (McEwan and Whitehead 1972).

Table 1. Results of calibrations with the BayesB model on the spectra obtained with the three methods. Results (average, max and min) are from 15 replications, each with different calibration and validation sets.

	Labspec (350-1830 nm)		Foodscan (850-1050 nm)		Labspec-FS (850-1050 nm)	
	N	NDF	N	NDF	N	NDF
R^2_{TRN}[a]						
Average	0.87	0.79	0.23	0.17	0.31	0.13
Max	0.93	0.85	0.31	0.24	0.42	0.27
Min	0.82	0.74	0.13	0.05	0.20	0.02
R^2_{VAL}[b]						
Average	0.72	0.59	0.23	0.07	0.33	0.07
Max	0.88	0.78	0.51	0.24	0.68	0.29
Min	0.40	0.38	0.02	0.00	0.00	0.00
$RMSE_{VAL}$[c]						
Average	0.29	3.56	0.52	5.43	0.49	5.83
Max	0.35	4.61	0.66	7.20	0.65	7.49
Min	0.24	2.72	0.38	4.15	0.40	4.43
TRN[d]	115	115	115	115	116	116
TST[e]	32	32	33	33	33	33

[a] *R^2_{TRN}= determination coefficient of TRN set calibration;*

[b] *R^2_{VAL}= determination coefficient of validation;*

[c] *$RMSE_{VAL}$= Root mean square error of validation;*

[d] *TRN= average number of samples in the 15 calibration sets;*

[e] *TST= average number of samples in the 15 calibration sets;*

Table 2. Results of calibrations with the BayesB model on the spectra obtained with the three methods with the entire dataset, and descriptive statistics of predicted values.

	Labspec (350-1830 nm)		FoodScan (850.1050 nm)		Labspec-FS (850-1050 nm)		Chemical	
	N	NDF	N	NDF	N	NDF	N	NDF
R^2_{CAL}[a]	0.88	0.78	0.24	0.18	0.32	0.09	--	--
$RMSE_{CAL}$[b]	0.18	2.68	0.45	5.17	0.43	5.40	--	--
TRN[c]	147	147	148	148	143	149	--	--
Predicted values[d]								
Average	2.47	43.47	2.44	43.78	2.37	43.67	2.42	43.78
Max	3.58	56.04	2.75	45.25	3.43	47.45	3.72	56.27
Min	1.63	30.75	2.25	37.16	1.93	38.80	1.44	29.93
SD	0.44	4.75	0.09	0.98	0.25	1.39	0.52	5.70

[a] *R^2_{CAL}= determination coefficient of calibration;*

[b] *$RMSE_{CAL}$= Root mean square error of calibration;*

[c] *TRN = number of samples in the calibration set;*

[d] *=valuesare given on an air-dried basis;*

Table 3. parameters of the regression of FN and FNDF from chemical analysis on FN from NIRS methods. The P values indicate the probability for intercept = 0 and b = 1.

	Intercept		b	
N%	Mean ± SE	P	mean ± SE	P
Chemical - LabSpec	0.026 ± 0.136	0.80	0.986 ± 0.055	0.85
Chemical - FoodScan	-0.815 ± 0.660	0.21	1.335 ± 0.270	0.22
Chemical – LabSpec-FS	-0.197 ± 0.144	0.58	1.069 ± 0.144	0.63
NDF%				
Chemical - LabSpec	3.22 ± 2.75	0.23	0.931 ± 0.063	0.27
Chemical - FoodScan	-50.86 ± 19.59	<0.01	2.162 ± 0.447	<0.01
Chemical – LabSpec-FS	10.54 ± 14.54	0.47	0.761 ± 0.333	0.47

Table 4. model selection for FN within Chemical and the different NIRs methods.

