Life-history, demography and behaviour of the Alpine chamois (Rupicapra rupicapra): the role of climate and environmental change

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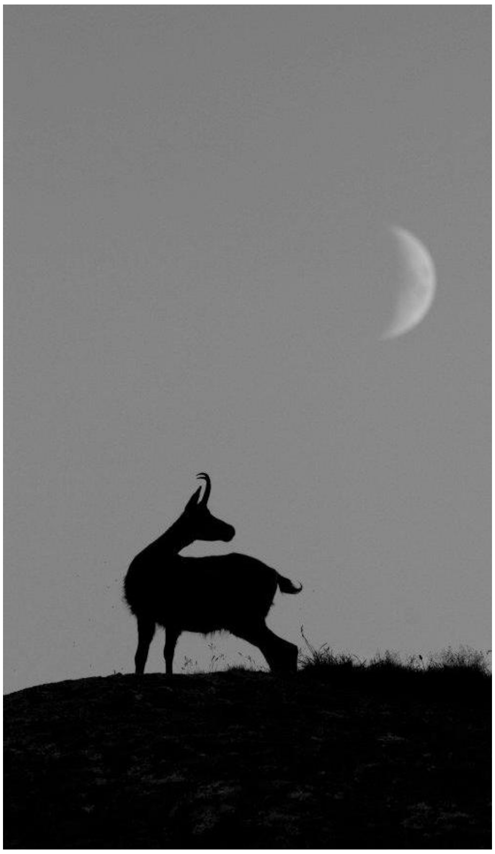

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Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Thomas H.E. Mason
July 2013

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Abstract

Climate change is altering ecology in myriad ways; the distributions, dynamics, phenology, morphology and life-histories of species are changing. Establishing the relative importance of these changes in different ecological traits is important to fully understand how climate and environmental change threatens populations. However, until recently, studies have often focused solely on range-shift responses and have rarely examined multiple forms of ecological change in a single species. Case-studies focusing on multiple aspects of ecology, for example demography, life-history and behaviour, could provide important general insights into how climate change will most threaten the persistence of species and populations. In this thesis, I investigate ecological variation, and the influence of climate and environmental change, in a common species of considerable cultural, economic and ecological importance, the Alpine chamois (*Rupicapra rupicapra*). Using a 38-year dataset on body masses and demography, augmented with demographic and behavioural data collected during this thesis, I examine variation in the life-history, demography and behaviour of this species, making both species-specific and general inferences. I find variability in reproductive strategies in the study populations, providing considerable insight into poorly understood area of this species' ecology. Male chamois in neighbouring populations adopt contrasting reproductive strategies, likely due to climatic differences among areas. Interestingly though, males time investment in reproduction similarly in the different populations. However, there is a strong pattern of age-dependent investment; young males delay reproduction until the end of the breeding season, apparently as a strategy to avoid high levels of competition. This is the first clear evidence for such a strategy in a male mammal. Next, focussing on the effect of climatic and environmental factors on chamois ecology, I found a strong influence of climate on body size, demography and foraging behaviour. Climate change appears to be driving declines in body size and climatic variation exerts a strong influence on demographic variation and foraging behaviour. However, the effects of local anthropogenic drivers in some cases exceed these effects. High hunting pressure has a profound effect on survival, with hunting mortality largely replacing natural mortality. Furthermore, the influence of disturbance by livestock grazing on altitudinal migration is very pronounced, forcing chamois to much higher altitudes. This project illustrates that climate change can affect diverse aspects of ecology. Despite the overriding research focus on range-shifts, climate-driven life-history and demographic change could influence populations more strongly. Furthermore, my results show that effects of other drivers, such as harvesting and biotic interactions, can also have profound effects on ecology, at times exceeding the influence of climate.

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Chapter 1

General introduction

1.1 Introduction

1.1.1 Motivation

The Earth's climate is changing due to the emission of greenhouse gases; the global mean temperature has increased by 0.74^{o}C over the past century and the rate of warming is accelerating (IPCC 2007, Meehl et al. 2007). The influence of anthropogenic climate change on ecology is a rapidly expanding area of research. An array of pronounced effects across a broad range of organisms have already been observed, including changes to phenology (e.g. Hoye et al. 2007, Menzel et al. 2006), life-histories (e.g. Musolin 2007, Stenseth and Mysterud 2002), community structure (e.g. Drigo et al. 2008, Glynn 1991), morphology (e.g. Husby et al. 2011, Ozgul et al. 2009), population dynamics (e.g. Ozgul et al. 2010, Thompson and Ollason 2001) and spatial distributions (e.g. Parmesan and Yohe 2003, Root et al. 2003).

Studies predicting the influence of future climate change on species are vital for highlighting the potentially severe impacts on biodiversity and its services, and for effective management strategies to be implemented (Pearson and Dawson 2003). Until recently, despite the variety of impacts that have been identified, research has been strongly focused on predicting future spatial range-shifts (e.g. Hickling et al. 2006, Parmesan and Yohe 2003). However, in some cases, other forms of climate-driven ecological change, such as changes in life-history and demography, could be more pronounced than range-shifts. More focus is required on the relative importance of different forms of ecological change so that this information can be incorporated into predictive models, producing improved projections of both population and range changes (Pearson and Dawson 2003, Thuiller et al. 2008). Such models could project more accurately how the life-histories and dynamics of populations will be affected and, thus, whether populations will persist in the future. Also, biotic and anthropogenic factors can have important effects on ecology, interacting with or even overriding the influence of climate (Pearson and Dawson 2003). Models linking climate-driven changes in spatial distributions, life-histories, demography and behaviour, and also considering the influence of non-climatic drivers, could be vital tools for the conservation of biodiversity in a changing climate.

Studying species most vulnerable to climate and environmental change is important in ameliorating the impacts of climate change on biodiversity. However this can be difficult because species are often already rare by the time they are acknowledged as being threatened (Gaston 1994). By contrast, common species, which exert a profound influence on their environment and provide key ecosystem services to human populations (Gaston and Fuller 2008, Gaston 2010), are more easily studied and can be useful indicators of the impacts of climate change on wider ecology (Duelli and Obrist 2003, Pearman and Weber 2007). This project focuses on the Alpine chamois, an ungulate species of considerable ecological, cultural and economical importance. Chamois are found throughout the European Alps (Shackleton 1997); an area particularly vulnerable to climate change (Bohm et al. 2001). Chamois are relatively understudied, despite their abundance and widespread distribution, and some aspects of their ecology remain poorly understood (Corlatti et al. 2011). I aim to shed further light on the life-history of this species, using it as a model system to provide general insights into the influence of climatic and environmental variation on the ecology of species living in vulnerable mountainous areas. I investigate the potential effect of climate change on life-history, demography and behaviour, moving on from the traditional focus on range-shifts, also exploring the influence of other drivers such as harvesting and inter-specific interactions.

1.1.2 Outline of structure

Firstly, I briefly overview the range of influences that climate change can exert on different facets of ecology, including changes to distribution, demography and life-history. I then focus specifically on mountain ecosystems, examining why these regions are particularly vulnerable to climate change. I will then narrow my focus to chamois, discussing in detail the value of studying common and economically important species. I provide an overview of climatic and environmental impacts on the ecology of chamois. I present two case-studies which have used data on life-history, demography and behaviour to make detailed predictions about the effects of climate change and show how such modelling techniques can contribute to management, both generally and specifically to alpine ungulates. Finally, I outline the specific aims of this project.

1.2 The impacts of climate change on ecology

1.2.1 Range-shifts

Despite change having a wide array of effects on ecology, spatial range-shifts have probably received the most focus in recent research (e.g. Chen et al. 2011, Hickling et al. 2006, Parmesan and Yohe 2003). This is understandable given, firstly, the tangible and widespread nature of observed range-shifts and, secondly, their relevance to conservation and reserve selection. Abundant palaeoecological evidence from the last post-glacial period shows that range-shifts, rather than *in situ* adaptation, are the fundamental responses of plant species to large-scale climate change (Huntley and Webb 1989, Huntley 1991, Huntley et al. 1995, Prentice et al. 1991). Range-shifts could also be the primary response of species to anthropogenic climate change (Huntley 1995). A number of studies performed across wide ranges of taxa have detected a globally consistent trend of range-shifts in the directions expected based on the physiological constraints of species (Chen et al. 2011, Devictor et al. 2008, Hickling et al. 2006, Parmesan and Yohe 2003, Root et al. 2003). For example, Hickling et al. (2006) found, across a range of British vertebrate and invertebrate taxa, northward shifts of 12.5-19 km decade^{-1} and upslope shifts of 4.7-10.7 m decade^{-1}.

Despite these documented shifts, evidence suggests that there may be a ‘colonisation lag’ between climate change and the distributional shifts of species; some species, such as habitat specialists, are less likely to respond rapidly to change (Devictor et al. 2008, Menendez et al. 2006, Warren et al. 2001). For instance, an analysis of French bird distribution data, collected between 1989 and 2006, revealed that, whilst bird communities had shifted on average 91km northward, they were nonetheless lagging about 180km behind climate warming (Devictor et al. 2008). Recent evidence shows that species’ ranges are moving much more rapidly than previous thought; however, in many cases, these range-shifts are still lagging behind climate change (Chen et al. 2011). This highlights the threat that anthropogenic climate change poses to many species, particularly considering that the expansion rates observed after the last ice age were up to an order of magnitude slower than the rates that are likely to be required to track future projected changes (McLachlan et al. 2005, Pearson 2006). Particularly long-lived and poor dispersing species may have survived the last ice age in glacial refugia rather than tracking changes in climate (McLachlan et al. 2005, Pearson 2006). Limitations in dispersal ability are thought to explain a species’ absence from a significant proportion of its fundamental range (the climatic range across which a species could physiologically survive) (Guisan and Thuiller 2005, Svenning and Skov 2004). Plant species in particular may be unable to migrate fast enough to track the rapid rate of anthropogenic climate change (Huntley 1991, Neilson et al. 2005). For some taxa, prospects may be even more pessimistic; for example, butterfly and bird range-shifts are lagging considerably behind climate warming (Devictor et al. 2008, Willis et al. 2009). Herptiles (reptiles and amphibians), noted for their poor dispersal and corresponding high levels of endemism (Williams et al. 2000), may be particularly at risk (Araujo and Pearson 2005). The distribution of European herptiles highlights a pattern of low dispersal: three of the main regions of herptile concentration coincide with refugia from the last ice age (Hewitt 2000). Many species will not be able to track future climate change and could become extinct without human intervention (Devictor et al. 2008, Hoegh-Guldberg et al. 2008, Menendez et al. 2006, Warren et al. 2001).

1.2.2 Adaptation and phenotypic plasticity

Adaptation can play an important role in how species respond to climate change, particularly when species are unable track their climatic niche (Davis and Shaw 2001). It may be particularly important in environments where dispersal is constrained by landscape characteristics; in mountainous environments, the rate of upslope migration in many species is lagging behind climate change, possibly as a result of a lack of suitable habitat at higher elevations (Chen et al. 2011). Rapid micro-evolutionary change can allow short-lived species to adapt to a new climate, although this is difficult to demonstrate in wild populations (Bradshaw and Holzapfel 2006, Hoffmann and Sgro 2011). Long-lived species, however, retain largely the same climatic tolerances over large geological timescales and, until recently, were thought unlikely to adapt rapidly (Huntley et al. 1989). However, there are now a number of examples of vertebrates adapting to climate and environmental change, not only through phenotypic plasticity, but also through evolutionary change. For instance, there is thought to be a heritable basis to advances in reproductive timing in Canadian red squirrels (*Tamiascurus hudsonicus*) (Reale et al. 2003) and to a recent migratory division in European blackcaps (*Sylvia atricapilla*) (Bearhop et al. 2005).

In general, phenotypic plasticity is considered more important than microevolution in responses to climate change (Gienapp et al. 2007, Ozgul et al. 2009, Ozgul et al. 2010). Life-histories and behaviour are being altered by climate change across a range of taxa and are, in turn, affecting the demography and dynamics of populations. The most pronounced life-history changes have been phenological; there have been widespread changes in the timing of key life-history events (e.g. Moyes et al. 2011, Winkler et al. 2002). In many populations, individuals are breeding earlier in the season due to warmer spring temperatures. For instance, across Europe, 78% of recorded leafing, flowering and fruiting events have become earlier, with springs occurring on average 2.5 days decade^{-1} earlier (Menzel et al. 2006). Animals, particularly mammals and birds, are performing key behaviours earlier, such as reproduction (e.g. Dunn and Winkler 1999, Moyes et al. 2011) and migration (e.g. Cotton 2003, Marra et al. 2005), in order to track the availability of resources. However, populations are responding individualistically, and in some cases spring dates and life-history events are not changing or are even becoming later (Lane et al. 2012, Yu et al. 2010). For example, data on vegetation phenology from the Tibetan plateau show that springs have become later, despite increasing temperatures, due to warmer winters delaying a period of winter dormancy (Yu et al. 2010).

Changes in life-history have affected populations both positively (e.g. Ozgul et al. 2010) and negatively (e.g. Both et al. 2006, Lane et al. 2012). For example, a population of yellow-bellied marmot (*Marmota flaviventris*) in Colorado, USA, has undergone significant phenological change in response to environmental change, with knock-on effects on body mass and population dynamics (Ozgul et al. 2010). In response to warmer springs, marmots have been emerging earlier from hibernation (Inouye et al. 2000), giving individuals more time to accumulate reserves during spring and becoming larger (Ozgul et al. 2010). Higher body masses have led to increases in survival and population growth rates (Ozgul et al. 2010). In some cases, life-history change in one species can adversely impact another. For instance, several Dutch populations of pied flycatcher (*Ficedula hypoleuca*) have dramatically declined over the past few decades as a result of earlier springs (Both et al. 2006). Advancing springs have led to earlier abundance peaks in caterpillars, the flycatcher’s prey, but flycatchers have been unable to adjust the timing of their breeding. As a result, there has been a shortage of food for chicks and some populations have crashed by as much as 90%.

Despite the abundance of evidence of adaptive and plastic responses to climate change, the majority of studies have discovered responses to changing patterns of seasonality rather than to shifts in thermal optima (Bradshaw and Holzapfel 2006). It remains to be seen whether species will be able to adapt physiologically to new climatic niches.

1.2.3 Biotic factors

It is widely accepted that species respond individualistically to climate (e.g. Pearson and Dawson 2003, Thuiller 2004), which could in turn lead to disruptions to the complex interactions between trophic levels during climate change, even if species composition within communities remained the same (Schmitz et al. 2003). For instance, the influence of bottom-up and top-down drivers of population dynamics may be altered by climate change. As an example, expected declines in snowfall on Isle Royale, Michigan, are predicted to decrease the hunting efficiency of wolves (*Canis lupus*), causing moose (*Alces alces*) populations to rise and, in turn, reducing the productivity of balsam fir (*Abies balsamea*) due to increases in foraging intensity (Post et al. 1999, Schmitz et al. 2003). Such trophic cascades can have significant impacts on the state of an ecosystem and, at small scales, could drive changes in species distributions (Schmitz et al. 2003).

Several studies have examined the effect of climate on tightly linked species interactions, such as those between parasites and their hosts, and have found that interactions were altered by changes to climate (Araujo and Luoto 2007, Davis, Jenkinson, et al. 1998, Davis, Lawton, et al. 1998). These findings highlight that alterations to interactions within a community may have larger impacts on species distributions than climate change will directly (Davis, Jenkinson, et al. 1998). There is even evidence that inter-specific interactions can reverse the responses of species to climate change. In an experimental study on grassland communities in California, USA, precipitation was manipulated to simulate future projections of rainfall change for the region (Suttle et al. 2007). In plots where rainfall was increased during spring, there were initial increases in plant species richness and primary productivity in response to increased water availability. This in turn led to increases in the abundance of invertebrate herbivores, predators and parasitoids. However, after several years of the study, competition between grass and forb species led to significant declines in the latter, an important resource for invertebrates, and consequent declines in invertebrate abundance and total species richness. These studies highlight the importance of considering inter-specific interactions when investigating climate change impacts on ecology, as well as the ability of climate and environmental change to alter the species composition of communities and the interactions within.

1.2.4 Predicting future climate change impacts

To ameliorate the impacts of climate change, it is clear that studies need to predict not only where populations will be in the future but also whether individuals will be able to acquire sufficient resources to survive and reproduce, and ultimately, whether populations will be able to persist. Incorporating more complexity into predictive models, for instance by using data on behavioural, life-history and demographic responses to climatic variation, will help to create a more detailed picture of how individuals and populations will respond to climate change. For well-studied groups such as ungulates, there is much data on the responses of populations to climatic variation, such as changes to demographic structure and population dynamics, which could be used to model responses to climate change (Saether 1997).

