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CICLO XXIII

ECOLOGY OF ALPINE IBEX (*Capra ibex ibex*, Linnaeus 1758) IN RELATION TO MANAGEMENT ACTIONS IN THE MARMOLADA MASSIF, ITALY

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Ad Andrea, a Chiara e a Marina, con affetto
Alla mia famiglia
Alla Natura, la più meravigliosa ricchezza che possa esistere

Premessa

La presente tesi è stata realizzata utilizzando i dati raccolti grazie a studi promossi da vari Enti:

- Amministrazione Provinciale di Belluno – Corpo di Polizia Provinciale
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(Photograph by **Vittorio Poli**)

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Abstract

ABSTRACT

An effective management or conservation of a species passes through the acquisition of a deep scientific based knowledge of its life history, population dynamic and ecological needs, as well as an objective evaluation of the results obtained. In the optic of adaptive management, in fact, we can "learn by doing", and therefore it is necessary to provide a scientific evaluation of the management actions made. When managing a population, decisions should be taken considering the general natural history of the species, but keeping in mind that distinct populations of the same species may differ significantly in behavior, population dynamics and resource selection, and need therefore further investigations.

This thesis dealt with several aspects of the ecology of alpine ibex (*Capra ibex ibex*, Linnaeus 1758) in the Marmolada massif, located in the Eastern Italian Alps (Dolomites, 46°26'13" N; 11°51'54"E). This population is peculiar because it was affected by an epizootic of sarcoptic mange, experiencing a severe decline, with the loss of about 3/5 of the individuals, and because it was object of different management interventions and monitoring programs. As a result, a significant proportion of the population was marked and/or equipped with a radio device, and followed for 7 years. In 2003-2006 the population was regularly surveyed by transects on foot and radiotracking. In 2004, a veterinarian management intervention took place: mangy ibexes were captured and treated with the parasiticide ivermectin. In 2006-2007, 14 male ibexes were translocated in the Marmolada group, in the frame of a restocking program. Regular monitoring of radio tagged animals and of the colony went on up to 2009. The large amount of data collected gave me the opportunity to broaden the knowledge on this population and to test the effectiveness of the management interventions adopted. The aim of this thesis were: to furnish useful suggestion for increasing monitoring quality, to increase knowledge on range extent, spatial behavior and resource selection of the Marmolada ibex colony,to provide a first insight on the consequence of a sarcoptic mange epizootic, and evaluate the consequences of translocations on ibex spatial behavior.

I firstly investigated on the demography of the population and, provided a critical assessment of the survey method used for ibex monitoring in the Marmolada. Ground counts likely underestimates population size, and can be improved by performing replicates and by recording the identities of marked animals sighted to be able to perform CMR estimations.

I then examined the pattern of age and sex specific survival rates of the population using CMR techniques, testing the factors linked to the population crash, including the sarcoptic mange epidemic peak, winter harshness and the effect of ivermectin treatments. As expected,

I found a strong impact of the epizootic, demonstrated by a sharp decrease in survival of both sexes and all age classes during winter 2003-2004, with a higher mortality rate for senescent males, while survival was high in the following years. Winter harshness did not seem to be crucial in explaining this higher mortality of ibexes, but this can be due to confounding effects of mange and winter severity, which are difficult to disentangle, especially with a relatively short term data set.

The second part of the thesis deals with the factors shaping space occupancy and habitat selection by ibex in the Marmolada massif, and focused on the adaptation process to the new area and colony by the translocated male ibexes. I first described the spatial pattern exhibited by adult resident males by computing their home ranges and examining which environmental factors shaped the ranging behavior. Ibexes showed a pattern of high stability with little variations in home range size across the years and the seasons, thought in winter they confined their home range in a smaller area, in response to snowpack depth. A significant inverse relation was found between home range size and the percentage of grassland inside it, indicating that the availability of preferred habitat resources is one of the main factors influencing spatial behaviour. Grassland was in fact positively selected by males throughout the years, as testified by the habitat selection analyses conducted at a yearly and a seasonal level.

I then compared the habitat selection exhibited by translocated and resident males at different spatial scales. At the II order level of selection, relocated individuals selected resources different of those selected by resident males. This result was probably linked to the exploratory movement that relocated ibex made in the new environment to create their own map of the surrounding, testified by the larger extent of the range occupied by translocated animals in relation to resident ones. However, no differences were found at III order level, indicating that within their home range all ibex selected the same resources. These results showed that the relocated ibexes needed even two years to conclude explorative movements, settle down to home ranges comparable in size to those of resident males and fully associate with them. Individual heterogeneity in behaviour played an important role in the length of the adaptation process, as well as social behavior: our analysis indicate that the settlement coincide with an increased association between resident male and translocated ones. This confirms the need of monitoring translocated individuals for at least three years, or longer, and to further investigate on social interaction, to better understand its influence in the settlement process.

In conclusion, the results of this thesis highlighted the importance of conducting a long-term monitoring program to assess the effectiveness of management actions and suggest the need of behavioural studies to improve conservation and management of populations of wild ungulates.

RIASSUNTO

Un'adeguata strategia di conservazione e gestione di una specie si basa sull'impiego di conoscenze scientifiche, e sulla valutazione dell'efficacia delle misure adottate attraverso un appropriato monitoraggio. Secondo il principio della gestione adattativa, infatti, è necessario infatti acquisire una solida base scientifica che consenta di migliorare l'efficacia della gestione nel tempo.

Conoscere le caratteristiche biologiche (quali la *life history*, la dinamica di popolazione, e le esigenze ecologiche) tipiche di una specie è fondamentale per poterla gestire correttamente. Tuttavia ogni popolazione è soggetta a specifiche pressioni biotiche a abiotiche e può differire dalle altre in termini di comportamento, dinamica e selezione delle risorse. Lo studio degli specifici adattamenti delle singole popolazioni al loro contesto ambientale riveste perciò un'importanza considerevole.

In questa tesi ho considerato diversi aspetti dell'ecologia della colonia di stambecco alpino (*Capra ibex ibex*, Linnaeus 1758) del gruppo della Marmolada (46°26'13" N; 11°51'54"E, Dolomiti orientali). Questa popolazione è stata colpita nell'inverno 2003/2004 da un'epizoozia di rogna sarcoptica e ha subito una drastica riduzione degli effettivi. Di conseguenza, è stata oggetto di diversi interventi gestionali e programmi di monitoraggio, nel corso dei quali una proporzione significativa della popolazione è stata marcata e/o dotata di radio-collare, e studiata per 7 anni. Nel 2003-2006 è stato condotto un programma di monitoraggio radiotelemetrico e visivo, mirato all'acquisizione di conoscenze sulla demografia, lo status sanitario e la distribuzione spaziale della colonia. Nel 2004 e 2005, è stato attivato un piano di trattamento farmacologico per contrastare l'epizoozia, e 58 stambecchi affetti da rogna sarcoptica sono stati catturati e trattati con ivermectina, un medicinale acaricida. Nel 2006-2007 è stato avviato un progetto di *restocking* nel corso del quale 14 stambecchi provenienti dalla colonia dei massicci Jôf-Fuart- Montasio (Alpi Giulie) sono stati traslocati nel gruppo della Marmolada. Gli animali traslocati e la colonia ricevente sono stati monitorati regolarmente fino all'estate 2009.

L'elevato numero di dati acquisiti ha fornito l'opportunità di approfondire le conoscenze su questa colonia e allo stesso tempo di fornire una valutazione scientifica degli interventi gestionali operati. Gli obiettivi di questa tesi sono infatti: fornire indicazioni utili per migliorare la qualità dei conteggi; migliorare le conoscenze sulla distribuzione, comportamento spaziale e selezione dell'habitat degli stambecchi della Marmolada;

comprendere l'influenza della rogna e di altri fattori limitanti sulla mortalità; valutare le conseguenze della traslocazione sul comportamento spaziale dei maschi di stambecco.

In primo luogo ho descritto la struttura demografica della popolazione, attraverso un utilizzo critico dei dati forniti dai conteggi. Questi dati si sono rivelati in gran parte inaffidabili, e tendono a sottostimare la popolazione. Stime più precise e accurate possono essere effettuate ripetendo più sessioni di conteggio e annotando ogni volta gli animali marcati avvistati.

In una fase successiva ho esaminato l'andamento dei tassi di sopravvivenza età e sesso specifici, utilizzando la tecnica del CMR, e ho testato l'effetto sulla sopravvivenza di diverse variabili connesse al crollo demografico, incluse la presenza di rogna, la severità invernale e il trattamento con ivermectina. Come atteso, il tasso di sopravvivenza ha mostrato un drastico calo nel 2004, quando la diffusione dell'epizoozia di rogna sarcoptica ha raggiunto il suo massimo, e i maschi senescenti sono stati il segmento di popolazione maggiormente colpito. La severità invernale non sembrerebbe spiegare invece l'elevato tasso di mortalità, ma questo risultato potrebbe essere legato al fatto che è complesso separare efficacemente le diverse fonti di mortalità in un intervallo temporale relativamente breve, come quello a mia disposizione.

Nella seconda parte della tesi ho esaminato i fattori che determinano l'utilizzo dello spazio (in termini di *home range*) e la selezione dell'habitat dei maschi e ho studiato il processo di adattamento al nuovo ambiente da parte degli stambecchi traslocati. Gli stambecchi della Marmolada mostrano un'elevata stabilità dell'utilizzo dello spazio: le dimensioni degli *home range* hanno mostrano una modesta fluttuazione stagionale, ad eccezione dell'inverno in cui le aree occupate si registra una contrazione delle aree occupate, probabilmente legata alla consistenza del manto nevoso, che ne limita gli spostamenti. La dimensione degli home range è risultata essere negativamente correlata con la percentuale di prateria in esso compresa, indicando che la presenza di adeguate risorse trofiche influenza il comportamento spaziale dei maschi. Le praterie alpine sono infatti fonte di foraggiamento e sono positivamente selezionate dai maschi nel corso di tutte le stagioni, come testimoniato dalle analisi di selezione dell'habitat.

La selezione dell'habitat degli stambecchi traslocati è stata studiata a diverse scale spaziali. Gli stambecchi rilasciati hanno selezionato risorse diverse dagli animali locali nel corso del primo anno, tuttavia questa differenza emerge solo al II livello di selezione, mentre nessuna difformità è emersa al III livello. Questo indica che all'interno del proprio home range la selezione delle risorse è la stessa per tutti gli individui, ma all'interno dell'area di studio gli stambecchi traslocati selezionano ambienti diversi da quelli selezionati dai locali. Infatti, una volta rilasciati nel nuovo ambiente, gli stambecchi necessitano di movimenti esplorativi per poter localizzare le risorse ottimali. Gli animali traslocati hanno mostrato un'elevata instabilità spaziale e hanno occupato home range più estesi di quelli degli animali locali. I risultati mostrano che il processo di ambientamento post-rilascio può prolungarsi per almeno due anni, anche se è influenzato da altri fattori quali l'eterogeneità individuale, e l' integrazione sociale nella nuova colonia. Questo conferma la necessità di monitorare regolarmente gli animali traslocati per almeno tre anni. Inoltre ulteriori studi andrebbero effettuati sull'effettivo ruolo rivestito dalle interazioni sociali nell'adattamento a un nuovo ambiente.

In conclusione, questa tesi dimostra la necessità di un monitoraggio a lungo termine per la verifica degli interventi gestionali attuati, e l'importanza di condurre studi comportamentali per migliorare la gestione e la conservazione degli ungulati selvatici.

General Introduction

1.THEORETICAL BACKGROUND

1.1. Science and applied wildlife conservation and management.

In the last decades, a growing concern on the effectiveness of conservation and management actions is arising (Pullin & Knigth 2009). One of the most problematic issue related to conservation (and management) programs is the gap between research and conservation plans. Several flaws are related to many conservation/management policies, and they all are related to the lack of a scientific based approach, and of a correct communication between theoretical studies and applied wildlife practices. As observed by Sutherland (2000) the absence of experimentation, correct monitoring and documentation leads to useless, or even detrimental conservation strategies.

Management and conservation are difficult decision making processes: choosing the best strategy to achieve management objectives is often problematic, as the objectives are controversial, resources are limited and often the possible management actions are restricted (Lyons et al 2008). The lack of an extensive documentation before setting an action is a widespread difficulty. Often management decision are taken on the basis of commonsense, personal experience and interpretations of traditional land management practices (Sutherland et al. 2004), and little evidences are collected to support applied practices. In a survey conducted on conservation programs in UK, Pullin et al. (2004) showed how, to support decision making, the most frequently used sources of information were existing management plan, not the achieved scientific knowledge or information gained within an experimental survey. Managers are confronted with the need to execute action fast and often with a small budget, and it is more convenient for them to rely on an established but unevaluated practice.

Acquiring information on a system is fundamental for improving conservation (Sauer & Knutson 2008, Stern et al. 2004). Monitoring is "the process of gathering information about some system state variables at different points in time for the purpose of assessing system state and drawing inferences about changes in state over time." (Yoccoz et al 2001). As a consequence of a growing public awareness towards loss of wilderness and biodiversity and problematic environmental issues as global warming, in the last years most developed Countries have established monitoring program for conservation purposes. Nevertheless, most of these programs lack the essential constitutive elements: the definition of the objectives and the planning of how to achieve them (Sutherland et al. 2004, Yoccoz et al. 2001). Even the best-aimed conservation program will fail when a correct plan is lacking. Without defining a statement of the project objective, monitoring end up in a simple gathering of information that may be useless.

Another flaw associated with conservation actions is that often project reporting is inadequate and does not provide the information necessary for assessing the effectiveness of the program and derive useful guidelines (Brooks et al. 2006). Moreover, even when a correct plan has been made it provide no gain in knowledge because it often remains in the memory of the practitioner that applied it (Sutherland 2000). In fact most of the conservation programs produce gray literature (technical reports, thesis dissertations, informal literature from nongovernmental organizations…) which is unevaluated and difficult to access. If shared knowledge is not easily available, in actual fact an evaluation of the conservation (management) practice is hard to be made. As pointed out by Pullin & Knigth (2009) without an effective monitoring and evaluation it is impossible to understand whether a conservation policy is doing “more good than harm”. In addition, people involved in wildlife conservation (and research) are used to be asked by the public opinion what is the meaning of their job, also because conservation programs are often expensive, and an evaluation of effectiveness is necessary to justify the costs of the programs and provide accountability (Ferraro & Pattanayak 2006, Stern et al. 2004).

An effective way to contrast all these flaw associated with conservation policies, is the adoption of the adaptive management approach procedure, based on the “learn by doing” principle. Adaptive management in fact incorporates research into conservation action: it is the integration of design, management, and monitoring to systematically test assumptions in order to adapt and learn (Salafsky et al. 2002). The idea of adaptive management is that the knowledge of ecological systems is not only incomplete but elusive (Walters and Holling 1990), therefore this approach require the willing to invest effort in systematically learning about whether and why conservation (management) actions work or do not work (Salafsky et al. 2001). Using this approach it is contemporaneously possible to achieve management objectives and acquire information on how the system functions and responds to management (Lyons et al. 2008). In the frame of an adaptive conservation strategy several developing steps are required: (1) to define clear objectives (2) to determine a structured plan for conservation strategies (3) to develop the knowledge and skills in individuals and organizations for practicing adaptive management (4) to produce efficient reports of the consequences of the policy applied, in relation to the underlying objectives (Lyons et al 2008, Salafsky et al. 2002). For a correct planning and development of the strategy, monitoring plays a central role

(Sauer & Knutson 2008, Yoccoz et al. 2001). Monitoring serves in the preparation for active conservation, to assess the status of the system, as well as during and after the application of the conservation program to evaluate the effectiveness of the applied actions (Nichols & Williams 2006, Yoccoz et al. 2001). As suggested by Pullin and Knight (2001) actions need to be critically evaluated to continually seek for increasing effectiveness. This can be achieved also by a systematic review, following a standard protocol (Pullin & Stewart 2006) and aiming in summarizing, evaluating and communicating the results. Increasing dialog between the academic scientific community, the managers who deal with everyday problem-solving and the general public is strongly desirable and will provide benefits for all the actors involved (Festa-Bianchet 2003b). Applied research can achieve interesting results, worthy of publications in peer-referred journals, on the ecology and behavior of the target species. As a demonstration, several successful long-term researches on marked animals are rooted in the cooperation between researchers and institutions (Festa Bianchet 2003b). In turns, the information acquired can help in significantly improving the quality of monitoring.

As a final point, I would like to stress on the importance of employing different tools for disseminating results. Since one of the most important steps in adaptive management is learning from actions, I believe that improvement in communication can have a significant impact on both applied conservation (or management) and science. As stated before, the presence of incorrect reporting of information or the difficulties to access it prevent from an evaluation of the conservation action as well as from the spreading of achieved results. Sometimes even very interesting and well conducted applied researches unfortunately end up in reports or thesis accumulating dust sitting on shelves. In example, although in the last decades translocation of wild animals has become a common strategy for contrasting population extinction and restoring the historical range of wild animals, most of the realised projects produced only technical reports that are not easy to be found through conventional channels (Fisher & Lindenmayer 2000). In my own experience, despite the large number of successful relocations and establishment of new populations of alpine ibex (*Capra ibex ibex*) in the Alps, I got troubles in finding materials on post release monitoring and planning of the action. On the counterpart, peer-referred articles, written in English and using scientific and statistical languages, are not truly providing useful information for practitioners, and information acquired by researchers are not always applied to conservation programs (Stinchombe et al. 2002). For this reason, I acknowledge the importance of reports for disseminating science, also because often scientific publication are not accessible to the public and require a long time interval to be published, but I advocate the need of an integration of gray literature and published results, that are easier available to a large audience. The communication gap between science and managers may results in ineffective duplicate efforts (Mace et al. 2000), that are no useful for conservation purposes, especially in the context of the actual difficulty in the gathering sufficient economic resources necessary for a correct monitoring. To this purpose an excellent tool for divulgating conservation studies and intervention is internet. In particular, particular useful is the website http://conservationevidence.com, held by the Department of Zoology of the University of Cambridge (England), that provide a useful interactive web database in which store reports, summaries and peer-referred papers.

1.2. Research and management: the case of large herbivores

Large herbivores have high economic value since they provide an important source of revenue through hunting and ecotourism, but in the meantime can be agricultural pests, affect forest productivity, act as vector of diseases for domestic livestock, cause car accidents (Apollonio et al. 2010, Gordon et al. 2004). As stated above, also an effective management/conservation of large herbivores will require an efficient integration between research and management (Festa-Bianchet 2007). Despite the growth of literature demanding the use of scientific based knowledge to improve their management (e.g. Apollonio et al. 2010, Festa-Bianchet 2003 a, 2007, Gaillard et al. 2003, Garel 2006, Gordon et al. 2004, Morellet et al. 2007), in many cases the management of ungulate populations is still limited in taking decisions relying on simple counts (Gaillard et al. 2008, Williams et al. 2002). In the case of mountain dwelling ungulates, the status of the population is assessed with a single yearly counts (Largo et al. 2008) that most likely do not provide a reliable estimate of the population size. In fact these yearly counts are often affected by an important bias (Gaillard et al. 2003, Morellet et al. 2007) related to the behaviour of animals, visibility on rough terrain, weather condition (Garel et al. 2005 b, Hutchins & Geist 1987) as well as observers training (Garel et al. 2005 b). Moreover, being performed once in a year, the level of precision is not computable (Loison et al. 2006). Since management decisions are taken on the basis of the estimated abundance (or on growth rates estimates derived by counts) this can have detrimental consequences both on hunted species (by setting wrong hunted quotas) and on protected ones because the size of a population is important for its persistence (Berger 1990). Even in the case counts furnish a correct estimate, they might not provide useful information on the underlying factors affecting the demographic processes that are important for achieving the desired goals (Morellet et al. 2007).

For a correct management, it is important to acquire information related to the species life history and on the variability over time of demographic parameters (Gaillard et al. 2003). Density dependent factors and environmental stochasticity act simultaneously as limiting factors on population dynamics of large herbivores (Owen Smith 2010). Climate (Coulson et al 2001, Moen et al. 2006, Mysterud et al. 2001), population density (Bonenfant et al 2009), predation (Andersen et al 2006, Berger et al 2001), competition (Darmon 2007, Owen-Smith 2002), habitat and forage quality (McLoughlin et al. 2006, Pettorelli et al 2003), diseases (Loison et al. 1996, Wilson et al. 2004) and human interferences such as hunting (Festa-Bianchet 2007) are all factors that can influence demographic parameters. However, their effects vary according to the age class composition of the population. In fact ungulates have strongly age structured populations: different age classes show different survival rates as well as a different reproductive output (Gaillard et al. 2000). Typically the life cycle of large herbivores shows three main stages: juvenile, prime age adults and senescent ones. Juvenile survival (which determines recruitment) is variable and affected by both density- dependent and density-independent mortality, while prime age adults show constant and high survival rates (Festa-Bianchet et al. 2003, Gaillard et al. 1999). As age increase, survival and fecundity decrease: in the senescent phase individuals are more sensitive to environmental variations and other source of mortality (Loison et al. 1999a). Moreover, most ungulate species show sex-biased survival rates, males being more sensitive to adverse environmental conditions (Toïgo & Gaillard 2003).

Also behavioural ecology can provide insight relevant for solving conservation problems (Blumstein & Fernández- Juricic 2010, Sutherland 1998). Many of the behavioural adaptation of a species in fact affect its performance in the environment and influence population dynamic, including diet, habitat use, mating systems, social organization, antipredatory response (Gosling & Sutherland 2000). In particular, understanding ranging behaviour and identifying the sources of variation in resource acquisition, would be particular useful for management /conservation purposes (Apollonio et al. 2003). Habitat selection is a complex hierarchical process of behavioural responses (Garshelis 2000, Johnson 1980) requiring investigations in multiple spatial and temporal scales to be understood, as at each level different resources and limiting factors act on individuals (Bowyer & Kie 2006). Resources are not uniformly distributed within a landscape, and animals have to move in response to patch composition, determining changes in local density (Morrison et al 2006).Wild animals normally restrict space use to a confined area (Börger et al. 2006), selecting locations where to live and breed, and this affect distribution, but also intra- and inter-specific interaction, and, as a consequence, population regulation (González-Suaréz & Gerber 2008, Morales et al. 2010, Revilla & Wiegand 2008). The integration of long-term demographic, habitat selection and movement studies allows to understand the link between individual fitness and habitat quality (Gaillard et al. 2010), and as a consequence consent to predict the probability of extinction, colonization, immigration and emigration in different patches in the landscape.

As a final point, we have to keep in mind that the world is not a static system. Nowadays, many ungulate species have recolonised spaces where they had gone extinct or have been declining, thanks also to management interventions and reintroduction (Gordon et al. 2004). Many species are now expanding their range of occurrence and present local overabundance, representing an hazard for vegetation (Festa-Bianchet 2007, Gill 2006, Hester et al. 2006, Loison et al. 2003). On the other hand, at the same time many other species are declining (IUCN red list: http://www.iucnredlist.org/), threatened by the expansion of human activities (Laliberté & Ripple 2004) and global climate change (Pettorelli et al 2007). In this dynamic system, it is necessary to adopt a plastic approach to management, and possibly to calibrate actions based on new acquired scientific knowledge. At this purpose, it is also important to assess species range not only on a large scale, but also at a population level (Darmon et al. 2007) and to disclose the processes underlying range expansion and contraction. In this way it is possible to define meaningful management units, over which geographical area a given management action or plan should be implemented, irrespective of artificial delimitations as administrative borderlines (Zannèse et al. 2006).

To conclude, as stated above, I believe that only an integration of information on habitat preference, behaviour, and demography of a population can help improve significantly the management of wild populations. To reach this objective, it would be necessary to increase the number of long term studies aiming at discovering life history characteristics that are formed by a long-term evolutionary process. Only with long term studies it will be possible to delineate a general pattern in the ecological needs of a species, linked to its natural history. Notwithstanding this approach requires considerable amount of funding and continuous cooperation between different institutions (Festa-Bianchet 2003 b), so this goal can be difficult to reach. Finally, it is necessary to keep in mind that distinct populations of the same species may differ significantly in behavior, population dynamics and resource selection due to the different environmental constraints to which they are subjected. Therefore it would be desirable to acquire information for each populations, and routinely assess and evaluate scientifically the status of the population and the effectiveness of management plans.

2. AIMS AND STRUCTURE OF THE THESIS

The aim of this thesis is to provide some insights on the ecology of the alpine ibex colony of the Marmolada massif, and to perform a critical evaluation of the management and conservation actions applied to furnish some suggestion for implementing the current monitoring programs in the massif.

In **chapter 2** we provide an overview on the history of the colony, as well as a critical analysis on the current monitoring programs. In **chapter 3** we used capture mark recapture techniques to investigate survival of ibexes. Survival is an essential component of population dynamics and it is important to understand which factor shape survival rates in a given population. We tested the effects of a epizootic of sarcoptic mange and local weather variability on survival and verified the effectiveness of the adoption of a treatment against mange. In **chapter 4** we analyzed the environmental factors determining ranging behavior of ibex in the Marmolada massif. The last two chapters deals with the consequences of translocation on ibex spatial and social behavior (**chapter 5**) and on habitat selection (**chapter 6**), in order to provide information useful for following translocationa as well as useful insights on the factors shaping selection in a new environment.

3. THE STUDY SPECIES

1.1. Systematic, history and current status

Alpine ibex (*Capra ibex ibex* Linnaeus, 1758) belong to the family *Bovidae* and to the subfamily *Caprinae*. Genus *Capra* is composed by 5 species distributed over Europe, Asia and North Africa: the East Caucasian tur (*Capra cylindricornis*), the Wild Goat (*Capra aegagrus*), the Markhor (*Capra falconeri*), Spanish ibex (*Capra pyrenaica*), and 5 different subspecies of *Capra ibex*: alpine Ibex (*C.i. ibex*), Siberian ibex (*C.i. sibirica*), Nubian ibex (*C.i. nubiana*), Walia ibex (*C.i. walie*) and West Caucasian tur (*C.i. caucasica*).

Capra ibex originated during the Riss glacial stage, in the Pleistocene, and reached its maximum expansion during the Wurm glaciation, occurring throughout the Alps and the neighbouring territories. In Italy, during the Wurm period, ibex were distributed also in the Apennines. At the end of the last glacial stage, alpine ibex remained confined to all Alps, from France to Slovenia. The number of ibex decreased sharply throughout the Alps during the 16th-19th century due to overhunting. Alpine ibex was hunted for its meat, for the trophy, but also because it was believed that its blood and certain body parts had pharmaceutical properties, or could be used as talismans.

The introduction of firearms in the XVI century was particularly detrimental for the species, that, as all *Caprinae*, have a flight response in which it flees to steep cliffs : this is an effective antipredatory strategy against ground predators, but not against firearms. By the XVIII century, ibex disappeared from the majorityof the Alps, and by the beginning of the XIX century,the Alpine ibex was on the verge of extinction, with an extremely small population (about 100 individuals) surviving in the north-western Italian Alps. In 1821 the king of Savoy proclaimed the first banning of hunting for ibex. In 1856, king Vittorio Emanuele II reserved the exclusive hunting rights of Alpine ibex for himself, establishing a Royal preserve. In order to prevent poaching, a unit of royal gamekeepers was created from local villagers. Owing to the strict control of poaching from that time on, the population of Alpine ibex in the Gran Paradiso area recovered rapidly even with royal hunting continuing. In 1922 the preserve was transformed into a protected area, the first national park in Italy, Gran Paradiso National Park. The following recovery of the species can be considered an exemplary history of conservation success: thanks to active conservation strategies (many reintroductions were performed), hunting restrictions and natural colonization processes (Stuewe & Nievergelt 1991) during the rest of the XX century the species reoccupied part of its original alpine range and increased in abundance. Today alpine ibex is no longer at risk of extinction, it is classed as “Least Concern” by IUCN (Temple and Terry 2007). Currently alpine ibex occur in Austria, France, Germany, Italy and Switzerland. In Italy, following the National law 157/92 hunting is not allowed for alpine ibex, thought a few heads are legally shot every years for control operation in the autonomous province of Bolzano (Apollonio et al. 2010). According to the survey conducted by the Institute for Environmental Protection and Research (ISPRA) the estimated total Ibex population in the Italian Alps in 2005 was about 15,000 individuals (Carnevali et al. 2009). The Ibex is currently present throughout the Italian Alps, from the Tarvìsio area (Friuli-Venezia Giulia) to the Maritime Alps (Piedmont). However distribution is still extremely fragmented (Duprè et al 2001, Pedrotti et al 2007, Carnevali et al 2009), and, especially in the eastern Alps, far below the potentiality (Boitani et al. 2002, Carnevali et al

2009). It is possible to identify 53 different colonies. Many adjacent colonies merged in the last decades, indicating a positive connectivity. The number of colonies is equally distributed between the central-western Alps (29 colonies) and the eastern Alps (24). However, the largest populations are located in the central and western Alps (Carnevali et al. 2009, Figure1).

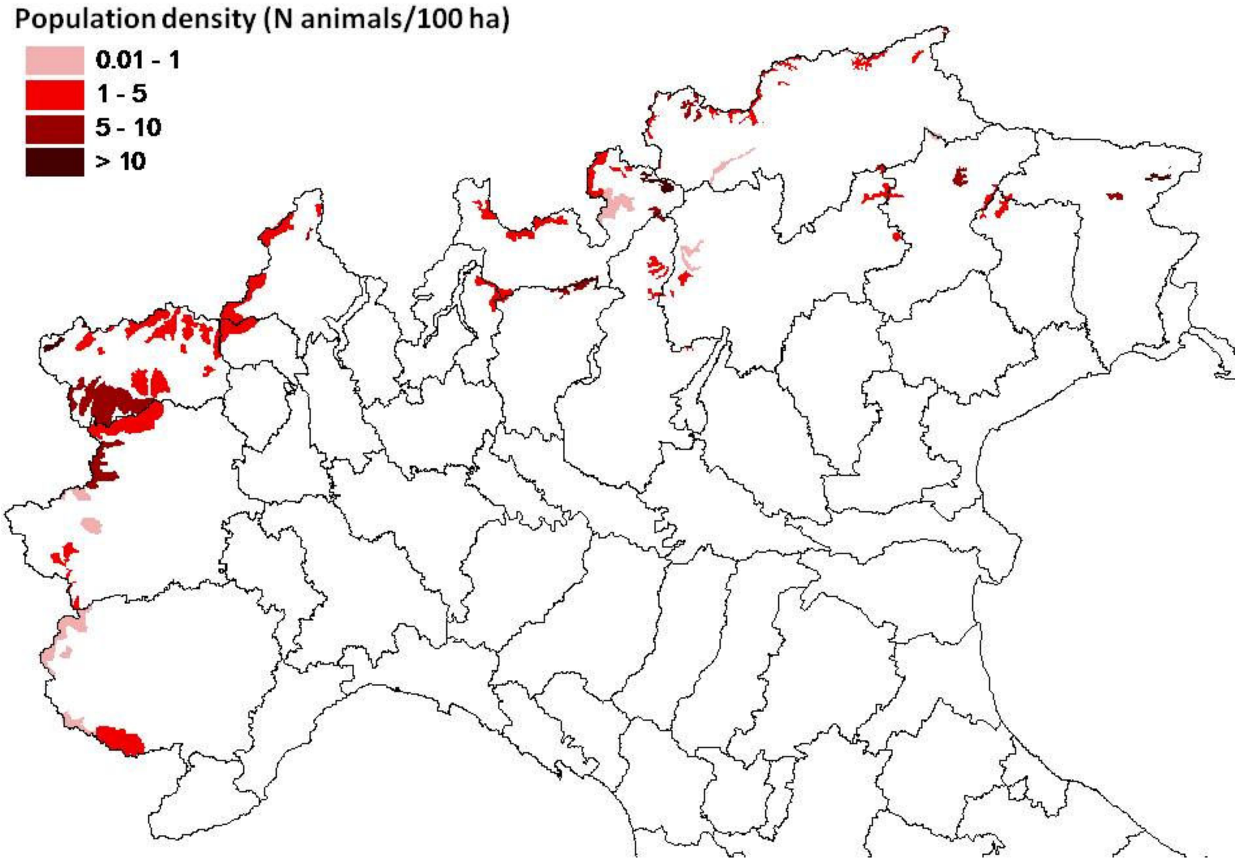

Figure 1: Distribution and densities of the Ibex populations present in the Italian Alps in 2005 (source: Carnevali et al. 2009)

3.2. Notes on the biology of Alpine ibex

Ibex are characterized by a strong sexual dimorphism (Figure 2): sexes differ in body size and horn length. The body is heavy and supported by short and solid legs. Adult males generally weight 65- 100 Kg, but in late Autumn can reach 120 kg, while females weight 40- 60 kg (Giacometti et al. 1997). The horns of males are curved backwards and can reach a length of 98 cm; frontal surfaces are ribbed with prominent transverse ridges. Females have much shorter horns, reaching about 34 cm (Tosi & Pedrotti 2003). Horns grow continuously through life, and age can be determined by counting the yearly horn increments (Couturier

1962). Ambient temperature and plant phenology influence horn growth (Giacometti et al. 2002, von Hardenberg et al. 2004). The coat length varies seasonally, being short and fuzzy during the summer and growing thicker wool and long guard hairs during the winter, winter coat is shed in April-May, while winter coat regrow in September.