	Category	Julian date	NDVI	AIC	Δ AIC
	X	X	X	122.7	15.8
Chemical	**X**	**X**		**106.9**	**0**
		X		**108.8**	**1.9**
	X	X	X	94.7	17.7
LabSpec	**X**	**X**		**77.0**	**0.1**
		X		**76.9**	**0**
	X	X	X	-125.7	24.3
FoodScan	X	X		-146.0	4
		X		**-150.0**	**0**
	X	X	X	-8.9	21.1
LabSpec-FS	X	X		-27.2	2.8
		X		**-30.0**	**0**

Table 5. Solution of fixed effects category and Julian date for the mixed linear models analysing FN data.

	l.s. estimate	SE	T	P
Intercept				
Chemical	4.731	0.366	12.94	<0.001
LabSpec	4.356	0.298	14.62	<0.001
Foodscan	2.898	0.110	26.31	<0.001
LabSpec -FS	2.952	0.234	12.61	<0.001
Females vs Males				
Chemical	0.263	0.127	2.08	<0.05
LabSpec	0.165	0.103	1.61	0.118
Foodscan	-0.033	0.038	-0.87	0.392
LabSpec -FS	0.052	0.081	0.64	0.528
Julian date				
Chemical	-0.0101	0.0015	-6.81	<0.001
LabSpec	-0.0083	0.0012	-6.81	<0.001
Foodscan	-0.0018	0.0004	-3.92	<0.001
LabSpec -FS	-0.0022	0.0010	-2.32	<0.05

Table 6. Model selection for FNDF within Chemical and the different NIRs methods.

	Category	Julian date	NDVI	AIC	Δ AIC
Chemical	X	X	X	862.4	10.9
	X	**X**	**--**	**851.5**	**0**
	--	X	--	856.8	5.3
LabSpec	X	X	X	789.5	10.1
	X	**X**	**--**	**779.4**	**0**
	--	X		783.9	4.5
FoodScan	X	X	X	408.3	16.4
	X	**X**	**--**	**392.5**	**0.6**
	--	**X**		**391.9**	**0**
LabSpec-FS	X	X	X	501.8	14.6
	X	**X**	**--**	**487.2**	**0**
	--	**X**	**--**	**488.3**	**1.1**

Table 7. Solution of fixed effects category and Julian date of the mixed linear models analysing faecal NDF.

	l.s. estimate	SE	T	P
Intercept				
Chemical	26.293	4.734	5.55	<0.001
LabSpec	24.13	3.421	7.06	<0.001
Foodscan	40.491	0.0745	54.40	<0.001
LabSpec -FS	43.841	1.254	34.95	<0.001
Females vs males				
Chemical	-2.606	1.640	-1.59	0.122
LabSpec	-1.802	1.183	-1.52	0.137
Foodscan	0.127	0.257	0.50	0.623
LabSpec -FS	-0.409	0.434	-0.94	0.352
Julian date				
Chemical	0.079	0.020	4.07	<0.001
LabSpec	0.085	0.014	6.08	<0.001
Foodscan	0.013	0.003	4.22	<0.001
LabSpec -FS	0.001	0.005	0.10	0.92

Figure 1. Julian date and trend of FN estimated with chemical and predicted with the three NIR methods