1.3 Climate change in mountainous regions

Mountainous areas cover about 20% of the Earth's surface (La Sorte and Jetz 2010) and contain a large proportion of its biodiversity (Lomolino 2001, Orme et al. 2005), including a range of species with unique adaptations and particularly high extinction risk (Jetz et al. 2004, Ricketts et al. 2005). Furthermore, these regions are home to 26% of the planet's human population (Meybeck et al. 2001) and provide vital ecosystem services such as water provision, erosion prevention and economic benefits through tourism, energy supply and agriculture (EEA 2010a, Körner and Spehn 2002, Nogués-Bravo et al. 2007). Mountainous regions are being particularly affected by climate change; for instance, temperature increases in alpine regions have been double the global average (Bohm et al. 2001). In addition, pronounced changes have been observed in precipitation, snowfall, glacier extent, the frequency of severe weather events and avalanche risk in these regions (Barry and Seimon 2000, Beniston et al. 2003, Dyurgerov 2003, Martin et al. 2001), posing significant threats to ecology.

1.3.1 Impacts on montane species

Not only have mountainous regions been particularly affected by climate change but montane species appear to be particularly sensitive to this change. Some of the first examples of extirpations due to anthropogenic climate change have been in high altitude mountainous species such as pika (*Ochotona princeps*) (Beever et al. 2003) and various butterfly species (McLaughlin et al. 2002, Wilson et al. 2005). The well-documented extinctions of the Monteverde golden toad (*Bufo periglenes*) and the Monteverde harlequin frog (*Atelopus* sp.), once endemic to the Monteverde mountains of Costa Rica, are thought to be the first global extinctions driven by anthropogenic climate change (Pounds et al. 2006). In these cases, global climate change is thought to have translated into micro-scale temperature range-shifts; favouring growth of the pathogenic chytrid fungus (*Batrachochtrium dendrobatidis*) and accelerating the development of the deadly disease Chytridiomycosis in these amphibians.

The most evident responses of montane populations to climate change have been upslope range-shifts, which have occurred globally across a range of taxa (Parmesan 2006). However, the geography of mountainous regions places large constraints on range-shifts (La Sorte and Jetz 2010). Mountains tend to be isolated, limiting the potential for lateral dispersal between mountains, and the potential for vertical dispersal is obviously restricted. Furthermore, even if there is suitable habitat at higher elevations, it can be low quality and inaccessible (La Sorte and Jetz 2010). This could explain why the upslope migration of many montane populations is lagging considerably behind climate change (Chen et al. 2011). Montane species can experience ‘range-shift gaps’, physical gaps between the upper limit of their current range and the lower limit of suitable habitat predicted in the future (Colwell et al. 2008, La Sorte and Jetz 2010), limiting further the potential for upslope migration. For these reasons, many montane populations are experiencing range retractions, as the trailing edge of their range tracks climate change upwards, but their leading edge is limited by a lack of available habitat (Colwell et al. 2008, Morelli et al. 2012, Wilson et al. 2005). This can result in the extinction of populations; for example in the Belding’s ground squirrel (*Urocitellus beldingi*), an alarming 42% of 72 populations in California have been extirpated along its lower altitudinal range due to climate change, with no evidence of newly colonised sites at higher elevations (Morelli et al. 2012). In lower altitude ground squirrel populations, a physiologically critical temperature may have been reached, limiting the ability of individuals to acquire resources and survive. Fortunately in this case, areas of human land-use, where supplementary food and water is available, have acted as refugia, ameliorating the impacts of climate change on this species. This is surprising, given that anthropogenic areas generally pose a significant barrier to the lateral dispersal of populations both among and between mountain ranges, for example due to the presence of roads and railways (Andersen 1991, Mysterud and Saether 2011). The extent to which species will move across lower lying areas between mountains when upslope dispersal is not a feasible option is currently unknown (La Sorte and Jetz 2010). Changes in precipitation, if not in step with temperature change, could also cause problems for populations migrating upslope. Populations tracking their thermal niche could encounter entirely novel precipitation regimes, dramatically increasing their risk of extirpation (McCain and Colwell 2011). This could particularly impact hydrophilic taxa, such as amphibians, in drying environments.

Aside from altitudinal range-shifts, there is a range of other, less documented, effects of climate change on montane ecosystems. For instance, as a side-effect of individualistic range-shift responses, the structure of communities can change rapidly (Klanderud and Totland 2005, Walther et al. 2005). Changes in species composition and diversity can in turn affect inter-specific interactions, altering dominance hierarchies (Klanderud and Totland 2005). Also, the physiology of montane vertebrates, particularly mammals, can be very sensitive to changes in temperature, being adversely affected by both heat and cold stress (Aublet et al. 2009, Pörtner 2002, Storz et al. 2010). As such, they can be forced to adjust their behaviours, for instance to avoid overheating during summer, which can impair their ability to acquire resources, leading to reductions in fecundity and survival (Pörtner 2002, Storz et al. 2010). For montane mammals, climate change can also influence demographic parameters indirectly via effects on vegetation quality and phenology (Inouye et al. 2000, Pettorelli et al. 2007). Changes in precipitation and temperature can affect snow depth and the duration of snow cover, influencing the ability of montane herbivores to forage (Pettorelli et al. 2007). Since reproductive cycles of montane mammals tend to be tightly linked to seasonality, alterations in vegetation availability can have a pronounced impact on their population dynamics (Inouye et al. 2000, Pettorelli et al. 2007).

1.4 The Alpine chamois as a model system

1.4.1 Why study chamois?

The focus of this study is the Alpine chamois, a species of alpine ungulate of considerable ecological, economic and cultural importance throughout the Alpine region. Chamois are the most abundant ungulate species in the European Alps, being found throughout the Alpine arc and across a large range of elevations, from 500m to 3,100m above sea level (Shackleton 1997, Spitzenberger et al. 2001). The value of studying the ecology of common and widespread species has recently been highlighted (Gaston and Fuller 2008, Gaston 2010). Chamois are a key component of Alpine ecosystems and are an important cultural symbol of the Alps. Furthermore, they contribute to the region’s economy through hunting tourism, being widely hunted throughout the Alps by both foreign and local hunters, and providing a culturally significant source of food and trophies.

The importance of studying rare and threatened species is obvious: they may be at risk of extinction due to anthropogenic drivers such as overexploitation, habitat loss and environmental change (Gaston and Fuller 2008, Gaston 2010, Mace et al. 2007). However, due to their sheer abundance, common species are more affected by these processes, and the loss of common species could have devastating and far-reaching impacts on ecosystems, due to their involvement in a large number of biotic interactions (Gaston and Fuller 2008, Gaston 2010). In a number of cases, common species are currently in decline (Donald et al. 2001, Green et al. 2004, Snook 1996), and there are abundant past examples of population crashes, and even extinctions, of previously common species, often due to overexploitation (e.g. Lockwood 2004, Milner-Gulland et al. 2001, Wilcove 2000). Common species are also threatened by climate and environmental change, particularly those that are specialised to environmental conditions that are currently widespread, but may be altered by climate change (Lindenmayer et al. 2011). For instance, the greater glider (*Petauroides volans*), which is distributed throughout the forested areas of eastern Australia, a region which has experienced drought, high temperatures and an increased frequency of wildfires in recent decades, is in rapid decline, which is thought to be due to environmental change in this habitat (Lindenmayer et al. 2011). Studying the ecology of common species in regions threatened by climate change is of great value to climate change research. Chamois are a very good study species in this respect, being widespread across a region which is very sensitive to climate change and has already experienced marked shifts in temperature, precipitation and phenology. Information on the influence of climate and environmental change of this species could be used to provide insight into the future plight of rarer, less conspicuous alpine species.

Frequently, much information is available on common species, allowing them to be readily studied and used as indicators of the effects of environmental change for rarer species (Duelli and Obrist 2003, Gaston and Fuller 2008, Pearman and Weber 2007). Despite this, there are still considerable gaps in our knowledge of the ecology of such species, for instance on life-history, reproductive and behavioural traits, which are important for studying how species interact with their environment (Gaston and Fuller 2007, Tyler et al. 2012). Until recently, chamois have been relatively understudied and several important aspects of their ecology, such as their reproductive biology, remain poorly understood (Corlatti et al. 2011). As such, this study provides an opportunity to improve our knowledge of this species, as well as providing general insights into the threat climate changes poses to mountain-dwelling species. There are frequently data on the demography and abundance of hunted ungulate species such as chamois (e.g. Coltman et al. 2003, Mysterud et al. 2005, Yoccoz et al. 2002), which can be used to study life-history and demography of these species. Whilst such data only provide information on a cross-section of a population and so lack information on individual variation (Nussey et al. 2008), and particularly individual variation over time, they provide a rich source of ecological information, at the population level, on commercially and culturally important species. This study draws heavily on a long-term 38-year dataset on chamois age, sex and body mass collated from hunting records (see chapter 2 for more information). Using these data, supplemented with further information collected in field studies, I investigate the influence of climate and environmental change on the life-history, demography and behaviour of this species, considering both the species-specific and general implications of this work.

1.4.2 Background to chamois ecology

In the recent past, information on chamois ecology was restricted to a rich anecdotal literature (Couturier 1938, Knaus and Schröder 1983, Kramer 1969). However, over the past few decades, there has been a considerable increase in studies on chamois, focusing largely on reproductive behaviour (von Hardenberg et al. 2000, Willisch and Ingold 2007), demography (Loison et al. 1994, Rughetti et al. 2011) and management (Corlatti et al. 2011, Skonhoft et al. 2002). Despite this increase, some features of their ecology remain poorly understood. Chamois are generally polygynous (Loison, Gaillard, et al. 1999, von Hardenberg et al. 2000) and yet, in terms of horn and body size (Couturier 1938, Knaus and Schröder 1983, Kramer 1969), are surprisingly sexually monomorphic (although body mass dimorphism does increase considerably before the annual rut (Rughetti and Fiesta-Bianchet 2011)). Furthermore, mortality rates in males and females appear to be relatively even (Bocci et al. 2010, Gonzalez and Crampe 2001). The presence of both monomorphy and even mortality rates is surprising, given the high cost of male-male competition and reliance on large body and weapon size in most polygynous ungulates (Clutton-Brock et al. 1985, Coltman et al. 2002, Preston et al. 2003). This study may help shed more light on this 'Darwinian puzzle' (Corlatti et al. 2011).

Chamois generally inhabit steep, rocky areas but can occupy a wide range of habitat types, including alpine meadows, broadleaf woodland and coniferous woodland (Pedrotti and Lovari 1999). They feed on a variety of vegetation, including grasses, herbs, buds, shoots and fungi (Sägesser 1986). During the autumn, the annual rutting season takes place and males compete to mate with females. Gestation lasts for approximately 170 days and one kid is born per female in early spring. Kids are weaned after about 6 months and reach sexual maturity at 2.5 and 3.5-4 years in females and males respectively. Females and juveniles generally form large groups of up to about 30 individuals, particularly during spring and summer, whereas males are more solitary (Couturier 1938, Knaus and Schröder 1983). Maximum lifespan is 19 years in males and 21 years in females (see chapter 2).

1.4.3 Climate change and chamois ecology

The climate of the European Alps is predicted to change considerably over the next century, with winters becoming milder and wetter and summers becoming warmer and drier (Beniston et al. 1995). These changes, and particularly their effects on the spatial distribution of snow, are predicted to influence the distributions and dynamics of alpine ungulate populations significantly (Mysterud and Saether 2011). However, such impacts are yet to be fully explored.

Range-shifts

The ability of alpine ungulates to track climate change in mountainous regions will be strongly governed by the migratory ability of their forage plants. Encouragingly, the upslope migration of alpine plant species has already been recorded, over long (Lenoir et al. 2008), medium (Pauli et al. 2007) and short time-scales (Erschbamer et al. 2009). Furthermore, alpine ungulates undertake altitudinal migrations at different times of the year and at a variety of temporal scales. These range from daily migrations during summer to avoid high temperatures (Aublet et al. 2009), to intra-seasonal medium-term displacements due to disturbances or harsh weather (Boldt and Ingold 2005), to seasonal migrations, for instance to lower elevations during winter, in order to follow changes in forage availability (Mysterud 1999). This plasticity suggests that there is much potential for alpine herbivores to track areas of suitable habitat, if they are accessible.

It is difficult to estimate how rapidly ungulates will expand their ranges in response to climate change. In chamois, as in most mammals, immigration and emigration regularly occur between populations; however, it remains to be seen whether such habitual migration will form the mechanism for range-shifts under climate change. Also, difficulties in predicting dispersal distances arise from variation within populations. For example, whilst female chamois generally exhibit a more exploratory pattern of movement, males are the main dispersers (Loison, Jullien, et al. 1999a). Furthermore, both resident and migrating male morphs exist (Lovari et al. 2006). This may reflect a system similar to the conditional dispersal strategy observed in roe deer (*Capreolus capreolus*) in areas of marginal habitat at range boundaries (Andersen et al. 2004) and may be a mechanism for range expansion when unsuitable habitat is encountered. Chamois are thought to be relatively rapid dispersers compared to other ungulate species, for instance in their colonisation of New Zealand, chamois exhibited dispersal rates of 8.7 km year^{-1}, which was considerably faster than the rates of other introduced ungulate species (Caughley 1963), offering encouragement for this species being able to track its climatic niche.

Population dynamics

Abundant data on how climatic and environmental variation influence alpine ungulate population dynamics could be used to predict potential impacts of climate change. The most significant impacts of climate on alpine ungulate population dynamics are thought to arise indirectly through effects on plant abundance, quality and phenology (Mysterud, Langvatn, et al. 2001, Pettorelli, Mysterud, et al. 2005, Post and Stenseth 1999). Various climatic factors can impact on the spatial and temporal variability of forage plants, which in turn can affect the body condition of individuals and consequently their reproduction and survival (Mysterud, Langvatn, et al. 2001). The timing of spring emergence of vegetation, patterns of snow cover and the nutritional quality of plant tissue are controlled by climate and can all have lasting effects on ungulate populations (Loison, Jullien, et al. 1999b, Mysterud, Langvatn, et al. 2001, Post and Stenseth 1999, Van Soest 1994). (Pettorelli et al. 2007).

Spring weather is thought to control the length of the growing season and ultimately the duration over which herbivores have access to high quality vegetation (Pettorelli, Mysterud, et al. 2005). As a result, there could be significant consequences if the emergence of spring vegetation becomes earlier and spring temperatures rise, as is predicted (Chmielewski and Rotzer 2002, Diaz and Bradley 1997). Earlier springs have been linked to higher body masses in juvenile chamois, due to a longer period of forage availability (Garel et al. 2011). However, rapid green-up during spring, related to warmer temperatures, are correlated with reduced survival in juveniles of alpine ibex (*Capra ibex*), and this is thought to be a result of decreasing the period of access to the best forage due to higher plant growth rates and a consequently shorter growing season (Pettorelli et al. 2007). However, with precipitation also predicted to increase during winter in the northern hemisphere (Christensen et al. 2007), a disjunction in plant phenology could be created across different altitudes due to precipitation falling as rain at lower altitudes and snow at higher altitudes (Mysterud, Stenseth, et al. 2001). This could be beneficial to alpine ungulates, providing a more variable snow melt and thus access to high quality forage over a longer period (Mysterud, Stenseth, et al. 2001, Post and Stenseth 1999). The effects of increasing spring temperatures are likely to vary between alpine ungulate species. For instance, higher temperatures in late spring are thought to benefit alpine chamois survival by coinciding with late season rainfall which may improve plant nutritional quality (Loison, Jullien, et al. 1999b). For Pyrenean chamois (*Rupicapra pyrenaica*) however, these higher temperatures negatively affect survival as they coincide with a period of low rainfall, and thus are thought to affect plant quality adversely. This highlights individualistic nature of responses to climate that can be evident across different populations.

Changes to winter climate are also likely to impact alpine ungulates, primarily due to changes in patterns of precipitation and, consequently, snow cover. In chamois, survival has been shown to be higher following snowy winters, which is thought to be an effect of snow cover protecting vegetation and extending the period of plant growth (Loison, Jullien, et al. 1999b). So with winter temperatures predicted to increase and snow cover predicted to decrease (Beniston 1997, Diaz and Bradley 1997), chamois survival could be negatively affected in the future. However, there is evidence from other chamois populations that extremely snowy winters can lead to significant reductions in survival in adults and juveniles, particularly if high snowfall occurs in late winter (by which time the body condition of individuals has generally declined significantly) (Rughetti et al. 2011, Willisch et al. 2012). The frequency of such extreme climatic events is predicted to increase in the future (Beniston and Stephenson 2004) and could lead to mass die-offs in some alpine ungulate populations. However, how frequent such events would have to be to threaten the persistence of populations is currently unknown (Mysterud and Saether 2011). Overall, changes to the amount of snowfall in alpine regions could have significant and varied impacts on ungulate populations.