Breeding occur once a year in December-January. Mating system is polyginous (Loison et al. 1999b). Sexual maturity, form a physiological point of view, is reached at 1.5 years in both sexes (Couturier 1962). However, age of primiparity in females is delayed to a later age in response to population density (Parrini et al. 2009), and in males reproductive success is mainly regulated by the acquisition of a dominance relationship (Willish 2009). Gestation is 167 ± 3 days (Couturier 1962).

Life history strategy is conservative: body growth is slow and prolonged through life. Ibex exhibit

the typical survival pattern of large herbivores with a very high prime aged adult survival, but survival of yearling and males is much higher than in other large herbivores (Toïgo et al. 2007).

Figure 2: Adult male (M88) lip-curling at an adult female in the Marmolada massif area.
Photograph by Vittorio Poli.

Alpine ibex typically inhabit open, rocky habitats at high altitude, above the tree line. The species is highly adapted to rocky environments, thanks to the morphology of the hoofs, clearly adapted to climbing. Alpine ibex have an almost completely herbaceous diet: it is a typical grazer with a certain degree of selectivity (Hofman 1989).

Ibex are highly gregarious, and sexes are spatially segregated (Ruchstül & Neuhaus 2001, Villaret et al. 1997). Outside the mating season, ibex live in separate male and maternal (females with young and subadults) herds (Toïgo et al. 1995, Villaret & Bon 1998).

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Chapter 1:
Study area and general materials and methods

1. STUDY AREA

The Marmolada group is located in the mountain range of the Dolomites, in the north-Eastern Italian Alps. The group encompasses two different administrative units: the province of Belluno, Veneto region, and the autonomous province of Trento. The group is composed by 8 subgroups and chains: the Marmolada massif, which gives the name to the entire group, the Padon chain, the Colac-Buffaure subgroup, the Ombretta-Ombrettola subgroup, the Cime dell'Auta chain, the Vallaccia subgroup, the Monzoni subgroup and the Cima dell'uomo chain (Figure 1).

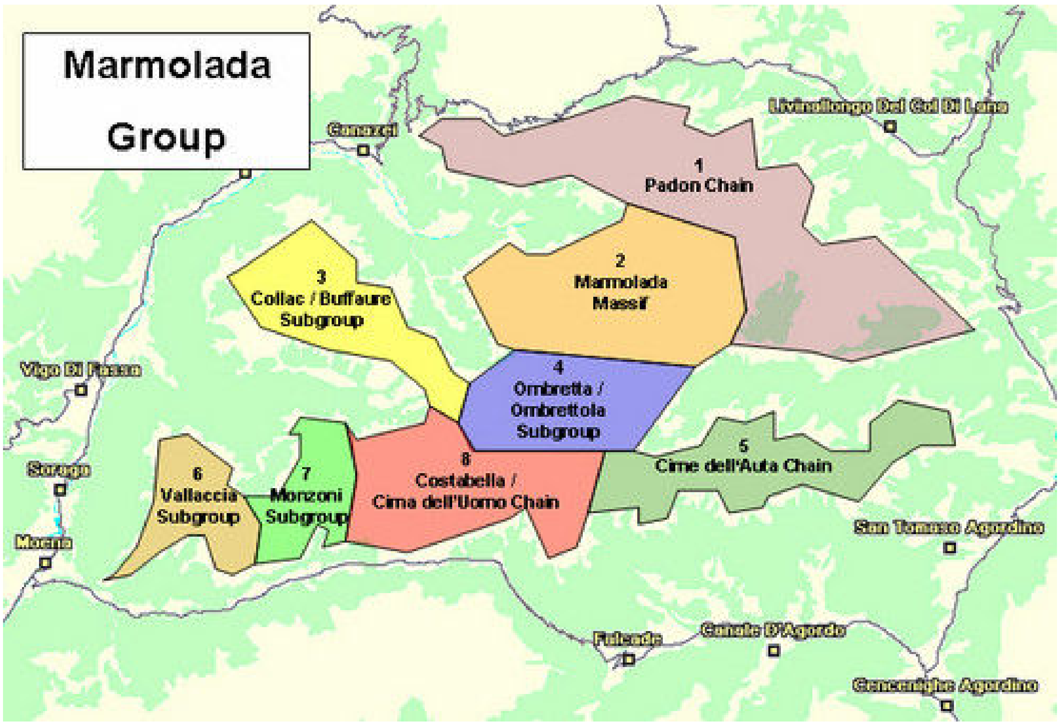

Figure 1: Overview Map of the Marmolada Group; subgroups are indicated in different colours source: http://www.summitpost.org/marmolada-group/152899

The area extends over about 150 km^2. The eastern and southern boundaries are represented by deep valleys (the Falcade and Cordevole valleys). The main peaks are: Punta Penia (3,343 m a. s.l.), Punta Rocca (3,250 m a.s.l.), Monte Serauta (3,009 m a.s.l.),all in the Marmolada massif, Cima dell'Auta (2,623 m a.s.l.), Padon (2,520 m a.s.l.) and Cima dell'Uomo (3,010 m a.s.l.). The group is characterized by steep mountains with a high ridge complexity. The main ridge axis orientation is east-west. Mountains are composed by dolomitic limestone, thought volcanic rocks and grey limestone are also present. A glacier lies at the summit of the Marmolada mountain, but it covers less than 2% of the total area (Duprè et al 2001).

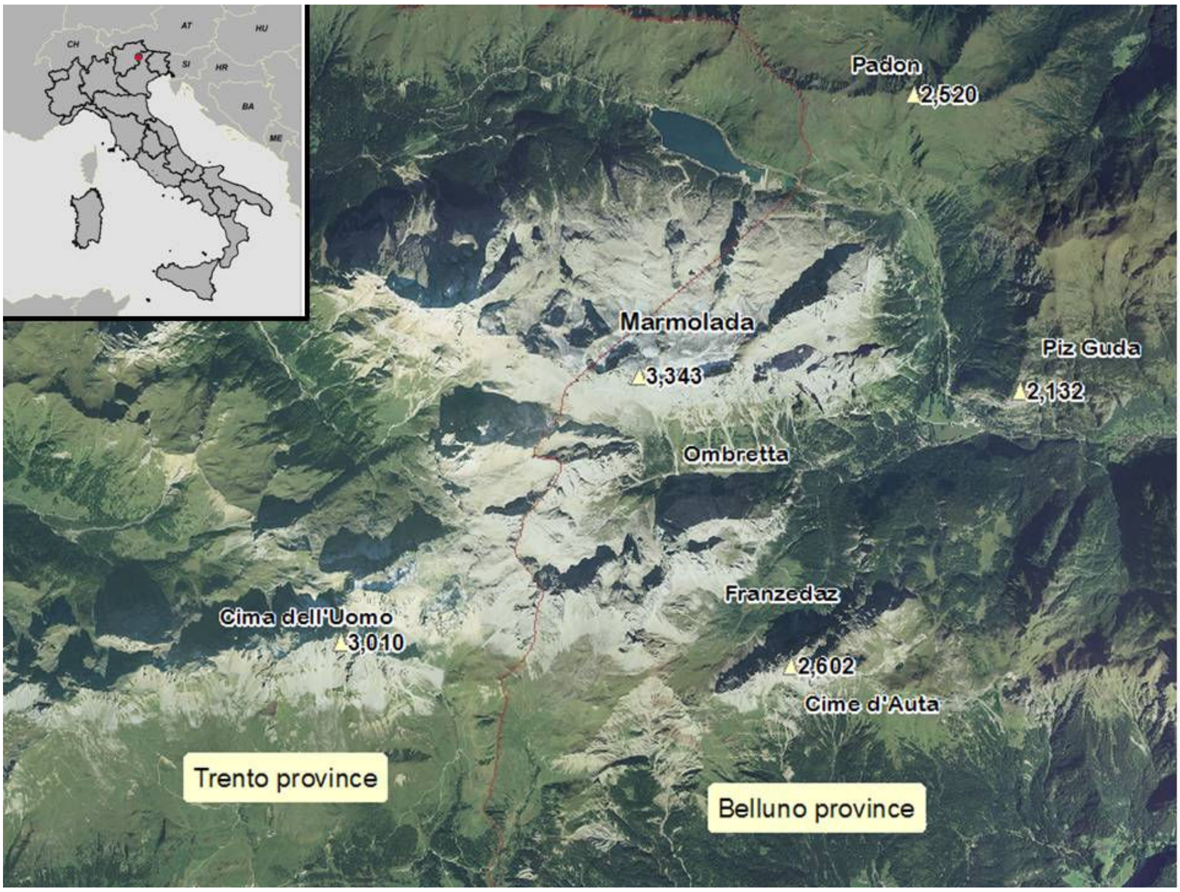

Figure 2: Map of the study area and its location in Italy; the red line indicate the boarderline between the Belluno province and the autonomous province of Trento.

At lowest elevations vegetation is mainly represented by mixed woodlands made by common beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*) and sycamore maple (*Acer pseudoplatanus*) interspersed with Norway spruce (*Picea abies*). At higher altitudes (>1600 m) woodlands are mainly composed by Norway spruce and larch (*Larix decidua*). Above the timberline (1900 m) vegetation is mainly represented by alpine meadows and shrubs as mountain pine (*Pinus mugus*), hairy alpen rose (Rhododendrum hirsutum), willows (Salix sp.), and green alder (Alnus viridis). Greenlands are composed by different herbaceous species (Sesleria varia, Carex sempervirens, Nardus stricta, Carex firma). Other large herbivores species present in the area were chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), mouflon (*Ovis gmelini musimon*).The study area is intensively used for touristic activities, such as skiing and hiking. Selective hunting is allowed for all ungulate species present except ibex. Several alpine pastures grazed by domestic cattle are present during summer. No large mammalian predator was present in the study area, except an occasional Brown bear (*Ursus arctos*) presence during summer

2009. Golden eagle (Aquila chrysaetos) are regularly present in the area and may predate ibex kids.

2. CAPTURES AND DATA COLLECTION IN THE FIELD

Ibex were immobilised with with xylazine hydrochloride (Rompum ®) injected by dart gun (Bassano et al. 2004, Dematteis et al. 2008). During handling time, ibex were hobbled, blindfolded and placed in lateral recumbency, marked with a unique color combination of ear-tag, and when possible weighted. Age was estimated by horn notches and tooth eruption and wear. Blood samples were collected from the jugular vein. Anaesthesia was monitored to assess signs of stress related to capture and reversed using atipamezole (Antisedan®). In 2002-2009 a total of 95 males and 46 females were captured in the study area, of those 31 males and 23 females were equipped with a VHF radiocollar. In 2006-2007 14 male ibexes and 2 females were captured in the Jof-Fuart massif, in the Giulie Alps (46°25'49" N; 13°29'38"E). They were then ear-tagged, equipped with a radio-transmitter, placed on a stretcher and carried to the nearest vehicle to be transported into individual wooden cages to to a stable, where they were housed until transportation to the study area, where they were released.

Field work was conducted from September 2003 to the end of August 2009 in the frame of two different studies (see chapter 3 for details). Radio-tagged ibexes were located mostly by sightings, and also by triangulation with a portable receiver and a hand-held yagi antenna. In 2003-2006 the area was also surveyed on a monthly basis with pedestrian transect, during which no radio device was employed for locating collared ibexes. Once located the animals, the estimated position was reported into a map of the study area (1:10000 scale). For each sighting we recorded: group size and composition (age class and sex of individuals) and the kind of habitat (vegetation and geomorphology) occupied by the group. For individual identification we used a 60x magnifier telescope (Swarovski CT85). Sighting were georeferentiated in ArcView 3.2 (ESRI ®) and stored in a Access (Microsoft ®) database. In 2003-2006 3,261 locations were obtained by triangulation, and 2,474 by visual sighting. In 2006-2009 2,805 sightings were obtained.

3. STATISTICAL ANALYSIS

Statistical analysis were conducted using R version 2.9.2. (R Development Core Team 2009) for windows and SAS ®version 9.1 (Copyright SAS Institute Inc.). Spatial analysis (including map digitalization) were conducted with the software ArcView GIS 3.2 and ArcGIS 9.2 (ESRI ®), while habitat analysis were performed using the package Adehabitat fo R software (Calenge 2006). CMR analysis were performed with M-SURGE (Choquet et al. 2004).

Detailed descriptions of the analysis performed are provided in the "Materials and method" section of each chapter.

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Chapter 2:

History , status, distribution and evolution of the ibex colony of the Marmolada

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The aim of this introductory chapter is to give some information on the distribution and demography of the alpine ibex colony of the Marmolada massif and provide some management tips. We will present here an overview of how ibexes used different parts of the study area as well as some demographic indexes derived from count data and transects.

The ibex colony of the Marmolada massif was established in 1978 with the release of 6 animals (3 males and 3 females) coming from the Gran Paradiso National Park (GPNP). In the following summer, other 4 individuals (2 males and 2 females), also captured in the GPNP, were added to the neo-colony. The population increased regularly and in 2002 the estimated population size was 456. In winter 2003/2004, characterized by exceptional snow precipitations, the population was affected by an epizootic of sarcoptic mange, a disease caused by the submicroscopic mite *Sarcoptes scabiei* var. *Rupicaprae*, and carried in the area by the chamois (Rossi et al. 2007). At the end of winter the colony was strongly reduced in numbers, and the province of Belluno, in collaboration with the University of Torino prompted an action plan with the aim of limiting the short-term effects of the epidemic. At this purpose ibexes were captured and injected with a 1% solution of ivermectin (Ivomec®, Rossi et al. 2006). Between 2006 and 2007 a restocking project was started and 14 adult males were translocated from the Jof Fuart-Montasio (Giulie Alps) in the study area (Rossi et al. 2006).

The Marmolada population has been strictly monitored from summer 2003 up to summer 2009 by two different projects conducted by different institutions. The first study, funded by the Trento province, was conducted in 2003-2006, and aimed to assess demographic and sanitary issues related with the insurgence of sarcoptic mange in the population (Monaco et al. 2005 b). During that period radio-telemetry monitoring, as well as monthly transect were conducted. From 2006 a second study jointly designed by the University of Padova and Torino was started (Scillitani et al. 2009). The population has been regularly surveyed to monitor post release behavior of collared translocated individuals and establish a comparison with resident individuals. Details of captures and data collection are provided in the general overview on material and methods in the introductory chapter of this thesis.

Distribution

The sightings and radio locations obtained in the entire study period (2003-2009) allows to draw with accuracy the distribution of ibexes on the massif (figure 1). The population occupy an overall area of about 140 Km^2. Few exchanges with neighboring colonies have been documented, indicating the overall site fidelity of the colony. In fact, since 2003 only two cases of dispersal of marked animals have been documented. In 2004 a male from the new-funded colony of Paneveggio-Pale di San Martino Natural park (about 20 km south-west from the Marmolada massif) joined the Marmolada colony (Monaco et al. 2004), and a male captured in 2008 in the Marmolada massif was observed in 2009 in colony of the Sella Massif (about 10 Km north west from the Marmolada, Brugnoli S., *personal communication*).

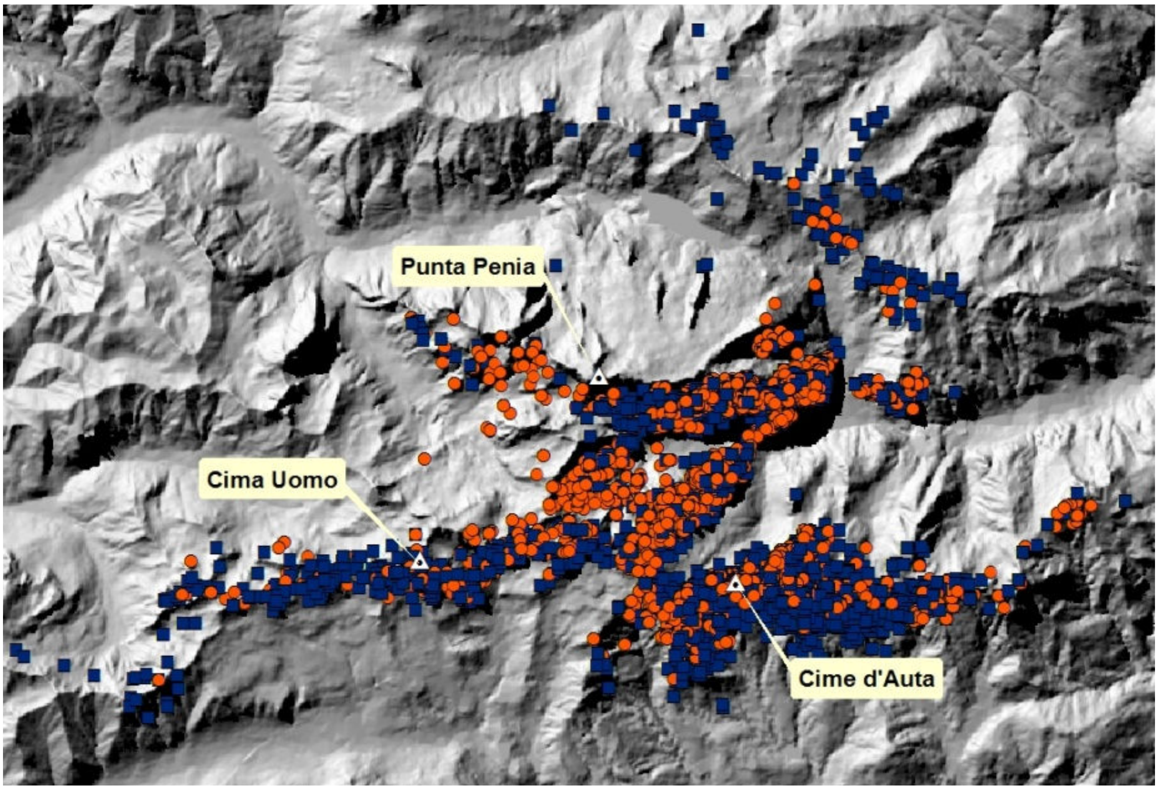

Figure 1: Sightings collected for females (red circles) and males (blue squares) in 2003-2009

As generally observed in ibex (Tosi & Pedrotti 2003), it is possible to distinguish wintering areas and summering ones. Ibex are highly dimorphic and sexes are ecologically segregated except during the winter months, when rut occur (Villaret & Bon 1995). In the Marmolada massif area, in contrast to what reported in other populations (Girard 2000) most ibex, especially males, do not travel considerable distances to reach their summer range, but rather make altitudinal movement within the same mountainside. Nonetheless, wintering areas are smaller than summering ones, and localized in two main subgroups (Ombretta and Auta) with south facing slopes rich in grassland (figure 2).

Ranges occupied by males and females overlap throughout the year, but core areas remain distinct, and they were observed in mixed herds mostly during winter. Moreover, outside the

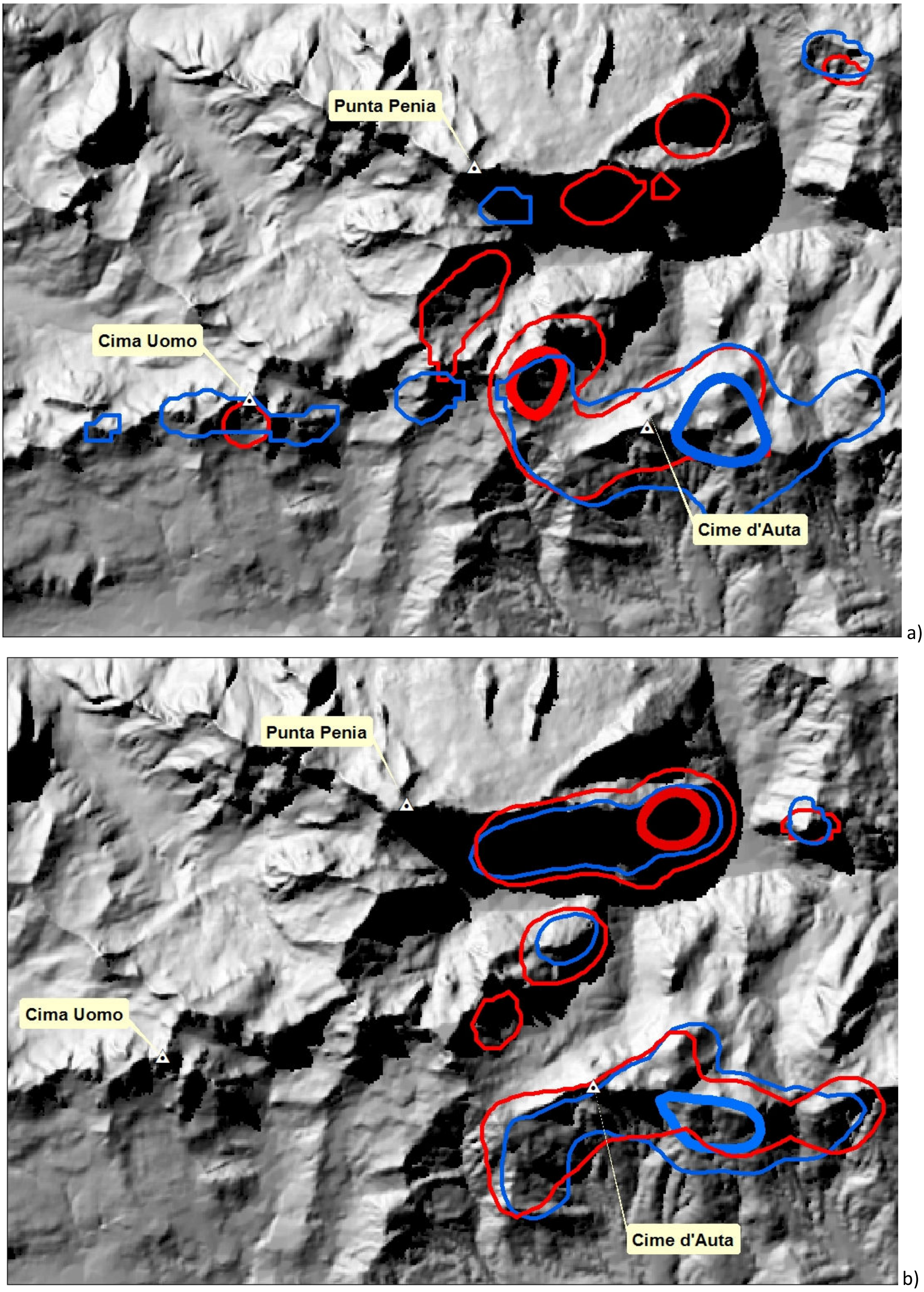

Figure 2: Summer (a) and winter (b) ranges occupied by ibexes in the Marmolada massif computed with 95% kernel estimators. Blue polygons refer to males, red ones to females. Core areas (50% Kernels) are represented with bolded contour.

rutting season, although they roam over the same areas, they select different environments: males use predominantly high-altitude grassland, and females rocky slopes. This has been reported as well in other population as well, and the stronger sselection of rocky environments exhibit by females can be explained as an antipredatory strategy (Grignolio et al. 2007). It is interesting to notice that females have a different core area in winter and summer, while the core area of males is always located in the Cime d'Auta chain.Despite the experienced change in density during the sudy period (see section "Demography and status" below) ibex showed a quite strong yearly site fidelity toward their summer and winter ranges. As an example, winter ranges of males are shown in figure 3. In winter 2005/2006 and 2006/2007 the winter range was larger, and this can be explained partially by the fact that both those winter were relatively short and snowpack depth was lower than in other winters, and partially because of some differences in the sampling intensity that results in different shapes of the estimated kernel. A similar site fidelity was observed for summer, and also females showed an high site fidelity in the overall study period.

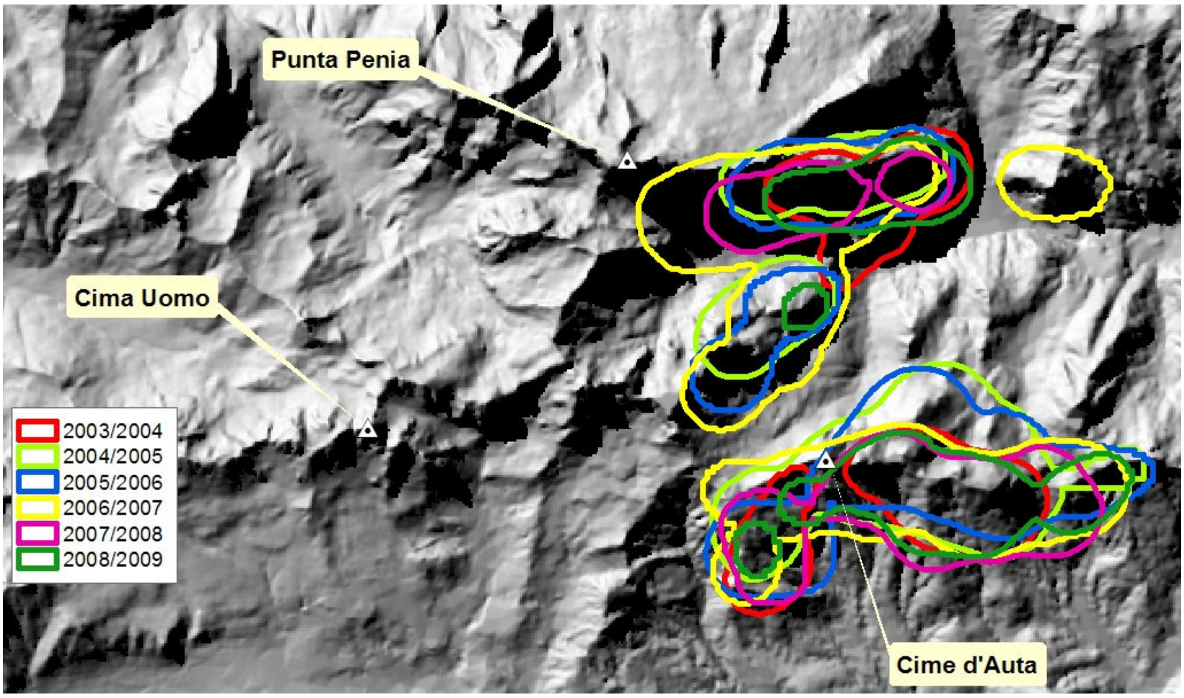

Figure 3: Wintering areas occupied by males in the study period.

Demography and status

Ibex were regularly counted from 1978 up to 1994, afterwards the yearly counts were irregularly performed (in 1996, 2000, 2002), until 2004, after the die off, when they were resumed and conducted regularly each year (figure 4). Counts are performed once in a year in summer with the ground count method (or block census- Maruyama & Nakama 1983). The area is divided into several blocks using features such as ridges, roads, streams and foot paths as boundaries. Within each block observers count ibexes using binoculars and telescopes from vantage point or while conducting transects on foot. Observers surveying different blocks are in contact via radio or mobile phone in order to communicate any displacement of animals that might result in a double count. All individuals sighted are recorded according to sex and age (kid, yearling, 2-10 years old, more than 11 years old and unidentified). In 2008-2010 also the number of marked individuals within a group was recorded and, when possible marked individuals were identified (in 2010). Since the Marmolada massif encompasses both the Belluno and the Trento province, counts are performed contemporaneously by the two administrations. Observers are local game keepers (Forest and Wildlife Service of province of Trento, and "Corpo di Polizia provinciale" province of Belluno) members of hunter associations ("Associazione cacciatore trentini") volunteers and, during 2003-2009, research personnel involved in fieldwork activities.

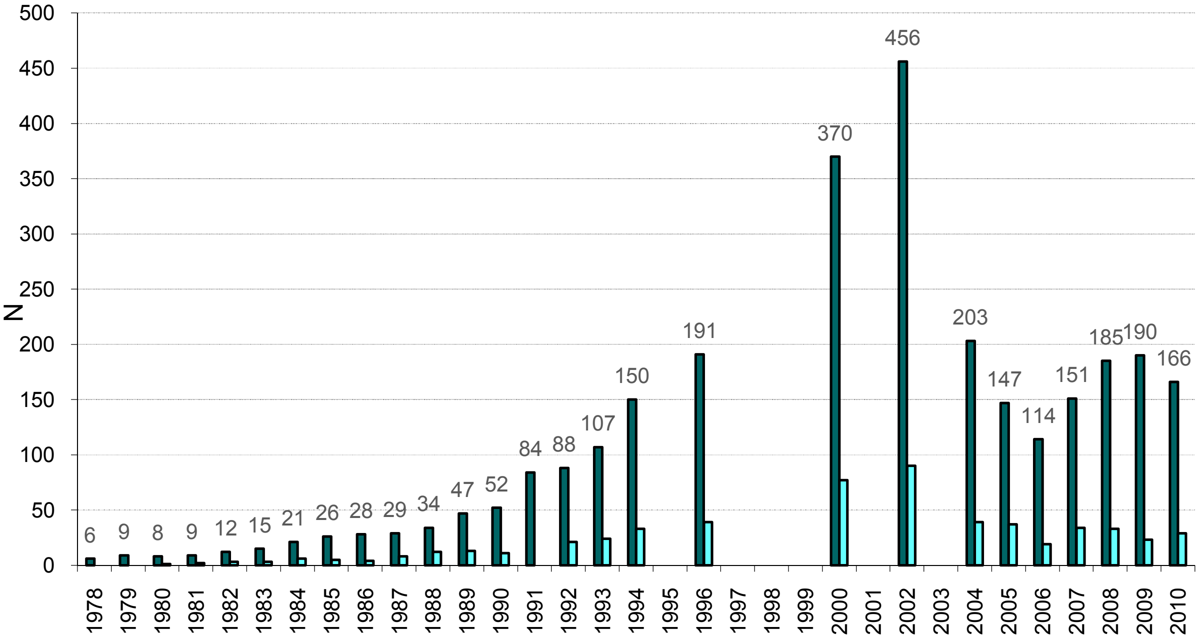

Figure 4: Yearly population counts conducted with the block census method in the Marmolada massif. In dark blue total number of animals counted, in light blue the number of kids. (Data taken from Monaco et al. 2005 a, and furnished by the Corpo di Polizia Provinciale, Province of Belluno)

The ensemble of data provided by the counts and by the entire monitoring program consent to delineate some demographic index, useful to understand the colonization process as well as the consequences of the die off on population structure, thought the analysis highlighted as well several problematic issue inherent to the way count are performed, that will be briefly discussed.

After its fundation, the population exhibited an exponential growth that it is typical for colonizing populations (Caughley 1977, Loison et al. 2002). In 1978-1994 (when annual count were regularly performed each year) the estimated growth rate was 1.21 when estimated by regressing the log transformed annual counts against time (figure 5), and 1.24 when estimated as the mean of the ratio of counts in t+1 to counts in t. This growth rate is high and proximate to the maximum rate of increase for ibex, which is 1.30 (Loison et al. 2002).

For the following period we did not calculate any trend since the counts were performed too irregularly. This is unfortunate as it is not possible neither to assess whether in 2003 the population was still in its exponential growth phase or already started to stabilize, either to have an estimation of the population size prior to the population crash. From the count data obtained in 2002, 2004-2010, we computed some simple indexes on sex ratio and number of kids per females (table 1) that might be useful to understand the effect of the crash on the population structure, and to critically evaluate counts. The population structure estimated by counts is reported in figure 6.