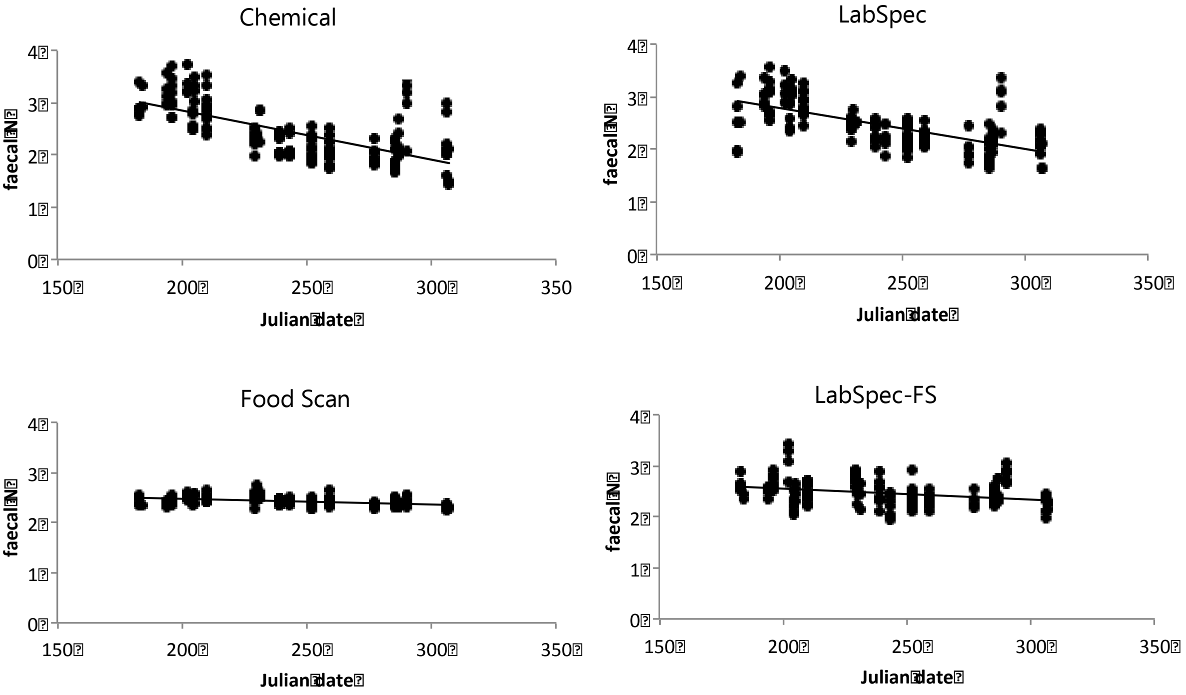
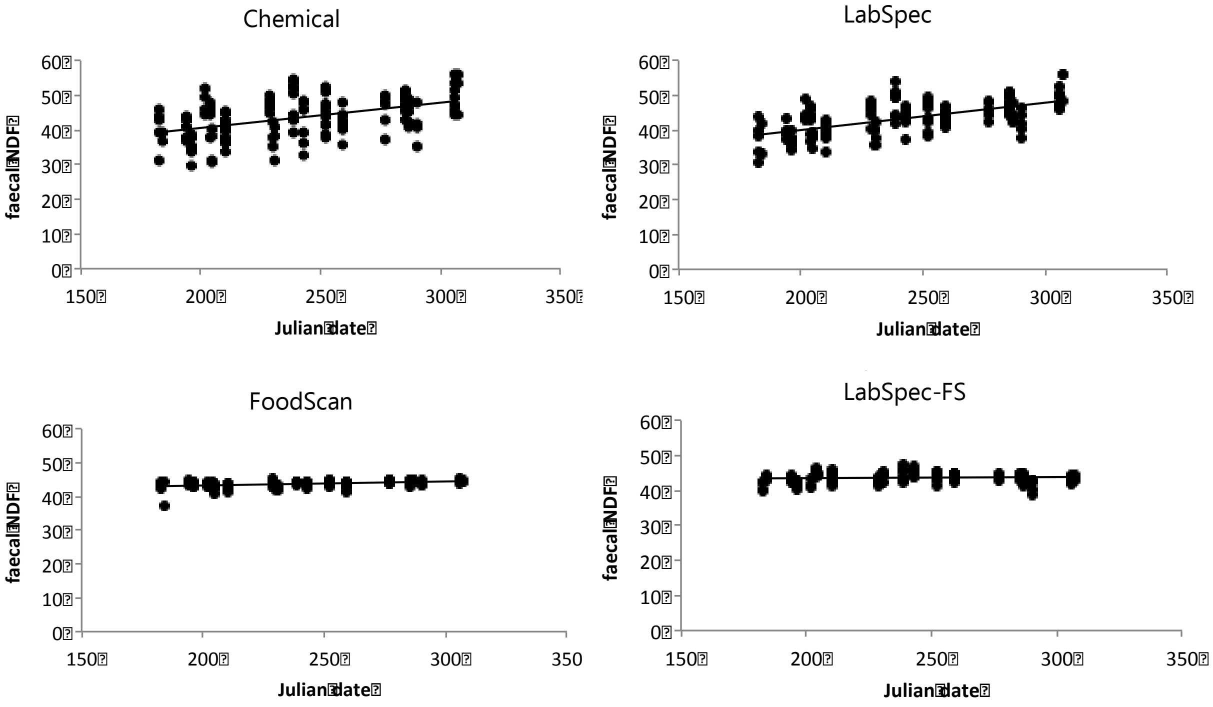


Figure 2. Julian date and trend of faecal NDF estimated with Chemical and predicted with the three NIR methods



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GENERAL CONCLUSIONS

This thesis provides new knowledge about the limitations and benefits of GPS tracking for monitoring large herbivores in Alpine landscapes, reports the first attempt, to my knowledge, to describe temporal patterns of spatial behaviour and the complex of intrinsic and extrinsic factors that influence them in Alpine ibex females, and evaluates a rapid and economic approach for assessing indirectly diet quality.