Behaviour and life-histories

There is potential for alpine ungulates to adjust their behavioural routines and life-histories, buffering against climate change effects and perhaps lessening the need to adjust their ranges. In the future, alpine ungulates will be subjected to higher temperatures during the spring and summer and may adjust their behaviours to compensate for these. For instance ibex can suffer heat stress at high temperatures, moving to higher altitudes and reducing the time they spend foraging when it is hotter (Aublet et al. 2009, Grignolio et al. 2004). Also, ungulates may avoid sunny slopes during the hottest part of the day (Escos and Alados 1992) and may even adjust the orientation of their body to the sun, to reduce the absorption of solar radiation (Maloney, Moss and Mitchell 2005). In the future, alpine ungulates may increasingly adopt such thermoregulatory behaviours to combat high temperatures. Decreases in snow cover during winter and hotter, drier summers are likely to affect the patterns of altitudinal migration at both daily and seasonal time-scales, as well as the amount of time individuals allocate to foraging and locomotion. However, how short-term patterns of altitude usage will translate to long-term altitudinal range-shifts is currently unclear.

1.5 Incorporating life-history, dynamics and behaviour into predictive models

To date, few attempts have been made to link the spatial distribution of a species with its life-history or population dynamics in order to make specific and applicable predictions about how species and populations will be affected by climate and environmental change. However, a small number of studies, focussing on well-understood systems, have started to examine the interplay among distributions, life-histories and dynamics in a changing climate (e.g. Keith et al. 2008, Willems and Hill 2009).

1.5.1 Distribution and population dynamics

Keith et al. (2008) coupled a ‘species distribution model’ (SDM), a type of model which characterises the spatial range of a species based on several important climatic variables, with a population dynamics model, in order to make detailed predictions about climate change impacts on several South African fynbos plant species (see Fig.1.1). They first created a SDM to predict the probability of species occurring in different habitat patches in the future. They then linked this to a population model which, for different plant life-histories, predicted how population size (*N*) was affected by factors such as fire regime (which strongly affects survival and seedling recruitment for these species), seed dispersal, and stochasticity (both environmental and demographic). The carrying capacity (*K*) for a given patch was also determined, from habitat suitability and habitat area. This model also incorporated density dependence, by reducing the rates of survival and growth for specific life stages whenever *N* exceeded *K* for a particular patch. Also, because climate change may alter *K* for a given patch, survival and growth rates would be altered correspondingly. So, if *K* was reduced by climate change, vital rates would be reduced until *N* fell below *K*. If climate change increased *K* or created new suitable habitat patches, then population dynamics would be affected by density-independent factors and dispersal distances.

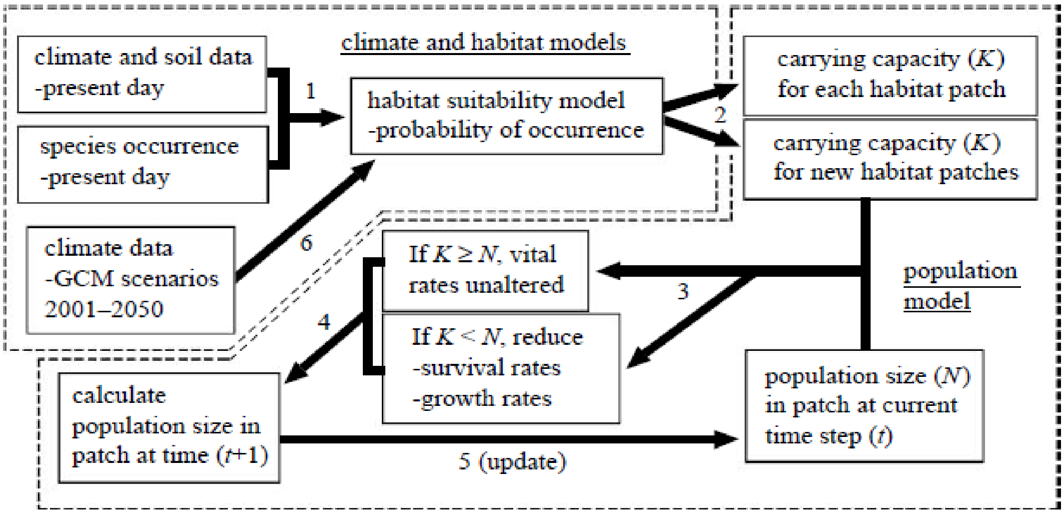


Figure 1.1 Representation of coupled climate and population models. From Keith et al. (2008).

The approach of Keith et al. (2008) enables robust predictions to be made about climate change, because it considers not only the projected availability of suitable habitat but also how populations will be affected in the future and whether they will be viable or at risk of extinction. Further robustness is created from the use of seed dispersal data to determine the ability of species to spread to new habitat patches. Using this model, the authors discovered that whilst climate change reduced population viability when burning regimes were used with eight year fire intervals, it actually increased viability when 14 year fire intervals were employed. There is much potential for findings such as these to be applied directly to management. The results of this model indicate that the response of a species to climate change can be dependent on a large number of factors. The probability of a population declining was dependent on a highly complex four-way interaction between distribution pattern, life-history, density-dependence and fire regime; this complexity highlights the importance of approaches which incorporate demographic information.

1.5.2 Distribution, behaviour and life-histories

Despite a relative dearth of data on climate effects on life-histories and behaviour, attempts have been made to incorporate such information into predictive models. A good example is the application of activity budget models, which have successfully used life-history information and environmental data to predict the spatial distributions of populations (Korstjens et al. 2006, Korstjens and Dunbar 2007, Willems and Hill 2009). These models have significant potential to predict responses to climate change. For a number of primate species, activity budget models have been shown to describe well their current geographical distribution, achieving comparable success to SDMs despite the datasets used often being limited (e.g. Korstjens et al. 2006, Willems and Hill 2009). These models are based on the theory that individuals must balance the time they spend in different behaviours each day in order to meet minimum energy requirements. Populations can only persist in areas where individuals are successful in performing core activities such as foraging and territory defence, without running out of time (Dunbar 1992a, b, Korstjens et al. 2006). The ability of individuals to survive in a given location is dependent on the local vegetation which provides both resources and shelter. In turn, climate variables such as rainfall and temperature exert a strong influence over vegetation quality and phenology so can be strong predictors of activity budgets (Korstjens et al. 2006).

Willems and Hill (2009) created an activity budget model to predict the distribution of vervet monkeys (*Cercopithecus aethiops*) across Africa (Fig. 1.2). Data on the amount of time individuals allocated to certain behaviours (feeding, moving, resting and social behaviour) was related to environmental data, including Normalised Difference Vegetation Index (NDVI), an index of plant productivity. The model performed well, successfully predicting presence at 78% of test sites and presence/absence at 87% of map pixels, a comparable predictive power to a SDM which successfully predicted 91% and 82% of sites and pixels respectively.

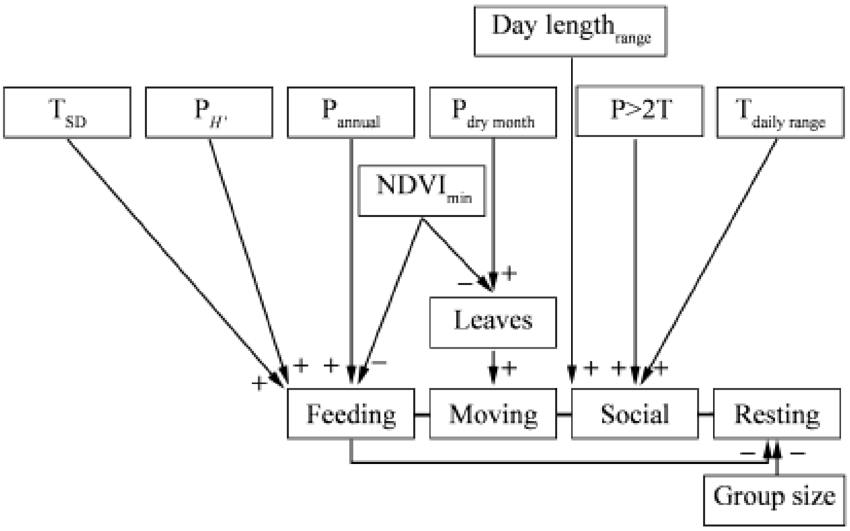


Figure 1.2 Path diagram of activity budget model of vervet monkey distribution, displaying relationships between climate, primary productivity, diet, time allocation and group size. Day length$_{range}$, annual range in day length; T$_{SD}$, temperature seasonality; P$_{H'}$, rainfall seasonality; P$_{annual}$, annual total precipitation; P$_{dry\ month}$, total precipitation of driest month; P>2T, growing season length, T$_{daily\ range}$, mean diurnal temperature range; NDVI$_{min}$, NDVI of least productive month. From Willems and Hill (2009).

Unlike SDMs, which are correlative, the activity budget model has the advantage of an explicit ecological mechanism, focussing on the relationship between time allocation, climate, local ecological conditions and group size (Korstjens et al. 2006). Due to its success in predicting current distributions, the use of activity budget models could see much success in predicting changes to future distributions. However, as yet, primates have been the only species with sufficiently detailed data for such models to be created, although with intensive behavioural studies there is potential for further mammal species, such as ungulates, to be modelled in such a way.

1.6 Implications for management

The approaches of Keith et al. (2008) and Willems and Hill (2009) indicate that there is much potential for detailed biological information to be incorporated into predictive models. These studies also highlight that, by focussing on a single or several species and using specific life-history and demographic information, predictions can be made which are directly relevant to conservation practitioners. Cross-species analyses are frequently used and often give general insights into threat (e.g. Bagchi et al. 2013, Levinsky et al. 2007); however, they can be less applicable to management. For many species, detailed life-history and demographic data for predictive models are not available. Applying dynamic modelling techniques to study common species, for which data can be abundant (e.g. Freeman et al. 2007, Mysterud, Yoccoz, et al. 2001), would inform the management of those species that most influence their environment and which, if lost, would most affect the functioning of ecosystems (Gaston and Fuller 2008, Gaston 2010). Furthermore, their use would provide an indicator of the threat of climate and environmental change to populations of other species in threatened ecosystems such as mountainous areas (Duelli and Obrist 2003, Pearman and Weber 2007).

Biologically detailed model predictions could contribute greatly to nature conservation in a changing climate. The traditional reliance on static protected areas is losing relevance in a rapidly changing climate where species ranges are shifting upslope and towards the poles (Araujo et al. 2004, Hannah et al. 2007). For example, it has been shown that a system of European reserves based on only current distributions could lose 6-11% of plant species within a 50-year period (Araujo et al. 2004). The use of modelling to predict range-shifts, and whether populations will be viable in new areas, could be applied in combination with reserve selection techniques which account for dynamic range boundaries (Araujo et al. 2004, Hannah et al. 2002, Hannah et al. 2007). Similar modelling techniques could be applied to link existing reserve networks using conservation corridors (Chetkiewicz and Boyce 2009, Williams et al. 2005).

For some poor dispersers, connected reserve networks may still be insufficient to allow migration into climatically suitable areas (McLachlan et al. 2007). In these cases, further human intervention may be required for species to track climate change, for example by assisted colonisation through the translocation of individuals. It is thought that, if carefully controlled and well planned, assisted colonisation could be a cost-effective and important management tool for enabling species with poor mobility to expand their ranges (Hoegh-Guldberg et al. 2008, McLachlan et al. 2007). For example, Willis et al. (2009) used a SDM to identify climatically suitable release sites for two British butterfly species beyond their range boundaries. After visiting the sites to make sure suitable habitat was available, translocations were successfully carried out, with both new populations growing steadily over the following six years. Well-planned assisted colonisation may be a viable and effective management strategy for those species unable to track climate warming.

1.6.1 Implications for alpine ungulate management

Traditionally, the management of European ungulate species has been very intensive, often with regimented hunting protocols in place (Wright 1999). Coupled with the high sensitivity of ungulate populations to environmental variation (e.g. Saether 1997), this highlights the need for well planned management strategies to mitigate the effects of climate change on ungulate populations (Colchero et al. 2009). Careful monitoring of the dynamics of these populations, particularly those that are heavily harvested, will be vital for management plans to be modified under climate change. Given that climate influences different demographic parameters in different ways, climate change is likely to alter the sex- and age-structures of populations. As such, changes in the hunting pressure on different segments of populations are likely to be necessary in the future. Models linking the impacts of management strategies (e.g. Skonhoft et al. 2002) and climate change (e.g. Colchero et al. 2009) on alpine ungulate populations will be of great value in the future.

A lack of suitable high-altitude habitat, which is thought to be restricting the upslope migration of montane populations (Chen et al. 2011), could pose a problem for alpine ungulates. If they are unable to track changes in climate, assisted migration could be an important management approach, used in conjunction with modelling to pinpoint suitable release sites. Assisted migration is a real option for alpine ungulates such as the ibex, a species that (as a result of uncontrolled hunting) was confined to a single population of only 90-200 individuals, before reintroduction programmes were started in 1938 into areas of its former range. These translocations led to the species recovering from a single population of about 4,000 individuals in Gran Paradiso National Park (GPNP), Italy, to around 40,000 individuals existing today, spread across more than 100 Alpine populations (Grodinsky and Stuwe 1987, Stuwe and Nievergelt 1991, von Hardenberg 2009).

Overall, it appears that different aspects of alpine ungulate ecology, particularly their distribution and demography, are likely to be influenced by climate and environmental change. Detailed case-studies of alpine ungulate populations, such as this one, will help to reveal which aspects of their ecology are most vulnerable to climate change, informing management and possibly mitigating negative impacts of climate change. Furthermore, such case-studies could provide general insights into how climate change threatens populations, informing the management of species from a wide range of taxa and from a variety of environments.

1.7 Project aims

1. **How does life-history vary across space and time?**

   Firstly, I will investigate the plasticity of chamois life-histories over both space and time. Using a long-term dataset on chamois hunting records, I will analyse variation in important life-history strategies among populations. Specifically, I will assess how males allocate resources to reproduction, both across their lives and within individual breeding seasons. I will discuss the potential influence of climate on the observed life-history patterns.

2. **How is body mass influenced by climate and environmental change?**

   I will then consider how body condition, an important life-history trait linked to reproductive success and fitness, has been influenced in these populations. I will investigate drivers of long-term trends in juvenile body mass, discussing links between condition, foraging behaviour and warming temperatures.

3. **How is demography influenced by climate?**

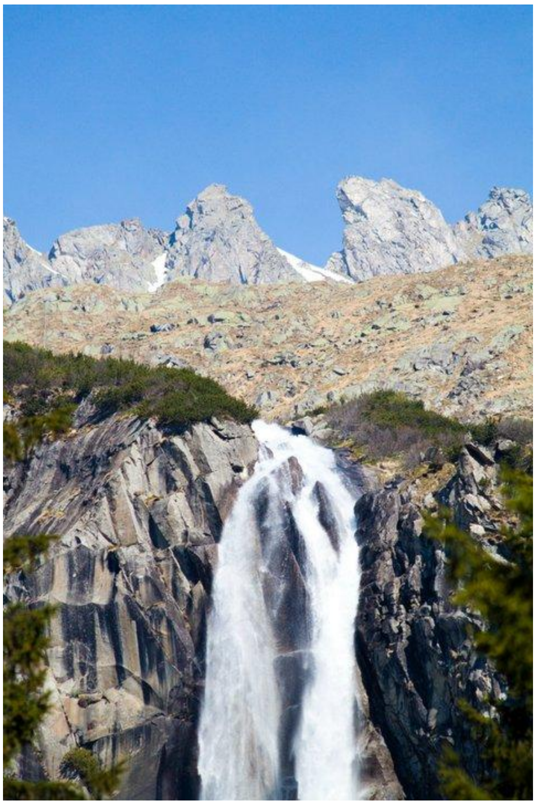
   Next, I will investigate the importance of climatic and environmental factors to chamois demography and population dynamics, combining data from censuses, hunting records and field-based observations. These analyses will reveal the potential influence of climate change, and also hunting, on chamois population dynamics.

4. **How is behaviour influenced by climate and inter-specific interactions?**

   Finally, using data on variation in chamois foraging behaviour during summer, from a different study population, I will examine the importance of temperature, as well as other factors such as inter-specific interactions, on chamois activity budgets and altitude use. Using the models I develop I will be able to predict the potential effects of climate change on chamois behaviour and distribution in the future.

Chapter 2

Trentino study area background and data collection



2.1 Background

The study area used in chapters 3-6 is located in the Central-Eastern Italian Alps, across a 1,333km^2 area of Trento Province (46°02'N, 10°38'E) (Fig. 2.1). The elevation of the study area ranges from 52 to 3,558m a.s.l., with a mean altitude of 1,586m. It is forested up to the tree-line at about 2,000m, above which habitat consists of Alpine meadows, sparse vegetation with rocky outcrops, scree fields, permanent snow patches and open rock faces. The study area consists of three chamois hunting districts: Adamello, Presanella and Brenta. There is considerable variation in altitude among the areas (mean altitude: Adamello, 1,979m; Presanella, 2,182m; Brenta, 1,675m). Adamello and Presanella are characterised by nutrient-poor siliceous vegetation whilst Brenta is characterised by nutrient-rich calcareous vegetation (Chirichella, Ciuti, Grignolio, et al. 2013). Typically, meadows in Adamello and Presanella are dominated by *Festuca scabriculmis* and *Carex curvula*, whilst those in Brenta are composed of *Sesleria albicans* and *Carex firma* (official data of Adamello Brenta Nature Park, Trento Province, Italy).