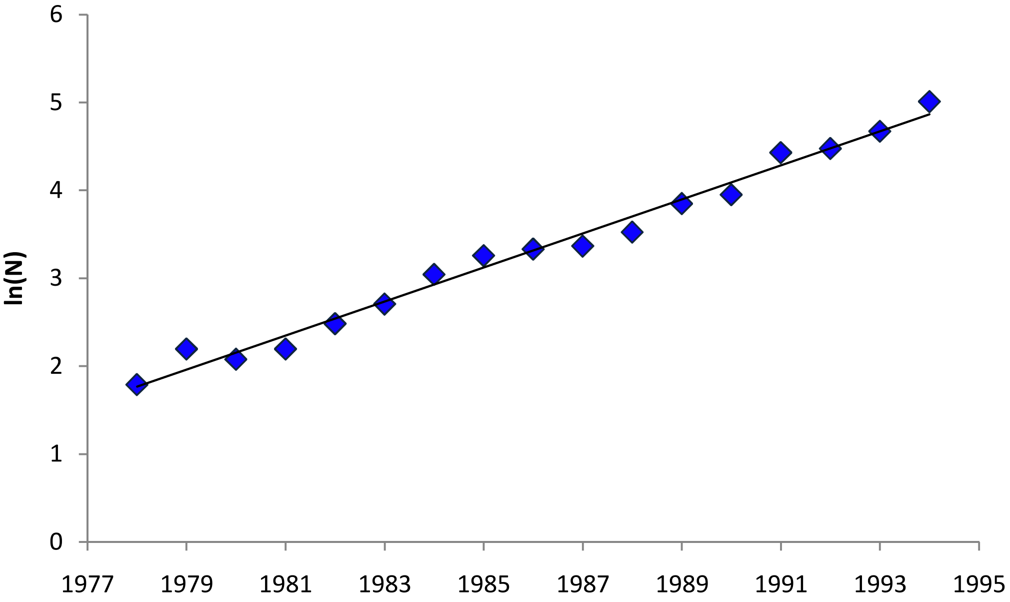

Figure 5: Trend of the log-transformed population counts performed in 1978-1994, with the regression linear curve best fitting the data.

Table 1: Total number of females, males, kids, yearlings and undetermined individuals counted in the Marmolada colony in 2002 and 2004-2010, and relative sex ratio and kids per females ratio.

Year	N females	N males	N Yearling	N Kids	Undetermined	Sex ratio (M/F)	kids/F
2002	133	176	39	90	18	1.32	0.68
2004	104	61	3	39	1	0.59	0.38
2005	57	33	12	37	8	0.58	0.65
2006	38	39	12	19	6	1.03	0.50
2007	67	33	12	34	5	0.49	0.51
2008	57	62	22	33	11	1.09	0.58
2009	54	79	32	23	2	1.47	0.43
2010	49	77	11	29	0	1.57	0.59

The detailed examination of the estimations obtained by count highlights several flaws associated with ground counts in Marmolada. In example in 2007 only 33 adult males were counted. From data on marked ibexes, we know for certain that at that time in the population at least 69 prime aged males were present in the population. It is therefore evident the high underestimation of population size, at least of the male segment of the population. As a result of this wrong estimation also all derived statistics are unreliable. The underestimation of the population size obtained by ground counts is clear also in the following years, when we have at our disposal also the number of marked animals sighted. In fact in example in 2008 only 32 marked males were sighted, when the number of marked males were 82. The number of marked females sighted was even lower: only 5 when 37 marked females were present at that time in the population. Similar results has been obtained in 2009 and 2010.

Some simple statistics can be derived from data collected with transect walk in 2003-2006. Figure 7 represents the observed proportion of senescent ibex (males older than 11 years of age and females older than 13 years of age) as respect to prime aged ones.

There was a sharp decrease in the number of senescent males sighted: in 2005 in 2006 no sightings of males older than 13 years was reported. Although we cannot exclude that some old male still occurred in the population at that time (senescent ibex are solitary and can be more difficult to spot) it is clear from this graph that this segment of the population was the most affected by the die off. Also sightings of senescent females showed a negative trend, thought is less accentuated than that of males.

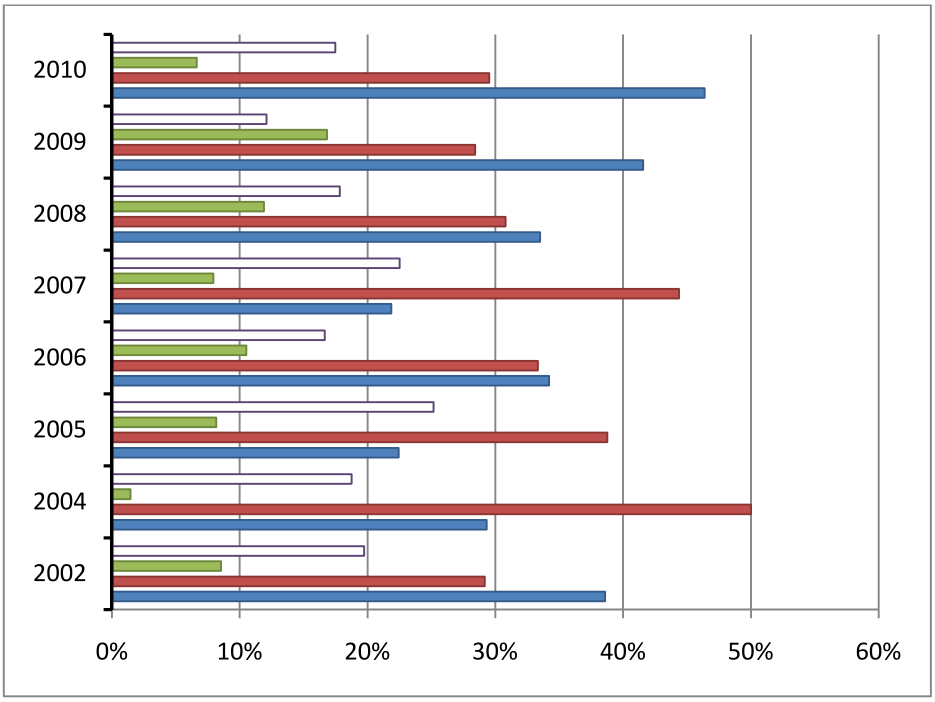

Figure 6: Population structure of the ibex colony in Marmolada as determined by ground counts performed in 2002 and 2004-2010. In blue males, in red females, in green yearlings and in white kids.

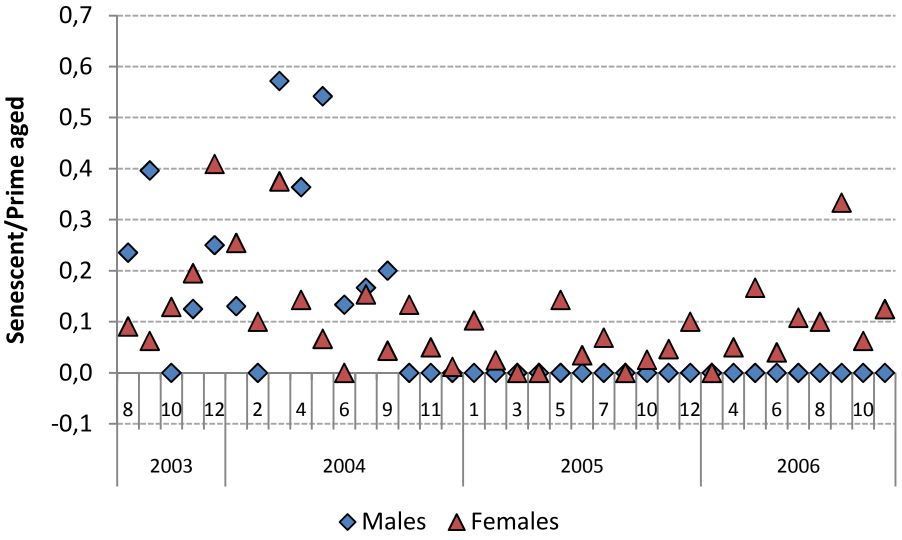

Figure 7: Proportion of Senescent and Prime age adults seen in the monthly transect surveys conducted in 2003-2006

A rough estimate of recruitment can be derived computing the monthly proportion of kids per females (Figure 8). The proportion show a negative trend when considering the whole period (slope of the linear regression=-0.004, R2=0.09, p=0.07) but no significant variation was found in the three years. However, when comparing 2003 and 2004 the negative trend was stronger suggesting a marked negative effect on reproduction in 2004 (Monaco et al. 2005b). In 2005 and 2006 the proportion of kids per females remain constant and lower than in 2003, suggesting that a prolonged effect of the epizootic on recruitment. Unfortunately, the lack of data on reproductive performance of marked females on regular intervals prevent from delineating a more precise index of variation in recruitment.

An estimation of the trends of abundance of large herbivores can be as well achieved by utilizing ecological indicators (Morellet et al. 2007): in particular, in Alpine ibex male group size can be a good proxy of variation in population density (Toïgo et al. 1996): the higher the density the bigger the group size is. We retained only the observation collected from June to October, because in that period the study area was more intensively surveyed; in addition in winter groups tend to be smaller and during rutting season the number of solitary males increase.

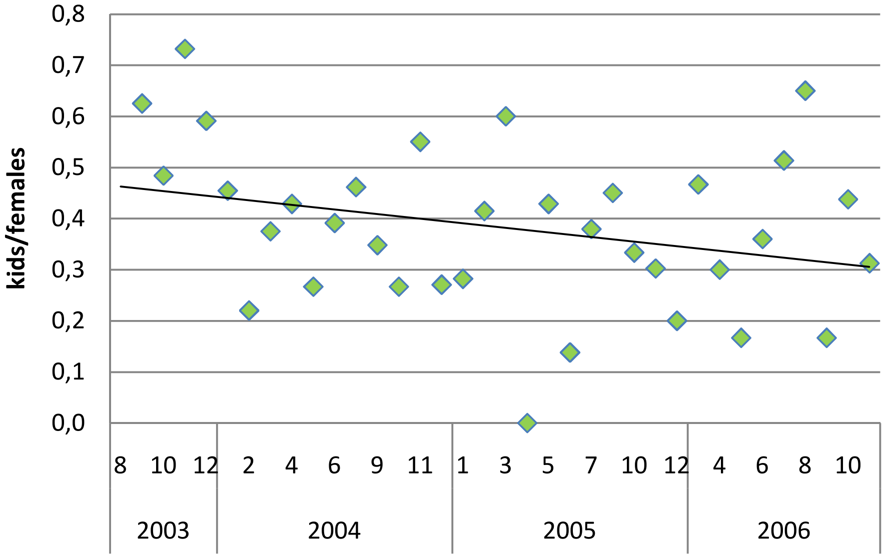

Figure 8: Proportion of kids and prime aged females seen in the monthly transect surveys conducted in 2003-2006

The mean group size follow an evident pattern of variation, with a steady drop in 2004 (Figure 9), corresponding with the population crash. The same pattern was observed when computing the typical group size (TGS, Jarman 1974) that quantifies the group size experienced by an average individual (Table 2). The Kruskal-Wallis test confirmed a significant variation of group size over the 7 years of study (H=118.82, df=6, p<0.001). The post-hoc pairwise comparison, made with the Mann-Whitney U-test, highlighted how group size observed in 2004 was highly significantly different ($p<0.001$ in all pairwise comparison) from all other years. It is very interesting to notice that in 2004 the proportion of solitary males was very high, though some rare observations of large groups still were possible (Table 2). The group size observed in 2003 was highly significantly different from group size observed in 2004-2006, and significantly different from group size observed in 2008 ($U=10,575$ $p=0.02$) and 2009 ($U=4,602$ $p=0.05$). The trend observed suggest a gradual increase in population size, not confirmed by data obtained with ground counts.

Table 2: Typical group size, maximum value of group size observed and proportion of solitary males sighted in June-October over the entire study

Year	TGS	Maximum Group size	% solitary males
2003	26.59	54	17%
2004	7.27	23	46%
2005	11.66	24	27%
2006	16.24	28	15%
2007	15.26	37	19%
2008	21.30	36	18%
2009	22.72	37	34%

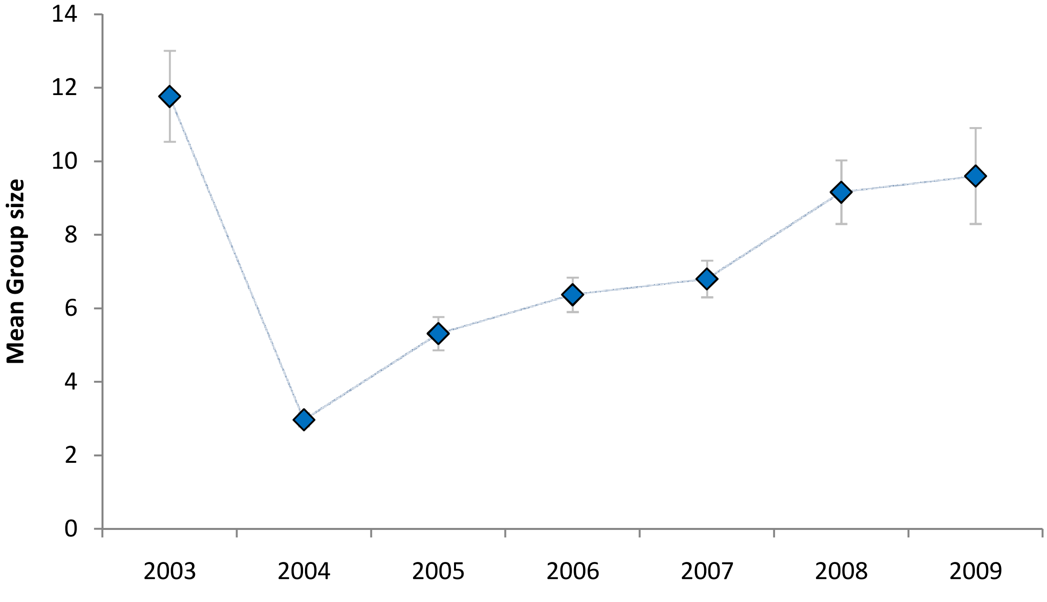

Figure 9: Mean male group size observed in June-October during the study period. Error bars represent standard errors associated with the estimates

CONCLUSIONS

In the study period, ibex showed a marked fidelity to their summering and wintering area, as demonstrated by the high overlap of kernels computed in different years. This is interesting considering that the population dropped in number and we might expected also a contraction in the range occupied. The senescent individuals in the population were those most affected by the high mortality experienced by the population in 2004, although a more detailed investigation on this topic is required, and will be developed in chapter 3, with the estimation of survival rates with respect to age and sex. Our data indicate as well a negative trend in recruitment, thought unfortunately, without a regular assessment of female reproductive success estimated on a representative sample of marked females, we are impeded to assess this trend with precision.

The descriptive analysis summarized in this chapter allows to make some critical evaluation on the actual monitoring of the colony. The assessment of population size and the monitoring of changes in abundance over time are fundamental prerequisites for choosing the right management action and assess the performance of the actual management strategies (Lancia et al. 2005, Synclair et al. 2005). Therefore the improvement of counting technique should be a priority both for managers and for scientists, in the perspective of adaptive management (Yoccoz et al. 2001). However, to be useful, population counts need to be accurate and precise. Biased and highly imprecise estimations can lead to wrong conclusions and end up in erroneous decisions (Garel et al. 2005). Estimating population size with low bias is difficult: sometimes even repetitions leads to an increase in precision that not necessarily coincide with accuracy (Lancia et al. 2005). Nonetheless in many cases, even when counts give unbiased estimates, population size alone provide no information on the underlying demographic processes as individual performance, reproductive success, survival, emigration/immigration…etc… (Morellet et al. 2007). Precision and accuracy of an estimates are affected by the probability of detection of individuals and by the sampling efforts. In the case of ibex, the most important factors affecting the quality of the estimation are different sightabilities by terrain, behavior of animals (in terms both of grouping and spatial behavior), changes in weather conditions and survey effort. Alpine ibex live in open habitats situated above the tree line, and therefore are considered relatively easy to spot, if compared to similar sized ungulates inhabiting forested habitats. For that reasons censuses are generally performed by ground counts (some published examples of other populations surveyed with ground counts: Girard 2000, Jacobson et al. 2004, Largo et al. 2008, Pedrotti 1995). In the Marmolada colony, as well as in other populations (Largo et al. 2008), ground counts are performed only once a year since managers assume that one count is sufficient for providing an accurate counts. However, this assumption is wrong for at least two reasons. First of all, although ibexes inhabit open areas, sightability in rocky environments is not forcedly high (due both to the accessibility to human observers and to the mimetic coat of ibex, likely to be confounded with rocks, at distance) and individuals can be missed resulting in an underestimation of population size. A comparison of population sizes obtained by ground counts and CMR estimate highlighted how estimations obtained with ground counts can lead to a rate of underestimation of 20-60% . Furthermore, the rate of underestimation increased as population size increased (Toïgo 1998), indicating that ground count may give a reliable estimates of the population size only when the population is at low density and in the colonization phase. Also in the Marmolada colony, as shown by the graph in Figure 5, count data collected on a regular basis in the colonizing phase were effective to estimate population trend, though unfortunately we did not have at our disposal data on the population structure.Nonetheless, the level of underestimation is highly variable among populations: a study conducted over 6 populations living in protected areas showed that estimates obtained with ground counts could lead to acceptable results, though inaccurate counts occurred as well (Largo et al. 2008). Secondly, conducting only one survey per year is incorrect because when there are no repetitions it is impossible to have a measure of variation. Sampling design lacking proper replication, not only may results in biased estimates, but also prevent from a reliable statistical analysis of data obtained (Lancia et al. 2005, Williams et al. 2002). The repetition of counts allows to computing standard error and confidence intervals associated to the estimation and allows to define the sampling effort needed to increase precision of the estimates, as well as computing index as the minimum number of animals alive in the population (Fattorini et al. 2007, Loison et al. 2006).

We wish to emphasize the need for an improvement of censuses in Marmolada, because as pointed out by Largo et al. (2008) the presence in a time series of only one inaccurate value, compromise the overall estimated growth rate. In the present study the presence of biased counts, the absence of a regularly collected time series count and the lack of repetition compromised the assessment of reliable population trends, especially when the population was at its highs and in the post epidemic phase when inaccurate counts may prevent from assessing the real entity of the die off.

Among the methods at disposal for estimating wild animals numbers, capture mark recapture (CMR) techniques are considered among the most reliable (Gaillard et al. 2003) also because they allow to estimate confidence intervals and detection probability (Yoccoz et al. 2001). To be effective and provide precise estimates a large sample of marked animals is necessary, and this normally constitutes a limit as the costs associated might be prohibitive (Morellet et al. 2007). However, since at present a good fraction of the Marmolada population is already marked, we strongly suggest to take advantage from it, and to keep on marking and sighting animals, as done in the census of 2010. We propose as well the adoption of several repetitions per years of ground counts. Moreover, during repeated surveys group size should be noted as well, since, as demonstrated by Toïgo et al. (1996) and highlighted with the simple tests presented here, group size variability over time can be a good proxy of the trend in abundance of population of ibexes.

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Chapter 3:

Survival estimates of Alpine Ibex in relation to disease, management intervention and weather variability. Preliminary results.

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INTRODUCTION

The change in abundance that occurs over time and the factors that influence that change are the subject of population dynamics (Skalski et al. 2005). Individual survival and reproduction are among the key parameters driving population dynamics (Krebs 2001, Williams et al. 2002). Diseases are important factors that can reduce individual fitness (Anderson & May 1978) and as a consequence population abundance and growth rates (Scott 1988). Disease is defined as a biotic interaction in which an individual host provides a suitable habitat for a disease agent (Krebs 2001). The impact of a disease is a complex process influenced by several factors related to the life history characteristics of both the host and the disease agent: virulence (or in the case of parasite, intensity of parasitization), immune-resistance of the host, rate of transmission, population density (Gortazar et al. 2006, Pérez et al. 2006). Mortality induced by a disease agent can be either compensatory either acting as an addictive effect therefore interacting with other major sources of variation in vital rates (Cross et al. 2009, Jolles et al. 2006, Pedersen & Greives 2008). In example, large herbivores population dynamic is affected by a complex set of interactions of several biotic and abiotic factors (Coulson et al. 2000, Gaillard et al. 2010), including habitat quality (Hobbs & Gordon 2010, Morales et al. 2010, Morrison et al. 2006), climate variability (Garrot et al. 2003, Loison et al. 1999 b, Moen et al. 2006, Mysterud et al. 2001, Owen Smith 2010), density dependence (Eberhardt 2002, Festa Bianchet et al. 2003, Fowler 1987), predation (Andersen et al. 2006, Messier 1991), stochasticity (Lande 1993, Sæther 1997). Large herbivores populations are strongly age-structured and different vital rates at different age stages respond differently to limiting factors (Loison et al. 1999 a, Gaillard et al. 1998, Gaillard et al. 2000). The role of diseases in wild ungulates population regulation is still understudied, due to the difficulties of monitoring. In free ranging animals it is in fact difficult to closely monitor the population and to know individual's history, as in the case of human and domestic animals (Gulland 1995). Often studies are started when the disease has already spread into the population and -especially in the case of epizootics- the outbreak has already caused a decline in population size, therefore it is impossible to establish causes of change in the pre-epidemic phase (Loison et al. 1996). Mortality may increase as a result of diseases (Cransac et al. 1997, Jorgenson et al. 1997, Loison et al. 1996, Monello et al. 2001). However it is difficult to disentangle the proportion of mortality due to diseases and other limiting factors. In example, Joly and Messier (2004) found an important regulative effect of predation on a bison population only when the prevalence of tuberculosis and brucellosis was high. Parasites and pathogens can increase host's vulnerability to predation by changing its skills to escape predators (Synclair et al. 2006): debilitated host may reduce flight ability or exhibit altered behavior (Milinski et al. 1990, Kortet et al. 2010, Raffel et al. 2008). Also climate stochasticity can act in synergy with diseases because debilitated animals are more likely to experience mortality due to inclement weather and vice-versa (Wilson et al. 2004).

Sarcoptic mange is a highly contagious infection caused by a submacroscopic mite of the species *Sarcoptes scabiei*. This mites burrow in the skin through the stratum corneum to the granulosum and spinosum. *Sarcoptes scabiei* complete all its life cycle within the host epidermis, triggering intensive itching and bacterial infection (Bornstein et al. 2001). Sarcoptic mange has been reported in more than 100 species of wildlife (Bornstein et al. 2001). In certain populations this disease can reach epizootic proportion, as reported for several mountain ungulate populations: chamois (Fernandez Moran et al. 1997, Rossi et al. 1995, Rossi et al. 2007), Iberian ibex (Leon-Vizcaino et al. 1999, Pérez et al. 1997, Sarasa et al. 2010), Barbary sheep (Gonzàlez-Candela et al. 2004). A sarcoptic mange otbreak caused by *Sarcoptes scabies* var. *rupicaprae* was first signaled in Austria, at the beginning of the XIX century. Since then, epidemic has been affecting chamois and coexisting alpine ibex populations in the Eastern Alps (Onderscheka 1982, Rossi et al. 1995). Since 1995, the epidemic front moved across the Dolomites, in Italy (Rossi et al. 2007), reaching the alpine ibex colony of the Marmolada massif in late 2003. This colony had been established in 1978 and 1979 with 10 individuals from the Gran Paradiso National Park (Italy) and in summer 2003 had become the biggest colony in the Eastern Italian Alps (Monaco et al. 2005 a). During Winter 2003/2004, characterized by extremely high snow depth and long persistence of snow cover in spring, the first mangy animals were sighted. In spring 2004 (April – May) the population experienced a dramatic crash (Monaco et al. 2005 b). In 2004- 2005 in the frame of an action plan promoted by Belluno province, ibexes were captured to receive a treatment with long-acting ivermectin (Ivomec ® Gold), a wide-spectrum antiparasitic drug (Rossi et al. 2006). From 2006 onward sighting of mangy animals were occasional, although the area was constantly surveyed for a study on spatial behavior of ibex. In 2009 and 2010 observation of mangy animals became more frequent and carcasses of affected animals were found as well, thought the mortality remained confined to few individuals.

Our aim here is to quantify survival rates of individual ibex in order to assess the outcome of the epizootic on individual vital rates, the relative effects of mange and climate and the influence of sex and age on mortality. Alpine ibex is a highly dimorphic species exhibiting a peculiar life history, characterized by slow body growth, high survival rates, late onset of reproductive success and a conservative reproductive tactic (Largo 2008, Toïgo et al. 2002, Toïgo et al. 2007). Survival of prime aged adult males is comparable to that of prime aged adult females: both sexes show a very high annual survival (95-99%) up to 10 years of age (Toïgo et al. 1997). Survival rates of yearling and males are higher than those observed in other ungulates of similar size (Toïgo et al. 2007). Senescent males represent the most sensitive segment of ibex populations (Toïgo et al. 2007), and are therefore more subjected to unfavorable environmental conditions. Harsh weather and density effects are reported to be the main regulating forces in healthy populations (Grøtan et al. 2008, Jacobson et al. 2004, Sæther et al. 2002). We expect therefore to find: 1) a mortality biased toward old males and young individuals and a lower impact on prime aged adults 2) a negative effect of winter harshness on survival: in particular we expect that winter 2003/2004 increased mortality acting in combination with mange epidemic, more than other similarly harsh winters occurring when disease was absent.

MATERIALS AND METHODS

Study Area

The study area was the Marmolada massif area, in the Eastern Italian Alps, (Dolomites - 46°26'13" N; 11°51'54"E). It encompasses about 150 km^2 and lies between 1200 and 3343 m a.s.l. The environment is typical alpine, with steep slopes even at low altitudes and characteristic dolomitic limestone rock. The main ridge axis orientation is east-west. Above the timberline (1900 m) vegetation is mainly represented by alpine grasslands and mugo pine bushes (*Pinus mugus*). Above 2500 m a.s.l. the area is mostly covered by rocks (59%) and screes (27%), with slopes higher than 30°.The study area is intensively used for touristic activities. Several alpine pastures are grazed by domestic cattle are present during summer. No large mammalian predator was present in the study area, except an occasional brown bear (*Ursus arctos*) presence during summer 2009.

Data collection

Captures occurred annually during late spring-summer from 2001 to 2009. Free-ranging ibexes were sedated by tele-injection of xylazine (Rompum ®, Gauthier 1993). A total of 108 males and 47 females were captured. In 2004 and 2005 capture sessions, 58 ibexes (41 males and 17 females) were treated once with ivermectin (Ivomec Gold ®). Age at first capture ranged from 1 to 15 years for males and from 1 to 16 years for females and only one kid was captured. All animals were aged by dentition and horn growth, measured, examined for health status and ear-tagged with a unique color and number combination. A VHF radiocollar (Televilt TXH3, Telonics CMM-320) was fitted to 31 males and 24 females. Twenty-three individuals were recaptured in 2004-2009; in recaptures damaged VHF collars were replaced or new VHF collars were put on already ear tagged animals. Since few ibexes were physically recaptured we considered subsequent sightings as a recapture event. Marked individuals were visually monitored all year-round from September 2003 to the end of August 2009. From 2003 to 2006 resightings occurred by systematic observations carried out monthly from transect walks and using homing techniques on radio-tagged animals. In 2006-2010 most resightings were obtained by homing techniques. However, when looking for radio collared animals all other individuals encountered were recorded. During the whole study period also sightings from vantage points observations recorded during the annual block censuses were considered.

Data analysis

Analyses were carried out using sightings of individually marked ibexes collected between June and November. We estimated survival by using Capture Mark Recapture modelling which relies on maximum likelihood estimators (Lebreton et al. 1992). We used the Arnason-Swartz survival model, a multi-state generalization of Cormack-Jolly Seber (CJS) models (Amstrup et al. 2005, Lebreton & Pradel 2002) with a logit link function in program M-SURGE (Choquet et al. 2004). We defined two states: state 1 corresponded to “seen in a given year ear-tagged” and state 2 “seen in a given year collared”. We tested for goodness of fit (GOF; Pradel et al. 2005) of the general CJS model φ_t p_t (fully time dependent survival and resighting probability) using the program U-CARE (Choquet et al. 2005). The directional test for trap dependence was highly significant, suggesting trap happiness effect (χ^2= 24.90 p<0.001). We accounted for different capture probability (p) of collared and ear-tagged ibexes by applying time dependence in capture probability of ear tagged animals.

On the basis of previous findings on sex specific differences in survival (Toïgo & Gaillard 2003, Toïgo et al. 2007) we considered males and females separately. We modelled survival according to several factors (Table 1) age structures, time effects, cohort of capture (year in which animals were captured) and treatment with ivermectin. We considered both addictive effects and interactions of the factors tested. Moreover, based on the presence of the massive die off in the population in spring 2004 we identified two time period for survival : a pre-epizootic period 2002-2004 and a post epizootic period 2005 onward. To model age-specific survival, we defined three-age-class: a yearling stage (survival from 1 to 2 yr), a prime-age adult stage (between 2 and 10 years of age), and a senescent stage (individuals older than 10 years of age). The cut-off point between prime-age and senescent stages was chosen from previous knowledge of survival curves for alpine ibex (Toïgo et al. 2007). We did not account for juvenile survival, since only one kid was captured.

Table 1: Symbols used in notation of CMR models for modeling survival of ibex in the Marmolada massif.

Symbol	**Explanation**
φ	Apparent survival rate
ac	Age class effect. 3 age classes:yearling, prime aged adults (2-10) and senescent (>10)
t	Time dependence over the entire study period
tre	Treatment with Ivermectin
Coh	Cohort of capture effect: we distinguished animals captured in 2002 and 2003 from those captured in 2004-onward
perA	time period A= survival vary in 2003 and 2004, costant afterwords
perB	time period B= survival vary in 2003, 2004 and 2005, costant afterwords
Tw	Air temperature in winter (December -March)
Tsp	Air temperature in spring (April and May)
Snow w	Snow depth in winter
Snow sp	Number of days in spring with snow deeper than 30 cm
INDVI	Sum of positive NDVI values over a given period
NDVImax	Maximum value of the NVDI over a year

Once defined the best reference model we tested for the effects of environmental covariates on survival probability. Since winter severity is one of the environmental factors most likely to influence ibex survival (Jacobson et al. 2004) we considered: snow depth in winter (January-March) and the air temperature in the same period, since the formation of ice crust on snow is one of the most limiting factors for foraging and movement (Moen et al. 2006). Also persistence of snow cover can be a limiting factor, therefore we considered as well the number of days with snow depth higher than 30 cm in spring (April and May) and the air temperature in the same period. Lastly we took two indexes derived from the Normalised Difference Vegetation Index (NDVI), that has been described as a good proxy of vegetation dynamics (Pettorelli et al. 2005): the maximum annual value of NDVI and the INDVI, which corresponds to the sum of all the positive NDVI values over a given period. Both these indexes give a measure of the annual plant productivity. All covariates were standardized (mean set to 0 and variance to 1).

Weather data were collected by Avalanche Centre of Arabba (Regional Agency for Environment Protection of Veneto Region, ARPAV) at the Monte Ornella meteorological station, about 10 km north of the study area at 2,250 m of elevation. Figure 1 reports the pattern exhibited by mean monthly temperature and snow depth during the entire study period.

We used an information-theoretic approach and selected the best-approximating model using Akaike's Information Criterion corrected for small samples (AIC_c ; Burnham and Anderson 2002).