In the first chapter, by combining stationary GPS collars tests with data from free-ranging collared animals, I investigated on the habitat features affecting the probability of acquiring a location and the accuracy of received locations, and aimed at understanding how these features might interact with individual activity under different climatic conditions. To my knowledge, such kind of information was very limited for Alpine habitats, where the rugged land morphology and the extreme seasonality in climate shape habitat features and animals behaviour. With stationary trials I found, not surprisingly, that the probability of receiving a location was mostly influenced by physical obstructions limiting the proportion of the available sky, while accuracy was influenced also by land cover, with forest having a negative effect as respect to open areas. However, using an approach derived from the data collected on the free-ranging female ibexes to screen the acquired locations for outliers, I found that in properly edited databases the accuracy of retained locations can be fairly good, within 10 m for 50% of locations and 20 m for 75% of them. Therefore, limitations for the GPS-tracking technology in Alpine landscape seem to derive more from the biased proportion of locations that are received and retained across different habitats, than from their accuracy.

For this purpose, I used a database of over 90,000 attempted locations from free-ranging females to assess how fix acquisition rate and quality (as indexed by the NAV 2D/3D codes) varied throughout the year and the daytime, and which habitat, climatic, and behavioural factors influenced them. I confirmed the negative effects of physical obstructions to sky view on the probabilities of acquiring a location and of acquired locations to be in the 3D class, but, more interestingly, I found that these probabilities followed intra-annual and daily patterns, being lower in winter than in summer and during nightime than daytime. The intensity of activity of animals had a positive effect on the probability of acquiring a fix and on the proportion of 3D acquired fixes. These probabilities, in addition, increased in days without precipitations and with temperatures higher than average, especially in winter. I explained these findings as the result of an interaction between animals activity, habitats selections, and climate. Female ibex are more active during summer and, especially in winter, during daytime and in days with favourable climate and weather conditions, When animals are active they are more likely to use open instead than sheltered areas, thus explaining the patterns observed in fix acquisition rate and quality.

Therefore, the locations received (and finally retained) from GPS – collared Alpine ibex, and likely from other large herbivores living at high elevations, underestimate the use of habitats providing shelter and may drop in periods of adverse weather. This must be taken into account not only when studying habitat selection, but also when deciding temporal scales of home ranges estimates. For instance, while in our ibex population daily home range estimates might be reliable in summer, they could be biased in winter. Therefore, in the second chapter of my thesis I decided to use longer temporal scales in order to compare intra-annual patterns of home range size. Finally, a general conclusion of this first chapter is that, since GPS collars performance is the result of non-random interactions between two components, the habitat features and how and when the animals use these habitats, researchers should not only address the first component with stationary tests, but should also attempt to understand, using data from free-ranging animals, how the behaviour of their species in the specific of their study areas may influence the results.

In the second chapter, I examined temporal trends of weekly and monthly home ranges and core areas and how they were influenced by climate, food resources and individual conditions. I found marked intra-annual patterns that were positively correlated with daylight, but were more synchronized with indexes of climate and vegetation phenology. When I analysed the HR and CA sizes within seasons, I found that they were predominantly influenced by climatic variables in winter, and by idexes of food resources in summer. These results suggested that female ibexes adopt an extremely conservative strategy of spatial use, which in winter is shaped by the need of reducing the costs and the risks associated with movement. Only when snow starts melting and vegetation to grow they start moving, and expande their ranges presumably in order to include patches of vegetation in early stages of phenology.

My results are, to my knowledge, the first insight with GPS technology and at detailed temporal and spatial scales on the space use strategies of female ibex. These animals live in areas with an extreme seasonality and their spatial strategies have evolved to survive through long winters. Winter HRs and CAs are very small and most probably located in specific favourable locations that must be conserved. However, female ibex need also to make the maximum of the food available during the short summers, in order to recover from the winter and raise their kids. The suitability of wintering and summering area for Alpine areas might be in the future challenged by global climate changes. An increase in temperatures might modify the amount and temporal distribution of snow accumulation and its melting, and the temporal and spatial patterns of vegetation phenology. Therefore, understanding how the spatial strategies of female ibexes, and likely of other species of high mountain herbivores, are shaped by climate and habitat constraints is fundamental to predict how they could adapt to changes in these conditions and to devise effective conservation actions.