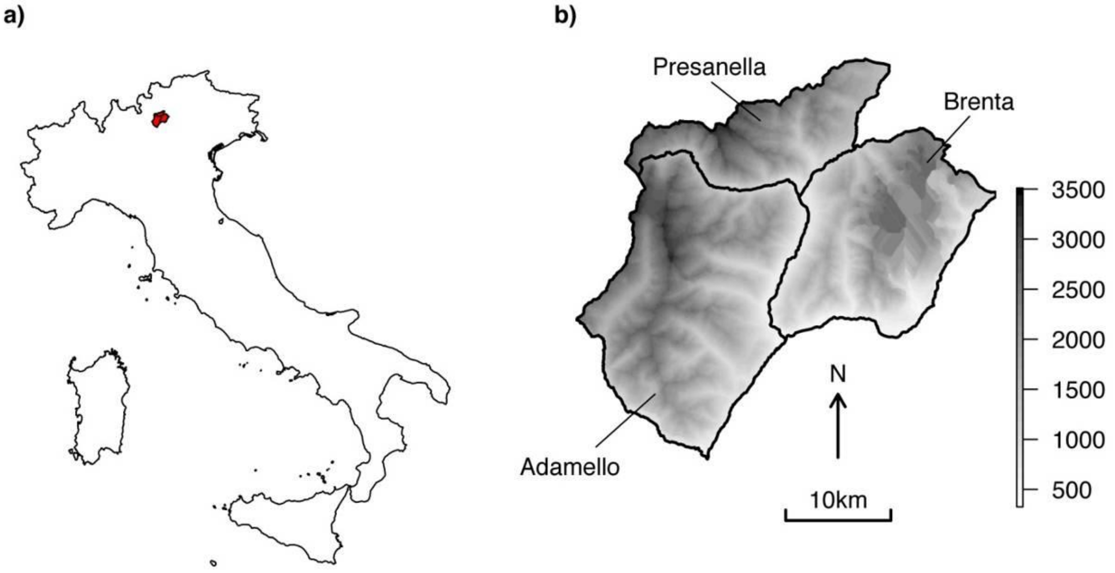


Figure 2.1 Map of **a)** Italy, indicating the location of the study area in red, and **b)** the study area, displaying the locations of the three hunting districts. Shading indicates altitude in metres.

In total, there are approximately 8,800 Alpine chamois found across the three study populations (4,300 in Adamello; 2,000 in Presanella; 2,500 in Brenta). There are a range of other ungulate species found in the area, including red deer (*Cervus elaphus*), roe deer, mouflon (*Ovis orientalis musimon*) and Alpine ibex. Red and roe deer are abundant but are rarely found in the high altitude areas above the tree-line frequented by chamois. In contrast, mouflon and ibex, which are both high altitude species, are restricted to several small populations, having been introduced and reintroduced, respectively, to the area in the recent past. There are several potential predators of chamois in the study area, including a small, stable population of brown bear (*Ursus arctos*) in Brenta, a very small number of Eurasian lynx (*Lynx lynx*) and the golden eagle (*Aquila chrysäetos*). However, predation on chamois is rare in the area, indeed predation by lynx has never been recorded (official data of Adamello Brenta Nature Park, Trento Province, Italy).

2.2 Data collection

Data were collected on the eviscerated body mass, sex, age and date shot of 28,966 Alpine chamois (15,155 males and 13,811 females) culled over 38 consecutive hunting seasons between 1973 and 2010. Ages were estimated from counts of horn growth annuli (Schröder and Von Elsner-Schak 1985). Males varied between 1 and 19 years old and females varied between 1 and 21 years old. Dates of shooting were converted to Julian day of year and ranged from day 247 to 365.

Table 2.1 Mean sex and age-specific chamois hunting quotas in Trento province.

Sex	Age-class	Age (years)	Mean proportion of quota (%)
Male	I	≥6	16
Male	II	2 - 5	10
Male	III	1	22
Female	I	≥11	13
Female	II	2 - 10	17
Female	III	1	22

Chamois are hunted with rifles every year from mid-September to the end of December. Hunting is controlled through licenses issued by local wildlife boards. Hunting quotas are set for each area by local wildlife boards, based on population density estimates from censuses performed prior to the hunting season. The proportion of different sex and age-classes in the quota are also decided annually (mean proportions shown in Table 2.1). There is little potential for artificial selection by hunters (e.g. by shooting the largest individuals at the start of the season) because flight distances (distance from hunter when chamois takes flight) in these hunted populations are large (personal observation) and, due to the generally open habitat, hunters can be easily detected. As such, whilst trophy hunting is practised in Trento Province, hunters have limited shooting opportunities per day and will typically shoot the first animal of a suitable age-class that they encounter. Also, since both males and females are trophy hunted, one would expect to see pronounced patterns of decreasing mass with season in adults of both sexes if artificial selection was occurring. This is not the case in females (see chapter 3). Furthermore, there was no evidence of hunter selection for larger bodied age classes earlier in the season, which might be the case if there was strong hunter selection for larger body mass (Fig. 2.2).

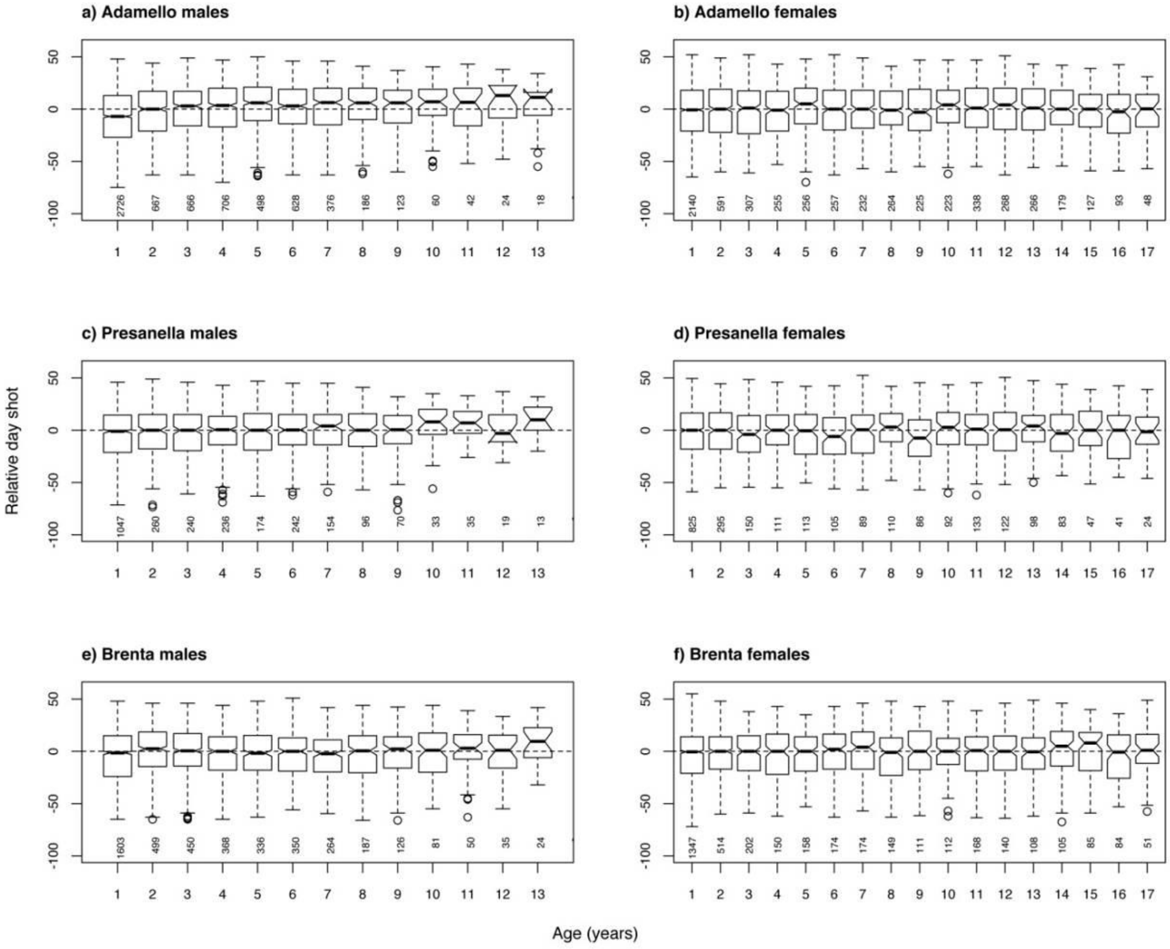


Figure 2.2 Variation in relative day shot with age in males and females in the three study populations. Relative day shot was calculated for each individual by shooting day minus median day of shot animals in the same year and site. Thick lines represent median values, boxes display inter-quartile ranges (IQRs) and the extents of the vertical dashed lines show maximum and minimum values. Outliers represent values more than 1.5 of the IQR higher or lower than the mean and, in such cases, the extents of dashed lines represent maximum and minimum values within 1.5 of the IQR. Non-overlapping notches on boxes provides strong evidence that the medians of these age classes differ. Note that, if artificial selection (for larger-bodied animals) was occurring, one would expect to see a U-shaped curve in these plots (with prime-aged individuals targeted earlier in the season, and older and younger individuals typically shot later in the season); this is not the case.

Chapter 3

Lifetime reproductive strategies in male chamois*

*Now published as:

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3.1 Abstract

A fundamental life-history question is how individuals should allocate resources to reproduction optimally over time (reproductive allocation). The reproductive restraint hypothesis predicts that reproductive effort (RE; the allocation of resources to current reproduction) should peak at prime-age, whilst the terminal investment hypothesis predicts that individuals should continue to invest more resources in reproduction throughout life, owing to an ever-decreasing residual reproductive value. There is evidence supporting both hypotheses in the scientific literature. I used an uncommonly large, 38-year dataset on Alpine chamois shot at various times during the rutting period to test these two hypotheses. Assuming that body mass loss in rutting males was strongly related to RE and, using a process-based approach, I modelled how male relative mass loss rates varied with age. For different regions of the study area, I provide evidence consistent with different hypotheses for reproductive allocation. In sites where RE declined in older age, this appears to be strongly linked to declining body condition in old males. In this species, terminal investment may only occur in areas with lower rates of body mass senescence. These results show that patterns of reproductive allocation may be more plastic than previously thought. It appears that there is a continuum from downturns in RE at old age to terminal investment that can be manifest, even across adjacent populations. This work identifies uncertainty in the relationship between reproductive restraint and a lack of competitive ability in older life (driven by body mass senescence); both could explain a decline in RE in old age and may be hard to disentangle in empirical data. I discuss a number of environmental and anthropogenic factors which could influence reproductive life-histories, underlining that life-history patterns should not be generalised across different populations.

3.2 Introduction

In most stable populations, reproductive life-histories should be optimised to maximise lifetime reproductive success (Stearns 1992, Williams 1966a). Accordingly, the question of how long-lived iteroparous animals should allocate resources to reproduction over their lives is of great ecological importance (Stearns 1992, Williams 1966a, b). Trade-offs exist not only between survival and reproduction, but also between current and future reproduction (Clutton-Brock 1984, Pianka and Parker 1975, Stearns 1992, Williams 1966a, b). The allocation of resources to current reproduction is likely to be damaging to future reproductive potential (Williams 1966b). As such, a breeding individual must carefully balance yearly investment in reproduction against future reproductive potential in order to maximise lifetime reproductive success.

The classical view of reproductive allocation in iteroparous species is that reproductive effort (RE; the allocation of resources to current reproduction rather than to future reproduction, growth or survival) should increase throughout life following maturity, due to a decreasing residual reproductive value (Clutton-Brock 1984, Pianka and Parker 1975, Williams 1966a, b). This has been termed the terminal investment hypothesis (Clutton-Brock 1984). The hypothesis predicts that the trade-off between current and future reproduction becomes less relevant in later life as the potential for future reproduction diminishes. As such, RE is predicted to peak in old individuals in their final breeding seasons. There is support for terminal investment from a range of taxa (Candolin 2000, Creighton et al. 2009, Ericsson and Wallin 2001, Isaac and Johnson 2005) although, to date, there is little evidence for male terminal investment in natural populations (e.g. Evans et al. 2011).

Evidence from a number of species suggests that RE peaks at prime-age (here defined as the age of peak body condition) and subsequently decreases (Billing et al. 2007, Cameron et al. 2000, Mainguy and Cote 2008, Yoccoz et al. 2002). This could either arise as a by-product of reproductive senescence (Williams 1957) or could be a life-history tactic designed to maximise RE over a number of years. Specifically, a large allocation of resources to current reproduction might be sub-optimal if it is likely to cause death. Instead, individuals might show reproductive restraint, eking out future reproduction over a number of years (McNamara et al. 2009, Yoccoz et al. 2002). The results of a recent modelling study by McNamara et al. (McNamara et al. 2009) suggest that reproductive restraint and terminal investment should be favoured in different conditions, depending on the rates of intrinsic and extrinsic mortality (due, for example, to disease or predation). This raises the intriguing possibility that, if rates of intrinsic and extrinsic mortality vary among populations, different patterns of reproductive allocation could exist within a species.

Ungulate species provide good model systems with which to study the allocation of RE over time. Males and females generally have strongly contrasting life-histories, investing in reproduction in different ways and over different periods of the reproductive cycle (Clutton-Brock et al. 1985, Stearns 1992). Females invest heavily in gestation, lactation and parental care, with their reproductive success strongly dependent on raising young successfully (Krebs and Davies 1993). In contrast, male reproductive success usually depends on competing for access to females during a short rutting season (Clutton-Brock et al. 1988). Specifically, male reproductive behaviour consists of agonistic interactions with rival males and courtship behaviours to attract females (Forsyth et al. 2005, McElligott et al. 2001, Yoccoz et al. 2002). Male reproductive allocation remains relatively understudied, but can be investigated by measuring the somatic costs of reproductive behaviour during the rut. Rutting male ungulates often adopt a strategy of 'appetite suppression', which means that they lie towards the capital end of the continuum between capital and income breeding, relying on stored energy to breed (Apollonio and Di Vittorio 2004, Stephens et al. 2009, Willisch and Ingold 2007). As such, the proportion of body mass lost by a male during the rut can be used as an estimate of RE (Doughty and Shine 1997). Relative mass loss is an informative indicator of RE because there is known to be an important trade-off between body mass and subsequent over-winter survival for mammals living in unpredictable environments (Berube et al. 1999, Loison, Langvatn, et al. 1999).

Reproductive allocation by males has been studied in several ungulates, using both transversal (cross-cohort) and longitudinal approaches. Using a transversal hunting dataset, Yoccoz et al. (2002) found that RE peaked in prime-aged male red deer before declining; this is probably explained by a reduced ability of older males to hold a harem (Clutton-Brock et al. 1985, Yoccoz et al. 2002). Declines in effort in older individuals have also been observed in longitudinal studies on male bison (*Bison bison*) (Maher and Byers 1987) and mountain goats (*Oreamnos americanus*) (Mainguy and Cote 2008). Intriguingly, Mysterud et al. (2005) used a transversal analysis to put forward evidence "consistent with the terminal investment hypothesis" of increasing RE with age in adult male moose, although the authors noted that effort tended to stabilise or decrease in the oldest individuals (which were sparse in their dataset). Unfortunately, several of these studies were based on small sample sizes, particularly of individuals of prime-age and older, a common problem in life-history studies (Nussey et al. 2008). A consequence is that earlier studies have fitted RE to data from age-classes with only one or two individuals, inevitably constraining the inferences that can be made from the data (Mysterud et al. 2005, Yoccoz et al. 2002).

Here, I analyse the relationship between male age and RE using a large transversal dataset of Alpine chamois. During the rut, males allocate most of their non-rutting time to rest rather than foraging; they are thus capital breeders (Willisch and Ingold 2007). Variation in male RE with age was tested using the mean, relative rate of body mass loss during the rut, as an estimate of RE (Mysterud et al. 2005, Yoccoz et al. 2002). Rather than taking repeated measurements of the same individuals, mass loss was estimated across different individuals shot at different times during the season. Also, age-related patterns of body mass were predicted both before and after the rut, as these could reveal important life-history characteristics which influence the allocation of RE. Using a process-based model of mass loss, RE variation with age was assessed among sites and between years. In contrast to previous studies (e.g. Mysterud et al. 2005), RE was fitted to data directly, rather than indirectly inferring RE from body mass predictions at different times; this improved the estimation of uncertainty in the RE predictions.

3.3 Materials and Methods

3.3.1 Background

Breeding male chamois defend small clustered territories during the rutting season, excluding rival males and defending oestrus females (Kramer 1969, von Hardenberg et al. 2000). Male rutting behaviour consists of agonistic interactions with rivals such as chasing and posturing; and interactions with sexually mature females, including herding and copulation (Kramer 1969).