RESULTS

Male survival

As expected, the models with age class effect described the survival better than those that did not account for age structure (table 2). We found no improvement when accounting for full time dependence (φ_t) or when including time dependence in the age class model (φ_{ac+t} , φ_{ac*t}), instead we found a significant effect of time period. When looking for a varying survival in 2003-2004 and constant in 2005-2009 (models with perA) or varying survival over 2003-2005 and constant in 2006-2009 (models with perB) we improved our estimations. This indicate the fact that the outbreak of sarcoptic mange accounted for time variation in survival: survival estimates lowered in 2004, when the peak of epidemic occurred. When we included treatment effect in the age class model we obtained a better fit, indicating that treated animals experienced a higher survival than untreated ones. However, treatments started in 2004 and almost all animals captured were treated, while 14 of the ibexes marked in 2002/2003 died in 2004, before treatments started. Therefore, we compared survival based on the date of capture of ibexes (cohort of capture). The model considering age effects and cohort of capture was the one best explaining male survival (table 2). Males captured in 2002 and 2003 experienced a lower survival rate than ibexes captured in 2004-2008, and senescent males had a lower

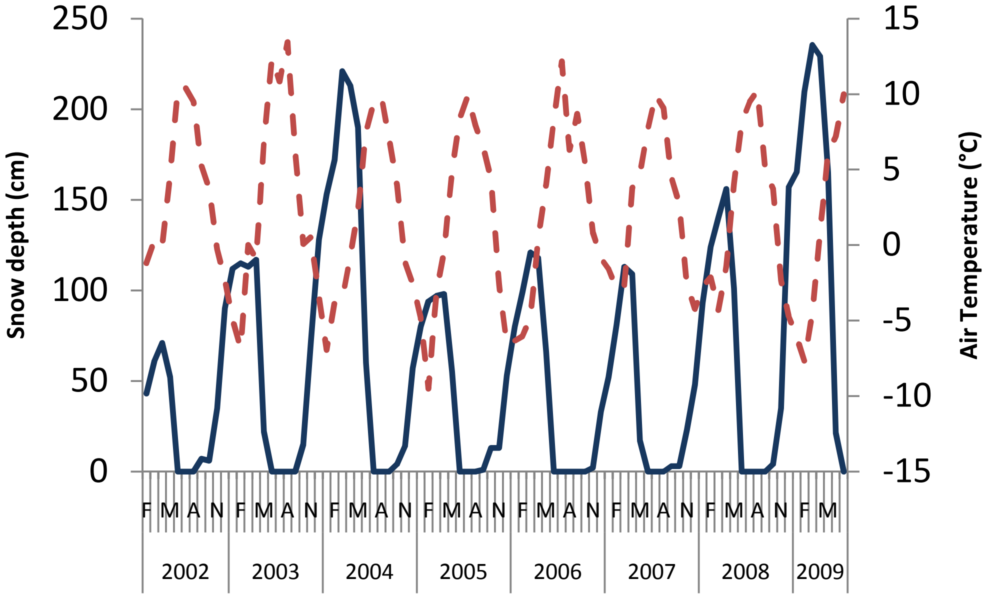

Figure 1: Mean monthly temperature (°C, dashed red line) and average monthly snow depth (in blue) in the Marmolada massif area over 2002-2009.

Table 2: List of model used for survival of male ibexes and relative number of parameters (NP), AICC and differences in AIC$_C$'s (Δ AIC$_C$) between each model tested and the best model (indicated in bold).

ModelNotation	**NP**	**Dev**	**AIC$_C$**	**ΔAIC$_C$**
φ	10	658.39	679.07	23.92
φ_{ac}	12	653.10	678.08	22.93
φ_{t}	16	647.82	681.54	26,39
φ_{ac+t}	18	643.94	682.12	26.97
φ_{ac*t}	25	634.32	688.55	33.40
$\varphi_{ac+perA}$	13	648.00	675.14	19.99
$\varphi_{ac+perB}$	15	641.51	673.02	17.87
φ_{ac+tre}	13	642.07	669.21	14.06
$\varphi_{ac+tre+t}$	19	630.08	670.50	15.35
$\varphi_{ac+tre*t}$	23	627.02	676.77	21.62
$\varphi_{ac+tre*perA}$	15	640.85	672.36	17.21
$\varphi_{ac+tre*perB}$	16	631.66	665.38	10.23
$\boldsymbol{\varphi_{ac+coh}}$	**13**	**628.01**	**655.15**	**0**
$\varphi_{ac+coh+t}$	19	622.22	662.65	7.50
$\varphi_{ac+coh*t}$	23	617.05	666.62	11.47
$\varphi_{ac+coh+perA}$	15	627.56	659.07	3.92
$\varphi_{ac+coh*perA}$	18	632.83	671.01	15.86
$\varphi_{ac+coh+perB}$	16	624.28	658.00	2.85
$\varphi_{ac+coh*perB}$	17	624.28	660.23	5.08

survival than prime aged ones (figure 2). Yearling survival is not reported in figure 2, since confidence intervals obtained were abnormally large, probably due to the very low sample size (only 6 individuals in total, 4 captured in 2004-2006).effect in the age class model we obtained a better fit, indicating that treated animals experienced a higher survival than untreated ones. However, treatments started in 2004 and almost all animals captured were treated, while 14 of the ibexes marked in 2002/2003 died in 2004, before treatments started. Therefore, we compared survival based on the date of capture of ibexes (cohort of capture). The model considering age effects and cohort of capture was the one best explaining male survival (table 2). Males captured in 2002 and 2003 experienced a lower survival rate than ibexes captured in 2004-2008, and senescent males had a lower survival than prime aged ones (figure 2). Yearling survival is not reported in figure 2, since confidence intervals obtained were abnormally large, probably due to the very low sample size (only 6 individuals in total, 4 captured in 2004-2006).

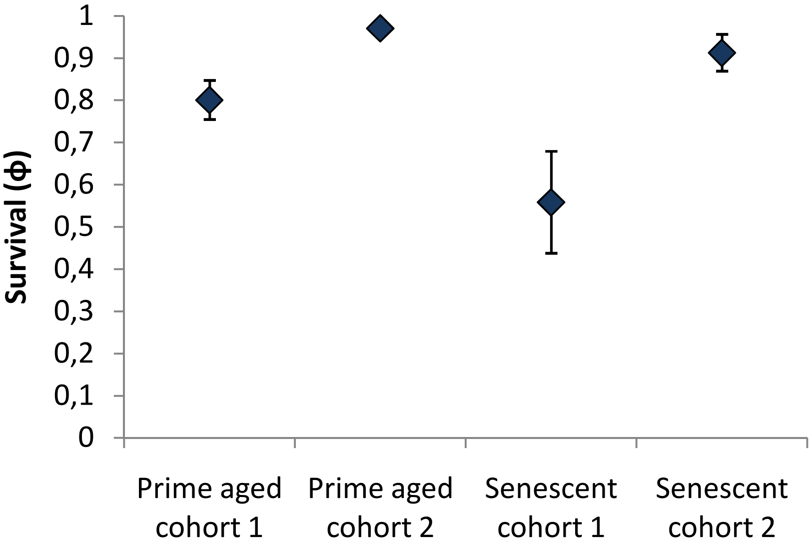

Figure 2: Estimated apparent survival for adult (2-9 years of age) and old (10-onward years of age) male ibex in relation to cohort of capture: cohort 1 means captured in 2002 and 2003, cohort 2 correspond to animals captured in 2004 onward. Error bars correspond to standard errors.

Effects of covariates on male survival

Among all the tested covariates, the one that explain better variation in survival was snow depth in winter (table 3). However the difference in AIC_C from the model with constant survival over time was only 0.36, indicating no significant improvement in the estimation. In contrast to our expectations snow depth had a positive effect on survival (estimated β=0.80) though the confidence interval was quite large (95%C.I. inf= -0.52, sup= 2.11). The second environmental variable likely to affect survival was NDVI max: the slope associated with this covariate was very high, suggesting a strong positive effect (β= 13,26, ES=11,92).

Table 3: List of model used for testing effect of climatic factors on survival of male ibexes and relative number of parameters (NP), AIC_C and differences in AIC_C's (ΔAIC_C) between each model tested and the best model (indicated in bold). In italic models with a **ΔAIC_C<2**

Model Notation	NP	Dev	AIC_C	ΔAIC_C
$\varphi_{\text{ac+coh}}$	13	628.00	655.14	*0.36*
$\varphi_{\text{ac+coh+t}}$	19	622.22	662.65	7.87
$\varphi_{\text{ac+coh*t}}$	23	617.05	666.62	11.84
$\varphi_{\text{ac+coh+snow w}}$	**14**	**625.46**	**654.78**	**0**
$\varphi_{\text{ac+coh*snow w}}$	15	625.05	656.57	*1.79*
$\varphi_{\text{ac+coh+snow sp}}$	14	627.53	656.85	2.07
$\varphi_{\text{ac+coh*snow sp}}$	15	626.32	657.83	3.05
$\varphi_{\text{ac+coh+Tw}}$	14	627.82	657.14	2.36
$\varphi_{\text{ac+coh*Tw}}$	15	624.75	656.26	*1.47*
$\varphi_{\text{ac+coh+Tsp}}$	14	628.00	657.32	2.54
$\varphi_{\text{ac+coh*Tsp}}$	15	626.98	658.50	3.71
$\varphi_{\text{ac+coh+NDVImax}}$	14	626.32	655.64	*0.86*
$\varphi_{\text{ac+coh*NDVImax}}$	15	625.46	656.98	2.19
$\varphi_{\text{ac+coh+INDVI}}$	14	763.76	793.09	138.3
$\varphi_{\text{ac+coh*INDVI}}$	15	626.12	657.63	2.84
$\varphi_{\text{ac+coh+snow w + Tw}}$	15	624.98	656.50	*1.71*
$\varphi_{\text{ac+coh+snow w + Ts}}$	15	624.67	656.18	*1.39*
$\varphi_{\text{ac+coh+snow sp + Tsp}}$	15	627.45	658.97	4.18
$\varphi_{\text{ac+coh+NDVImax+snow w}}$	15	623.75	655.26	*0.48*
$\varphi_{\text{ac+coh+snow sp +snow w}}$	15	625.37	656.88	*0.36*

Female survival

Contrary to males we found no age class effect in females: when including age class in the model of survival, AIC_c increased (table 4). Also treatment and time period did not improve our estimates, although treated animals seemed to experience a higher survival. The best model for females was the one considering only different survival rates for animals captured in 2002 and 2003 and those captured in 2004-2008 (figure 3), with females captured in the first cohort of capture experiencing a low survival. Due to the small sample size for females, we did not test for the effects of environmental covariates.

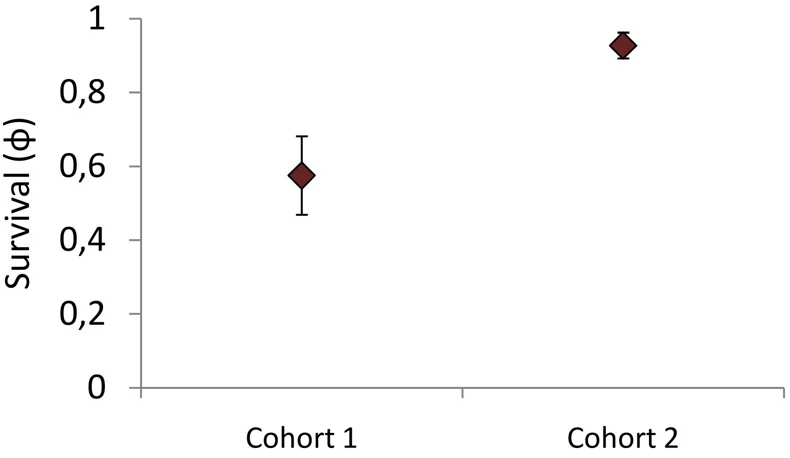

Figure 3: Estimated apparent survival for female ibex in relation to cohort of capture: cohort 1 means captured in 2002 and 2003, cohort 2 correspond to animals captured in 2004 onward. Error bars correspond to standard errors.

Table 4: List of model used for survival of female ibexes and relative number of parameters (NP), AIC_C and differences in AIC_C's (ΔAIC_C) between each model tested and the best model (indicated in bold).

Model Notation	NP	Dev	AIC_C	ΔAIC_C
φ	10	218.16	240.34	10.50
φt	16	206.87	244.59	14.75
φac	12	217.02	244.17	14.33
φac+t	18	203.24	246.59	16.75
φac*t	18	212.98	256.34	26.50
φac+tre	13	215.41	245.12	15.28
φtre	11	216.25	240.89	11.04
φtre*perA	12	213.44	240.59	10.74
φac+coh	13	203.31	233.02	3.18
φac+coh*t	23	188.69	247.23	17.39
φac+coh+perA	16	199.60	237.33	7.49
φac+coh*perA	15	201.08	236.08	6.24
φac+coh+perB	17	199.54	240.05	10.21
φac+coh*perB	17	201.00	241.51	11.68
φcoh	**11**	**205.20**	**229.84**	**0.00**
φcoh*t	20	193.09	242.32	12.48
φcoh*perA	13	203.63	233.34	3.50
φcoh+perB	14	203.48	235.81	5.97
φcoh*perB	15	203.48	238.48	8.64

DISCUSSION

This study confirmed the occurrence of changes in vital rates associated when the outbreak of sarcoptic mange occurred. As expected, survival of both males and females was lowered in 2004, when the outbreak of sarcoptic mange occurred. Sarcoptic mange is one of the most severe diseases of wild ungulates and, especially in the first outbreak, naïve populations may experience dramatic crashes (Gonzales-Candela et al. 2004, Rossi et al. 1995, Rossi et al. 2007). Mangy animals in the consolidated phase of the disease show hiperkeratotic and dry skin, alopecia and self-inflicted lesions induced by the intense itching (figure 4), that may in turn cause bacterial infections (Bornstein et al. 2001, Menzano 2003). As a consequence movements are hampered and flight and climbing activity are strongly reduced. Affected animals become undernourished, with a significant reduction in fat reserves, as reported in chamois (Fernandez-Moran et al. 1997), fox (Newman et al. 2002) and wombat (Skeratt et al. 1999). Disease in fact can cause anorexia in infected animal and, in the case of mange, the

Figure 4: Prime-aged male affected by sarcoptic mange in the cronic stage of infection. Photograph by Mirco Piccin

lesions around the mouth in the final stages may reduce feeding efficiency (Leon-Vizcaino et al. 1999, Pence & Ueckermann 2002) hence remarkably lowering the body condition of sick individuals. In our study population, mange affected survival of all animals irrespective of age and sex. We expected to find a stronger mortality in males, as in several dimorphic ungulate species a male biased mortality or prevalence of disease has been reported (Ferrari et al. 2010, Moore & Wilson 2002, Wilson et al. 2004), however our results indicate that in 2004 survival of both males and females was lower. Large herbivores have strong age structured populations (Festa Bianchet et al. 2003) with age specific mortality rates (Gaillard et al. 1998). Accordingly, we found an important effect of the age class in explaining survival pattern of males. The apparent lack of such effect for females is probably due to the small size of our sample, and to the fact that the majority of females were prime aged. Moreover, since senescent ibex are reported to be more sensitive to changes in environmental conditions (Toïgo et al. 2007), we expected as well a higher sensitivity of this age class to disease. This was in part confirmed by our results. In fact, although the impact of the disease was high for all animals, in 2004 older males seemed to suffer a higher mortality (survival of prime aged males = 0.69, ES=0.10 , survival of senescent males =0.32 ES=0.17). Anyway, the lowered survival seemed confined in time to 2004, while in the years following the epidemics, our results (2005-2009 : survival of prime aged males = 0.98, ES = 0.01, survival of senescent males = 0.93 ES = 0.04) confirmed the very high survival rates reported for alpine ibex (Girard et al. 1999, Largo 2008, Toïgo et al. 2007). The elevated mortality in 2004 followed by a very high survival in the following year can be explained by several concomitant causes. Almost all animals captured in 2004 and 2005 were treated with injection of ivermectin, which efficiently reduces mange and cures animals (Leon-Vizcaino et al. 2001, Soll et al. 1992). Therefore our sample for estimating survival was mostly composed by treated individuals, and this could have led to biased positive estimates in 2005 in which we found very high survival rates, that might not correspond to the real average survival experienced by the population, since obviously it was not possible to cure all animals present in the colony. Secondly, we might infer that, when mange first infected the population in 2003-2004, it spread rapidly killing most of the animals. Eventually, the few survivors were the more resistant ones. In example, Jorgenson et al. (1997) observed a reduction in survival of prime aged bighorn sheep due to a pneumonia epizootic, but this reduction was limited to one year, suggesting a development of immunity against it. In other sarcoptic mange epizootics occurred in wild populations, a very high mortality was described on the first infection, followed by an epidemic silence due to the great size reduction experienced by the population (Gonzales-Candela et al. 2004). Also acquired immune resistance toward mites can play an important role in the length of the die off (Guberti & Zamboni 2000), but the development of the immune response to sarcoptic mange infestation is still a poorly understood phenomenon (Sarasa et al 2010). Duration of the high mortality phase is variable, and is related to population size and density and the probability of transmission between individuals (Guberti & Zamboni 2000).

Inter-individual transmission of mange is mainly by direct contact (Bornstein et al. 2001, Sarasa et al. 2009) although mites can also survive for some time off their host and still remain infective (Pence & Ueckermann 2002). As a consequence, it tends to be a density dependent disease (Pence & Ueckermann 2002). The epizootic occurred in Marmolada when the population was at its peak, and the high density might have improved the spread of the disease, as reported for pneumonia outbreaks in bighorn sheep (Monello et al. 2001). Being transmitted by direct contact, the spread of mange is also influenced by the social system of the host, as reported for other diseases (Böhm et al. 2008, Craft et al. 2008, Perkins et al. 2009). The biology of alpine ibex make it particularly vulnerable as the species is highly gregarious and groups have an unstable composition (Toïgo et al. 1995, Villaret & Bon 1998), favoring a quick spread of the disease within a colony. Males and females are ecologically segregated and herd in different groups, although during the rutting season they congregate in mixed herds. Within a group direct contact within individuals is common, for example contact and interactions between males serve to establish the hierarchy that regulate the access to reproduction (Willisch & Neuhaus 2010). In the Marmolada the epizootic peak occurred in April-May 2004 (Monaco et al. 2005b), as described in chamois (Rossi et al. 2007) and in Iberian ibex (Leon Vizcaino et al. 1999). This common trend is due to the fact that sarcoptic mange follows a seasonal pattern linked to the fertility and the survival of the mites: egg production reach its maximum in Autumn (Sokolova et al. 1989). The first symptoms appear after one month, and the complete evolution of the disease take 2 to 4 months (Menzano 2003), explaining the rise in sarcoptic mange episodes observed in winter and the mortality peak in spring (Rossi et al. 2007). The disease therefore takes place when animals are already exposed to the limiting conditions of winter, and the two factors can therefore act in combination (Ondersheka et al.1989 cit. in Rossi et al. 2007). In spring 2004 a total of 139 carcasses were found. Among these, 77 presented overt signs of sarcoptic mange, 33 were not affected and in 29 cases it was not possible to assess the cause of mortality (Fraquelli et al.

2004). In the following years the number of carcasses found decreased steadily (35 in 2005, 3 in 2006), confirming that most mortality was confined to 2004. We are aware that it is not possible to delineate a reliable estimate of mortality rate by using the number of carcasses found, since it may lead to high biased estimates (Ciucci et al. 2007, Gulland 1995). However, the finding of at least 33 carcasses not affected by mange indicate the presence of a source of mortality other than mange. Winter 2003/2004 was characterized by exceptional snow precipitations (figure 1), and could therefore act as an additive limiting factor, causing direct mortality and inducing starvation (Barret 1982, Young 1994). In fact winter severity has been described as one of the most important limiting factors in ibex dynamics (Grøtan et al. 2008, Largo 2008, Jacobson et al. 2004, Sæther et al. 2002). In particular high snow falls, height and persistence of snow cover can compromise survival in alpine ungulates (Crampe et al. 2002, Loison et al. 1999b). Snow may prevent free access to resources (Moen et al. 2006), cause direct mortality with avalanches, increase the cost of locomotion (Dailey & Hobbs 1989), especially in a mountain ungulate as ibex, well adapted to climbing in rocky environment but poorly performing in deep snowpack (Raye 1994). In addition, severe winter conditions can create favorable conditions for the onset of an epizootic, since it generate increased costs on animals, and malnourished and stressed animals most likely have depressed immune system defense (Festa Bianchet 1988, Monello et al. 2001). In this study we expected to find a negative influence of snow depth in winter and persistence of snow cover in spring on survival. In particular we expected a negative effect in survival over winter 2003/2004, which was characterized by exceptional snow precipitations, but on the contrary we detected a slight positive effect. One reason might be linked to the relative short time interval at our disposal and on the structure of our sample. However, the model with covariates was not consistently improving the model with constant survival over time, highlighting that the very different survival pattern exhibited by the males of the first two cohorts of capture (2002 and 2003) explained most of the variability in our data base. Moreover we lack information on kid survival, and our sample of yearling individuals was too small to provide a reliable estimate, and yearlings, together with kids, represented the age classes more sensitive to environmental factors (Gaillard et al. 2010), included winter severity (Crampe et al. 2002). A comparative study of alpine ibex population dynamics in different populations (Largo 2008) showed that prime aged males are less likely to be affected by severe winter conditions, although the response to climate varied across populations. A second explanation of our failure is that the relationship between snow depth and survival is not always clear to assess. First, snow depth significantly affect survival only above a certain threshold, also because ibex tend to avoid patches with heavy snow cover, selecting south facing areas with steep slopes with reduced snow accumulation (Tosi & Pedrotti 2003). Second, on the opposite, high snow fall can increase survival because it improves plant productivity and therefore body weight in the following spring (Loison et al. 1999b, Owen Smith 2010). Lastly, the use of local weather variables is not always the best descriptor of climatic influence on wild animals, as they fail to capture complex associations between weather and ecological process. Indeed, Hallet et al. (2004) demonstrated how a large scale index such as North Atlantic Oscillation (NAO) outperformed local weather variables in describing mortality pattern in Soay sheep (Ovis aries).

In conclusion, this study showed that immediately after the epidemic survival of remnant individuals was comparable to those reported in healthy populations, indicating a relative short term effect of sarcoptic mange on survival. Nevertheless, the results provided here are preliminary, and can be implemented to achieve more robust estimates. For example, an improved model for correcting trap dependence can be developed with the new software E-SURGE (Choquet et al. 2009) or data can be analyzed with an alternative approach, such as bayesian modelling. Moreover, adding data collected in summer 2010 could improve the estimates, since it would increase the sample size. The lack of negative effects related with weather in fact could have been reasonably linked also to the relatively short time interval sampled.

Finally, it is necessary to underline that here we provided an estimation of only one component of population growth, while it was not possible to account for the effect of mange on the reproductive output of the population, which is instead an important driver of population dynamic.In fact, parasites and pathogens can affect population growth also by reducing the reproductive output of the host population. Several studies report an effect of micro and macro pathogen on reproduction: disease can either directly cause abortion, as in the case of brucellosis (Rhyan 2001) or indirectly lower reproduction rates, as reported for chamois (Pioz et al. 2008), reindeer (Albon et al. 2002, Stien et al. 2002) and bison (Joly & Messier 2005). In addition, even when mortality is acute (as in the case of epizootic), the effects of disease on reproduction can be delayed and this may prolong the negative effect of disease on population growth over a longer time. In a chamois population affected by a keratoconjunctivitis epidemic, the population took 5 years to recover the previous rate of increase. In the first post-epidemic phase, in fact population experienced a low reproductive index due to a lowered maternal effort (Loison et al. 1996). A depressed reproductive output has been described as well in Soay sheep of St Kilda which experience an alternation of population boom and crashes due to the combination of starvation and parasite load (Coulson et al. 2001). Moreover, as a consequence of disease young individuals may experience lower weight gains and body size (Wilson et al. 2004). Since cohorts that show relatively low birth weights are more likely to suffer high mortality in their first year of life (Forchhammer et al. 2001) recruitment can lower during the first post epidemic phase.

Further studies based on marked animals are needed to better understand the relative effects of different limiting factors such as disease, density and winter severity on the studied population and on alpine ibex populations in general. In the Marmolada colony, the establishment of a standardized protocol of marking and resighting of individuals would be desirable, as it will provide the opportunity to detect the overall response of the population in terms of demographic parameters in the post epidemic phase. The acquisition of data on the reproductive output of this population of alpine ibex is strongly recommended, because it will help to delineate the response of the population to the epizootic over a longer term. Since ibex adopt a conservative reproductive strategy, limiting reproductive effort in poor environmental conditions (Toïgo et al. 2002), we might infer that as a consequence of mange females tend to maximize their own survival investing less on reproduction. This could likely explain the relative low population size of the Marmolada colony, that has still not recovered the pre-epidemic rate of increase and population size, as suggested by population counts data.

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Chapter 4:

Factors affecting home range size of male Alpine ibex (Capra ibex ibex) in the Marmolada massif.

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INTRODUCTION

Understanding the organization of animal in space and time is a fundamental issue in ecological studies. In general, animals tend to confine space use to a restricted area, the home range, classically defined as the area traversed by an individual in its normal activities of food gathering, mating and caring for young (Burt 1943, Powell 2000). Home range size is affected by several different factors, such as body weight and phylogeny (Mysterud et al. 2001, Ottaviani et al. 2006), energy requirement (McNab 1963), sex (Clutton-Brock 1989, Dahle & Swenson 2003, McLoughlin & Ferguson 2000), age (Cederlund & Sand 1994) and reproductive status (Dahle & Swenson 2003, Saïd et al. 2005) of individuals, and, in social species, social factors such as group size and composition (Loveridge et al. 2009). In addition, several extrinsic factors linked to the species ecological needs may act as important determinants of home range extension: population density (Kjellander et al. 2004, Massei et al. 1997), forage abundance and availability (Larter & Gates 1994, McLoughlin & Ferguson 2000, Nilsen et al. 2005, Shradin et al. 2010), landscape structure (Anderson et al 2005, Lamberti et al 2006, Saïd & Servanty 2005, Tufto et al 1996), climate variability (Börger et al. 2006 b, Fisher & Owens 2000), seasonality (McLoughlin et al. 2000), predator pressure (Creel et al. 2005) and human disturbance, as hunting (Scillitani et al. 2010, Vercauteren & Hyngstrom 1998). Therefore understanding variation in spatial behaviour (including home range size and habitat selection) and identifying which factors shape this variation is crucial for a better knowledge of the species biology (Morales et al. 2010) and help to reach an improved management and conservation (Apollonio et al. 2003, Sutherland 1998). At a population and individual level, availability of resources is most likely one of the major determinant of home range size (McLoughlin & Ferguson 2000). At this purpose, important knowledge on the causes of intra-specific variations can be gained by the acquisition of information on different populations of the same species because, due to diverse geographical and –as a result– ecological constraints, availability and acquisition of resource may vary in different areas and time periods.

Alpine ibex (*Capra ibex ibex* L., 1758) is a gregarious species characteristic of mountain environment. Its native range is: the Alps of France, Switzerland, northern Italy, Austria and Germany (Shackleton 1997). The species typically inhabit open habitats at high altitude, above the tree line, and is linked to environments characterized by rocky steep slopes, which are actively selected by both sexes particularly in winter (Nievergelt 1966, Girard 2000, Tosi

& Pedrotti 2003). Alpine ibex exhibit a pronounced sexual dimorphism and sexes segregate during most time of the year (Ruchstul & Nehaus 2001, Villaret & Bon 1995). Spatial segregation seems to occur also between males of different age classes: males tend to group with individuals of similar age (Villaret & Bon 1995). Males use alpine grassland during all year (Grignolio et al. 2003, Lembke 2005, Pedrotti 1995), while females, especially in summer after parturition, are more linked to cliffs and rocky slopes (Grignolio et al. 2007, Villaret et al. 1997). Seasonal altitudinal movements are made in relation to vegetation phenology gradient. In spring, males occupy low-elevation grasslands where fresh grass is available while in summer, they move to higher elevation (Grignolio et al. 2003, Pedrotti 1995). During winter, males select steep slopes where snow depth is minimal (Tosi & Pedrotti 2003). The gradient of slopes is one of the most important factors influencing habitat selection by Alpine ibex: generally ibexes select slopes between 30 and 45 degrees, particularly during the winter season (Girard 2000, Pedrotti 1995, Tosi & Pedrotti 2003).

Aim of this study was to understand which factors might shape the home range size of alpine ibex in the Marmolada massif, in the Dolomites (Eastern Italian Alps). We investigated on the effects of age, different landcover types and meteorological conditions on the home range size of males. We assumed that home range size should be linked to the extent of the preferred resources. We hypothesized that the preferred habitat features should be alpine grassland, which supply forage, and we expected that seasonal home range size should be inversely related to this habitat feature, especially in winter, when snow cover prevent free access to resources. We also expected to find a negative relationship between the home range size and snow depth, since deep snowpack may hamper ibex movements preventing them free access to all study area.

MATERIALS AND METHODS

Study Area The study area was the Marmolada massif area, in the Eastern Italian Alps (Dolomites - 46°26'13" N; 11°51'54"E, figure 1). It encompasses about 150 km^2 and lies between 1,200 and 3,343 m a.s.l.. The environment is typical alpine, with steep slopes even at low altitudes and characteristic dolomitic limestone rocks. The main ridge axis orientation is east-west. A glacier is present in the Marmolada massif, but it covers less than 2% of the total area (Duprè et al 2001). At the bottom of valleys are present mixed forest composed by common beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*) and sycamore maple

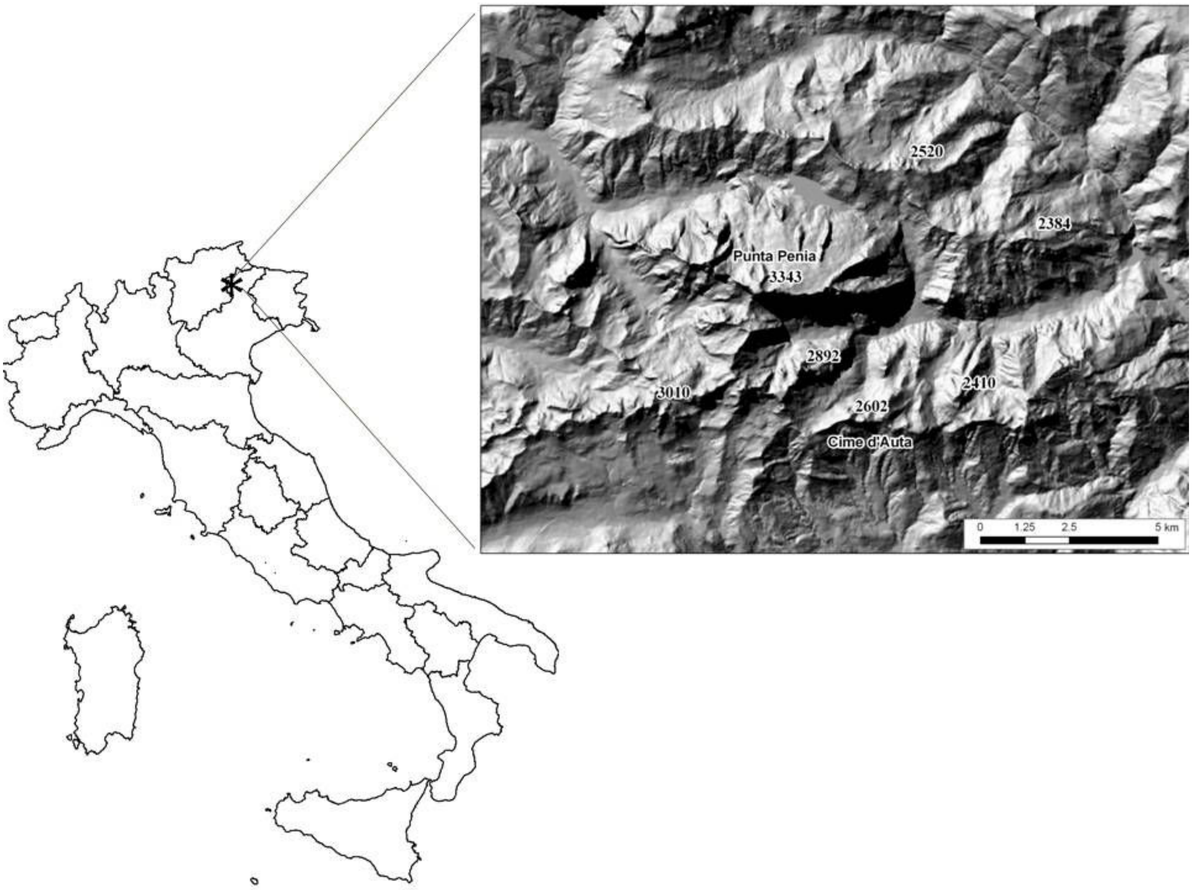

Figure 1: Map of the study area and its location in Italy.

(*Acer pseudoplatanus*) interspersed with Norway spruce (*Picea abies*). At higher altitudes (>1600 m) woodlands are mainly composed by Norway spruce and larch (*Larix decidua*). Above the timberline (1900 m) vegetation is mainly represented by alpine grasslands and bushes as mountain pine (*Pinus mugus*).