In the third chapter, I evaluated the use of faecal N estimated with NIRS approaches as a rapid and economic tool to describe biological patterns of the diet quality of both female and male Alpine ibex. I found that, provided a suitable NIRS technology is used, this approach can provide biologically meaningful results. In addition, I found that, in the high elevation habitats that characterize the environment of the Alpine ibex, where the availability of nutritional resources alternative to Alpine grasslands is restricted, the species cannot contrast the decline in vegetation quality from summer to autumn. This indirectly confirms that strategies to reduce energy costs are most important for the species during the long winters, and that only spring-early summer seem to be seasons when the benefits of increasing home range in search of better food may overcompensate the cost and the risks associated with movement, as I suggested in the second chapter. Females showed a tendency for higher indexes of diet quality than males, which suggests that the energy requirements of pregnancy and lactation lead them to a greater feeding selectivity. The fact that NDVI of the area surrounding faecal samples was unrelated wit indexes of diet quality might appear in contrast with the results of the second chapter, where NDVI of HRs was negatively correlated with their size. Possibly, my results in this third chapter might derive from an inability to correctly adapt the size of the buffer area to the spatio-temporal shifts of the animals, or by the need for refining NDVI indexes to take into account the disturbing effects of variable proportions of bare soil. These aspects should be investigated with larger spatial and temporal datasets. More in general, my results emphasize the need for improving the knowledge on foraging strategies of species living in highly seasonal environments, in order to better understand drivers of spatial behaviour and ultimately of evolution of life-history traits.

ACKNOWLEDGEMENTS

Questo lavoro è stato possibile grazie al sostegno alla ricerca scientifica della Fondazione Cassa di Risparmio del Veneto e Rovigo, la quale mi ha dato l'opportunità di ottenere una borsa di studio destinata allo svolgimento di un progetto di dottorato in Italia sostenuta dall'Università di Padova. Ringrazio anche la Regione del Veneto e in particolare la Sezione Caccia e Pesca per il supporto finanziario alla ricerca. Il Corpo Forestale delo Stato - comando provinciale del Veneto, Ufficio Territoriale per la Biodiversità (UTB) di Tarvisio e stazione di Canale d'Agordo - , e il Corpo di Polizia Provinciale di Belluno hanno fornito un insostituibile supporto logistico e per la cattura degi animali.

Vorrei ringraziare il mio supervisore, Maurizio Ramanzin, dal primo momento in cui mi ha dato l'opportunità di fare questo dottorato seguendo uno dei progetti più belli ed emozionanti. Quel giorno di estate sulla Marmolada presi una delle decisioni più significative della mia vita, e ad oggi non riesco ad immaginare che altra strada avrei potuto intraprendere che mi portasse più vicino alle mie passioni. Grazie per avermi dato la possibilità di vivere questa esperienza, per il fondamentale sostegno durante i tre anni di lavoro e per la comprensione nei momenti più difficili. Ringrazio anche Enrico Sturaro per avermi reso più facili i miei primi momenti in Italia, era l'unico capace di parlare la mia lingua!, ma soprattutto per il suo grande aiuto sia in aspetti lavorativi che personali.

Ringrazio con tutto il mio cuore Luca Rossi per avere incrociato il mio cammino, deviandolo verso l'esperienza più bella e intensa della mia vita. Ho avuto la fortuna di aver conosciuto una delle persone più rappresentative e stimate nell'ambito faunistico ma allo stesso tempo in grado di trasmettermi l'importanza dell'umiltà, della semplicità e del coraggio per raggiungere i propri sogni.

Un ringraziamento speciale vorrei dedicarlo ad Alberto De Luca, la persona senza la quale non sarei mai riuscita a sorpassare ogni ostacolo, avendomi dimostrato non solo una eccezionale capacità intellettuale, ma anche una enorme generosità. Nei momenti più difficili mi è stato sempre vicino,

anche nella lontananza. Mi ha spinto su dopo ogni caduta in un modo incondizionato, mi ha insegnato infiniti aspetti tecnici sul lavoro, mi ha trasmesso preziose conoscenze ma soprattutto mi ha convinta a guardare sempre avanti senza smettere di sorridere. Non potrò mai restituirgli tutto quanto la sua amicizia ha significato per me.