3.3.2 Data collection

Body mass data were analysed from the three hunting districts in the study area. Data collected prior to 1979 were limited, so these years were excluded from the analysis. Although timing of the rut is likely to vary slightly between sites and years, there were insufficient data to assess this reliably. Therefore, based on extensive field observations (Marco Apollonio, personal communication), a fixed rut period of days 300 to 340 was assumed. Given the strict criteria set out above, the sample size was 7,202 males and 6,415 females.

3.3.3 Statistical Analysis

Evidence was sought for age-dependence in the relative rate of male mass loss during the rutting period. Annual population density is a potentially important factor affecting the rate of mass loss and may vary across years at a given site (Yoccoz et al. 2002). As such, the number of individuals culled each year divided by the area of suitable habitat in each site was used as a proxy for population density. This proxy, *d*, is only a crude index but generally correlates well with population density values estimated from censuses performed since 1992 (Fig. 3.1). A modelling framework was developed that allows age-dependent change in mass either to vary annually in response to changes in *d*, or to exhibit a smooth trend across years. It was assumed that, during the rutting period of year *y*, individuals of age *a* lose mass at mean, relative rate $L(a,y,d,s)$, when in a population at density *d* and in a given site *s*. As *L* is independent of body mass, it can be used to compare RE directly across sexes and age-classes. Specifically, if the expected mean mass of individuals on day 300 (hereafter, the 'initial mass') is $\overline{m}_{300}(a,y,d,s)$, then their expected mass on day *t* ($t \geq 300$) is

$$\overline{m}_t(a,y,d,s) = \overline{m}_{300}(a,y,d,s)\exp\left[-L(a,y,d,s)(t-300)\right]$$

The objective is to estimate $\overline{m}_{300}(a,y,d,s)$ and $L(a,y,d,s)$ using model selection to assess the importance of age, year, population density, and site. Using these estimates expected mean mass of individuals at the end of the rut, on day 340, could be inferred (hereafter, 'final mass').

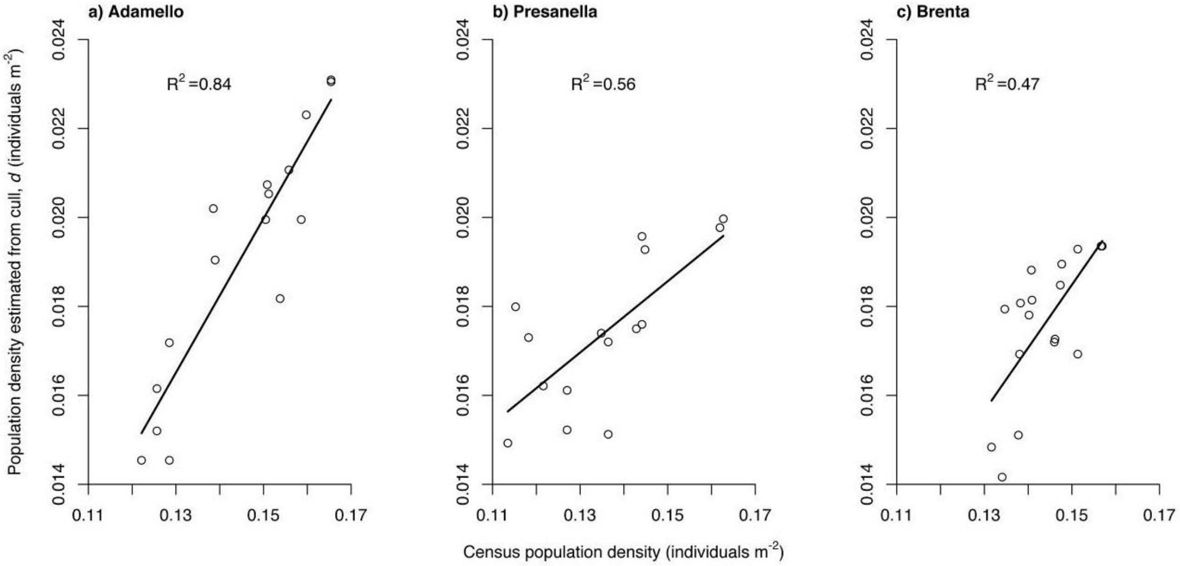

Figure 3.1 The relationship between *d*, the population density estimate, and population density estimated from censuses. Linear regressions plotted. R^2 values shown.

It was assumed that age-dependence for both the initial mass and mass loss functions could be characterised using cubic splines. Cubic splines were used to avoid numerical instabilities that are often characteristic of higher order polynomials (e.g. Kreyszig 1999). It was assumed that the shape of these splines was fixed across years for any site (i.e. age-dependence was fixed) but that their relative magnitude could vary among years to reflect annual environmental variation. Specifically, three cubic splines were used, each spanning 4 years of age, to describe complete age-dependency from 1 to 13 years of age. These three splines correspond broadly to pre prime-age (1-4 years), prime-age (5-9 years) and post prime-age (10-13 years). There were too few individuals older than 13 within each site to permit reliable predictions for these individuals. Using fewer than three splines resulted in a poor fit to the data, whereas using more than three splines did not improve the fit for either function. Initial mass, and mass loss rate, were described by

$$\overline{m}_{300}(a,y,d,s) = \frac{f(a)}{\alpha_0(y,d,s)}$$

and

$$L(a,y,d,s) = \frac{g(a)}{\beta_0(y,d,s)},$$

where *f*(*a*) and *g*(*a*) describe the two three-piece, cubic spline functions and satisfy *f*(1) = *g*(1) = 1. Thus, the scaling parameter α_0 represents the inverse of the initial mass of the youngest age modelled (yearlings). Similarly, β_0 describes the inverse of the rate of mass loss of yearlings. To identify long-term trends and density-dependence, models were constructed that allowed α_0 and β_0 to be either: constant, linearly dependent on *d*, linearly dependent on *y*, or quadratic in *y*. Incorporating yearly trends and density-dependence in life-history traits is plausible for long-term studies of mammalian life-histories. In total, 16 models were fitted to both male and female mass time-series data for each of the three sites (Tables 3.1 & 3.2).

When fitting the models it was assumed that variation about the predicted mean body mass was normally-distributed. Models most consistent with the data were selected using Akaike's Information Criterion (AIC; (Burnham and Anderson 2002)). To avoid selecting overly complex models the two-step selection criterion suggested by Richards (2008) was used. First, all models having an AIC within six units of the smallest AIC calculated were selected (i.e. $\Delta\text{AIC} \leq 6$). Second, in order to remove overly complex models, those with a higher AIC value than any simpler nested model were disregarded.

Ignoring site effects substantially reduced the model fit, justifying fitting separate models for each site (Tables A1 & A2). For each site, the most parsimonious model was fitted to 1,000 bootstrapped replicates (Efron and Tibshirani 1991), stratified by age, to determine 95% confidence intervals for initial mass, final mass and rate of mass loss. Statistical analyses were performed using R version 2.12.1 (R Development Core Team 2011). Results are reported with standard errors, where applicable.

3.4 Results

For males, the best AIC models explained a large proportion of the variation in the data (Fig. 3.2). For each site, the scaling parameter associated with initial mass, α_0, varied with year (Table 3.1), indicating long-term population change. The best fitting function varied between sites (quadratic in Adamello and Brenta but linear in Presanella) but the overall trends are surprisingly consistent: males have become consistently lighter in all sites across the study period (Fig. 3.3); for example, yearling males have become between 1.1 and 2.4kg lighter over the past 32 years. These changes may be a result of higher competition, as the data suggest that population density has increased over this period.

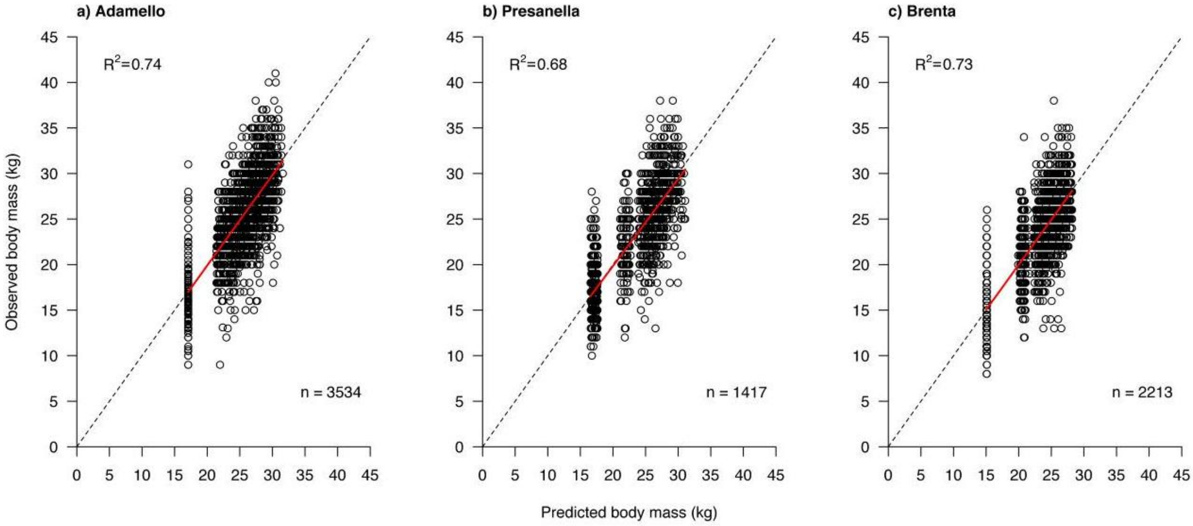

Figure 3.2 Plots of model fit for males. The relationship between observed body mass and predicted body mass by best model, in each site. Linear regressions plotted (red lines). R^2 values and sample sizes (n) shown. Dashed lines show 1:1 relationship.

Model selection indicated that β_0 was influenced by site and year and $g(a)$ differed between sites (Table 3.1), which suggests that the patterns of net rate of relative mass loss, L, differed across sites and have changed during the 30 years of the study. However, despite such differences there was clear evidence of a somatic cost of reproduction for males during the rut across all ages and sites (mean adult male proportional mass loss: Adamello, 19.1 ± 1%; Presanella, 17.1 ± 1.1%; Brenta, 18.1 ± 1.3%; Fig. 3.4). In contrast, female mass loss during this period was much lower (mean adult female proportional mass loss: Adamello, 7.2 ± 0.7%; Presanella, 8.0 ± 0.3%; Brenta, 7.7 ± 0.2%; Fig. 3.5).

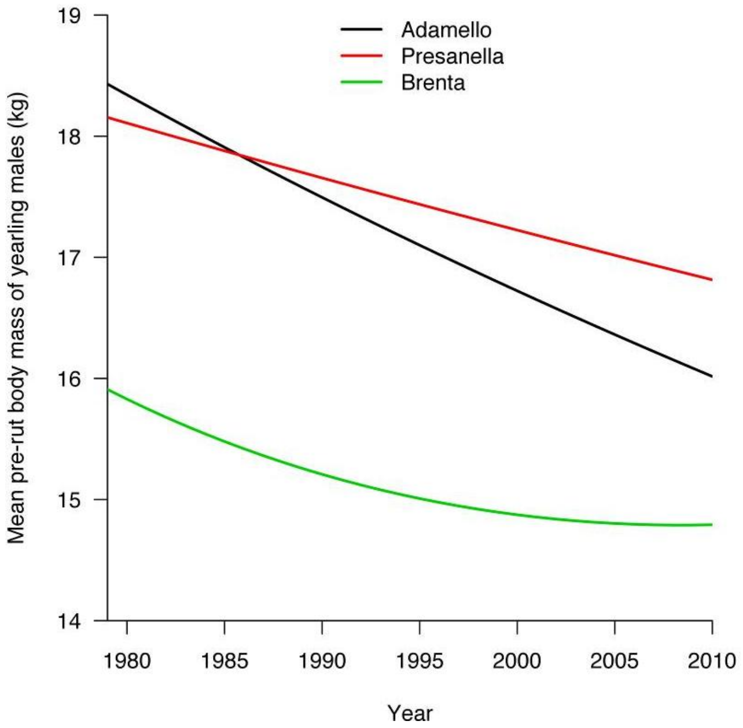

Figure 3.3 Change in predicted yearling male mass over time. Variation between predicted pre-rut body mass of yearling males (on day 300) with year in Adamello, Presanella and Brenta.

In adult females, initial and final mass are relatively constant with age (Fig. 3.5 a-c). However, male mass is highly age-dependent and the shape of this age-dependency varies among sites. Interestingly, initial mass shows a strong decline after 8 years in Adamello (Fig. 3.4 a) and a weaker decline after 10 years in Presanella (Fig. 3.4 b). However in Brenta, initial mass remains relatively constant throughout adulthood (Fig. 3.4 c). The age-related pattern of final mass also varies among sites. In Adamello and Presanella, adult males show a constant final mass (Fig. 3.4 a & b); however, in Brenta, final mass declines after 9 years (Fig. 3.4 c).

In females, confidence intervals suggest that there are no strong patterns of relative mass loss with age (Fig. 3.5). In contrast, male relative mass loss is highly dependent on age and there is considerable variation in the shape of this relationship among sites (Fig. 3.4). In Adamello, rate of mass loss initially increases rapidly with age, peaking in 8 year olds before dropping (Fig. 3.4 d). In Presanella, rate of mass loss increases more gradually, peaking at 10 years before apparently dropping (Fig. 3.4 e). In Brenta, after a slight plateau between 5 and 9 years, rate of mass loss continues to increase steadily through older ages (Fig. 3.4 f). In all sites, confidence intervals widen with increasing age (due to decreasing sample size); however, the general trends of mass loss with age in Adamello and Brenta appear robust (Fig. 3.4 d & f). In Presanella, whilst the best model predicts a decrease in mass loss after 9 years, due to the width of confidence intervals at old age I cannot rule out the possibility that RE levels off (Fig. 3.4 e).

Variation in male age-structure among the sites shows that there are increasingly fewer males in Adamello from 8 years onwards, relative to Presanella and Brenta (Fig. 3.6). This suggests that the survival of older males is lower in Adamello than in the other sites. 6 y.o. males in Adamello live an average of 1.3 additional years compared to 1.7 and 2 more years in Presanella and Brenta, respectively.

Table 3.1 Model selection results from cubic spline model fitted to male chamois body mass data. Models are distinguished by the functional forms of α_0 and β_0. Specifically, I allowed α_0 and β_0 to be constant across years (α_0; β_0), vary linearly with year (α_0(y); β_0(y)), quadratically with year ($\alpha_0(y^2)$; $\beta_0(y^2)$) or linearly with population density (α_0(d); β_0(d)). Maximum log-likelihoods (LL) and ΔAICs are shown for each site. K is the number of parameters in a given model. The most parsimonious models for each site are highlighted in bold (i.e. have a ΔAIC value that is ≤6 and lower than all simpler nested versions (Richards 2008)). *n* is sample size for each site.

Model	**K**	**Adamello**		**Presanella**		**Brenta**	
		LL	**ΔAIC**	**LL**	**ΔAIC**	**LL**	**ΔAIC**
n		3539		1426		2237	
M(α_0,β_0)	13	-8625.5	82.6	-3629.6	106.2	-5501.1	53.0
M(α_0,β_0(y))	14	-8621.8	77.3	-3602.6	54.2	-5487.4	27.6
M(α_0,$\beta_0(y^2)$)	15	-8621.8	79.3	-3584.6	20.1	-5483.9	22.5
M(α_0,β_0(d))	14	-8624.7	83.0	-3602.8	54.4	-5493.9	40.6
M(α_0(y),β_0)	14	-8597.2	28.1	-3581.3	11.5	**-5474.5**	**1.8**
M(α_0(y),β_0(y))	15	**-8582.6**	**0.9**	-3581.3	13.6	-5474.5	3.8
M(α_0(y),$\beta_0(y^2)$)	16	**-8581.2**	**0.0**	-3576.9	6.7	-5474.1	5.0
M(α_0(y),β_0(d))	15	-8594.6	24.8	**-3574.6**	**0.0**	-5474.5	3.7
M($\alpha_0(y^2)$,β_0)	15	-8597.2	30.1	-3578.3	7.5	**-5472.6**	**0.0**
M($\alpha_0(y^2)$,β_0(y))	16	-8582.5	2.7	-3578.3	9.5	-5471.9	0.6
M($\alpha_0(y^2)$,$\beta_0(y^2)$)	17	-8580.7	1.1	-3578.2	11.4	-5471.6	2.0
M($\alpha_0(y^2)$,β_0(d))	16	-8593.8	25.2	-3573.9	0.7	-5471.6	0.0
M(α_0(d),β_0)	14	-8606.9	47.4	-3586.8	22.6	-5483.3	19.4
M(α_0(d),β_0(y))	15	-8606.9	49.4	-3578.0	6.9	-5479.0	12.8
M(α_0(d),$\beta_0(y^2)$)	16	-8601.4	40.4	-3576.7	6.2	-5479.0	14.8
M(α_0(d),β_0(d))	15	-8590.4	16.4	-3585.8	22.5	-5483.0	20.7

Table 3.2 Model selection results from cubic spline model fitted to female chamois body mass data. Models are distinguished by the functional forms of α_0 and β_0. Specifically, I allowed α_0 and β_0 to be constant across years (α_0; β_0), vary linearly with year ($\alpha_0(y)$; $\beta_0(y)$), quadratically with year ($\alpha_0(y^2)$; $\beta_0(y^2)$) or linearly with population density ($\alpha_0(d)$; $\beta_0(d)$). Maximum log-likelihoods (LL) and ΔAICs are shown for each site. K is the number of parameters in a given model. The most parsimonious models for each site are highlighted in bold (i.e. have a ΔAIC value that is ≤6 and lower than all simpler nested versions (Richards 2008)). *n* is sample size for each site.