The study area was intensively used for touristic activities, such as skiing and hiking. Hunting was allowed, and the hunted ungulates species were Chamois (*Rupicapra rupicapra*), Roe deer (*Capreolus capreolus*) and Red deer (*Cervus elaphus*). Several alpine pastures are grazed by domestic cattle during summer. No large mammalian predator was present in the study area, except an occasional Brown bear (*Ursus arctos*) presence during summer 2009.

Data Collection

Free-ranging ibexes were sedated by tele-injection of xylazine (Rompum ®, Gauthier 1993). Captures were performed during late spring-summer of each year from 2001 to 2009, and we captured a total of 95 males of different ages (range 1-15 years old). All animals were aged by dentition and horn growth, measured, examined for health status and ear-tagged with a unique color and number combination. A VHF radiocollar (Televilt TXH3, Telonics CMM-320) was fitted to 31 males.

Field work was conducted from September 2003 to the end of August 2009. Radio-tagged ibexes were located mostly by sightings, and – during 2003-2006 – also by triangulation with a portable receiver and a hand-held yagi antenna; in case of triangulation, locations were computed using a minimum of three bearings obtained with LOCATE II (Nams, 1990). Each sighting was plotted in the field into a map of the study area (1:10000 scale). For individual identification we used a 60x magnifier telescope (Swarovski CT85). Sighting were georeferenced in ArcView 3.2 (ESRI ®) and stored in a Access (Microsoft ®) database.

Temperature and precipitation data from the nearest weather stations to our study area were provided by the Avalanche Centre of Arabba (Regional Agency for Environment Protection of Veneto Region, ARPAV).

Data analysis

All statistical analyses were conducted with the statistical software SAS 9.1 ® (SAS 2006), and spatial analysis were performed in ArcGIS 9.3 (ESRI ®).

We defined four seasons, on the basis of climatic characteristics and ibex biology: "summer": June-August; "autumn": September-November; "rutting season and winter": December-February; "spring": March-May. For all the analysis we employed a total of 48 different males ibexes (31 radio-collared) located more than 10 times per season, with a total of 236 home ranges.

In order to understand which environmental factors were most likely to affect home range size and therefore should be used as covariate when modelling home range size, we firstly performed an exploratory habitat selection analysis. We compiled a 1:5,000 land-use cover map by refining the forest cover maps produced by the Veneto Region and by the province of Trento using the orthophoto of the study area. We reclassified landcover data into eight habitat types most likely to influence ibex: "Grassland", "Grassland interspersed with rocks and scree", "Rocks", "Scree", "Shrubland", "Woods", "Glaciers", "Antropic features". We assigned to each ibex location the correspondent habitat type and computed the percentage of use of every habitat type by each individual ibex. We estimated habitat availability by generating 4,192 random locations (which equalled the total number of ibex locations) throughout the study area using the random point generation function of the Hawths Analyis Tool extension for ArcGIS 9.3 (Beyer 2004). We analysed habitat selection performing a compositional analysis of log ratios (Aebischer et al 1993) with the Compos analysis software

(Smith 2005). We obtained elevation (m), slope (degree) and aspect of the study area from a Digital Elevation Model (DEM), a raster map with a pixel size of 25 m×25 m, developed by the Veneto Region and the Trento Province. Finally, we computed the average slope, elevation and aspect of the preferred habitat type within each home range, and then we then tested for the presence of correlation between these different habitat variables in order to select the variables to be included into the following analysis of home range.

We estimated seasonal home range size with cluster estimators (Kenward 2001, Kernohan et al 2003) by using the software Ranges VI (Kenward et al 2003). Cluster estimators are built using nearest-neighbour distances between locations: locations are linked in clusters that minimize the mean joining distance (Kenward 2001). This estimator can be useful to describe the space use by ibexes, which generally use small areas connected by corridors (Pedrotti et al. 1995). In addiction, this method worked better on our data than Kernel estimator and Minimum Convex Polygon (MCP). Home range size (in hectares, ha) was log-transformed to meet a normality assumption. We modelled the logarithmic home range size with mixed linear models (Proc Mixed, SAS) in which we considered the individual as a random effect to take into account the intra-individual variance and pseudo-replication due to repeated observations on the same individual. Models tested the effects of the different combinations of the following explanatory variables on home range size: year, season or, in alternative, time period (a total of 23 different time periods obtained by the combination of season and research year) and individual's age as class effects, and percentage of the preferred habitat type, average slope, average elevation, average aspect of the preferred habitat type within the home range, and number of relocations used to calculate home range size as covariates. When testing periods instead of year and season, differences among seasons were assessed by orthogonal contrasts of periods. A multiple comparison post-hoc test was performed with the Tukey-Kramer adjustement. Model selection among the list of candidate models was performed using the Akaike Information Criterion (AIC, Burnham & Anderson 2002).

Finally, we assessed the effects of climatic variables on home range size by testing the presence of a correlation between winter and spring home range size and the average air temperature and snow depth.

RESULTS

The compositional analysis revealed a significant difference from random use (Wilk's $\lambda=0.001$, $p<0.001$), and the habitat types preferred by male ibex were: "Grassland interspersed with rocks and scree" and "Grassland" (table 1), followed by scree and rocks. Therefore we

Table 1: Simplified ranking matrix according to compositional analysis of ibex locations versus random locations within the study area (second-order selection)

	Grassland	Grassland with rocks and screes	Rocks	Scree	Shrubland	Woods	Glaciers & Antropic features	Rank
Grassland		-	+++	+++	+++	+++	+++	**5**
Grassland with rocks and screes	+		+++	+++	+++	+++	+++	**6**
Rocks	---	---		---	+++	+++	+++	**3**
Scree	---	---	+++		+++	+++	+++	**4**
Shrubland	---	---	---	---		-	+++	**1**
Woods	---	---	---	---	+		+++	**2**
Glaciers & Antropic features	---	---	---	---	---	---		**0**

proceeded by computing the percentage of grassland (merging both the types of grassland together) within each home range, and we estimated the average elevation, slope and aspect of grassland. The percentage of grassland was not correlated with slope ($r_{pearson}$= 0.071, p=0.278), poorly correlated with elevation ($r_{pearson}$= 0.128, p=0.049) significantly correlated with aspect, but with a small Pearson's correlation coefficient ($r_{pearson}$= 0.377, p<0.001). Slope was correlated both to elevation ($r_{pearson}$= -0.463, p<0.001) and aspect ($r_{pearson}$= 0.331, p<0.001), and also aspect and elevation were correlated ($r_{pearson}$= -0.209, p<0.001). In the subsequent analysis of home range size with mixed models we used percentage of grassland in all models and tested the addition of only one of the other variables at once.

Mean seasonal home range size was 182.1 ha (N=236, SD:210.39 ha; range:10.87-1611.89 ha). The list of candidate model is reported in table 2. The best model according to the AIC criterion was the one with the following explanatory variables: percentage of grassland nested within season, slope of grassland, number of locations, time periods (AIC=417.3). We found a highly significant effect of all the explanatory variables tested: time period ($F_{22,160}$ = 2.95; p <0.001), percentage of grassland nested within season ($F_{4,160}$ = 20.93; p <0.001), slope of grassland ($F_{1,160}$ = 49.50; p <0.001), and number of locations ($F_{1,160}$ = 15.72; p <0.001). The orthogonal contrasts did not show important differences between seasons (estimated home range size: autumn=9.62 SE=0.58; winter=8.62 ES=0.62; spring=9.78 SE=0.66; summer=9.15 SE=0.58); but winter home ranges were significantly smaller than spring ($F_{1,160}$=5.86 p=0.02) and autumn ($F_{1,160}$=4.83 p=0.03). In figure 2 are reported the least

Table 2: List of candidate models used to explain home range size in alpine ibex and relative AIC values. In bold the best model according to AIC criterion.

Model formulation	AIC
LogHRsize=β_0+ β_1 Season + β_2 Year + β_3 %Grassland+ β_4 SlopeGrassland + β_5 Nloc + β_6 Age	469.4
LogHRsize=β_0+ β_1 Season + β_2 Year + β_3 %Grassland(season)+ β_4 SlopeGrassland + β_5 Nloc+ β_6 Age	458.3
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland+ β_3 SlopeGrassland + β_4 Nloc+ β_5 Age	439.2
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland(season)+ β_3 SlopeGrassland + β_4 Nloc+ β_5 Age	425.8
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland(season)+ β_3 SlopeGrassland + β_4 Nloc	**417.2**
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland(season)+ β_3 AspectGrassland + β_4 Nloc	469.6
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland(season)+ β_3 SlopeGrassland + β_4 AspectGrassland + β_5 Nloc	428.0
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland(season)+ β_3 ElevGrassland + β_4 Nloc	462.3
LogHRsize=β_0+ β_1 time-period + β_2 %Grassland(season)+ β_3 SlopeGrassland + β_4 ElevGrassland + β_5 Nloc	426.2

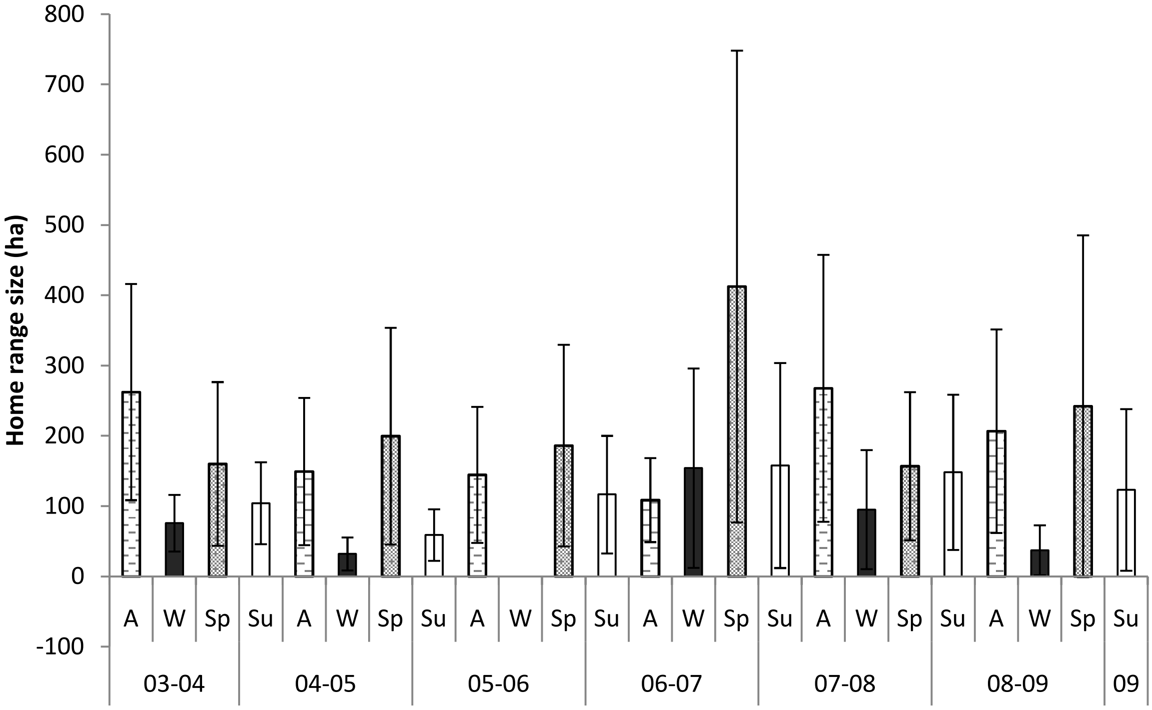

Figure 2: Seasonal home range size (least square means) of adult male ibex in the Marmolada massif. Error bars represent standard errors

squared means of the home range estimates obtained with the model. The percentage of grassland within the home range affected negatively home range size in all seasons, except in winter, and also slope was inversely related to home range size (table 3). As expected, the number of location was instead positively related to the size of home range, and this result is probably linked to the fact that some winter home ranges were not built with the asymptotic number of location required for stabilization of home range size (Kernohan et al. 2001).

Table 3: List of the β-estimates obtained for the covariates in the best model

Covariate name	b	SE	df	t- value	p
Grassland percentage in Summer	-2,15	0,61	160	-3,53	<.001
Grassland percentage in Autumn	-2,91	0,47	160	-6,13	<.0001
Grassland percentage in Winter	-0,68	0,58	160	-1,17	0.243
Grassland percentage in Spring	-3,03	0,53	160	-5,67	<.0001
Slope of Grassland	-0,11	0,02	160	-7,04	<.0001
Nloc	0,03	0,01	160	3,96	<.001

Home range size in winter and spring was inversely correlated with snowpack depth ($r_{pearson}$= -0.24, p=0.05). However, when we fitted a mixed model for the winter and spring home range size using as covariates snow depth, percentage of grassland and number of locations used we found no significant effect of snow ($F_{1,42}$=1.73, p=0.20). We found no correlation between home range size and temperature ($r_{pearson}$= 0.31, p=0.31).

DISCUSSION

As we hypothesized the change in percentage of grassland significantly explained variation in home range size in almost all season, with the exception of winter. This result is in agreement with an analysis conducted on male ibex in the Gran Paradiso National park (Grignolio et al. 2003) which reported a negative correlation between home range size and grassland. Most of the studies performed on the effects of landscape structure on home range size of large herbivores used deer as model species. Saïd & Servanty (2005) reported an important effect of edge density, and therefore of habitat heterogeneity, on roe deer home range size, and these findings are supported by other studies on the same species conducted in different study areas (Italy: Börger et al. 2006 b, Lamberti et al. 2006; Norway: Tufto et al. 1996). The importance of landscape heterogeneity at various spatial scales was reported as well in a study on mule deer (*Odocoileus hemionus colombianus*, Kie et al. 2002), that emphasized the importance not only of patch composition, but also of how habitat patches are distributed within the landscape: when different habitats are interspersed, deers may limit their ranging behaviour to a smaller area than when similar habitats are clumped together, because a small area might offer them resources for different needs. A study conducted on north American elk (*Cervus elaphus canadensis*) indicated that forest cover and forage biomass were the main determinants of seasonal home range size: when resources were abundant, elk confined their ranging behaviour to a smaller area (Anderson et al. 2005). Alpine grassland are the preferred habitat for adult male ibex, and are actively selected during active phase because they provide forage (Grignolio et al. 2003, Lembke 2005). The inverse relationship between grassland percentage and home range size found in this study therefore cope with the resource exploitation hypothesis suggested by several authors (Anderson et al. 2005, Larter & Gates 1994, McLoughlin & Ferguson 2000): when forage is easily available ibexes did not need to seek out it by moving important distances. However, forage availability alone can't completely explain changes in spatial behaviour exhibited by ungulates: as underlined by all the studies cited above, it is extremely important to consider the concomitant effect of several factors other than food, such as population density and predation, when analysing home range variation in size. In the case of the Marmolada ibex colony, predation was not a limiting factor for subadult and adult males, since no large predators were permanently present in the area. Instead, variations in population density were likely to affect spatial behaviour in the Marmolada colony, that experienced a population crash during winter 2003-2004 causing a dramatic decrease in population size, and consequently of population density (Monaco et al 2005). Unfortunately we had at our disposal only two seasons with high density (autumn and winter 2003), while after experiencing the crash, population size did not fluctuate significantly in the remnant years (Scillitani et al., unpublished data). Therefore we decided not to test this effect to avoid biased conclusions. Nonetheless the estimated home range sizes in 2003 did not differ significantly with the estimates obtained in the following years, suggesting the lack of a density effect .

Our results indicate also a negative relation between grassland slope and home range extension. First of all, this result can be linked to a simple geometry rule: an increase in slope correspond to a decrease in the surface. However, there might be also a biological-based explanation: in fact the importance of slope in ibex habitat selection has been described by several authors (Couturier 1962, Girard 2000, Pedrotti 1995, Wiersema 1983).This is particularly true for winter and the beginning of spring when ibexes concentrated on south facing mountainside, in grassland characterized by steep slope, which are free of snow in relation to other areas. As a result, it is not the extent of grassland in itself which is limiting, but the extent of grassland located in steep slopes that might become a resource limiting home range size when deep snowpack is present. This might as well explain why in winter we found a significant effect of slope but not of grassland on home range size. Estimated seasonal home range sizes were similar to those reported for other alpine ibex populations (Girard 2000, Parrini et al. 2003), and, as expected, were smaller than those reported in studies on relocated ibexes, which usually tend to occupy larger areas as a consequence of their exploratory movement in the new environment (Michallet 1994, Pedrotti 2005, Scillitani et al. 2009).

We found no remarkable differences of home range estimates throughout seasons, although winter home ranges were in general significantly smaller than the home ranges used during the other seasons, in agreement to what found in former studies (Girard 2000, Parrini etr al 2003, Terrier et al. 1994). For most species inhabiting Northern or alpine environments, the availability of resources, in terms of quantity and quality, is reduced during winter and the beginning of spring, since they are covered by snow (Collins & Smith 1991, Festa Bianchet 1988, Nordengren et al. 2003). Alpine ibex, as other members of the genus *Capra* are well adapted to climb in rocky environment with steep slopes (Geist 1987), but their movements are hampered by the presence of a high snow depthh (Raye 1994, Tosi & Pedrotti 2003). The extent and depth of snow cover may affect cost of locomotion (Dailey & Hobbs 1989) and limiting movement to confined patches free from snow can be a strategy to save energy (Rivrud et al. 2010). In this study we observed a tendency to a negative trade off between the snow depth and the extension of home range, and this slight negative correlation might partially explain the small home range size we observed in December-February. The tendency of male alpine ibex to reduce ranging behaviour in winter has been reported for other populations (Girard 2000, Parrini et al. 2003). Other studies (Pedrotti 1995) reported home ranges of similar extent during winter and spring, however this was probably linked to the fact that the studied population was located in central Italian Prealps, where snow depth was likely less deep in respect to alpine areas.

The importance of the different environmental characteristics acting on seasonal fluctuations of home range behaviour of ibexes was underlined by Girard (2000) which found differences in the variations of seasonal home range size exhibited by different subpopulations of ibex occupying areas with different climatic constraints – such as snowpack depth – inside the Vanoise National Park (France). Our results indicate the tendency of a stable space use pattern throughout the year, and in different years, as testified by the lack of significant seasonal variation in size. However, this result should be taken carefully since sample size during winter was smaller than in other seasons, and this can lead to biased estimates (Börger et al. 2006 a, Kernohan et al. 2001). Moreover, as pointed out by Börger et al. (2006 b), an *a priori* definition of "season" (even if based on biological assumptions on the case study species) can lead to biased estimates of home range size and of the individual sources of variations. According to these authors, the individuation of the appropriate time-scale on which conducting the analysis should be determined with a hierarchical approach, but unfortunately, we were not able to apply such approach due to the relatively large time intervals between locations and sample size. The lack of substantial seasonal differences in home range size found in this study is probably also linked to the strategy adopted by ibexes in respect to seasonal fluctuations of climate. In the Marmolada massif most males, especially after the population crash, did not migrate across wintering and summer ranges located in distinct geographical sites., but remained all year in a relatively confined area, displacing seasonally along an altitudinal gradient within the same mountain ridge. This behaviour contrasted with what described for other populations (Gauthier et al 1991, Girard 2000, Girard et al 2009), although the same authors reported also the presence of several different strategies adopted by ibexes: the majority of individuals used always the same wintering and summering areas, while others changed geographic location every year and a minority did not migrate at all. The change in the altitude gradient or the use of migration routes in response to seasonal weather variability and forage availability is a common strategy for mountain ungulates (Alpine ibex: Francisci et al 1985, Girard 2000, Grignolio et al. 2004; Bighorn sheep -*Ovis Canadensis*-: Festa Bianchet 1988; Chamois: Lovari et al. 2006; Mountain goats-*Oreamnus americanus*-: Hjeljord 1973, Rice 2008; Red deer: Bocci et al. 2010, Luccarini et al. 2006; Roe deer: Mysterud 1999, Ramanzin et al. 2007) and allows them to exploit resources with the highest possible income. In fact seasonal migrations mirror the temporal changes in vegetation phenology : in spring animals use patches at low altitudes where plant growth starts, while in summer they move to high altitude areas where the vegetation growth is delayed. This assures mountain dwelling species the acquisition of high quality food through several months (Festa Bianchet 1988). By reaching favorable habitats migrating animals do not need necessarily to enlarge the extent of the area used, therefore if we do not consider the movement connecting summering and wintering area we could also do not detect any variation in seasonal home range size.

We found no effects of temperature on home range size, but, once more, the pre-defined seasonal scale could hide the effects of climate variability (Börger et al. 2006 b, Rivrud et al. 2010) and, also, direct and indirect effects of climate are often difficult to separate (Mysterud et al. 2008). In fact, the relationship between local weather variables such as temperature and home range size is probably mediated partially by the effects of climate on forage availability in terms of plant productivity and quality (Pettorelli et al. 2005) and secondarily through the interaction between climatic variability and population density (Hallet et al. 2004, Moen et al. 2006), which in turn affect herbivores space use patterns (Owen-Smith 2002).

Finally, in contrast with the findings of other studies that highlight the importance of different personalities when studying spatial ecology (Morales & Ellner 2002, Réale et al. 2007), individual variability did not explain a substantial amount of variance in observed home range size. This result is probably linked to the gregarious nature of male alpine ibexes that in most part of the year live in large herds, and herding behaviour might partially reduce differences in individual behaviour in terms of settlement and ranging behaviour by influencing habitat selection (Fortin et al. 2009) and foraging decisions (Fortin & Fortin 2009). Another explanation lies into the morphology of the study area and the habitat preferences of male ibexes in geographical terms. In fact in the Marmolada massif area males tended to occupy the same mountainsides throughout the year. This high site fidelity shown by males might lead to the observed flattened differences between individuals. This possibly can also explain the lack of differences in ranging behaviour between males of different ages. We expected to find differences in space use pattern of younger males in relation to adult and old ones, in fact ibex males of different age have conspicuous differences in body size, and therefore in energy requirement, and studies on segregation indicated that younger males tend to associate more with females (Ruckstuhl & Neuhaus 2001, Villaret & Bon 1995). However this was true especially for yearlings and two years old males, while males older than 3-4 years did not differ that much than older males with respect to patterns of inter-individual associations (Villaret & Bon 1995). For this analysis we had only two individuals younger than four years at the first capture and this can probably explain why we did not find any effect of age on home range, as described in other studies using adult individuals (Parrini et al. 2003).

In conclusion, dissimilarities in landscape characteristics in terms of grassland extent help to explain home range size of male alpine ibex in the Marmolada massif. A further step in this analysis can be understanding the composition of vegetation (in terms of species richness, biomass and interspersion) within the grasslands in different mountainsides and test whether this plant diversity affect home range size and geographic location of male ibexes. In fact, as suggested by McLoughlin & Ferguson (2000), at the individual level forage abundance and quality is likely to be the most important factor affecting home range size. Another important factor that will need further investigation is the role of snow depth in determining ranging behaviour. Height of snow cover, persistence in spring are factors that are likely to prevent ibex movement. Detailed measures of snow cover and a model describing annual variation may allow a more precise description.

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Chapter 5:

Post-release spatial and social behaviour of translocated male alpine ibexes (Capra ibex ibex) in the Eastern Italian Alps.

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Submitted

ABSTRACT

Alpine Ibex (*Capra ibex ibex*) distribution is still highly fragmented, especially in the Eastern Italian Alps. For conservation purposes it is therefore necessary to enhance connectivity between different populations by management tools such as reintroductions and restocking interventions aimed at reinforcing small and isolated colonies. In this three years study (2006-2009) we describe the space-use and social patterns exhibited by a group of adult male alpine Ibex relocated into the colony of the Marmolada massif (eastern Italian Alps). Our aim was to analyze the post-release behavior of translocated alpine ibexes in comparison with resident males, in order to test the short-term success of the restocking, provide some insight on the duration of the adaptation process and to furnish some indications for future restocking programs. None of the translocated males abandoned the colony, and all survived showing no capture/transport related stress. However, their integration into the colony was a slow and complex process. The released ibexes needed one or even two years to conclude explorative movements, settle down to home ranges comparable in size to those of resident males and fully associate with them. Individual heterogeneity in behaviour played an important role in the length of the adaptation process. These results highlight the importance of conducting a long-term monitoring program after restocking intervention and suggest the need of behavioural studies to improve knowledge on the process of integration of ibexes in a new colony.

KEYWORDS Alpine ibex, restocking, translocation, home range, association index.

INTRODUCTION

Alpine Ibex (*Capra ibex ibex*) came close to extinction at the beginning of the XX century due to overexploitation. However, thanks to active conservation strategies (such as introductions, reintroductions and hunting restrictions) and natural colonization processes (Stuewe & Nievergelt 1991) during the rest of the century the species was able to reoccupy part of its original alpine range and increase in abundance. Today it is classed as “Least Concern” by IUCN (Temple & Terry 2007). Despite alpine Ibex is no longer at risk of extinction, its distribution is still highly fragmented, especially in the Italian Alps (Duprè et al. 2001, Pedrotti et al. 2007, Carnevali et al. 2009). The species distribution range is below the potentially suitable area in Italy, and 85% of the entire Italian population is present in the western and central Italian Alps (Carnevali et al. 2009). In addition, alpine Ibex are characterized by a high spatial stability and are confined to high mountain ranges due to their ecological constraints (Gauthier et al. 1994). As a consequence, expansion of the existing colonies is very slow. For conservation purposes it is therefore necessary to boost management actions such as reintroductions and restockings, and to enhance connectivity between different populations (Pedrotti et al. 2007, Carnevali et al. 2009). Relocations have been adopted as an effective tool for conservation of large herbivores (Fisher & Lindenmayer 2000, Singer et al. 2000, Soorae et al. 2008). Survival of reintroduced populations of alpine ungulates can be affected by several factors, such as the initial size of the population (Berger 1990, Pedrotti et al. 2007) age and sex composition of the founders (Komers & Curman 1998, Apollonio et al. 2003), genetic variability (Randi 2005), habitat suitability (Owen-Smith 2003), pathogens (Cunningham 1996, Mathews et al. 2006) and connectivity between populations (Festa- Bianchet 2002). Translocation can affect significantly behavior of the animals because they are subjected to the multiple stresses of capture, handling, transportation and adaptation to a new environment (Letty 2007). Therefore, it is necessary to assess post-release behavior and settlement patterns with an intensive monitoring program (IUCN 1998, VV. AA. 2007, Soorae et al. 2008). In particular, in the first months after release, translocated animals may exhibit an altered ranging behavior, because they need to know the new environment (Jones & Witham 1990, Tosi et al. 1996, Michallet & Toïgo 2000, Dolev et al. 2002) and locate resources (Owen Smith 2003). Furthermore, interactions with conspecifics may play an important role in the duration and success of the adaptation process (Sjöåsen 1997), especially for gregarious species (Apollonio et al. 2003, Stanley-Price 1989).

Here we describe the space-use and social patterns exhibited by a group of adult male alpine Ibex relocated into the colony of the Marmolada massif (Dolomites, eastern Italian Alps). The Marmolada colony was founded in 1978 and the reintroduction was successful: the population increased steadily and up to 2003 this colony was one of the biggest of the eastern Italian Alps (Brugnoli 1999, Monaco et al 2004). However, during winter 2003-2004 the population experienced a dramatic crash caused by the combined effects of a sarcoptic mange epidemics and harsh weather conditions (Monaco et al 2005). In 2006 and 2007, a total of 14 male ibexes were translocated into the colony with the aims of improving its genetic variability and long term viability (Rossi et al 2006). Aim of this study is to analyze the post-release behavior of translocated alpine ibexes, in comparison with that of resident males, in order to assess the short-term success of the relocation and provide indications for future restocking programs.

We expected that relocated ibexes exhibited a post-release spatial instability, and were therefore interested in assessing the extent of such instability and verifying whether, and when, relocated ibexes eventually settled to spatial patterns similar to those of resident males. In addition, given the high gregariousness of male ibex (Tosi and Pedrotti 2003), we were interested in verifying the patterns of association of relocated males with resident males.

STUDY AREA

The study was carried out in the Marmolada massif, in the Eastern Italian Alps, (Dolomites - 46°26'13" N; 11°51'54"E, figure 1). The study area (about 150 km^2) lies between 1,200 and 3,350 m a.s.l. (highest peak, Punta Penia 3343 m a.s.l.). It is a typical alpine environment, characterized by steep slopes and dolomite limestone peaks. The main ridge axis orientation is east-west. A glacier lies at the summit of the Marmolada mountain, but it covers less than 2% of the total area (Duprè et al. 2001). Vegetation at the lowest elevations is mainly mixed woodlands made by common beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*) and sycamore maple (*Acer pseudoplatanus*) interspersed with Norway spruce (*Picea abies*). At higher altitudes (>1600 m) woodlands are mainly composed by Norway spruce and larch (*Larix decidua*). Above the timberline (1900 m) vegetation is mainly represented by alpine meadows and shrubs as mountain pine (*Pinus mugus*).

The study area is intensively used for touristic activities, such as skiing and hiking. Selective hunting is allowed for chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). Several alpine pastures are grazed by domestic cattle during summer. No large mammalian predator was present in the study area, except an occasional brown bear (*Ursus arctos*) presence during summer 2009.

MATERIALS AND METHODS

Ibex captures.- Translocated males were captured in the Jof-Fuart Montasio Massif (46°30'19.45"N 13°34'42.57"E) located about 200 Km east of the Marmolada massif (figure 1), and with geomorphological characteristics similars to those of the study area. Ibexes were released into the study area in May 2006 (9 individuals, hereafter also called TR1) and May 2007 (5 individuals, hereafter also called TR2). During the study period, age of relocated ibex was between 5 and 11 years (mean: 8, SD: 1). Resident males were 10 individuals which had been radio-tagged during a previous research project (Monaco *et al.* 2005) and 8 individuals which were captured and radio-tagged in August 2008. All individuals were equipped with

VHF radio-transmitters (Televilt TXH3, Telonics CMM-320). In addition, 18 resident males were individually recognisable from ear-tags. Age of resident males considered for the analysis (average: 7, SD: 2) was comparable to that of relocated ibex. All captures for this study were performed by tele-injection of xylazine (Rompum ®, Gauthier 1993), under the supervision of a veterinarian. All sedated ibex were aged from annual horn growth and examined for health status, before being equipped with the radio transmitters and/or ear-tagged with a unique colour combination.