Per il loro inestimabile aiuto vorrei anche ringraziare le persone che hanno dedicato il suo tempo, sforzo e passione al lavoro svolto sulle cime della Marmolada. Sono stati giorni di intensa fatica fisica e mentale, ma anche delle più indescrivibili sensazioni di libertà e unione con ogni singolo elemento della Natura. Ho avuto la fortuna di vivere a più di 2.000 m di altitudine i momenti assolutamente più emozionanti di tutto questo lavoro. Ringrazio Matteo Mosconi, per la sua l'inesauribile energia e l'avermi regalato tante preziose fotografie, alcune delle quali utilizzate in questa tesi. Ma soprattutto grazie a Mattia Ferramosca, per avermi aspettato in ogni curva di ogni ardua salita, in tutti i sensi della vita, con infinita pazienza, forza e positività, sollevando il peso dalle mie spalle e convinto dalla mia forza e capacità. Raggiungere la cima non sarebbe stato possibile senza di lui.

Quisiera dar un saludo especial a Encarna por demostrarme tanta fortaleza. A pesar de su ganas de ayudarme y aprender, de colaborar en el proyecto y de disfrutar de cada momento, la mala suerte se nos adelantó, pero me dió la oportunidad de conocer una persona esplendida y sobretodo indestructible!

Un profondo ringraziamento lo dedico alle "squadre cattura" del Corpo Forestale dello Stato e del Corpo di Polizia Provinciale di Belluno. Con loro ho vissuto dei momenti fra più divertenti e appassionanti di tutto questo percorso. Mi hanno dimostrato come l'uomo a volte possa correre sulle rocce più veloce di uno stambecco, e come la tua passione possa diventare il tuo modo di vivere. Hanno svolto un lavoro fondamentale per questo progetto, il quale senza di loro non sarebbe stato possibile nemmeno cominciare, ma hanno anche avuto la capacità di agevolare la fatica con il loro entusiasmo e semplicità. Grazie tante, con tutto il mio sincero affetto, alla squadra di catture più coraggiosa e che io abbia mai conosciuto.

Ringrazio Francesca Cagnacci e Ferdinando Urbano per aver messo a disposizione dei dati fondamentali (NDVI) che hanno permesso un maggior approfondimento e conoscenza degli aspetti ecologici e comportamentali dello stambecco alpino, ma anche per l'aiuto ricevuto durante i miei primi passi nell'utilizzo di programmi di gestione di ampi database.

Ringrazio l'Agenzia Regionale per la Prevenzione e Protezione Ambientale del Veneto (ARPAV) per la velocità e disponibilità con cui hanno procurato i dati meteorologici indispensabili per raggiungere gran parte delle conclusioni di questo lavoro.

Ringrazio con tantissimo affetto tutti i meravigliosi colleghi e ormai cari amici che ho potuto conoscere in questi tre anni, Eirini, Serena, Erika, Alessandro, Miriam, Francesco, e un lungo eccetera. Non è mai semplice tornare al punto di partenza lasciando alle spalle tutto quello che conosci, ma loro mi hanno fatto sentire come a casa dal primo momento, e la loro accoglienza sarà sempre indimenticabile per me.

Aunque llegar a Italia supuso un antes y un después, muchas personas permanecen siempre ahí, en mi pasado, presente y futuro, dándome la certeza de que los buenos amigos duran toda la vida. Quisiera agradecer todo el apoyo a mi querida Isis, a Patri, a Gloria, a Marisol, y a tantas otras personas que me han demostrado su cariño cuando más lo he necesitado a pesar de la distancia.

A mi madre y hermanas no solo quiero agradacerles el apoyo que he siempre recibido para alcanzar mis metas, si no tambièn el pilar fundamental que han supuesto en los momentos más dificiles. Doy las gracias a mi madre por su amor incondicional, la paciencia de tantas despedidas y la fortaleza con la que a pesar de todo aún sonríe a cada instante de la vida. A mis hermanas, porque han sido siempre mi punto de referencia y las piezas de un puzze capaz de afrontar cualquier obstáculo.

Finalmente quisiera agradecerlo todo a la persona que me trajo hasta aquí, a mi padre. Quiero darle las gracias por transmitirme los valores más sólidos y fundamentales de mi vida, por entusiasmarme con sus enseñanzas sobre cada planta, cada pequeño insecto, cada pájaro o cada

curva de los senderos que tantas veces recorrimos juntos, por haberme maravillosamente contagiado su pasión por la Naturaleza antes incluso de aprender a caminar. Esta tesis la dedico a él, porque la fuerza de cada uno de mis pasos ha tenido solo un objetivo, demostrarle que cada día estoy más cerca de hacer realidad el sueño que un día compartimos.