Model	**K**	**Adamello**		**Presanella**		**Brenta**	
		LL	**ΔAIC**	**LL**	**ΔAIC**	**LL**	**ΔAIC**
n		2990		1329		2096	
$M(\alpha_0,\beta_0)$	13	-7092.9	78.4	-3187.6	95.7	-5002.0	25.2
$M(\alpha_0,\beta_0(y))$	14	-7076.4	47.4	-3155.7	34.0	-4997.1	17.5
$M(\alpha_0,\beta_0(y^2))$	15	-7062.0	20.6	-3147.8	20.1	-5000.5	26.2
$M(\alpha_0,\beta_0(d))$	14	-7083.5	61.5	-3174.9	72.3	-5002.5	28.4
$M(\alpha_0(y),\beta_0)$	14	-7073.3	41.1	-3142.8	8.1	-4995.1	13.5
$M(\alpha_0(y),\beta_0(y))$	15	-7063.6	23.8	**-3138.5**	**1.7**	-4995.3	16.0
$M(\alpha_0(y),\beta_0(y^2))$	16	-7063.5	25.6	**-3138.4**	**3.5**	-4992.1	11.4
$M(\alpha_0(y),\beta_0(d))$	15	-7066.2	29.0	-3140.8	6.3	-4995.1	15.4
$M(\alpha_0(y^2),\beta_0)$	15	-7073.6	43.8	-3142.7	9.9	**-4989.0**	**3.2**
$M(\alpha_0(y^2),\beta_0(y))$	16	-7061.2	21.0	**-3136.7**	**0.0**	-4988.9	5.1
$M(\alpha_0(y^2),\beta_0(y^2))$	17	-7060.5	21.6	-3136.4	1.4	-4989.5	8.3
$M(\alpha_0(y^2),\beta_0(d))$	16	-7071.3	41.3	-3139.9	6.4	**-4986.4**	**0.0**
$M(\alpha_0(d),\beta_0)$	14	-7068.0	30.7	-3168.8	60.2	-4999.4	22.1
$M(\alpha_0(d),\beta_0(y))$	15	-7066.7	30.1	-3151.2	27.0	-4998.1	21.4
$M(\alpha_0(d),\beta_0(y^2))$	16	**-7050.7**	**0.0**	-3147.5	21.7	-4997.6	22.4
$M(\alpha_0(d),\beta_0(d))$	15	-7060.5	17.5	-3167.4	59.4	-4998.4	22.0

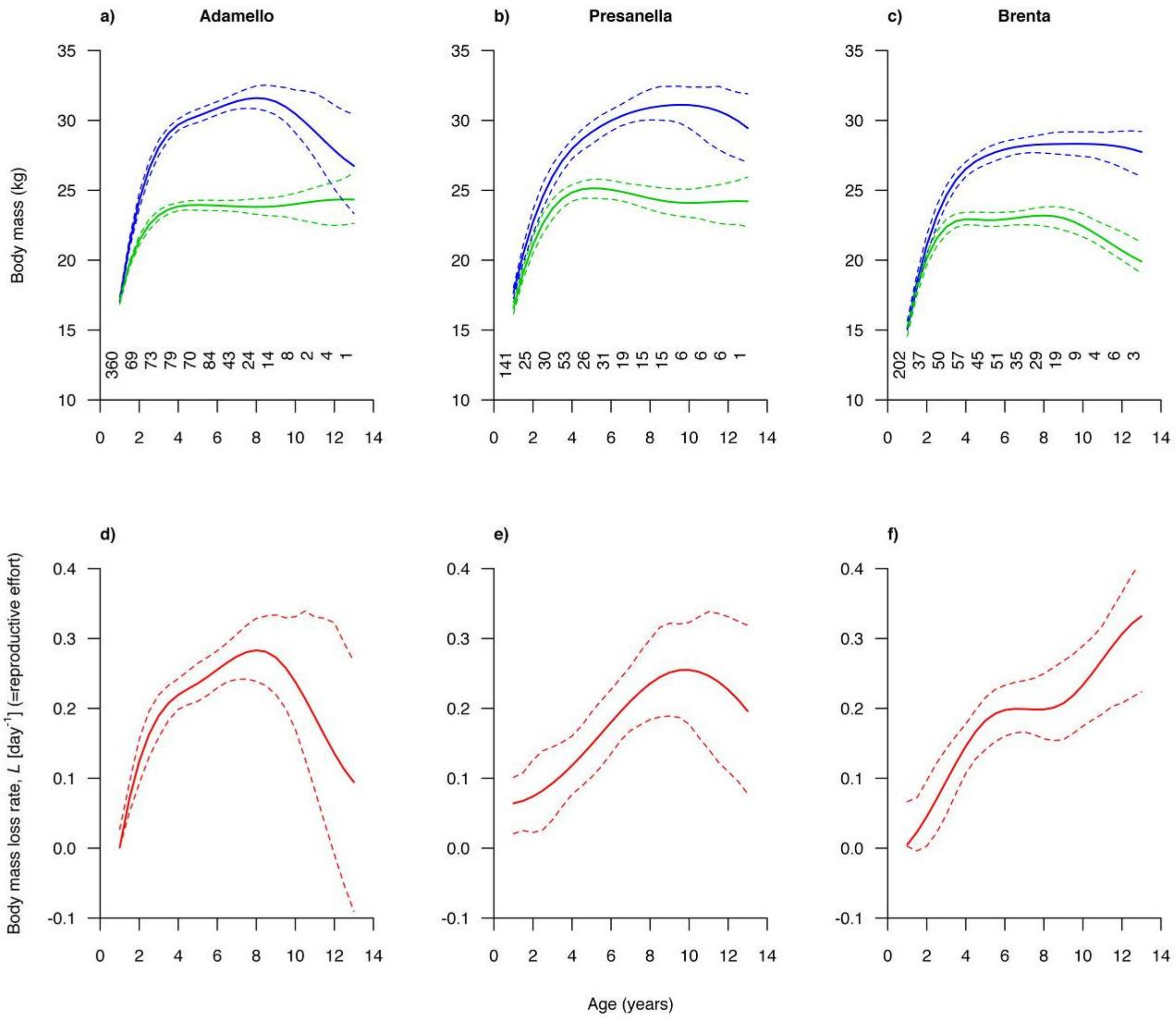

Figure 3.4 Patterns of male mass and mass loss with age. Variation in mean predicted male chamois initial body mass (blue lines), final body mass (green lines) and body mass loss rate, *L* (red lines), with age across the three study sites; Adamello (**a** & **d**), Brenta (**b** & **e**) and Presanella (**c** & **f**). Predicted values for each age are mean values across all years. Dashed lines represent 95% confidence intervals from 1,000 bootstrapped replicates (Efron and Tibshirani 1991). Sample sizes are displayed for each age.

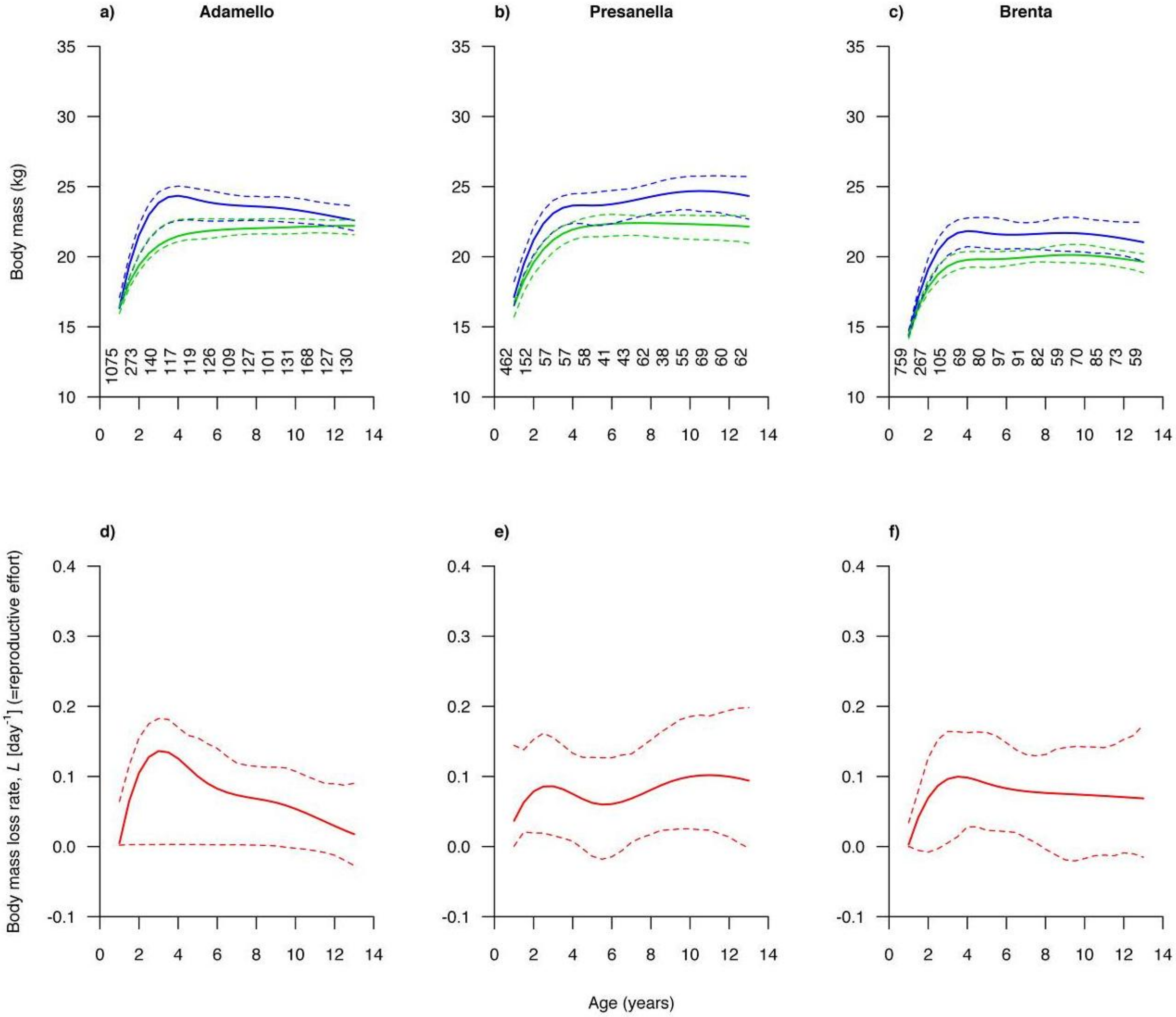

Figure 3.5 Patterns of female mass and mass loss with age. Variation in mean predicted female chamois initial body mass (blue lines), final body mass (green lines) and body mass loss rate, *L* (red lines), across the three study sites; Adamello (**a** & **d**), Brenta (**b** & **e**) and Presanella (**c** & **f**). Predicted values for each age are mean values across all years. Dashed lines represent 95% confidence intervals from 1,000 bootstrapped replicates (Efron and Tibshirani 1991). Sample sizes are displayed for each age.

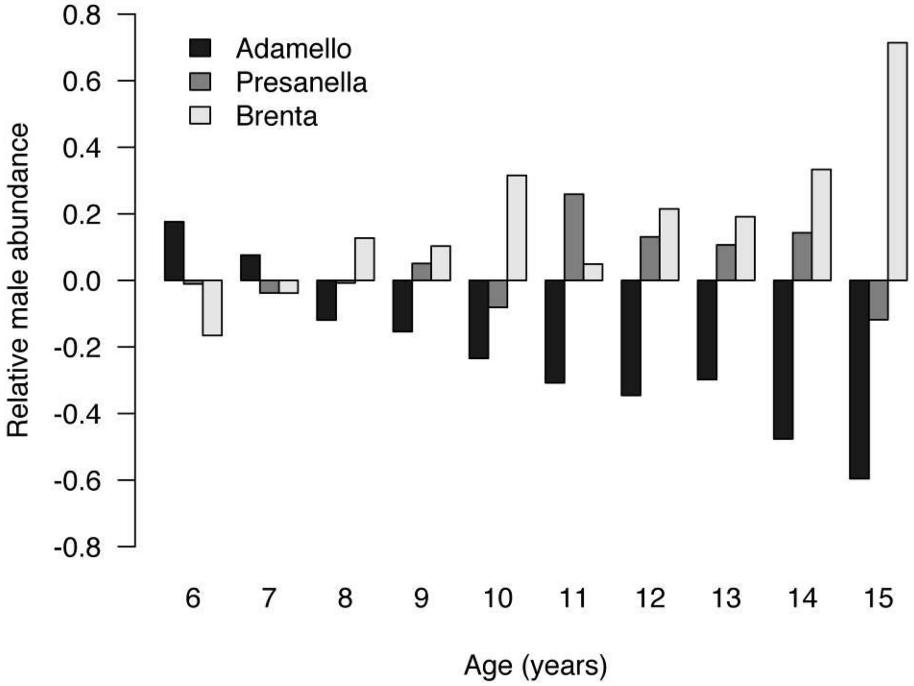

Figure 3.6 Age-structure of males. The abundance of males in each site at each age, from 6 years upwards (hunting age-class I, see Table 2.1), relative to the area-wide age-distribution. Assuming that individuals within each hunting age-class are shot randomly, the proportions of different ages shot represent the age-structure of that class. A value of 0 indicates no difference to the mean population age-structure.

3.5 Discussion

Male chamois suffer a substantial somatic cost during the rut, with breeding males losing as much as 28% of their body mass (Fig. 3.4). Unsurprisingly, female relative mass loss during this same period is considerably lower and less affected by age (Fig. 3.5), underlining that male mass loss is a consequence of RE. How males allocate resources to reproduction across their lives varies considerably among sites (Fig. 3.4 d-f). Within two of the sites there are declines in RE after prime-age, whereas males in the other site appear to show terminal investment. Several aspects of male life-history, including rates of decline in initial mass at old age and the consistency of final mass with age, differ substantially across the study area, strongly influencing the patterns of RE. Such variation between neighbouring populations is surprising.

In Adamello and Presanella, RE peaks at prime-age before decreasing in old individuals (Fig. 3.4 d & e). The downturn in RE at old age is particularly pronounced in Adamello. Studies of other male ungulates have found similar results (Maher and Byers 1987, Mainguy and Cote 2008, Yoccoz et al. 2002), as have studies on males from other taxa (Billing et al. 2007). This pattern is consistent with the predictions of reproductive restraint but could also arise simply as a by-product of body mass senescence. That the initial mass of males strongly decreases after prime-age, particularly in Adamello (Fig. 3.4 a & b), indicates such senescence (decline in fitness due to physiological degradation (Jones et al. 2008)). This is likely to hinder the ability of old males to defend oestrus females as large body size is important for male-male competition in polygynous ungulates (e.g. Coltman et al. 2002, McElligott et al. 2001). As such, one might expect that old chamois adopt alternative mating strategies, as seen in red deer (Clutton-Brock et al. 1985). The pattern of final mass with age also influences the pattern of male reproductive allocation in these sites. Final mass is largely unaffected by age among adult males in Adamello and Presanella (Fig. 3.4 a & b), hinting at a ‘giving-up mass’ which could be important for over-winter survival (Berube et al. 1999, Loison, Langvatn, et al. 1999). This would further constrain the ability of males to invest resources in reproduction, consistent with the reproductive restraint hypothesis. It is, however, difficult to disentangle senescence-driven declines in RE and reproductive restraint. After all, high senescence rates in later life could be the consequence of a life-history designed to maximise RE early in life. Whether an inability to compete in later life (owing to body mass senescence) is consistent with reproductive restraint is currently unclear.

In Brenta, RE appears to increase throughout life, a result consistent with terminal investment (Fig. 3.4 f). There is evidence for terminal investment from a range of taxa (Creighton et al. 2009, Ericsson and Wallin 2001, Isaac and Johnson 2005) but this study provides some of the first evidence in males (see also (Velando et al. 2006)). The ability of old male chamois to continue to increase their RE can be partly explained by their ability to hold on to breeding territories. Data from other chamois populations suggests that males show high levels of site-fidelity year by year and profit from a ‘prior residence advantage’ in territory ownership (von Hardenberg et al. 2000). As such, experienced males that have defended a given territory in the previous year’s rut are more likely to defend it successfully in the present rut, provided they are in good condition (von Hardenberg et al. 2000). This means that male chamois at least have the potential to increase RE throughout their lives, in contrast to species such as red deer where males past their prime cannot hold harems (Clutton-Brock et al. 1985). Unlike in the other sites, initial mass declines little after prime-age in Brenta (Fig. 3.4 c). This means that old males in Brenta are better at acquiring resources in between rutting seasons and are likely be more competitive as a result. Perhaps unsurprisingly, terminal investment may only be optimal where old individuals are able to compete effectively with their younger rivals. Also, in contrast to the other sites, there is no consistent final mass across adult males in Brenta (Fig. 3.4 c); old males end the rut in worse condition than young males do, presumably putting themselves at a greater risk of over-winter mortality due to a reduction in fat reserves. High RE and reduced body condition could also result in immunosuppression and a high parasite burden, as has been recently shown in this species (Corlatti et al. 2012). In line with terminal investment, the benefits of high RE would outweigh such costs (Clutton-Brock 1984, Pianka and Parker 1975, Williams 1966a, b).