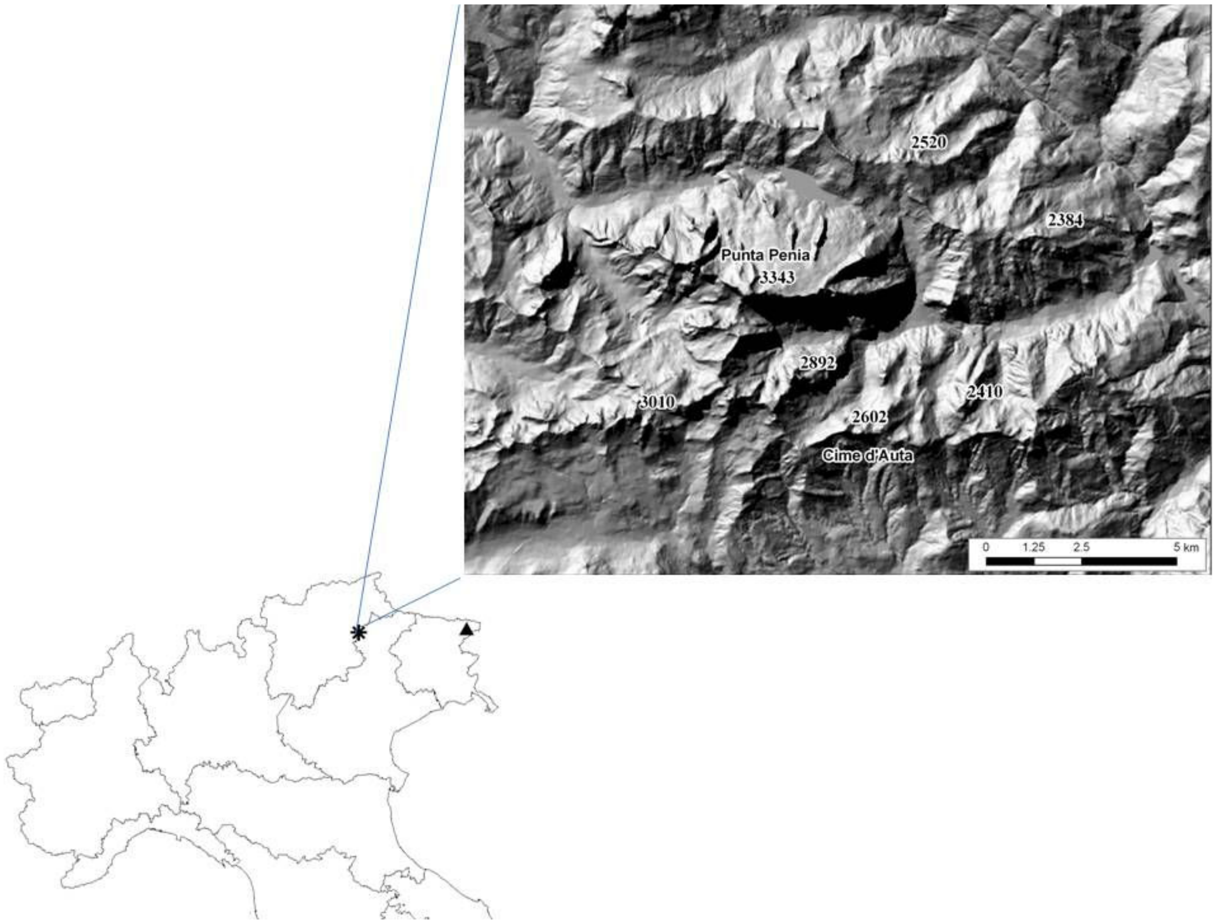

Figure 1: Map of the study area and its location in Italy: the asterisk indicate the Marmolada massif, the triangle Tarvisio (where translocated ibexes where captured)

Data Collection.-From June 2006 to August 2009 we searched (5 days/week) the study area to locate all radio-tagged and ear-tagged ibexes. We used radio-assisted sightings to locate radio-tagged individuals, since in the alpine environment used by ibex the presence of rocky peaks, cliffs and canals causes reflection and refraction of radio waves, and therefore locations obtained by the triangulation technique may be highly inaccurate (Kenward 2001, Pedrotti et al. 1995). However, we were able to locate also ear-tagged individuals with a similar frequency. We achieved an average number of sightings per individual and month of

4.8 (SD: 1.5) for radio-tagged males and 4.2 (SD: 1.3) for ear-tagged males. For each sighting we recorded: group size and composition (age class and sex of individuals) and plotted its location into a ortophotograph of the study area (1:10000 scale). For individual identification we used a 60x magnifier telescope (Swarovski CT85). Sightings were georeferenced in ArcView 3.2 and stored in an Access (Microsoft ®) database

Data treatment and analysis

We used data collected from 1 June 2006 to 31 August 2009. The statistical software employed for statistical analyses was SAS 9.1 ® (SAS 2006).

Home range size. We estimated annual home ranges from June 1st to May 30th 2006-2007, 2007-2008, and 2008-2009. For seasonal home ranges, we defined the following seasons, based on climate seasonal changes and the biology of ibex: "Summer": June-August; "Autumn": September-November; "Rut and Winter": December-February; "Spring": March-May. We computed home range size by means of Minimum Convex Polygon (MCP) and cluster estimators (Kenward 2001, Millspaugh and Marzluff 2003) by using the software Ranges VI (Kenward et al., 2003). MCP allowed us to make comparisons with other studies, but it is well known that this method tends to overestimate home range size (White & Garrot 1990, Millspaugh & Marzluff 2003, Fuller et al. 2005). Cluster estimators are built with a nearest neighbour joining rule, based on the distance between locations (Kenward 2001). They can be useful to describe the space use by ibexes, which generally use small areas connected by corridors (Tosi & Pedrotti 2003). Therefore, the combined use of these two methods allowed us to estimate the maximum (MCP) and the minimum (Cluster) area used by ibex. Since we had a similar location frequency for radio- and ear-tagged resident males, and in a preliminary ANOVA we found no differences in seasonal home range size between radio-tagged and ear-tagged resident individuals (MCP; LS means ± ES: radio-tagged = 169.9 ± 36.0; ear-tagged = 136.2 ± 34.1; $F_{1,95} = 0.01$; P = 0.93), we decided to use also home ranges of ear-tagged individuals. For statistical analyses, home range size was log-transformed to meet a normality assumption. For all analyses we used mixed linear models (PROC MIXED, SAS), where individual was treated as a random effect. Differences between Least Square (LS) means were tested by performing a multiple comparison post-hoc test with the Tukey-Kramer adjustement. Age was tested as a covariate. For annual home ranges, we were interested in detecting changes with time after release in the spatial behaviour of relocated as compared to resident males, and hence in the interaction between provenance (resident, TR1, TR2) and research year (1,2,3). However, this was not possible since TR2 were translocated in year 2 and were absent in year 1. Therefore, we first defined a simplified provenance (resident and translocated) and tested its effect in a model with all years. Having ascertained in this way that there was indeed a significant interaction between simplified provenance and year (see results), and in order to compare all available provenances in all years, we then defined a combined variable where each level was the combination of each provenance and year, and tested it in a simple one-way model.

For the analysis of seasonal home ranges we used home ranges with at least 10 locations. This number is lower than that suggested as the minimum required to obtain accurate estimates in other species (Saïd et al. 2005, Börger 2006). However, we were principally interested in a relative comparison of spatial behaviour between ibexes of different provenances, and less interested in an accurate estimate of home range size. To take into account possible effects of sample size on home range size estimates, in all models we used number of locations as a covariate. Since we had only one season (summer) in year 4, we defined as "period" the combination of each season and year. As above described for annual home ranges, we first analysed data with a model with the simplified provenance, period and their interaction (see results). Then, to compare all available provenances in all periods, we obtained a combined variable where each level was the combination of each provenance and period and tested it in a simple one-way model. Although analyses were performed on log transformed data, results will be presented as hectares.

Movements within seasonal home ranges. - We analyzed more in detail the spatial strategies of ibexes by quantifying their rate of movement within their seasonal home range. Based on morphological and land use features that are known to affect habitat suitability for ibex, and on spatial distribution of sightings, we split the study area into 10 different sub-areas. By using the Geoprocessing extension in ArcView 3.2 (ESRI ®) we assigned each sighting to a sub-area, and then we calculated the number of times each ibex shifted between different sub-areas within each season. We analyzed the rate of change of sub-areas by performing an "event" (location in a different cluster)/"trials" (number of location available) logistic regression analysis with a model with 13 periods (as above described), 3 provenances (resident, TR1 and TR2) and their interaction. Odd ratios were estimated with resident males in summer of year 2 as reference class.

Experienced group size - According to Jarman (1974), the group size experienced by an average individual ("typical group size") is better described by calculating the frequency distribution of all sightings of a given sex/age category in groups of different size. Since male ibex are highly gregarious and segregate from females during most of the year (Villaret et al. 1997, Bon et al. 2001), we used only observations of groups composed uniquely by males. We defined 5 classes in relation to the group size: "solitary males", "small groups" (2 to 5 individuals), "intermediate groups" (6 to 10 individuals), "large groups" (11 to 20 individuals) and "very large groups" (more than 20 individuals). We then calculated the distributions of sightings of resident, TR1, and TR2 males in each group size class for each year of monitoring. Distributions were compared with a χ^2 test with a post-hoc Bonferroni test for confidence intervals.

Inter-individual association index – Inter-individual associations were quantified on a monthly basis by computing a modified Ginsberg e Young (1992) association index: $I_{ab}=x/(x+y_a+y_b)$ where: x=number of sightings in which a and b were together in a given month; y_a= number of sightings of a without b in a given month; y_b= number of sightings of b without a in a given month. The index varies between 0 and 1. Dyads were assigned to the following categories of association: resident (association between resident males); TR1 (association between TR1 males); TR2 (association between TR2 males); resident-TR1; resident-TR2; TR1-TR2. The difference between the association index observed in those categories was tested by using a Kruskall-Wallis test (hereafter KWt), followed by Dunn post-hoc test with Bonferroni adjustement. Since summer is the period of the year in which adult males form larger groups and therefore interact most (Toïgo et al 1995, Tosi & Pedrotti 2003, Villaret & Bon 1995), a more detailed analysis was performed by testing the effect of the category of association on the observed association index during each summer in different years.

RESULTS

Dispersal and survival.- All translocated ibexes remained within the target colony, restraining their exploratory movements within the area used also by resident males. Two translocated males died engulfed by avalanches during the winter 2008/2009, characterized by exceptional snow precipitations.

Annual home ranges.- We obtained 89 home ranges for 40 individuals (26 Resident; 9 TR1 and 5 TR2 – Figure 2). The mixed model with the effects of simplified provenance and year showed significant effects for provenance (MCP: $F_{1,45}$=34.35, p<0.001; Cluster: $F_{1,45}$= 13.62,

$p<0.001$), year (MCP: $F_{2,45}$=16.35, $p<0.001$; Cluster: $F_{2,45}$= 3.44, $p<0.05$) and their interaction (MCP: $F_{2,45}$=3.65, $p<0.05$; Cluster: $F_{2,45}$= 2.22, p=0.12). There was no effect of age (MCP: $F_{1,45}$=0.84, p = 0.365; Cluster: $F_{1,45}$= 0.24, p = 0.627). The one-way model showed highlys significant effects of the combined provenance by year variable (MCP: $F_{7,44}$=10.82, $p<0.001$; Cluster: $F_{7,44}$= 3.59, $p<0.01$). Resident males had comparable home ranges in all 3 years (figure 2), while TR1 males had significantly larger home ranges than resident males in year 1 (MPC: $p<0.001$; Cluster: p = 0.07) and year 2 (MPC: $p<0.001$; Cluster: $p<0.05$;), but not in year 3 (MPC: p = 0.49; Cluster: p = 0.80). Translocated males TR2 used larger areas than resident males in year 2 (MPC: p =0.05; Cluster: p =0.40), but not in year 3 (MPC: p =0.94; Cluster: p =0.98). Differences between provenances were more marked with MPC (total area explored) than with Cluster (area used within that explored). Translocated males TR1 settled to similar home ranges than resident males after 2 years from release, while TR2 settled after 1 year.

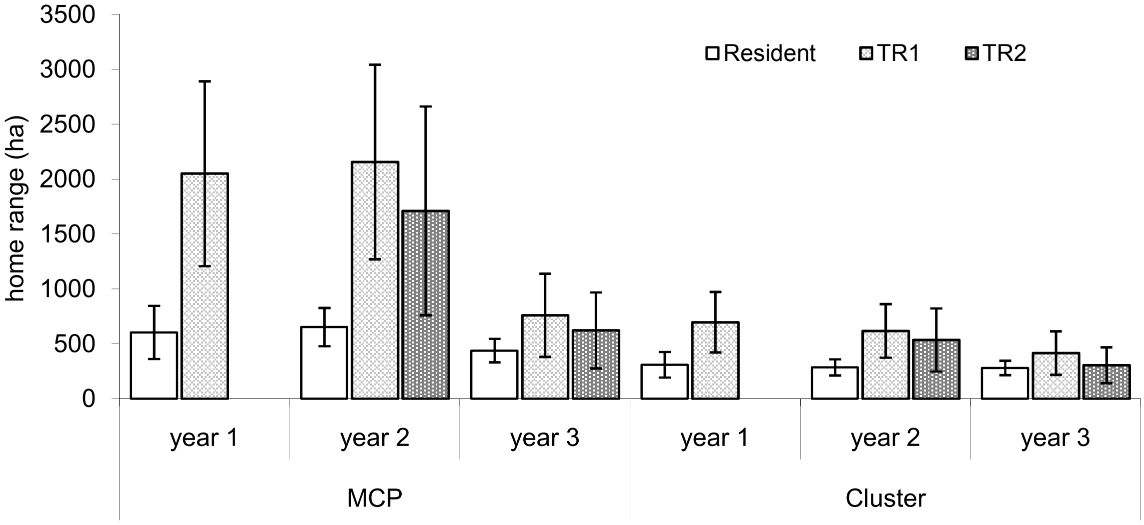

Figure 2: Annual home range (least squares means) of resident and translocated adult male ibex in the Marmolada massif. Error bars represent standard error.

Seasonal home ranges.-We obtained 270 home ranges with 42 individuals (28 resident, 9 TR1 and 5 TR2). Size of seasonal home ranges was on average 391 hectars (SD= 494) for MCP and 230 hectars (SD = 353) for Cluster estimators. Since statistical analyses produced similar results for MCP and Clusters, we will discuss hereafter only the MCP estimator. The mixed model with the effects of simplified provenance and period showed significant effects of provenance ($F_{1,203}$ = 11.05, $p<0.01$), period ($F_{12,203}$ = 14.63, $p<0.001$) and their interaction ($F_{12,203}$ = 4.04, $p<0.05$). Age had no effects ($F_{1,203}$ = 0.64, p = 0.426). With increasing number of locations there was a tendency for increasing home range size estimates ($F_{1,203} = 4.03$, $p<0.05$). The one-way model showed a highly significant effect of the combined provenance by year variable ($F_{34,195} = 7.04$, $p<0.001$); number of locations was again significant ($F_{1,195} = 4.82$, $p<0.05$). Least square means are given in figure 3. Translocated TR1 ibexes used much larger home ranges than resident males in the summer and autumn following their release (in year 1), although this difference was significant only for summer ($p < 0.05$) due to a very high individual variability of TR1 males. In winter and spring, they used areas similar to those of resident males, but had again larger home ranges ($p<0.05$) in the summer of the second year. Afterwards, and up to the summer of year 4, they maintained a tendency for using larger areas than resident males in summer and autumn, but differences became less remarkable and were not statistically significant. Translocated TR2 ibexes settled faster than TR1 males, since they used larger home ranges than resident males only during the summer of the year of their release ($p<0.05$).

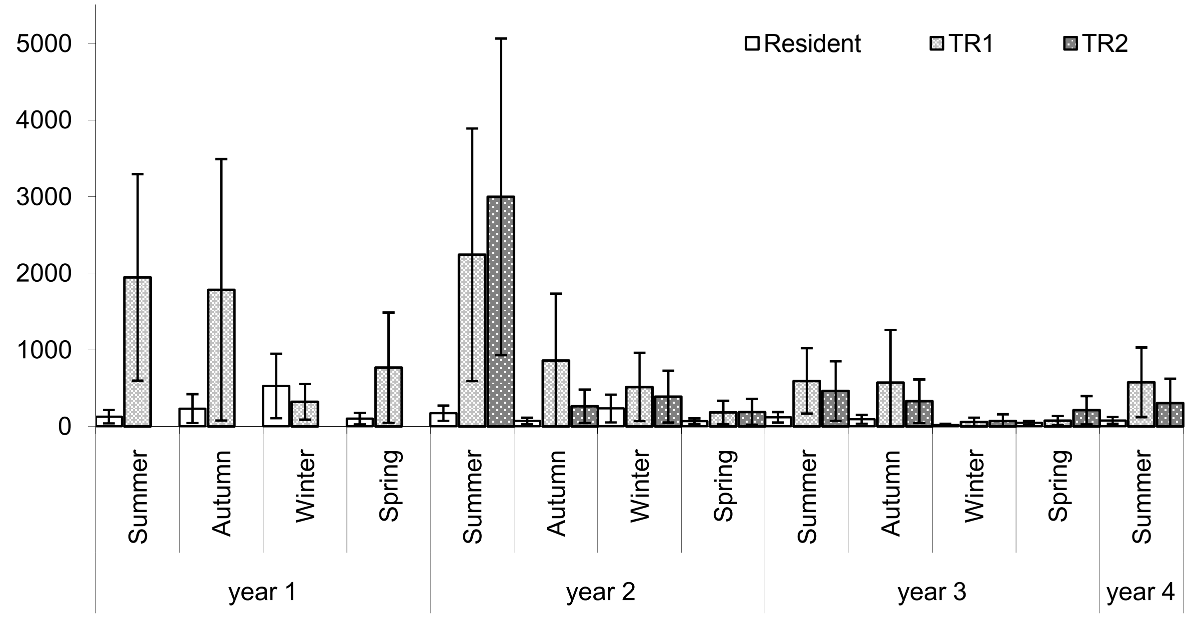

Figure 3: Seasonal home range (least square means) of resident and translocated (TR) adult male ibex in the Marmolada massif. Error bars represent standard errors.

Males of all provenances tended to have smaller home ranges in spring than in the other seasons. In addition, they all had extremely low home ranges in the winter of year 3.

Movements within seasonal home ranges. - The logistic regression analysis of the rate of change of sub-areas within seasonal MCP home ranges gave highly significant effects for provenance (χ^2=20.9 df = 2 p<0.001), period (χ^2=24.0 df = 12 p<0.001) and their interaction (χ^2=120.3 df = 20 p<0.001). Odd ratios are shown in figure 4. Both TR1 and TR2 males showed a higher rate of change than resident males in the summers of their release year, but not in the other periods. In general, there was a tendency for ibexes of all provenances to show lower rates of change in spring than in the other seasons.

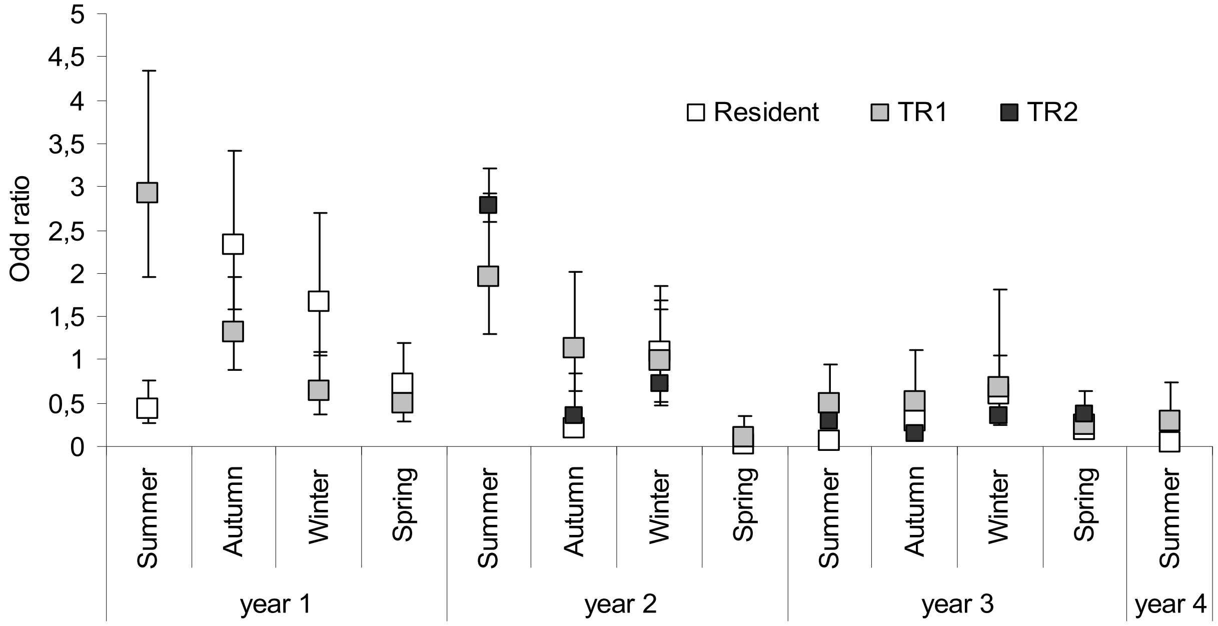

Figure 4: Odd ratios for the rate of change of sub-area within seasonal home ranges for resident and translocated (TR1: translocated in year 1; TR": translocated in year 2) adult male ibexes. Error bars represent confidence intervals for P<0.05. Resident males in summer of year 2 are taken as reference class (odd ratio = 1).

Male group size- Experienced group size is shown in figure 5. In the year of release, TR1 males differed in grouping behaviour from resident males (χ^2=878.22 df=4 p<0.001). The Bonferroni test showed that they were significantly more solitary and joined less frequently "very large" groups with more than 20 individuals. Grouping behaviour differed significantly also in years 2 (χ^2=154.37 df=4 p<0.001) and 3 (χ^2=93.37 df=4 p<0.001). However, TR1 males increased their use of "intermediate" and "very large" groups (years 1-2: χ^2=734.94 df=4 p<0.001; years 2-3: χ^2=42.37 df=4 p<0.001; years 1-3: χ^2=1290.63 df=4 p<0.001), in that reducing their disparity as compared to resident males. Translocated TR2 males differed from resident males only during the first year after release (year 2: χ^2=35.29 df=4 p<0.001; year 3: χ^2=4.47 df=4 p=0.35), when they used more "small" groups and less "very large" groups. Instead, they differed significantly from TR1 males in both years (year 2: χ^2=18.60 df=4 p<0.001; year 3: χ^2=38.90 df=4 p<0.001), since they tended to be less solitary and used

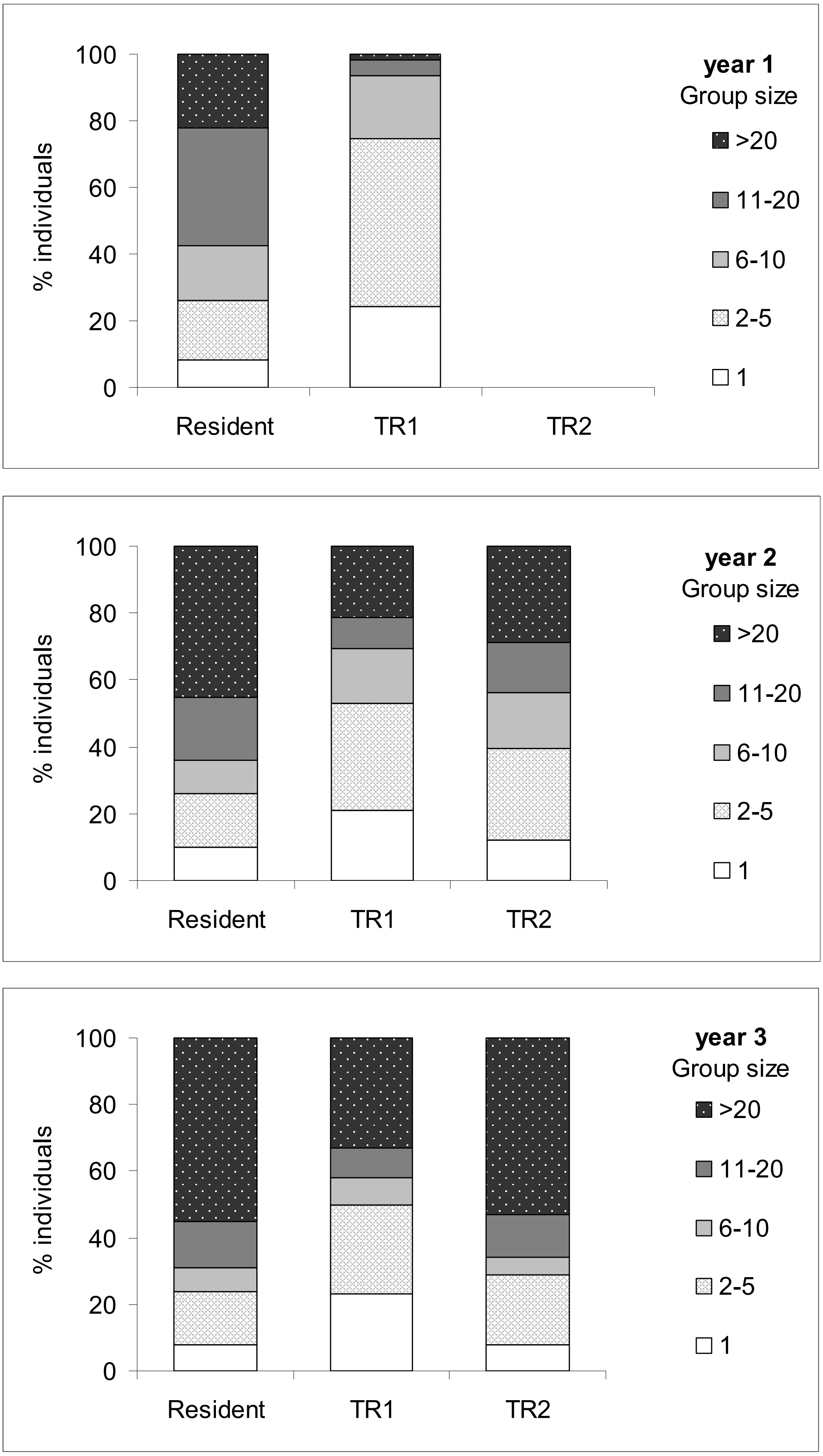

Figure 5: Group size experienced by resident and translocated (TR1: translocated in year 1; TR2:translocated in year 2) adult male ibexes during the three years of research.

more frequently “large” and “very large” groups. We also observed, in resident males, an increased use of “very large” groups passing from year 1 to years 2 and 3 (years 1-2: χ^2=198.34 df=4 p<0.001; years 2-3: χ^2=35.74 df=4 p<0.001; years 1-3: χ^2=533.10 df=4 p<0.001).

Inter-individual association.- The average monthly association index observed for resident males and the association between resident males and, respectively, TR1 and TR2 males are shown in figure 6. During the summer months males tended to form the largest groups and consequently also the association index assumed the highest values, while during winter males became more solitary, and therefore the association index was almost null. We observed a highly significant difference of the association index in relation to the different categories of association (KWt: H=1212.65, df= 5, p<0.001). The Dunn test indicated that in the overall period of study the association index observed for resident males differed from the values observed for all the other categories of association. Table 1 summarizes the results obtained for the analysis of association indexes observed in summer.

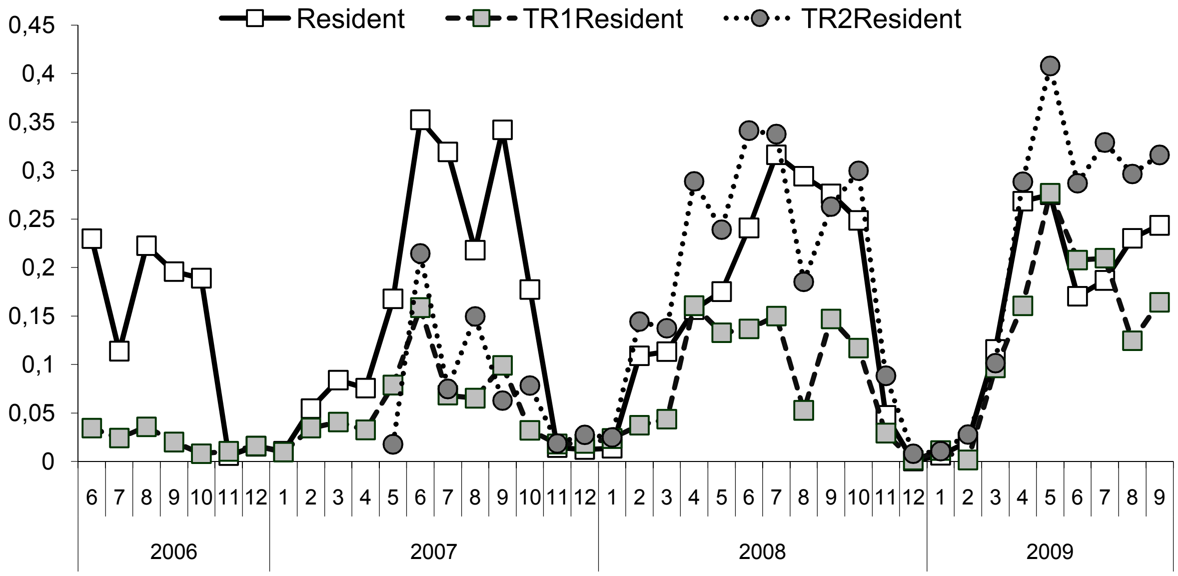

Figure 6: general patterns of monthly association index (average values) observed within resident males (white); TR1 with resident males (light grey), and TR2 with resident males (dark grey)

Association indexes showed significant differences between categories of association in all summers (KWt = summer 1: H=146.8, df= 2, p<0.001; summer 2: H=241.3, df= 5, p<0.001; summer 3: H=304.9, df= 5, p<0.001; summer 4: H=84.0, df= 5, p<0.001). After release, TR1 males associated more among themselves than with resident males, and only in the fourth summer we observed a comparable level of association between the animals belonging to the two different provenances. Translocated TR2 males showed instead a higher degree of association with both resident and TR1 males from the summer of their release year.

Table 1 Descriptive statistics (number of observations, mean value and standard deviation) of the association index calculated during the four summers (2006-2009) of the study. The letters indicate the similarities between couples of values obtained with Dunn post-hoc comparison (p=0.05).

Category	Summer 1			Summer 2			Summer 3			Summer 4		
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Resident	825	0.19^{B}	0.29	939	0.30^{C}	0.28	939	0.28^{B}	0.26	1328	0.20^{A}	0.23
TR1	108	0.15^{B}	0.20	108	0.18^{AB}	0.27	108	0.09^{A}	0.17	83	0.19^{A}	0.26
TR2				30	0.23^{C}	0.18	30	0.35^{B}	0.28	18	0.49^{B}	0.28
TR1Resident	687	0.03^{A}	0.08	687	0.10^{A}	0.16	684	0.11^{A}	0.18	344	0.18^{A}	0.23
TR2Resident				372	0.15^{B}	0.16	372	0.29^{B}	0.24	720	0.30^{B}	0.29
TR1TR2				132	0.15^{AB}	0.18	132	0.12^{A}	0.20	94	0.30^{AB}	0.30

DISCUSSION

This study highlights how the adaptation to a new colony by translocated male alpine Ibex is a complex process, that may involve a prolonged spatial and social instability. This altered behaviour is particularly evident when compared with the behaviour of resident animals.

Resident males exhibited a conservative space use, occupying areas of comparable size during different years and also showing a high overlap between annual home ranges (Scillitani et al. 2009). A similar pattern of high stability in space use, with home range sizes (MCP) comparable to those of the resident males of our colony, has been described for the autochthonous ibex population of the Gran Paradiso national park (Parrini et al. 2003). In our study seasonal home ranges tended to be smaller in winter and spring, in agreement with other studies (Michallet 1994, Parrini et al. 2003, Terrier et al. 1994). However, we did not record seasonal migrations across different seasonal quarters, as observed in other ibex colonies (Gauthier et al. 1991, Girard 2000). This high site fidelity is probably linked to the morphology of the study area, in which the sites most suitable during winter coincide with those preferred in summer. In fact the largest alpine grasslands which constitute the preferred environment for males (Grignolio et al. 2003, Bassano 2006) are south facing and characterized by steep slopes and therefore during winter are covered by a lower snow depth. During the other seasons the same areas are probably selected in relation to forage availability.

Although in general seasonal home ranges of resident males did not vary significantly between different research years, we observed smaller winter home ranges during 2008-2009, especially if compared with winter 2006-2007. A possible explanation of this pattern is the difference in timing and amount of snowfalls between winters. In winter 2006-2007 snowfalls were late and shallow, with snow cover being less deep than 40 cm until February, but in winter 2008-2009 snow cover had already reached a depth of 130 cm at the beginning of December. In early winter males generally move to reach females in reproductive quarters, showing therefore larger home ranges (Parrini et al. 2003, Pedrotti 1995), but the depth of snow cover may hinder movements of ibex that is scarcely adapted to snow (Tosi & Pedrotti 2003). This might explain why resident ibexes had larger home ranges when snow was scarce, but greatly reduced the areas used when it was abundant.

During the first and second year after release, translocated ibexes used annual home ranges which were bigger than those of resident males, both when calculated with MCP which index the total area explored, and with clusters which estimate that more intensively used. Translocated ibexes used the largest home range size during summer, while they used areas of a similar size than resident males in winter and spring. In accordance with this result we also detected a higher rate of movement within sub-areas during summer. This was most probably because translocated males were released in late spring and because during summer and autumn risks correlated to exploration and climatic constrains are lowest. Several studies already showed that after translocation animals generally exhibit wandering movements that result in larger home range sizes (Pedrotti 1994, Tosi et al. 1996, Jones et al. 1997, Michalet & Toïgo 2000, Dal Compare 2008), as we observed for the males translocated in the Marmolada massif. In particular, other studies on reintroduced ibex populations showed how released animals progressively increased the extent of the area explored but within 6 months or one year they settled down or at least used preferential directions in their movements (Tron 1994, Terrier et al. 1994, Monaco and Carnevali 2002, Mustoni et al. 2008). In our study this phase of instability was more prolonged and lasted until the second or third year after release. Home range size of translocated ibex (about 2,000 ha) during the years interested by exploratory movements was in average similar to those reported in other studies on reintroduced populations (Michallet 1994, Pedrotti 1995, Terrier et al. 1994, Tron et al. 1994, Monaco & Carnevali 2002).

In general, however, we recorded a shorter wandering phase in ibexes released in 2007 (TR2) which exhibited smaller home ranges than TR1 males and settled down more quickly. In fact a reduction in home range size to values similar to those of resident males was achieved in the second summer after release by TR2 males, but in the third summer by TR1. However, we found a large variability in behaviour among different individuals, in accordance to other studies (Terrier et al 1992). In example, one of the males released in 2006, "mTAR2" settled down in a small area the summer after the release. The following year, instead, he wandered over a large area, while in the third and the fourth summer after release he occupied permanently the area used during the first year. On the contrary the male "mTAR3" did most of his exploratory movements within the first summer after release, and settled down from the second year after release.

Numerous studies on reintroductions highlighted how the age of released animals may play an important role in the establishment process and usually younger individuals disperse less from the release site (Sempéré et al. 1986, Michalet & Toïgo 2000, Calenge et al. 2005). The translocation of adult and old animals can therefore be more problematic because they may be less adaptable to the colonization of a new environment they are not used to (Letty et al. 2007). In our study, age of translocated ibexes varied from 5 to 9 years at release, but we did not observe any difference due to age in spatial behaviour.

Althought they exhibited a marked post-release spatial instability, none of the translocated ibex dispersed outside the target area, as was instead observed in previous reintroductions of ibexes in nearby massifs (Sommavilla G., personal communication). This can be partly due to the fact that our study area has only few high altitude corridors that ibexes can use for dispersing toward other areas. However, the area is not isolated, as confirmed by one ibex immigrating into the Marmolada colony after his reintroduction in the neighbouring park of Paneveggio-Pale di San Martino (Monaco et al. 2005), and by an ibex captured in 2008 in the Marmolada massif which was observed in 2009 outside the study area (about 12 Km, Brugnoli S., personal communication). Probably the presence of an already established colony facilitated the settlement of reintroduced ibexes, as it has been reported in other studies (Pedrotti 1995). However, there are cases in which such facilitation was not observed (Monaco & Carnevali 2002, Terrier et al. 1992). Anyway, other studies where dispersal was observed were reintroduction studies, and in various instances dispersal ended into nearby colonies (Dal Compare, 2008). Our results may suggest that when translocations are made to reinforce existing populations the risk of dispersal is lower than when they are made to establish new populations.

It is also possible to hypothesize that social behaviour plays a central role in the adaptation process of translocated males to the new area. Alpine ibex, as other species of the *Caprinae* subfamily, is a highly gregarious species (Tosi & Pedrotti 2003, Bassano 2006). It shows an extreme variability of group composition which is characterized by open membership since social bonds are commonly loose (Girard 2000, Toïgo et al 1995, Villaret & Bon 1995). In general older males tend to be more solitary than younger ones (Toïgo et al. 1996, Villaret & Bon 1998). Even if the pattern of social bonds between male alpine ibex is still not clearly understood, it has been suggested that males engage confrontations during the pre-rutting season in order to reduce the agonistic behaviour during the rut, which take place in the harshest months (Willisch 2009). Therefore for the success of a restocking intervention it is important to take into account the social interactions with established conspecifics. In addition in some cases the presence of conspecifics may slow the adaptation process because it can result in agonistic behaviours that prevent reintroduced individuals the access to the most suitable areas, as suggested for Fallow deer (Dolev et al. 2002).

In this study we observed a dissimilarity in the social behaviour exhibit by resident and translocated males. In agreement with literature, in the Marmolada colony resident males gathered frequently into large groups of 11 to 20 individual, and were often observed in groups composed by more than 20 individuals. It is also important to notice how, from 2006 to 2008, we recorded an increase in frequency of individuals observed in "very large" groups. The Marmolada colony experienced a severe demographic decline, due to the outbreak of sarcoptic mange in winter 2003-2004, which also caused a decrease in group size (Monaco et al. 2005). The observed tendency toward an increase of the group size could therefore be considered an encouraging signal of the growth of the colony, since in Alpine ibex, group size is correlated with population density (Toïgo 1996).

Nevertheless, associations within males were not stable, as indicated by the low average values of inter-individual association indexes amongst resident males.

The interaction with local males showed by TR1 differed from that exhibited by TR2, and this may partially explain the different length of their wandering phase. After release, ibexes translocated in 2006 associated mostly within themselves. Because they grouped among themselves, TR1 males tended to be solitary or formed small groups. This lower tendency to gregariousness was observed also in the second and third year after release, although during this time they showed an increased use of groups made by more than 10 individuals. Only in the fourth summer after release TR1 started to associate regularly with resident males. In contrast, ibexes released in 2007 showed a quicker social integration process, since they segregated from local males only in the first summer after release, were seldom solitary and joined more often larger groups than TR1 males.

These temporal patterns of experienced group size and association indexes match those observed for spatial behaviour, with translocated males reducing their homes ranges to similar sizes than resident males when they started to associate with them. We may therefore hypothesize that, together with the progressive knowledge of the new area acquired from exploratory movements, the development of social connections with resident males influenced the spatial behaviour of translocated ibexes, which, when started grouping with resident males, started also to use the same spots. We do not have certain evidences of the reason why TR2 males were faster in the adaptation process. This difference might have been a consequence of individual variability, or maybe, since TR2 males associated with TR1 males soon after release, they took benefit from the experience and the social bounds already established by the males released the year before. Unfortunately, the lack of behavioural observations on the interactions between individuals before and after the translocation prevents us to test such hypothesis.

In conclusion, the integration into an established colony by adult male ibex appears to be a complicate process which involves several different variables and may take up to two or even three years to be completed. In addition, for all the spatial and social parameters analyzed we observed a highly remarkable individual variability, so that we cannot conclude by drawing a general pattern in the behaviour of ibexes translocated to reinforce an existing population. However, the experience gained by this study might be useful in designing future restocking interventions aimed at reinforcing small and isolated colonies. We recommend to continue post-release monitoring for at least three years after release, to contemplate the capture of resident males in order to be able to compare the behaviour of translocated and local animals and to incorporate into such monitoring behavioural observations, in order to detect the eventual occurrence of agonistic behaviour between translocated and resident ibexes, which might lower the success of the translocation affecting the reproductive success of released males.

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Chapter 6:

Habitat selection in translocated alpine ibex: is selection innate?

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INTRODUCTION

Describing the organization of animals in space and time is a primary task in ecological studies, necessary for a good understanding of the biology of a species (Gaillard et al. 2010, Morris 2003). In particular, the study of habitat selection is important because it expresses the connection between a species and the environmental context in which it lives (Basille 2006). The aim of habitat selection studies is in fact determining which environmental factors affect the distribution of a given species. According to the habitat selection theory, species select the habitats (*sensu* Hall et al. 1997) which maximize their fitness and allow them to coexist with other species (Manly et al. 2002). In general, resources are not uniformly distributed, but scattered within an heterogeneous landscape (Morrison et al. 2006, Garshelis 2000) and, since animals normally confine their movements in a restricted area, this generates space use patterns (Borger et al. 2006). The disproportionate use of a given resource in comparison to its availability is commonly considered an evidence of selection (Manly et al. 2002), although this is object of debate since it is often really difficult to define what is in point of fact available for an animal (Beyer et al. 2010, Garshelis 2000). Therefore, fully understanding of mechanisms underlying resource selection is one of the most controversial issues in ecology (Garshelis 2000, Lima & Zollner 1996). As most ecological processes (Levin 1992, Wiens 1989), habitat selection follows a hierarchy: precisely, according to Johnson (1980), it is possible to recognize four main hierarchical levels of selection. The first-order selection is the distribution range of a population, second-order selection is the selection of home range of an individual or a group, third-order selection detects the selection of a patch within the home range and fourth-order selection is linked to the microhabitat of an animal (i.e. selection of food items or resting sites..etc..). Selection mechanism may be different at each level, and different are the cues that influence decision-making at different scales (Bowyer & Kie 2006, Thomas & Tailor 1990, 2006). Therefore, conducting analysis at more than one scale is necessary to describe pattern of selection and can be a prerequisite for detecting the true explanatory variables that explain the ecology of a species. For this reason it is necessary both to consider different level of organization (from population to organism, Johnson 1980) and to investigate pattern of selection at different spatial (Boyce et al 2003, Dussault et al 2005, Kie et al 2002, Schaefer & Messier 1995) and temporal scales (Arthur et al 1996, Schaefer et al 2000, Schooley 1994).

The resource selection process is affected by several factors including forage availability and quality (Hochman & Kotler 2006, Owen-Smith 2002, Senft et al 1987, Wilmshurst et al 1995), patch distribution within the landscape (Kie et al. 2002, Morrison et al 2006), predation risk (Creel et al 2005, Hebblewhite & Merril 2009, Laundré et al 2001, Willem & Hill 2009), presence of competition (Darmon 2007, Forsyth 1999, Putman 1996), seasonality (Ager et al. 2003, Cransac & Hewison 1997, Squires et al. 2010, Rettie & Messier 2000), sex (Bleich et al. 1997, Clutton-Brock et al. 1987, Villaret et al. 1997), age class (Cransac et al. 1998) and kind of behaviour (Godvik et al. 2009, Moe et al. 2007).

Some features of resource selection are innate and intimately connected with the species ecology and life history: species are morphologically adapted to survive to the constraints of a given set of environmental condition as a result of their evolution (Darwin 1859). However, (especially in complex organisms as birds and mammals) the acquisition of subtle adaptations in habitat selection decisions can be the result of a complex learning process acquired by individuals throughout their lifetime and linked both to cultural transmission and personal experience (Giraldeau 1997, Manning & Stamp 1998). For example, the importance of learning in resource acquisition have been demonstrated for feeding behavior in primates (Lefebvre 1995), and also for the selection of plant species in herbivores (Edwards 1975, Villalba et al. 2004). According to the Natal Habitat Preference Induction (NHPI) theory (Davies & Stamps 2004) the experience with the natal habitat shapes the habitat preferences of individuals in the following stages of their lives. In fact the experience with the stimuli that an individual gain in its natal habitat increase the probability that the individual will select habitats that contain similar stimuli. This mechanism in turn plays an important adaptive role, since individuals are most likely to select features that can maximize their fitness.

In social species, moreover, selection can be mediated by the presence of other individuals: conspecific exert an important attractive effect in several species (Giraldeau 1997, Lima & Zollner 1996, Reed & Dobson 1993) and animals living in a group can make group based selection decision (Fortin et al. 2009) or follow decisions taken by the group leader (Michelena et al. 2010). On the other hand group members can compete for resource acquisition and as a consequence presence of conspecific becomes a limiting factor (Molvar & Bowyer 1994, Shrader et al. 2006).

At the home range level, (third level of selection) the major factor determining species range occupancy is forage availability and abundance (McLoughin & Ferguson 2000). In example herbivores feed on plant species that in turn are spatially structured, although their availability and nutritional value might change over time in seasonal environments (Owen- Smith et al. 2010). Therefore in terrestrial herbivores memory of the place where optimal resources are placed and consequently familiarity with the inhabited range (Bailey et al. 1996, Benhamou 1994, Owen- Smith et al. 2010, Stamps & Khrishnan 1999, Switzer 1993, Van Moorter et al. 2009) are key factors in resource selection.

A movement out of the familiar range of an individual lead to an increased cost due to the exploring behavior (Stamps et al. 2005) needed to locate optimal resources. As a result of this explorative movements animals undergo the risk of increased mortality due to increased predation (Hebblewhite & Merril 2007, Nicholson et al 1997), starvation and increased energetic costs of searching behaviour (Pärt 1995). This is certainly true for migrating and dispersing animals (Stamps et al 2005, Johnson & Gaines 1990, Ward 1987), and is even more problematic in the case of relocations. Unlike disperser, translocated animals do not change range as a consequence of an innate behavior or a natural decisions. Once relocated in the new habitat, translocated animals lack the knowledge of the surrounding areas and an acquaintance of the available resources to accommodate their needs. This may lead to inappropriate behaviours and consequently poor demographic performance (Letty et al. 2007, Stamps & Swaisgood 2007, Stanley-Price 1989). Moreover, it has been reported that some species actually avoid unfamiliar items, because they are afraid of them (“neophobia” - Greenberg 1984) and this can counteract a successful adaptation to the release site.

The aim of this study was to understand how translocated wild caught animals adapt to a new environment. In particular we want to verify if, after a relocation, animal have to learn the new habitat (H_0) or if habitat selection depends mainly on the ecological preference of a species (H_1), or it results from a combination of the two processes (H_2). If H_0 is true, we expect to find both a long explorative behavior and attraction to conspecific that will provide translocated individuals cues of the location of optimal resource. If H_1 is true, we expect males to have the same habitat selection, independently to their origin, and it should be stable over years. We tested these hypotheses by evaluating the habitat selection patterns exhibited by resident and translocated adult alpine ibex (*Capra ibex*) males. To do so we firstly described habitat selection by resident ibex (before the introduction of new individuals). We operated a comparison with the selection exhibited by translocated ibexes on different spatial and temporal scales. Moreover, since ibex is a gregarious species we expect to find a positive effect of conspecific attraction in the adaptation process.

MATERIALS AND METHODS

Study Area (and release site)

The study area was the Marmolada massif area, in the Eastern Italian Alps, (Dolomites - 46°26'13" N; 11°51'54"E, figure 1). It encompasses about 150 km^2 and lies between 1200 and 3343 m a.s.l. The highest peak is punta Penia (3343 m a.s.l.) and the main peak in the area most used by ibex is Cima dell'Auta (2623 m a.s.l.). The environment is typical alpine, with steep slopes even at low altitudes and characteristic dolomitic limestone rocks. The main ridge axis orientation is east-west. A glacier is present, but it covers less than 2% of the total area (Duprè et al 2001). At the bottom of valleys are present mixed woodlands made up of common beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*) and sycamore maple (*Acer pseudoplatanus*) interspersed with Norway spruce (*Picea abies*). At higher altitudes (>1600 m) woodland are mainly composed by Norway spruce and larch (*Larix decidua*). Above the timberline (1900 m) vegetation is mainly represented by alpine meadows and bushes as mugo pine (*Pinus mugus*). Above 2500 m a.s.l. the area is mostly covered by rocks (59%) and screes (27%), with slopes higher than 30°.

The study area is intensively used for touristic activities, such as skiing and hiking. Hunting is allowed, and the hunted ungulates species are chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). Several alpine pastures with domestic cattle are present during summer. No large mammalian predator was present in the study area, except an occasional brown bear (*Ursus arctos*) presence recorded during summer 2009.

Source Area

The translocated ibex were captured in the Jof Fuart (2666 m a.s.l.) and the Jof Montasio (2753 m a.s.l.) massifs in the Tarvisio area, Giulie Alps (46°25'49" N; 13°29'38"E, figure 1), about 200 Km eastern of the release site. This area is similar in the geological composition to the Marmolada massif area since also it is characterized by dolomitic limestone and steep slopes at relatively low altitudes too. Altitudes range from 500 m to 2800 m a.s.l., and treeline is around 1700 m a.s.l. The bottom of the valleys are mainly covered by deciduous woodland composed by common beech and by mixed woodlands composed by common beech, Norway spruce, European silver fir (*Abies alba*), Scots pine (*Pinus sylvestris*) and European black pine (*Pinus nigra*). Between 1000 and 1500 m the main cover types are forest of Norway spruce and larch. Alpine grassland and mugo pine bushland are the predominant habitat cover type

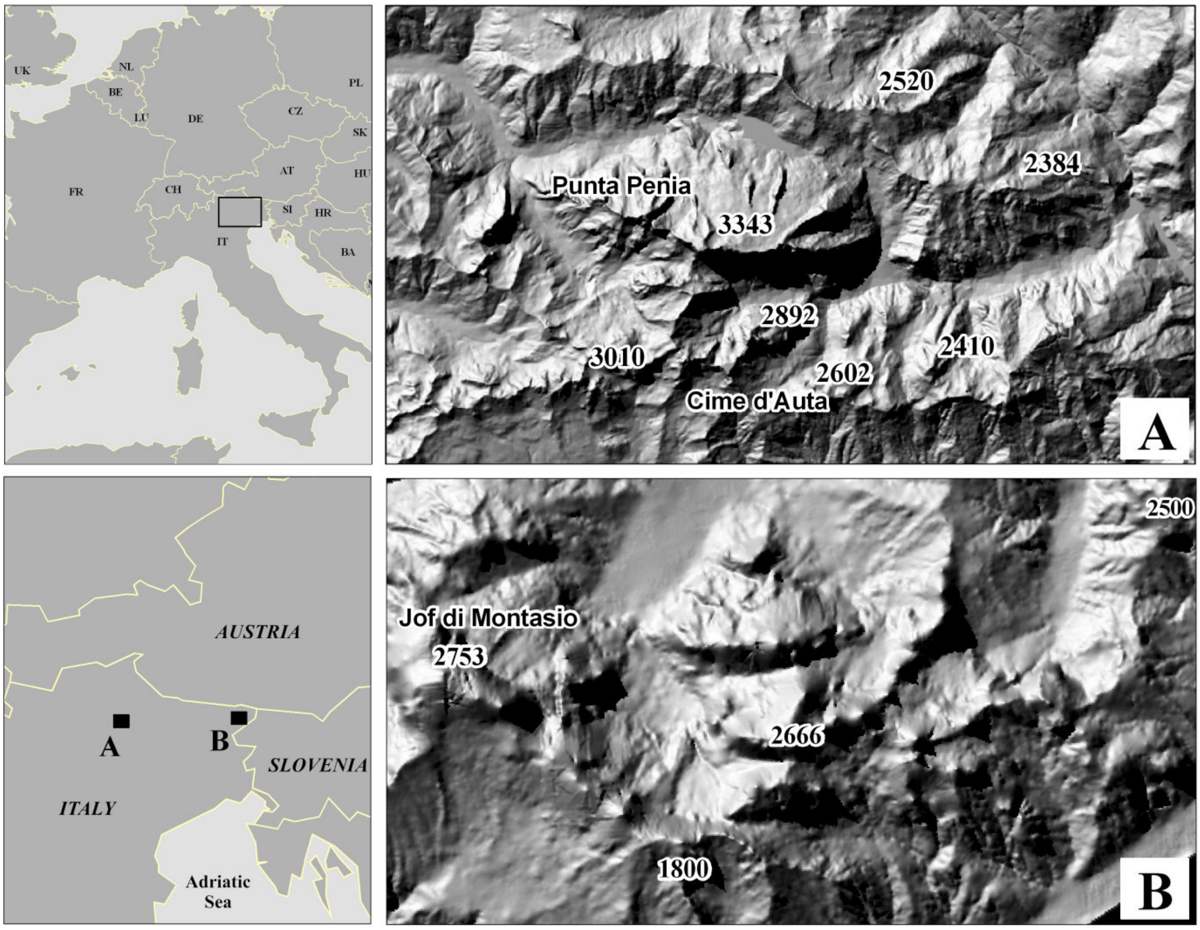

Figure 1: Map of the study area (Marmolada, A) and of the source area (Tarviso, B) and their location in Italy.

between 1500 and 2000 m a.s.l., while from 2000 m to 2500 m rock faces (66%) with steep slopes (above 45°) were predominant.

The area was less intensively used for touristic purposes than the Marmolada massif, and hunting was allowed. The other ungulate species present were the chamois, the red deer and the roe deer. Large carnivores, such as the brown bear and the Eurasian lynx (*Lynx lynx*), regularly occurred.

Data Collection

In the Marmolada massif free-ranging ibexes were sedated by tele-injection of xylazine (Rompum ®, Gauthier 1993). Captures were performed during late spring-summer of each year from 2001 to 2009, and we captured a total of 108 males of different ages (range 2-12 years old). All animals were aged by dentition and horn growth, measured, examined for health status and ear-tagged with a unique color and number combination. A VHF radiocollar (Televilt TXH3, Telonics CMM-320) was fitted to 31 males. Translocations from the Tarvisio area occurred in May 2006 (9 individuals) and 2007 (5 individuals). All translocated males were adult (age ranged from 5 to 9 years old) and equipped with a VHF radiocollar.

Field work was conducted from September 2003 to the end of August 2009. Ibexes were located by visual sightings. For individual identification we used a 60x magnifier telescope (Swarovski CT85). Radio tagged ibex were searched with homing technique, but we were able to locate also ear-tagged individuals with a similar frequency: in 2006-2009 we obtained an average number of sightings per individual and month of 4.8 (SD: 1.5) for radio-tagged males and 4.2 (SD: 1.3) for ear-tagged males. Each location was plotted in the field into a map of the study area (1:10000 scale). For each sighting we recorded group size and composition (age class and sex of individuals), and the kind of habitat (vegetation and geomorphology) occupied by the group. Sighting were georeferenced in ArcView 3.2 (ESRI ®) and stored in a Access (Microsoft ®) database.

Data Analysis

For all the analyses, we used the library adehabitat (Calenge 2006) in the software R.9.2 (R Development Core Team 2009).

Habitat structure and choice of the habitat variables

We considered resources that potentially supply forage or provide shelter (i.e. escaping terrains that act as refugees from predators or potential other perturbations, or vegetation types that may offer cover and may help in maintaining homeothermy). We compiled a 1:5,000 land-use cover map by refining the forest cover maps produced by the Veneto Region and by the province of Trento. We reclassified landcover types (i.e. resources) into 8 categories (Table 1): “alder shrubs”, “glacier”, “grassland”, “grassland interspersed with rocks and scree”, “lakes”, “mugo pines”, “rocks”, “scree”, “shrubland”, “pastures”, “woods with less than 30% of trees” (i.e. wooded pastures), and “woods with more than 30% of trees”(i.e. woods). To include the size and the shape of the habitat variables and to consider a possible selection for the edges (Conner et al. 2003), we compiled the maps of the distances to these 8 variables by calculating for each pixel of a map the mean distance to the pixel containing the considered variable. The obtained maps were thus all rasterized. We included in the analysis variables related to the topography, to consider the anatomical (elevations and slopes) and physiological (insolation) adaptations of the species. We derived elevation, slope and aspect of the study area from a Digital Elevation Model (DEM), a raster map with a pixel size of 25 m×25 m, developed by the Veneto Region and the province of Trento by using the spatial analyst tool in ArcGIS 9.3 (ESRI ®).To describe the habitat selection by male ibexes, we thus

Table 1: List of the 15 maps used for the analyses.

Variable	Abbreviation
Elevation	Elev
Slope	Slop
Insolation	Sun
Alder	dAldr
Glaciers	dGlac
Grasslands	dGrasl
Grasslands with screes	dGrasS
Lake	dLak
Mugo pine	dMugo
Pastures	dPastr
Rocks	dRock
Screes	dScree
Shrub	dShrub
Wooded pastures (less than 30%of cover)	dWoodI30
Woodlands (more than 30% of cover)	dWoodS30

used a total of 15 raster maps with a resolution of 50 m (Table 1). To help us to interpret our results, we first described the habitat structure by estimating the correlation between all pairs of variables with a Principal Component Analysis (PCA) and a table of the correlations. PCA in fact allows to quantify the interrelationship among a large range of variables and to explain them in terms of a smaller set of components (McGarigal et al 2000).

Habitat selection according to the provenance of individuals

We described the ibex males habitat selection at two different levels (that of groups and of individuals), with two types of factorial analyses, at design II and design III, *sensu* Thomas & Taylor (1990).

At the largest scale (i.e. corresponding to the level of the groups), we performed different Outlying Mean Index (OMI) analyses at the design II. This method corresponds to a niche analysis (*sensu* Hutchinson 1957), with the same area considered as available for all the individuals (Dolédec et al 2000). We first described the resident males ecological niches, independently of the translocated males, to evaluate if there were a temporal variation from 2003 to 2009. We calculated the available area by computing the minimum convex polygon (MCP) encompassing 95% of the locations collected from 2003 to 2009. We then considered the provenance of individuals (i.e. resident, noted as “Res”, of from Tarvisio, noted as “Tar”) to evaluate if the males of different provenance had different ecological niches. We integrated the year (from 2006 to 2009) to take into account a potential learning of the habitat by the relocated males. Then we integrated the effect of seasonality (6 seasons: "Autumn"from September to October, "Pre_rut" in November, "Rut" in December and January , "Winter" in February-March, "Spring" in April - May, "Summer"from June to August) to test if the residents and the introduced males had the same ecological niches according to the temporal variations of the resources availability.

We tested the same parameters (years, provenance and seasons) at the smaller scale (i.e. third order selection, corresponding to the level of individuals, Johnson 1980), but in this case we employed another niche method, the K-select analysis (Calenge et al 2005 a) that considers a different availability for each individual. We thus compared the locations (i.e. observations) of each individual with the area (MCP 95%) occupied during the considered period by the individual animals.

Inter-annual overlap between resident and introduced males

We tested the presence of conspecific attraction at two spatial scale. At a larger scale we compared the size of the whole areas occupied by the resident males and by the males coming from Tarvisio (since their introduction in 2006), by calculating the MCP of the males according to their provenance with 95% of the locations. At the smaller scale (i.e. level of the individuals), we estimated more precisely the area used by each individual using the Kernel method with 95% of the locations and we calculated the mean annual overlap between the individual home ranges of the males of different provenance (i.e. the proportion of the home range of one animal covered by the home range of another one)..

RESULTS

Habitat structure and choice of the habitat variables

The PCA showed 2 axes (explaining respectively 41,78% and 13,57% of the total variability). This analyses allowed us to choose the less correlated variables for the analyses. We deleted the maps representing the distances to rocks, that were highly correlated with the distances to grasslands (cor=0,87), the distances to screes, strongly correlated with the distances to grasslands interspersed with screes and rocks (cor=0,91), the distances to glaciers, correlated with the distances to pastures (cor=0,7) and the distances to lakes, highly correlated with the distances to shrubs (cor=0,82). We thus retained for the following analysis 11 variables (i.e. maps).

Inter-annual variations of the resident males ecological niche

We retained only one axis, since the first axis of the OMI explained 95,6% of the total variability (Figure 2A). We found no real variation in the habitat selection exhibited by the resident males during the 7 years of study, except a slight divergence in 2006. The resident males occupied always the areas situated far from the shrubs and closed to the pastures and the grasslands with and without screes (Figures 2B and 2C). This avoidance of shrubs and the selection for the grasslands seemed a little less underlined in 2006.

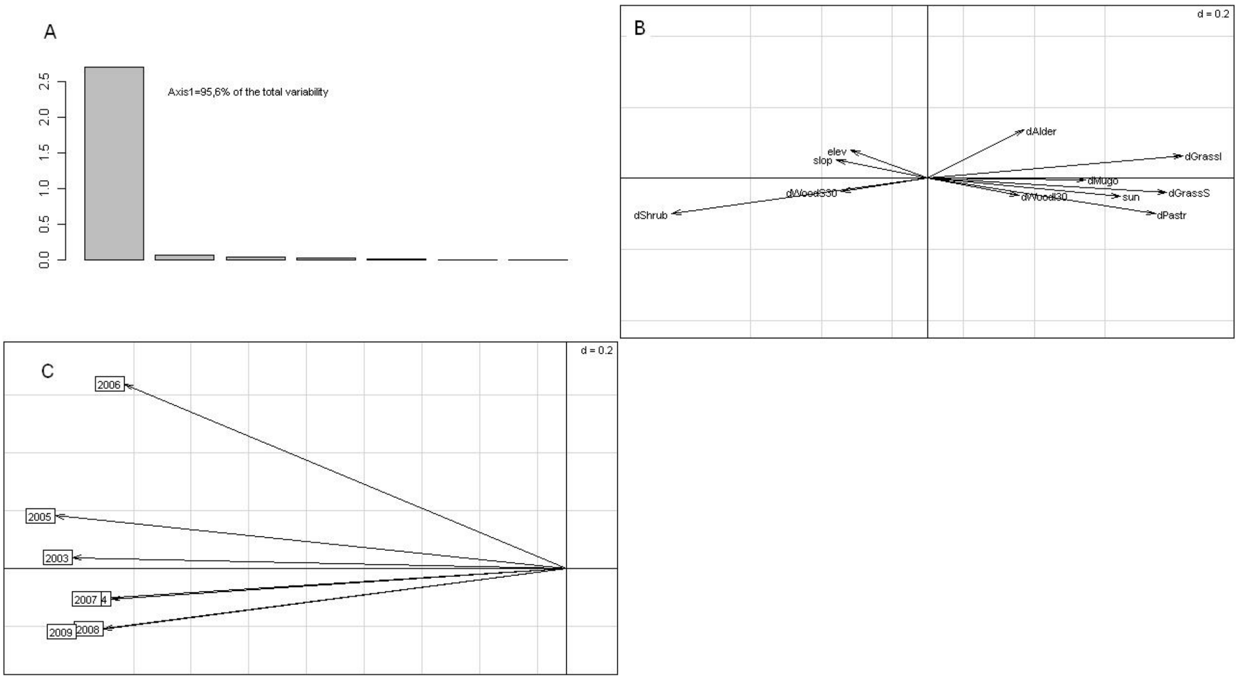

Figure 2: Results of the OMI analysis performed on the resident males to describe the annual pattern of variation of their ecological niches. A) Scree plot; B) Scores of the habitat variables; C) Marginality vectors.

Comparison of the ecological niches : Had the provenance of males an importance in their habitat selection?

Large scale (second order selection)

The OMI aiming to compare the temporal variation of the ecological niches of resident males with translocated males between years showed two axes that explained the most of the variability in the data (88,62% by the first axis and 10,03% by the second, see Figure 3A).

The year 2006 behaved differently to the other years on the two axes, both for resident males and particularly pronounced for the translocated males. In 2006, the males from Tarvisio were situated at higher elevation and steeper slopes, and closer to the shrubs, comparing to the next years. The habitat selection of the resident males was slightly different of the following years too, but this distinction was less pronounced than for the introduced males. From 2007, the ecological niche of the introduced males started to be more similar to that of the resident males. In 2008 and 2009, the ecological niches were all alike, both for the resident and for the introduced males. They were defined by an avoidance of shrubs and a selection for the two types of grasslands (with and without screes), for the pastures and the sunny areas.

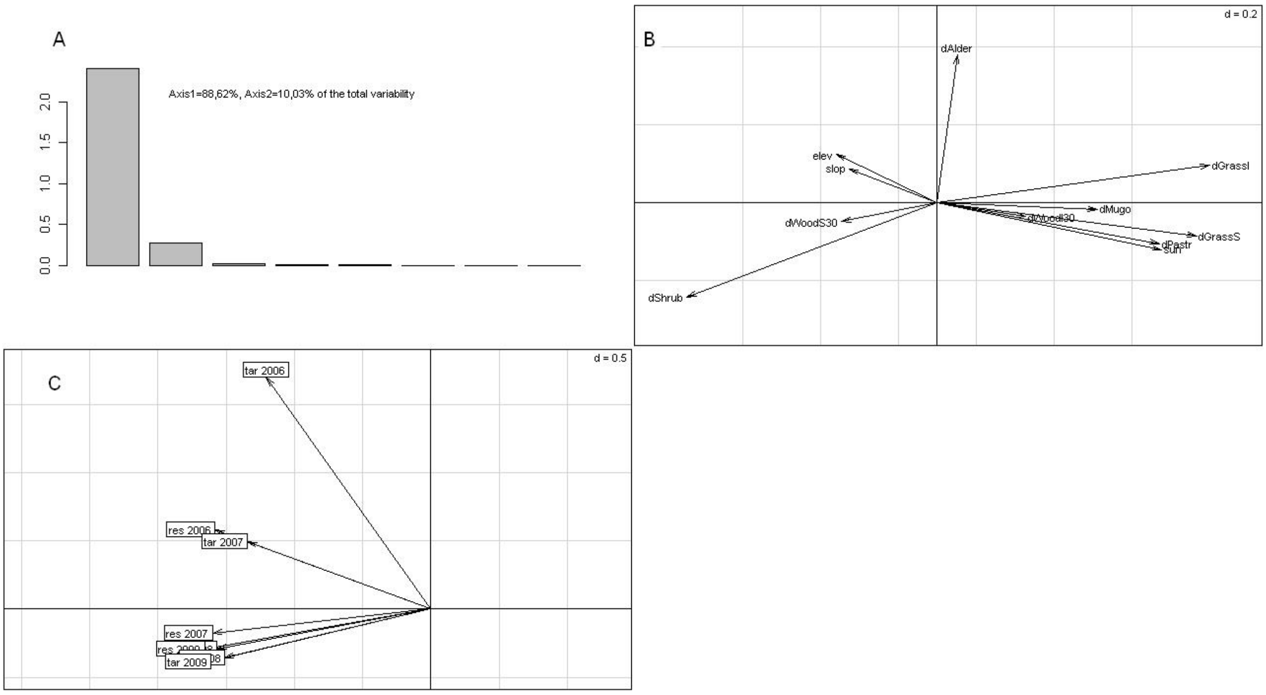

Figure 3: Results of the OMI comparing the annual pattern of the ecological niche of the introduced males and of the resident males (res=Resident males; tar= males from Tarvisio). A) Scree plot; B) Scores of the habitat variables; 3) Marginality vectors.