My results have shown that several key life-history characteristics vary between sites, and are important in influencing how RE is allocated with age. The variation among the age-related patterns of initial mass among sites appears particularly important. The low initial masses of older males in Adamello and Presanella might limit their ability to invest highly in RE, even if classical life-history theory suggests that they should. This, twinned with an apparent cut-off mass, appears to drive a downturn in RE at old age in these sites. Survival also appears to vary among sites. Adult male survival is considerably lower in Adamello (Fig. 3.6); 6 y.o. males live an average of 1.3 additional years compared to 1.7 and 2 more years in Presanella and Brenta, respectively. This, and the pronounced body mass senescence, could be linked to the apparent faster pace of life there (Fig. 3.4 d-f). RE increases much more rapidly with age in Adamello, suggesting that males start becoming involved in the rut at a younger age (mean 3 y.o. proportional mass loss: Adamello, 17.3%; Presanella, 8.9%; Brenta, 9.2%). There may be positive feedback between shorter life-spans and a faster pace of life, which in turn results in higher rates of body mass senescence in Adamello. Senescence rates are thought to be higher in faster living species, due to a faster accumulation of damage (Jones et al. 2008); the same might be true for faster living populations within a given species. In Brenta, where the pace of life is slower and life-spans are longer, body mass senescence is limited. It appears that only in such conditions can old males make use of their experience and continue to increase RE throughout their lives. The lower survival and faster pace of life in Adamello could be related to the higher hunting pressure there (mean proportion of adult males harvested per year (from census years): Adamello, 32.3 ± 1.5%; Presanella, 29.5 ± 2%; Brenta, 25.2 ± 1.6%). Hunting has been known to influence a range of life-history traits, including survival, mating behaviour and body mass (Coltman et al. 2003, Singer and Zeigenfuss 2002). Where hunting pressure is higher, and risk of mortality is greater, it could pay to allocate more energy to reproduction earlier in life.

The observed variation among sites could also be mediated by environmental differences. Life-histories, and specifically reproductive allocation, can be plastic with respect to the environment (Bardsen et al. 2011). Brenta is a calcareous area, whilst the other sites are siliceous, harbouring very different plant communities (Gensac 1990). In calcareous areas, plants are generally more nitrogen-rich (Gensac 1990), which could further explain the lower rates of body mass senescence in Brenta. It may be easier for older males there to acquire resources in between rutting seasons than in the siliceous sites, putting them in good stead for the rut. Differences in the patterns of final mass with age could be related to altitudinal variation among sites (mean medium elevation of shot males: Adamello, 1,979m; Brenta, 1,675m; Presanella, 2,182m). Due to the considerably higher altitudes of Adamello and Presanella, their winter climates are likely to be harsher and there may be a greater risk of over-winter mortality. As such, a cut-off mass to buffer against over-winter mortality would be more important in these sites than in Brenta, thus limiting their ability to expend energy during the rut. A harsher winter climate could also explain why pre-rut breeding males weigh on average 2.7 ± 0.16kg and 2.12 ± 0.07kg more in these sites than in Brenta (Figs. 3.4 a-c).

This study shows that comprehensive transversal datasets can still be of great value to ecology. Whilst longitudinal field studies have the obvious advantage of being focused on within-individual processes (Nussey et al. 2008), such data are difficult to collect, frequently unavailable and, typically, limited by a focus on relatively small numbers of known individuals (e.g. Cameron et al. 2000, Willisch and Ingold 2007). In comparison, transversal datasets can contain information on tens of thousands of individuals; although they cannot account for individual heterogeneity, they can outline broad life-history patterns at the population level. Previous studies have tended either to accept or to reject evidence of terminal investment (e.g. (Yoccoz et al. 2002)); here, by contrast, I demonstrate for the first time that patterns of reproductive allocation can vary readily across different, and even adjacent, populations.

Chapter 4

Intra-seasonal reproductive timing in male chamois*

*Now published as:

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4.1 Abstract

Age-dependent reproductive timing has been observed in females of a number of species; older females often breed earlier in the season and experience higher reproductive success as a result. However, to date, evidence for within-season variation in reproductive effort (RE) for males has been relatively weak. Males are expected to time RE in light of intra-seasonal variations in the availability of receptive females and competition with other males. Young males, which are typically smaller and less experienced, might benefit from breeding later in the season when male-male competition is less intense. Using a long-term data set of Alpine chamois, I seek support for the hypothesis that younger males allocate highest RE late in the breeding season, at a time when older male RE has decreased substantially. My results support this hypothesis, suggesting that intra-seasonal variation in RE may be an adaptive life-history trait for males as well as females.

4.2 Introduction

In a number of vertebrates, but particularly birds, old individuals breed earlier in the season than younger ones (Forslund and Part 1995, Perdeck and Cave 1992). Earlier breeding often increases reproductive success (Sydeman et al. 1991, Verhulst and Tinbergen 1991) because earlier-born offspring can profit from greater resource availability (van Noordwijk et al. 1995) and longer growing seasons (Cote and Festa-Bianchet 2001, Feder et al. 2008). Furthermore, they may have a competitive advantage over later-born rivals (Nilsson 1989). Reproductive timing can also affect adults directly, as late breeders can suffer from tighter time or energetic constraints after breeding (Nilsson and Svensson 1996). Age-dependent patterns of reproductive timing are generally attributed to increasing breeding competence with age, as individuals become larger and more experienced (e.g., Forslund and Part 1995). Young breeders may also be limited energetically due to their smaller size; breeding later in the season allows time for them to acquire sufficient energy reserves (Cargnelli and Neff 2006, Schultz et al. 1991).

To date, the vast majority of studies have focused on reproductive timing in females; however, life-history trade-offs are also expected to drive age-dependent patterns in male reproductive phenology (e.g., Mysterud et al. 2008). Despite the advantages of early breeding, younger, smaller or less experienced males might benefit from delaying breeding until later in the season. During the peak breeding season, when female receptivity is at its highest, male-male competition can be intense and breeding can be monopolised by a small number of dominant males (Clutton-Brock et al. 1985). Young males are known to increase their reproductive effort (RE; allocation of resources to current reproduction) in years when older males are scarcer (Singer and Zeigenfuss 2002). This might also hold true within a season, if older males exhaust their energy stores and cease to compete effectively before the end of the period of female receptivity. However, whilst male-male competition is known to influence male RE in a range of taxa (e.g., Galimberti et al. 2007, Neff et al. 2004), there is currently little evidence for its influence on the timing of male RE across the breeding season. Indeed, in some species there is no support for an effect of experience on reproductive timing (Ridgway et al. 1991). Intriguingly though, there is some support from a male mammal: in populations of red deer (*Cervus elaphus*) at low density, prime-aged male peak RE coincides with peak female receptivity, whereas young male RE peaks slightly later in the season (Mysterud et al. 2008). Whether this male life-history strategy occurs more widely among mammals is unknown.

Male chamois allocate RE annually to a short rutting season each autumn, during which they defend small, clustered territories, guarding estrus females from rivals (Kramer 1969, von

Hardenberg et al. 2000). Intriguingly, field observations of breeding chamois during the 2011 rut in the study area in the Central-Eastern Italian Alps suggest that peak breeding activity of younger males occurs near the end of the rut, much later than that of older males, supporting an age-dependent pattern of reproductive timing in this species (Fig. 4.1). However, due to the small sample size of observations, which were limited to a single year, it is unclear if this pattern of activity occurs consistently across years for this population.

Male chamois are capital breeders (Stephens et al. 2009), significantly reducing their food intake during their breeding season, and depending on stored energy to breed (Willisch and Ingold 2007). In capital breeders, RE is strongly related to the size of an individual’s energy store (Doughty and Shine 1997) and body mass loss rates can be used as estimates of RE (Mysterud et al. 2005, Yoccoz et al. 2002). In alpine chamois, breeding males experience pronounced mass loss during the rut, whereas the mass loss rates of non-breeding males and females during the same period are much lower (chapter 3; Mason et al. 2011), supporting the use of mass loss rate as an index of RE in this species. Based on this established link between RE and rate of mass loss, I assess support for the prediction that young male chamois in the system increase their RE later in the rut when larger, older males begin to reduce their RE. I do this by taking advantage of the long-term data set of hunting records taken during the rutting season and by estimating patterns of mass change across age-classes for three neighboring populations.

4.3 Materials and Methods

4.3.1 Mating data

Data were collected on the frequency of mating events during the rutting season of autumn 2011. Data collection started on the 29th October (day 302) and ended on the 13th December (day 347). Two survey sites were chosen within the study area, both consisting of a high proportion of open habitat and known to be used by rutting chamois. The survey sites were visited every few days during the season and visual scans of all individuals in the area were carried out at regular intervals during the day using spotting scopes and binoculars. All observed mating events were recorded and the ages of the males involved were classified as 3-5 years or 6+ years based on their body size and horn length (Knaus and Schröder 1983). Observer effort was constant throughout each day of data collection. Due to small sample sizes, data were aggregated across both sites (Fig. 4.1).

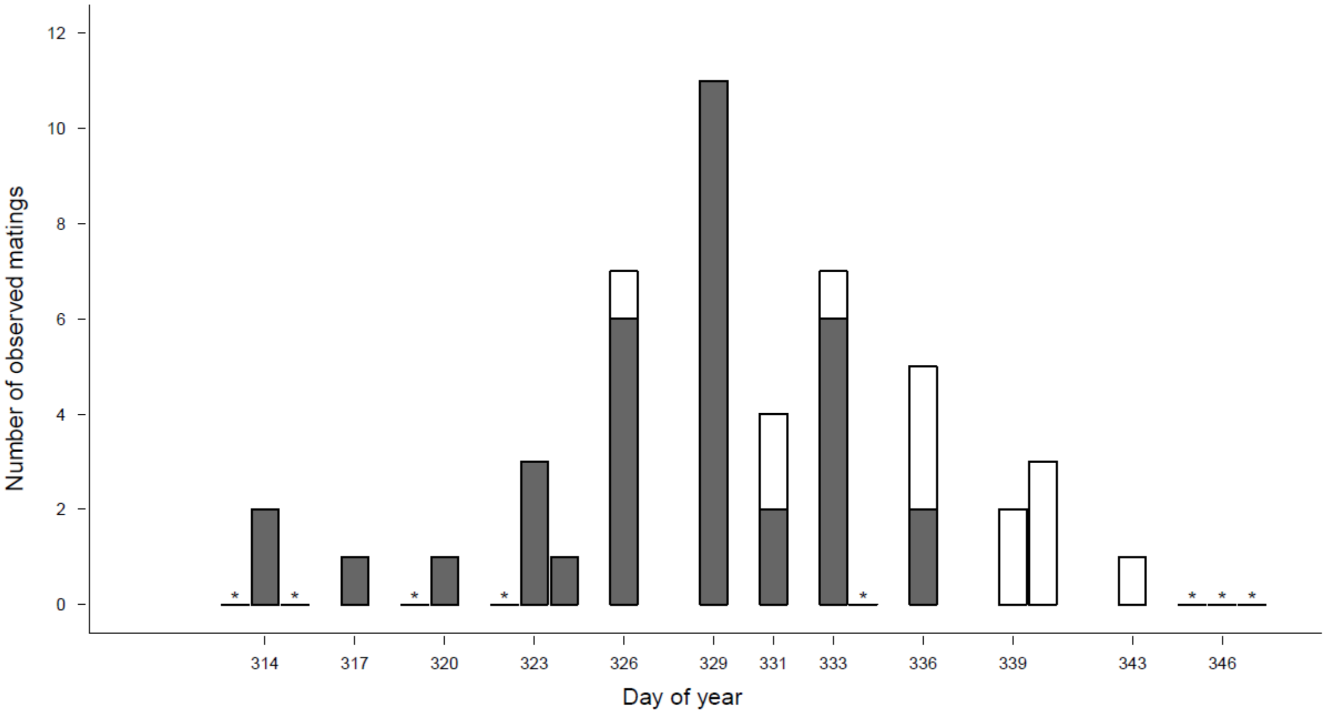

Figure 4.1 Variation in the frequency of observed mating events involving young (3-5 years; white bars) and old (6+ years; grey bars) males over time, during the rut. Asterisks indicate days on which surveys were carried out but no mating events were observed.

4.3.2 Body mass data

Body mass data were analysed from the three hunting districts in the study area. Data on shooting were converted to the Julian calendar and ranged from day 252 to 351 (9th September-17th December). This time period encompasses a pre-rut period as well as the entire rut (Forslund and Part 1995). Despite the strict criteria above, the sample size was still large (12,893 individuals).

4.3.3 Statistical analysis

Model of within-season body mass dynamics

I sought to characterise age-dependent, temporal patterns of male mass change across the rutting season. Let $\overline{m}_a(s,y,t)$ be the mean mass of an individual of age *a* in site (i.e., hunting district) *s* on day *t* of year *y*. Change in mass throughout the season is governed by,

$$\frac{d\overline{m}_a}{dt} = C_a(s,y,t)\overline{m}_a,$$

where C_a is the relative rate of mass change of individuals of age *a*. If the mean mass on day 252 (the earliest shot date recorded) is $\overline{m}_{a,y,252}$, then the solution to this equation is

$$\overline{m}_a(s,y,t) = \overline{m}_{a,s,y,252}\exp\left(\int_{\tau=252}^{t} C_a(s,y,\tau)d\tau\right).$$

Here, it was assumed that C_a, can be partitioned into a baseline rate, denoted $F_a(s,t)$, and a year-dependent offset, denoted $w_{a,s,y}$, which reflects annual variation due to environmental changes or factors such as population density (Mysterud et al. 2008, Yoccoz et al. 2002). Also, it was assumed that mean mass on day 252 can vary across years for age *a* in site *s* by factor $z_{a,s,y}$. Thus, the expected mass is

$$\begin{aligned}\overline{m}_a(s,y,t) &= z_{a,s,y}\overline{m}_{a,s,252}\exp\left(\int_{\tau=252}^{t} F_a(s,\tau) + w_{a,s,y}d\tau\right)\\ &= z_{a,s,y}\overline{m}_{a,s,252}\exp(w_{a,s,y}t)\exp\left(\int_{\tau=252}^{t} F_a(s,\tau)d\tau\right),\end{aligned}$$

where $\overline{m}_{a,s,252}$ is the average mass of individuals of age a at site s on day 252 across the study period. As there was no *a priori* prediction regarding the functional form of F_a with respect to day (*t*), five possibilities were considered: constant, linear, quadratic, cubic and double cubic spline, each spanning day 252 to 351 (for equations of the functions used to describe *F*, see Appendix A1).

Model fitting and model selection

Despite having access to a large data set of male masses, sample sizes were much reduced when data were subdivided among ages, sites and years. Such low sample sizes can result in high uncertainty in parameter estimates. Thus, I made use of my previous analysis (chapter 3; Mason et al. 2011), which indicated relatively low variation in patterns of mass change among adjacent ages. Age data were combined into four age-classes: 1-2 year olds (non-breeders), 3-4 year olds (young breeders), 5-6 year olds (early prime-age) and 7-13 year olds (late prime-age). Age-dependent parameters were estimated separately for each of these age-classes, which are distinguished using the subscript A.

It was assumed that the variation in the mass data for age *a* individuals at site *s* about the modelled mean is normally-distributed with variance $\sigma_{a,s.}$ Thus, the log-likelihood of the model parameters associated with age-class A at site s, denoted $\boldsymbol{\theta}_{A,s}$, given all the data, is

$$LL(\boldsymbol{\theta}_{A,s}) = \sum_{a \in A}\sum_{y}\sum_{j}\left(-\frac{1}{2}\ln(2\pi) - \ln(\sigma_a) + \frac{1}{2}\left(\frac{\overline{m}_A(s,y,t_{a,s,y,j}) - m_{a,s,y,j}}{\sigma_{a,s}} \right)^2 \right),$$

where $m_{a,s,y,j}$ and $t_{a,s,y,j}$ are the mass and the day of the *j*th aged *a* individual sampled in year *y* at site *s*, respectively. For each age-class at a site the five functional forms for *F* proposed above were fitted using maximum likelihood, and were identified the most parsimonious fit using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002, Richards 2008). Uncertainty in body mass predictions was assessed by fitting 1000 bootstrapped replicates stratified by year, site and age (Efron and Tibshirani 1991). Random sampling, stratified within season across four time periods (determined by the quartiles of available data with respect to time), was used to produce replicates with a representative spread of data. Statistical analyses were performed using R version 2.13.0 (R Development Core Team 2011).