The results of the OMIs performed for each year on a seasonal level highlighted : 1) a temporal variation of the ecological niche during the year according to the seasons, and 2) a difference in resource selection between the resident and the translocated males that was marked in 2006, lighter in 2007, and that disappears after 2008 (Figure 4).

During 2006, the two types of males followed the same seasonal variations in their habitat selection, principally based on pastures and grasslands. In Autumn, they were situated close to the shrubs and far from the Alder shrubs. In Spring, they were mostly situated in the sunny places. Except during the pre-rut and the rut, the resident males and the introduced males were

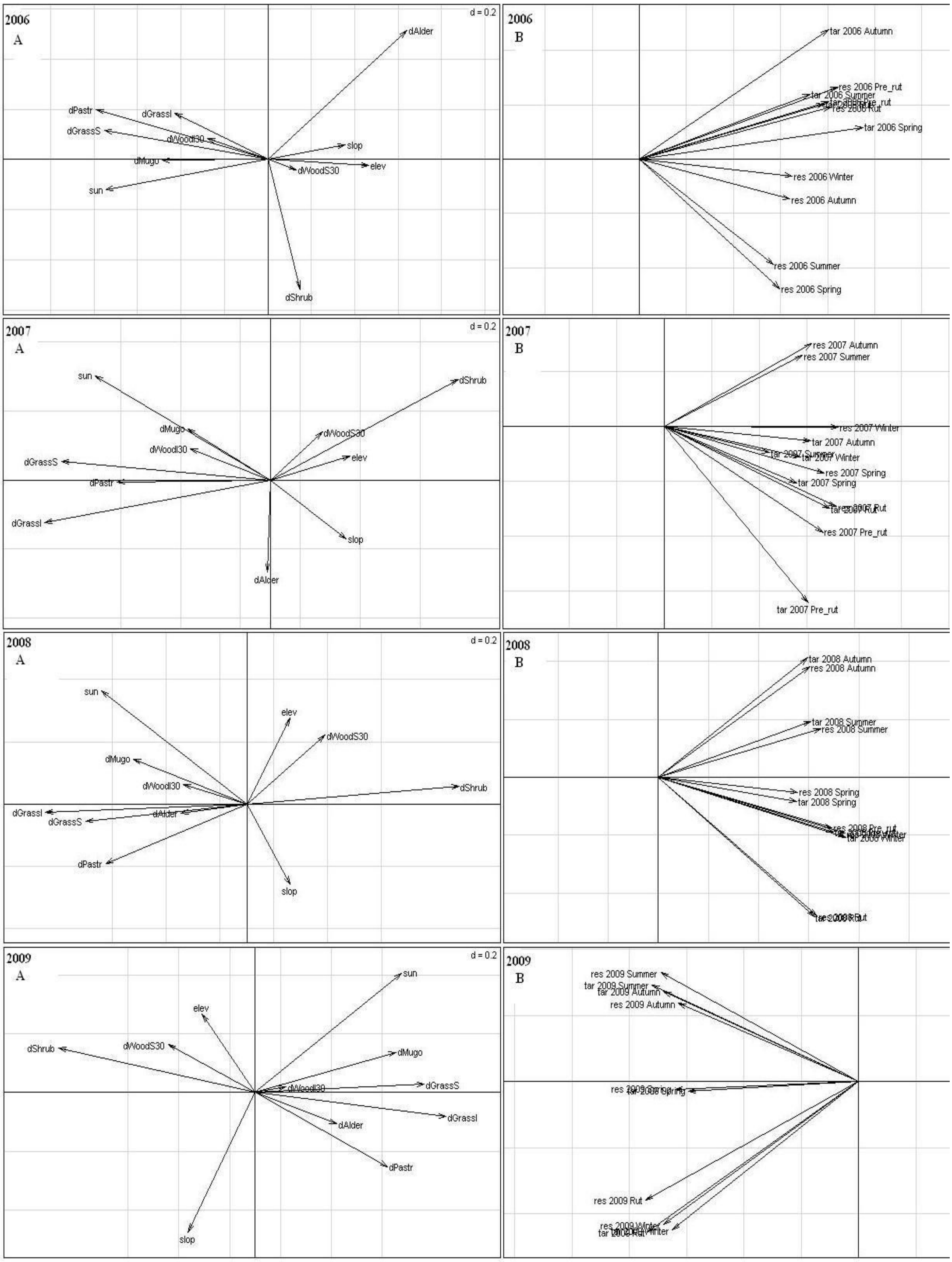

Figure 4: Vectors of the habitat variables (A) and marginality vectors (B) of the OMIs performed each year to compare the ecological niches of the resident males (“res”) and the introduced males (“tar”) in function of the seasons (“pre-rut”, “rut”, “winter”, “spring”, “summer”, “autumn”).

always segregated, the translocated males being closest to the shrubs and farthest to the alders compared to the resident males. In 2007, the ecological niches of the translocated and the resident males were more similar, but in Summer and Autumn, the resident males were situated at highest elevations and closest to alder woods compared to the introduced males that occupied highest slopes and areas closer to shrubs. In 2008, the two types of males inhabited the same areas during the year. The results showed that they performed a small altitudinal migration since Spring to Autumn. During the rut, the two types of males occupied the areas with the highest slopes. In 2009, there were no difference between the Tarvisio and the resident males.

Small scale (third order selection)

The first axis of the K-select aiming to compare all the individuals explained the best the variability in the data (93.15%). The majority of the males are situated exactly on the same place of this axis, indicating that all the individuals select the same habitat variables: the high elevations, the Mugo pines, the grasslands made with screes and the pastures (Figure 5). The results showed no differences between the resident and the translocated males. On the 76 males, only 4 individuals behave differently: 3 resident males (M40, MP1, and to a lesser extent M69) and 1 male from Tarvisio (M77).

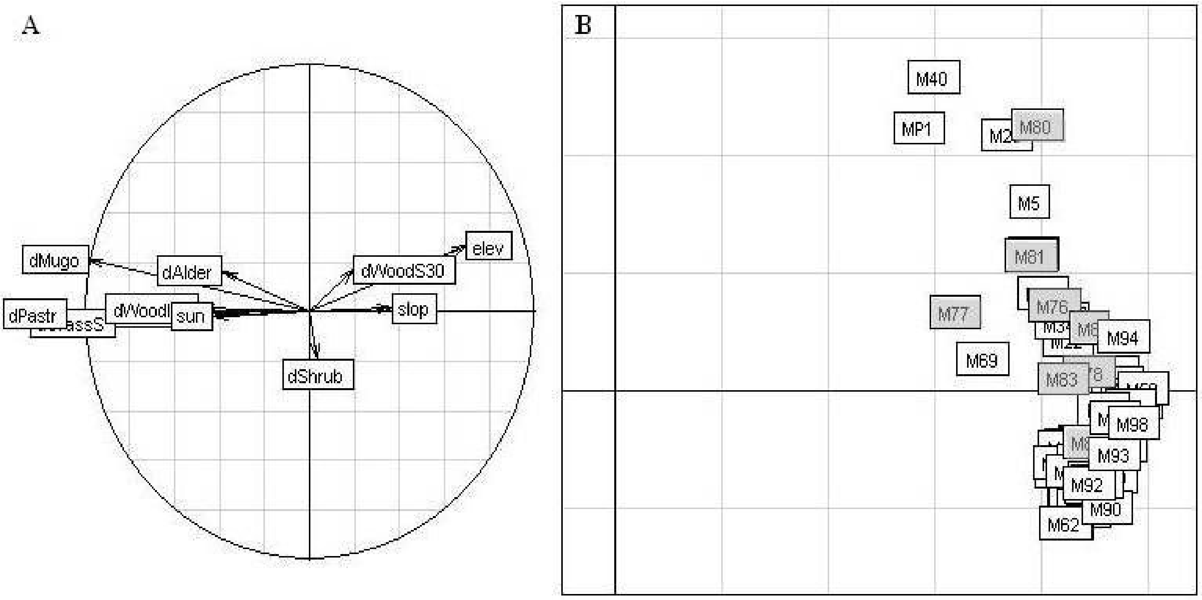

Figure 5: The ecological space formed by the first two axes of the K-select. A) Distribution of the habitat variables; B) Distribution of the individuals (in white: resident males, in grey: introduced males).

On the analyses performed on a yearly basis, the first axis was always the only one selected (explaining 92.33%, 93.69%, 93.75% and 90.41% respectively for 2006, 2007, 2008 and 2009). It is important to keep in mind that the interpretations have to be made only considering the first axes, since the second axes of the analyses have no explanatory value. In general, all the individuals presented a similar ecological niche characterized by a high elevation, and cover type made by pastures, mugo pines and grasslands with screes, and alders in 2008 and 2009 (Figure 6). However, the selection of some particular individuals for some habitat variables was less strong. In 2006 and 2007, the males M77 and M69 were situated at inferior elevations compared to the other males. In 2008 and 2009, the males M77, M69 and M80 selected the same habitat variable but not as too strong than the other males. The males M77 and M80 came from Tarvisio while the M69 is a resident male. These observed differences thus seemed to be proper to the individuals, independently to their origin. In 2006, the mean age of the males was 7.29 year ±7.29, with no difference between the Tarvisio and the resident males. The age thus could not explain the inter-individual differences of habitat selection.

Lastly, the results obtained at a seasonal level (all years pooled) showed that, in Summer, all males had the same ecological niches: they selected grasslands (with and without screes and rocks), high elevation and steep slopes, but the selction was weaker for the two translocated males M77, M69 and the resident male M26. Also in Autumn, all animals selected the pastures, the mugo pine, the grasslands containing screes and high elevations, the resident male MP1, and M69 being slightly different. In Winter, we decteted no differences among males, which habitat selection was very diversified for the pastures, the grasslands with and without screes, the mugo pine, the alders, the wooded pastures, the screes and the sunny sites, and with a slight avoidance for the shrubs. In Spring, the habitat selection was diversified too: principally animals preferred the Mugo pine, then the pastures and the grasslands with screes, then the grasslands without screes, the wooded pastures, and lastly the alders and the sunny areas. All the males had globally the same habitat selection, even if the resident males M77, M69 and M35 were barely different.

Inter-annual overlap between resident and introduced males

Overlap at the large scale

During all the study period, the introduced males occupied a larger area than the resident males, but the difference was not significant, neither considering the season (p=0.19) nor the year (p=0.62). The size of the surface occupied by the two types of males

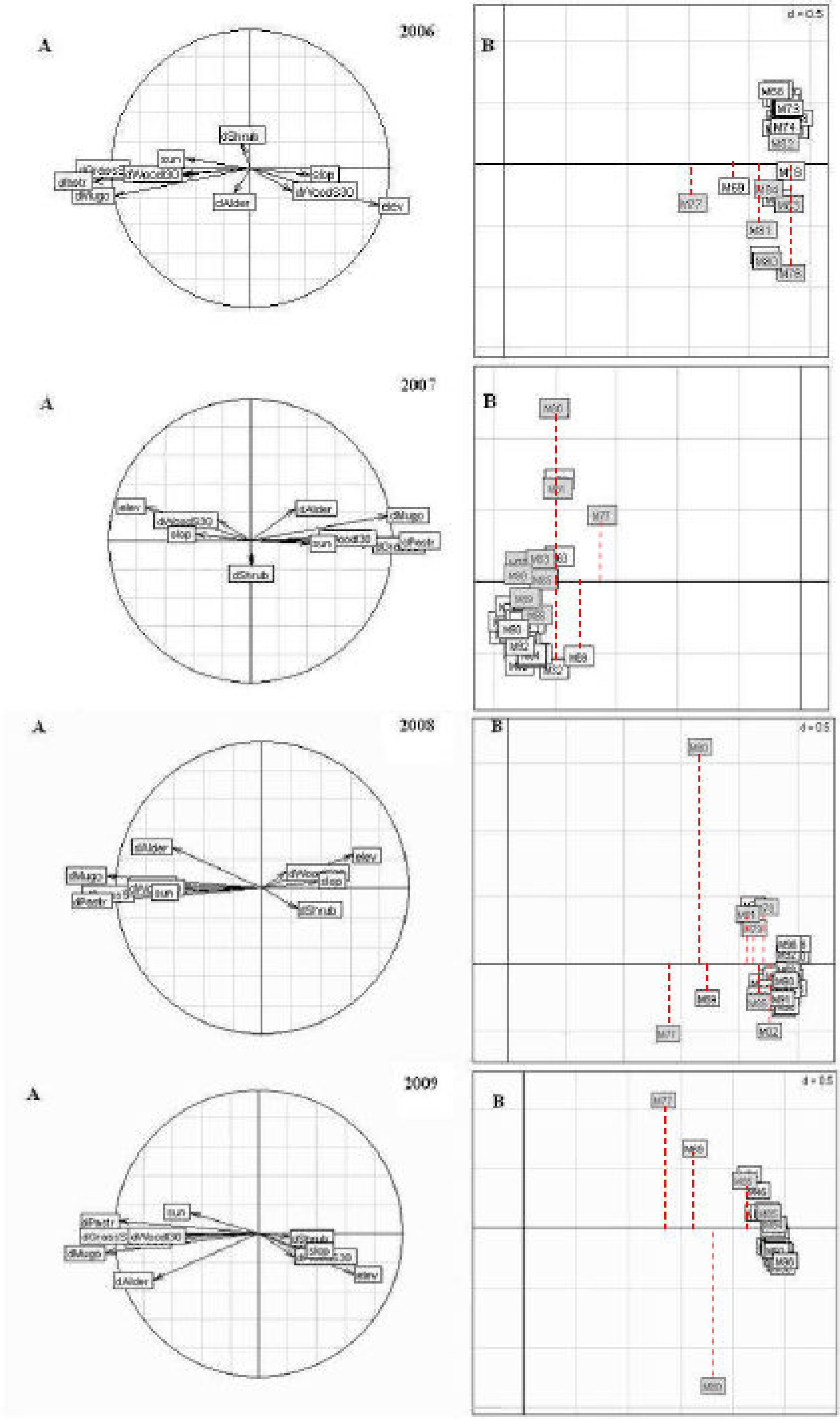

Figure 6: K-select performed for each year, from 2006 to 2009. A) Projection of the habitat variables in the ecological space composed by the first two axes (but in each analysis, only the first axis explains the structure of the data); B) Males. The grey boxes symbolize the males originated from Tarvisio, the white boxes, the resident males. As examples, the dash red lines showed the projection of some males on the first axes.

were subjected to the same annual variations. During the year of the introduction, the translocated males were distributed on a surface almost 2 times bigger than those occupied by the resident males (MCP 95% = 6411,77 ha for the introduced males versus 3278,11 ha for the resident males). Since then, they tended to restrict the ranging area.

At the smaller scale

For this analysis we kept only the males observed more than 10 times per year and per season. We deleted 690 observations corresponding to 48 males. We then tested 52 males, (among them 14 were translocated from Tarvisio).

We did not find a significant difference in the whole range size occupied by resident and translocated males, although the range occupied by translocated males was larger (3336,90 ha for the residents, 4724,18 ha for the introduced, t = -1,62, p=0,11). The mean home range size tended to follow the same annual variations whatever the origin of the males, except in the last year. In average, the overlap between the home range of the introduced and the resident males was 45,32 ±11,82%. Small in 2006, it increased in 2007 (64,70±56,20%) and 2008 (53,7±19,66%) and then stabilized in 2009 (50,6±20,84%).

The overlap between the resident and the introduced males always increased during the warmest seasons (spring and summer) from 2006 to 2009 (F=30.86, p=0,03, figure 7), although it was not the case during the coldest seasons (pre rut, rut, autumn and winter).

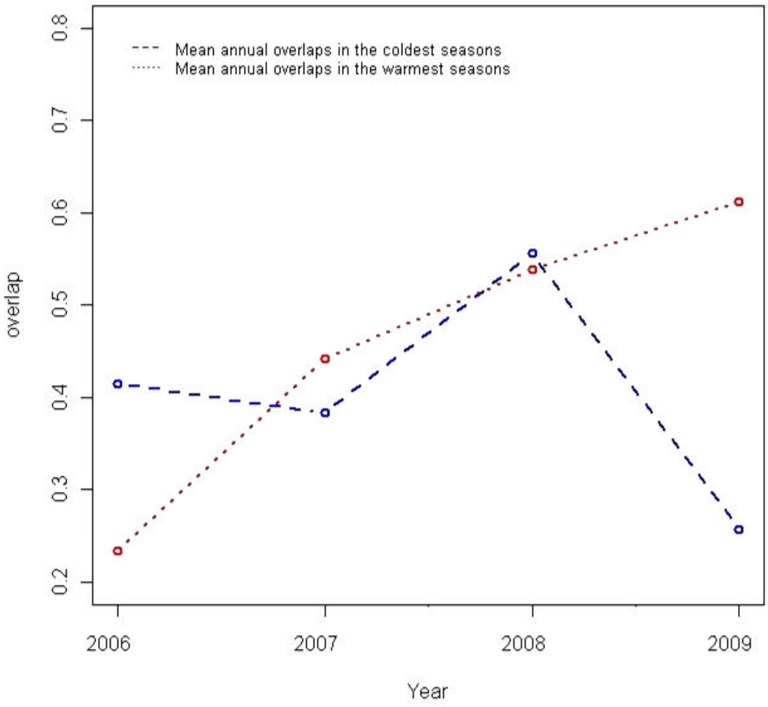

Figure 7: Mean annual overlap between the resident and the introduced males during the coldest seasons (pre rut, rut, autumn and winter) and the warmest seasons (spring and summer).

DISCUSSION

The habitat selection pattern exhibited by resident males was stable among years, showing also a moderate seasonal variation. Our results were consistent with other studies reporting habitat selection in alpine ibex (Grignolio et al. 2003, Lembke 2005, Pedrotti 1995, Villaret et al. 1997): males selected the grassland all year long. The observed seasonal variation in the habitat types reflected the seasonal altitudinal movement that ibex make in response to the variation in the phenology of the vegetation, as described in several mountain ungulate species (Festa Bianchet 1988, Grignolio et al. 2003). Our results indicate, at the larger scale (II order selection), the presence of dissimilarities in the resource selection pattern exhibited by translocated ibexes, which during the first year after release tended to use grassland at higher elevations in respect to resident males. This selection of higher altitudes areas may be caused by several different factors, that could have acted in synergy. First of all the differences found may be the result to the search behavior displayed by the translocated males, that needed to explore the new environment to locate the best resources and the appropriate habitat configuration. As a consequence of that, they ventured also in sites not used by local males, but when they familiarized with the environment they selected the same resources as local males. Secondly, they might select the higher altitudes in as a refugee area, since the steep and rocky sites present there might be useful as escape terrain (Hutchins & Geist 1987). Several studies reported how the adaptation to a novel habitat might be one of the most delicate phases in relocation programs (for a review see Letty et al. 2007, Stanley-Price 1989). The maladaptation to the new environment in fact may result in an ecological trap for the released animals (Frair et al. 2007, Rantanen 2010) determining even the failure of the reintroduction – or reinforcement- program (Griffith et al. 1989, Stanley-Price 1989, Wolf et al. 1996). This risk is particularly high in the case of release in the wild of captive-bred animals (Stanley Price 1989), that are often naïve in respect to a natural habitat. However the stress due to the novelty of the environment can increase mortality also in wild caught animals (Letty et al. 2003) or causing dispersal movements away from the desired area (Moorhouse et al. 2009). Resource selection is a complex process including both external resources and internal factors: the selection of a given resource depends both on the stimuli provided by the environment and on the response of the animal to these clues (Hilden 1965, Orians & Wittemberger 1991). In fact clues have to be acknowledged by the animals. An important role in this process lies in the natural history of the species (Wiens 1970) but also the experience developed in the natal habitat (NHPI, Davis & Stamps 2004) can act as an important determinant in the movement orientation. When an animal experience a new environment it sequentially search for discrete patches of habitat, and so the natal habitat experience helps the disperser to quickly recognize at least one suitable habitat in the current landscape (Stamps et al. 2005, Stamps & Swaisgood 2007). With longer searching the more the probability of finding a suitable habitat increase, even if the length of searching movements is in turn affected by habitat structure and by the sampling information acquired by individuals (Fortin 2002).

Once an animal settle down, the knowledge of where high quality resources are located act as an intensifier and orient animal space use. Familiarity with the environment combined with memory of the resource distribution are key components of resource selection pattern (Wolf et al. 2009), and confer individuals ecological benefits (Schaefer et al. 2000), because as animals move afield from their familiar area they are likely to experience a reduced fitness (Greenwood 1980). When animals are released in a new territory, as in this study case, they lack the knowledge of the spatial distribution of resources in the environment. Therefore they have to build their mental map relying on the clues collected while searching (Rittenhouse et al. 2008). Long explorative movements are characteristics in translocated animals (Jones and Witham 1990, Tosi et al. 1996, Michallet & Toïgo 2000) and have been reported in ibex as well (Pedrotti 1995, Mustoni et al. 2008, Tron et al. 1994) including the present population case study (Scillitani et al. 2009). During the first year after release translocated ibex as a whole occupy a larger range than resident males, and also the analysis on seasonal home range size (Scillitani et al. 2009) showed that ibex fully stabilized only during the third year of research. We can thus infer that, especially during the first year, translocated ibexes collected the clue necessary to build their memory map of the Marmolada area.

A third explanation of the abnormal selection of translocated males in respect to resident males considers the characteristics of the source site in comparison to the release site. The source area was similar to the release area in terms of geology and climate, but was also characterized by steeper slopes even at lower altitudes than in the Marmolada area. Therefore the mismatch in altitudinal selection could be linked by the habituation to the previous habitat by the translocated ibexes. When confronted with an unfamiliar environment, translocated animals may tend to search resources that resemble the ones present at the source habitat (Frair et al. 2007, Kenward & Hodder 1998, Warren et al 1996, Roe et al. 2010, Stamps & Swaisgood 2007). In particular, a study on the effects of herd source on habitat selection in bighorn sheep (Kauffman et al. 2009), a mountain ungulate similar in ecology to ibex, highlighted the presence of differences in the finer scale of resource selection. All animals showed a similar general pattern of selection, but some features of the adaptation to the source habitat were retained.

In the present study, differences in behavior were observed only on a broader scale. When looking at the resource selection within the home range instead, we found not only a lack of differences related to provenance but also an uniformity in the niche used by all individuals, except some few exceptions. This means that globally the range of translocated males was located in a different geographical area than that inhabited by resident males. Therefore at this scale we detected the dissimilarities due to the concomitant searching and learning behaviors. Inside the home range all animals selected the same resources: that corresponded to the innate component of the selection, inscribed in the natural history of alpine ibex. This means that the ecological preferences were basically the same for all ibexes, but the coarser scale analysis indicate that, especially during the first year after release translocated ibexes were not able to locate optimal resources in the new area.

It is interesting to notice how the shortening of explorative movement (Scillitani et al. 2009) and the reduction of the discrepancies in habitat selection was associated with a progressive increase in the overlap between the area used by translocated and resident males. This augmentation in the overlapping area was consistent with the results obtained in a previous study on the same population (Scillitani et al 2009) on the trend of interindividual association among males of different provenance. In the first year after release, translocated males were solitary or grouped between them, segregating from resident males. From summer 2008 instead they started to regularly assemble with resident males. Association was stronger during summer, when male ibex form larger herd, and weaker in winter, because during the rutting season male herds split in smaller groups and join females herd (Toïgo et al 1995) which in the rest of the year are segregated (Villaret & Bon 1995).

In gregarious species the presence of conspecific animals may act as an attractant (Reed & Dobson 1993). Sociality can fasten up adaptation to the new habitat because it provides translocated animals clues on where best resources are located by social facilitation (Galef & Giraldeau 2001, Reed & Dobson 1993, Shrader et al. 2006). Moreover habitat selection in social herbivores can be mediated by group size (Fortin et al. 2009). On the other hand we cannot exclude the presence of interspecific avoidance: translocated ibexes could have been forced to occupy suboptimal habitats because the optimal ones were already occupied by resident males. Unfortunately the lack of behavioral observations prevented us to test such hypothesis. Ibex groups are not stable in composition over time (Girard 2000, Toïgo et al. 1995, Villaret & Bon 1998) and the mechanism of group formation, as well as pattern of social dominance are still not clear. A recent study (Willisch & Neuhaus 2010) showed that the role of large male herd outside rutting season may favor the formation of a stable dominance relationship that regulate the access to receptive females. Social status is determined by body mass and horn length and apparently age do not directly affect the rank obtained (Bergeron et al. 2010). However, to our knowledge there is no study on the role of dominance relationship in alpine ibex on regulation of the access to resource and on the presence of interspecific competition.

We found no difference related to age in resource selection, but it must be considered that all translocated males were adults and similar in age. Nonetheless, it has been suggested for other species (Calenge et al. 2005 b, Michallet & Toïgo 2006), that also the age of released animals may affect the ranging behavior. In fact older animals have developed a deeper tie to their source habitat than younger ones and consequently they might suffer more the forced detachment from their familiar habitat (Letty et al. 2007).

In conclusion, this study indicated that the best hypothesis explaining the habitat selection in translocated ibexes was the H2 : resource selection was the result of both an innate behavior and of a learning process. Knowledge of the new habitat was acquired both by searching behavior and (probably) by social transmission. For following studies on the effect of translocation we strongly recommend the adoption of a multiscale approach. As highlighted by our case study and corroborated by several other multiscale studies (Bowyer & Kie 2006) animals may pursue different objectives at coarser and finer scales. As recommended by Bowyer & Kie (2006) it is therefore important to consider “not only the level of interest but also a level above that provide the context and one below to examine potential mechanism”. As guidelines for reintroductions (IUCN 1988) recommend post-release monitoring of released animals many of the monitoring programs concentrate on the spatial behavioral pattern exhibited by singular individuals. However, this might prevent the identification of potential source of variations, because comparing use and availability at the home range scale might reveal only the instinctive component of resource selection, and also because heterogeneity in results may arise as a result of individual personalities (Réale et al. 2007).

Finally, since source habitat provide animals a sort of "guidelines" regarding resource selection (Davis & Stamps 2004) in the frame of a translocation program and of a scientific based conservation a pre-release sampling in the source population and habitat might be relevant for acquiring information on the adaptation to the release habitat.

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General Conclusion

The findings of this thesis can be useful for delineate the ecological adaptation of alpine ibex to the dolomitic environment, and to evaluate the effectiveness of the management actions adopted.

The preliminary results of the CMR analysis on survival (chapter 3) showed us that, as expected, senescent individuals were the most sensitive to sources of mortality as sarcoptic mange and severe weather conditions. Apparently the die off of ibex in the Marmolada was confined to 2004, however I think that this result should be taken with caution, since our sample could be biased: most animals captured in 2004 were treated with ivermectin, and this might prevent us to understand how the natural mortality process evolved in the following years. At this purpose, our data suggest an increase in survival due to treatments. However, unfortunately we lack the presence of a balanced sample of treated and untreated animals in the same cohort of capture and this might compromise a correct evaluation of the effectiveness of treatments. A refinement of the model, would be required in particular to best investigate on the relationship of survival and weather, still not clear. Alpine ibex in the Marmolada were tied to their traditional home range, showing site fidelity at the population (chapter 2) and individual level (chapter 4). The population showed a stable use of the same summering and wintering areas, and, according to data on marked individuals, dispersal toward neighboring colonies was really rare. Home range size did not vary in relation to age, nor to individual, but it was influenced by the extent of grassland present in the area, and in part by snowpack depth and persistence. The higher the proportion of grassland, the smallest was the home range, except in winter, when probably the most important factors affecting home range size was the extent and the depth of snowpack. Grassland was in fact the preferred habitat in all seasons and years (chapter 6). When translocated in a new habitat, ibex tended to roam over a large area, and showed high individual variability in response to the stress of transplantation (chapter 5). Having no knowledge of the new area ibex needed to build their map of the environment including the location of resources as optimal foraging sites, safe bedding areas and escape terrains. This learning phase led them also to select different resources in respect to resident animals (chapter 6). Our results indicate that ibex employ at least two years to get familiar with their surroundings (chapters 5 and 6). In addition, they suggest that ibex settled down when "integrating" in the group of resident males. However, our data do not allow an exploration of the role of sociality in the adaptation process: did resident animals act as a deterrent, displacing the reintroduced ibex to suboptimal animals, or as an attractant? Further investigation in this direction, as well as on factors affecting habitat selection in a new habitat will be required.

One critical point of the studies collected in this thesis, is the sex biased monitoring of the population: most data were collected on males, and the limited sample size precluded the possibility to study females. Therefore further investigations on females are required. Study of marked females can help to understand population recruitment, which is one of the fundamental processes underlying demography. Moreover, being segregated from males over most of the year, females have different ecological requirements, that should be studied also in this population.

In conclusion, what kind of clues can be derived from these findings to improve management? For a good understanding of life history traits of a species, the establishment of long-term studies on marked individuals would be strongly desirable. Since the mechanism driving the demography of a species are depending on the local ecological constraints, more long term studies on different populations of the same species should be established. Nonetheless, long term studies are costly, require a big sample size, stable funding and extensive field seasons (Festa-Bianchet & Côté 2009). Although long-term scientific studies using cutting-edge technology are not always achievable, it is still possible to derive some useful indication from basic information that can be collected in a relatively inexpensive way.

As shown in chapter 2, data obtained with yearly single counts clearly do not provide an adequate estimate of population size of the Marmolada colony. Since management decisions are taken on the basis of population assessment, this lack of precision should be corrected. Counts should be repeated, in order to provide a measure of the precision associated to the data (Loison et al. 2006). Since at present a good proportion of animals is marked, during censuses marked animals should be identified whenever possible, as done in the count of 2010. This will allow not only to perform CMR estimates, but also to accomplish an immediate evaluation of the reliability of the count, by comparing the number of marked animals sight with the number of marked animals present in the population. Since age structure matter, when considering survival of ibex (Yoccoz & Gaillard 2006, Toïgo et al. 2007), particular attention should be paid to age evaluation in the field (Garel et al. 2005). At least for males, determination of age can be refined. At present the age classes recorded are "yearling", "2 to 10 years of age", "11 years of age and older". This might work for females, for which is quite difficult to estimate age at distance, but for males narrower categories can be established. In addition, since in census are often involved many different observers, with different level of experience, at least a training session can be performed in order to achieve an improved estimation. Our results indicate that not only the knowledge of population abundance, but also of its space use is important for an efficient conservation. We acknowledge that conducting radiotelemetry studies would be not easy feasible for local managers (due to time and money constraint), but some useful information can be achieved even if every location of sightings -also occasional ones- are collected, georeferenced and stored in a data base.

Finally, our study on translocated ibex indicate that at least 3 years of monitoring are required to assess the efficiency of the relocation. Furthermore, the collection of data on relocated animals can be of great interest for researchers too, since they provide the unique possibility to test which factor shape space occupancy in an animal that is naïve about the surrounding environment.

As stated in the introduction, the final step associated with a research aimed at evaluating management and improving knowledge on a population would be the communication of the achieved results to local managers and public. Many of the results obtained on this population have been disseminated in conferences and produced technical reports (e.g. Monaco et al. 2005, Rossi et al. 2006, Scillitani et al. 2009), and I state my personal commitment in divulgate through meeting to local managers the evaluation made in this thesis. As pointed out by Festa Bianchet (2003) the improvement of communication of the role of scientific research in conservation programs is crucial: in particular researchers should be encouraged in using medias for disseminating research in a way that can be easily understood by general public, but still based on strong scientific evidences, raising awareness for the need of conducting applied and theoretical research in this field.

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ancora non lo so

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cadeva la pioggia, segnavano i soli
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(Art. 9 Costituzione Italiana)