4.4 Results

Model selection indicates that the relative rate of change in male mass during the rutting season varies both with time and age; in no age-class is the constant growth model the most parsimonious (Fig. 4.2, Table 4.1). Importantly, the model formulation is clearly able to describe the observed variation in body mass during the breeding season for all age-classes (Fig. 4.3).

In each age-class, there is a highly consistent temporal pattern of mass change among the three sites. In 1-2 year olds, the rate of mass change remains close to zero throughout the season (Fig. 4.2 a, e & i). In 3-4 year olds, this rate is near zero at the start of the season before becoming increasingly negative throughout the rest of the season (Fig. 4.2 b, f & j). Such extended periods of mass loss are suggestive of RE. Importantly, in all sites, 3-4 year old mass loss rates continue to increase beyond the date on which the majority of rutting activity is generally thought to conclude (approximately day 340; Forslund and Part 1995). In contrast, in both older age-classes, the rate of mass loss peaks at about day 325, after which the rate of mass loss decreases. Interestingly, there is even a short period of mass gain at the end of the year for the older individuals (Fig 4.2 c-d, g-h & k-l). These findings suggest a relatively well-defined rutting period in older males, which is followed by a period of mass recovery. The confidence intervals suggest that, whilst uncertainty increases towards the temporal limits of the data, the observed patterns are robust.

Table 4.1 Model selection results. Models varied in the functional form used to described the relative rate of mass change (constant, linear, quadratic, cubic or double cubic spline). Maximum log-likelihoods and ΔAICs are shown for each age-class and site. The most parsimonious models for each age-class and site are highlighted in bold (these are models with a ΔAIC that is ≤6 and lower than all simpler nested versions; see Richards 2008).

			Adamello		**Presanella**		**Brenta**	
Age-class	**Model**	**K**	**LL**	**ΔAIC**	**LL**	**ΔAIC**	**LL**	**ΔAIC**
1-2	Constant	37	-7650.1	23.6	**-2886.2**	**1.6**	-4327.6	6.2
1-2	Linear	38	-7643.8	13.0	**-2884.4**	**0.0**	-4326.7	6.4
1-2	Quadratic	39	**-7636.3**	**0.0**	-2883.7	0.7	**-4322.9**	**0.8**
1-2	Cubic	40	-7636.2	1.9	-2883.5	2.3	**-4321.5**	**0.0**
1-2	Spline	41	-7636.1	3.7	-2883.3	3.9	-4321.4	1.9
3-4	Constant	37	-3260.0	152.0	-1167.9	11.2	-1687.9	26.1
3-4	Linear	38	-3214.5	63.0	**-1162.2**	**1.9**	**-1673.9**	**0.0**
3-4	Quadratic	39	-3185.7	7.3	**-1160.3**	**0.0**	-1673.6	1.3
3-4	Cubic	40	**-3181.0**	**0.0**	-1160.3	1.9	-1673.5	3.2
3-4	Spline	41	-3180.9	1.7	-1160.2	3.9	-1673.3	4.7
5-6	Constant	37	-2787.0	122.7	-1014.6	31.5	-1583.1	65.2
5-6	Linear	38	-2742.4	35.5	-1003.2	10.7	-1563.6	28.2
5-6	Quadratic	39	-2734.9	22.5	-1000.0	6.4	-1556.4	15.9
5-6	Cubic	40	**-2722.7**	**0.0**	**-996.2**	**0.7**	**-1547.5**	**0.0**
5-6	Spline	41	-2721.9	0.5	**-994.8**	**0.0**	-1547.4	1.9
7-13	Constant	37	-2072.9	82.8	-1031.2	36.5	-1808.3	77.4
7-13	Linear	38	-2042.6	24.1	-1019.1	14.3	-1784.8	32.4
7-13	Quadratic	39	-2040.3	21.6	-1015.3	8.8	-1776.7	18.1
7-13	Cubic	40	-2032.9	8.7	**-1011.4**	**3.0**	**-1766.6**	**0.0**
7-13	Spline	41	**-2027.5**	**0.0**	**-1008.9**	**0.0**	-1765.9	0.6

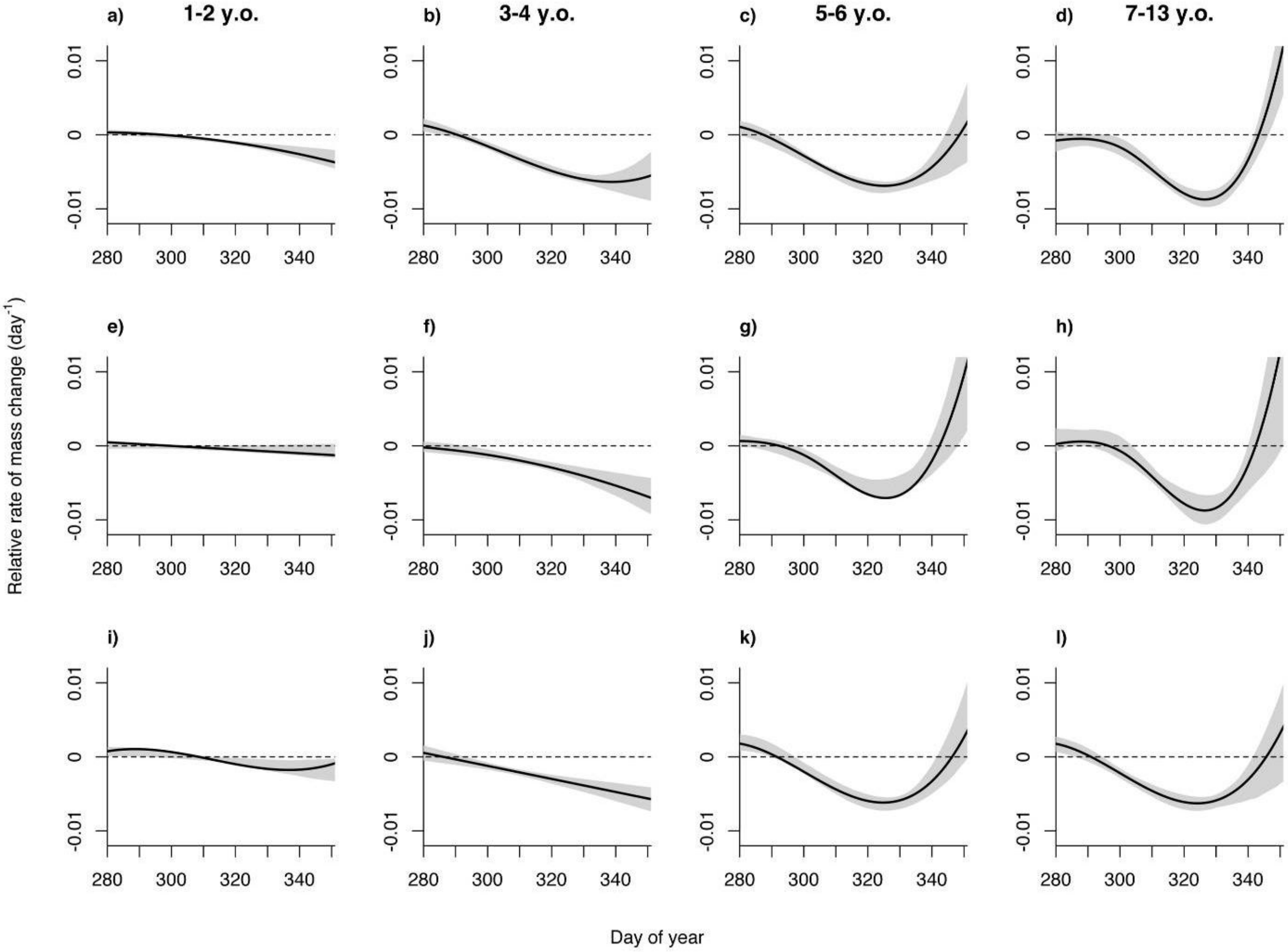

Figure 4.2 Variation in estimated relative rate of mass change during the rut for four male age-classes in the three study sites: Adamello (**a**-**d**), Presanella (**e**-**h**) and Brenta (**i**-**l**). Solid curves show the mean rate of mass change estimated for an average year using the best AIC model for each age-class in each site. Shaded grey areas show 95% confidence intervals for the mean. Horizontal dashed lines show hypothetical zero growth.

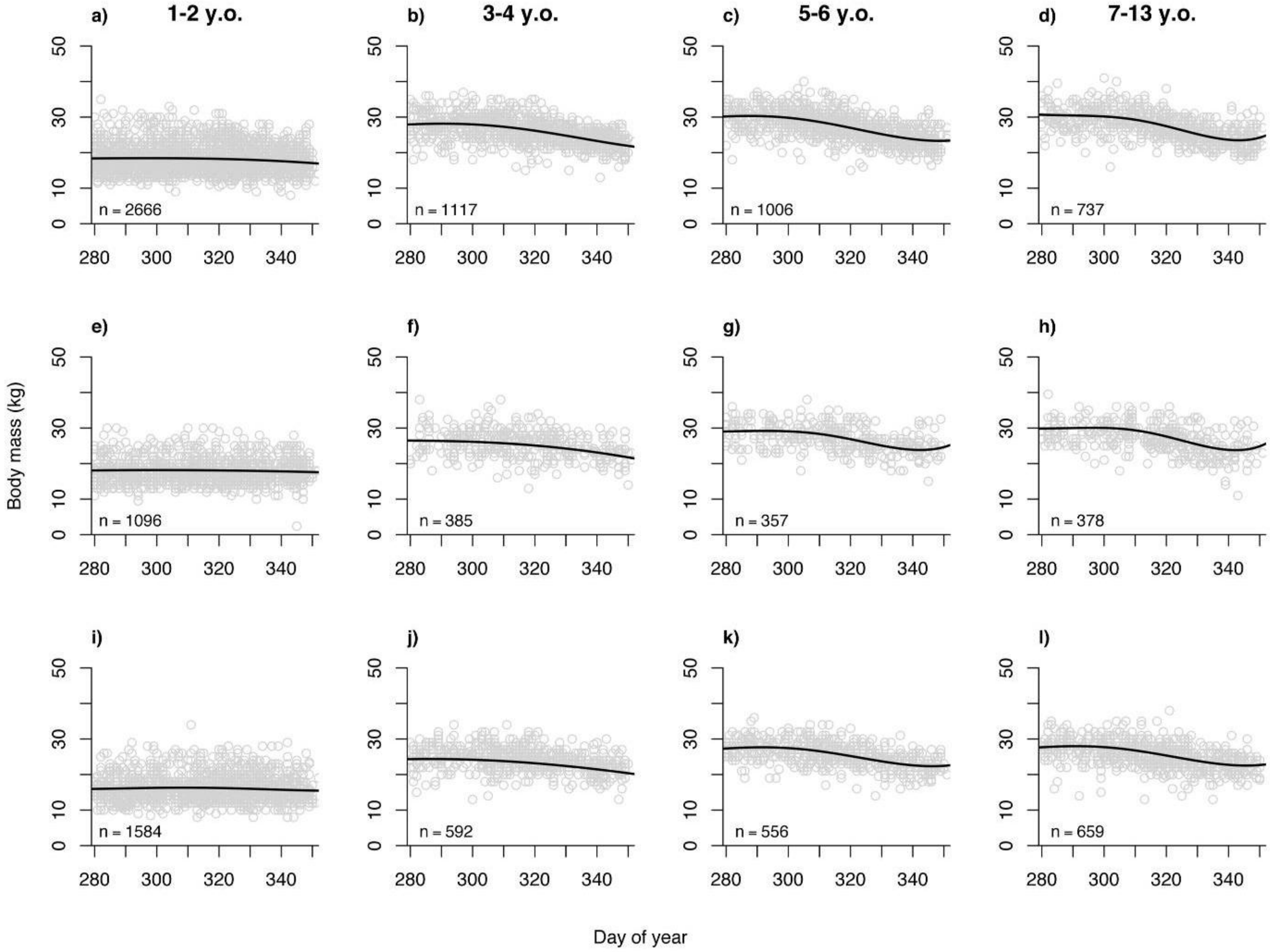

Figure 4.3 Variation in body mass with time during the rut for four male age-classes in the three study sites: Adamello (**a**-**d**), Presanella (**e**-**h**) and Brenta (**i**-**l**). Solid curves are the mean predicted mass in an average year, weighted by sample size of each age, estimated by the best AIC model for each age-class in each site. Points are the raw mass data. Sample sizes are also shown.

4.5 Discussion

Here, I sought support for the hypothesis that, relative to older males, younger males should allocate RE later in the breeding season when male-male competition may be less intense. For chamois, the data indicate that the timing of mass loss during the breeding season, which is a reliable measure of RE, varies strikingly between young and old breeding males (Fig. 4.2). Males of 3-4 years suffer their highest mass loss rates 13-27 days later in the season than older males, at a time when the loss rates of older males are significantly reduced (Fig. 4.2). As such, the results suggest that young chamois males allocate peak RE late in the season, when older males are significantly reducing their RE, providing considerable support for my hypothesis. Interestingly, this intra-seasonal pattern is highly consistent across the three districts investigated, despite considerable variation in how males in these populations allocate RE across their lives (Forslund and Part 1995).

These results concur with field observations from the study area. Specifically, the frequency of mating events involving young males increases towards the end of the rutting season (Fig. 4.1), in keeping with estimates of young male RE (Fig. 4.2 b, f & j). In contrast, peak mating activity in older males occurs much earlier, consistent with estimates of peak RE for older males (Fig. 4.2 c-d, g-h & k-l). This agreement strongly suggests that the observed high rates of young male mass loss late in the season are indeed a result of RE, rather than, for instance, an inability to halt mass loss following the rut. Reduced competition from older males late in the season could drive an adaptive life-history strategy, in which young males could be rewarded with late mating opportunities. Males of 3-4 years old are 7-10% lighter than older age-classes and are generally less experienced (males are sexually mature at 3-4 years; Couturier 1938, Knaus and Schröder 1983). Also, chamois males are more likely to defend a breeding territory successfully if they occupied it in the previous year (von Hardenberg et al. 2000). As such, young males may struggle to compete for territory ownership and could benefit from delaying peak RE until later in the season when male-male competition is reduced. Importantly, these findings strongly support those of Mysterud et al. (2008), who theorised that exhaustion of prime-aged males was driving a similar reproductive strategy in young red deer. There is some evidence that late breeding by subordinate males can be profitable in ungulates: in Soay sheep (*Ovis aries*) for example, whilst there is no data on the intra-seasonal timing of RE, the siring rate of smaller males increases towards the end of the season, in part due to sperm depletion in dominant males (Preston et al. 2001).

In this study, males of 5-6 and 7-13 years appear significantly to reduce their RE late in the season, eventually pulling out of the rut, as shown by mass gains (Fig. 4.2 c-d, g-h & k-l), at a time when few oestrus females are thought still to be present in the study area. It is likely that this withdrawal is necessary due to exhaustion following a long period of reduced food intake (Willisch and Ingold 2007). Indeed, there is evidence that males in these populations cease rutting once their mass drops below a particular threshold (Forslund and Part 1995). 7-13 year olds appear to stop rutting slightly earlier and gain more mass post-rut than 5-6 year olds. By quitting earlier, the oldest and most experienced individuals have more time to prepare for the coldest months. Body mass is positively correlated with over-winter survival in ungulates due to thermoregulatory costs (Berube et al. 1999, Loison, Langvatn, et al. 1999) and, as such, being in poor condition following the rut may put individuals at a greater risk of mortality. Males of 3-4 years continue to lose mass at a high rate at the end of the year (Fig. 4.2 b, f & j), apparently trading off any heightened mortality risk against the benefit of reproduction late in the season.

I have identified strong age-dependent patterns in the timing of mass loss across the breeding season for chamois and it is likely that this reflects variation in how different age-classes allocate RE over time. This suggests that age-dependent variation in reproductive timing can exist in males as well as in females. In chamois, this variation appears to be a result of an adaptive life-history strategy in young males, which favor delaying peak RE until older males have significantly reduced their RE, despite there being fewer receptive females present at this time. These findings highlight an important life-history strategy in subordinate individuals, adding substantial support to a similar result in another ungulate (Mysterud et al. 2008). I propose that late breeding by young males could be a general phenomenon in ungulates.

Chapter 5

Climate change and long-term trends in juvenile chamois body mass

5.1 Abstract

Widespread changes in body size, particularly declines, have been observed across a range of taxonomic groups in recent decades. Such declines could substantially impact on the functioning of ecosystems and could even lead to extinctions. There is strong evidence that climate change is responsible for these trends, with a number of different mechanisms having been proposed. There is a suggestion that, in line with Bergmann's rule, warming environments may select for smaller size as heat conservation requirements change. However, to date, most studies suggest that climate change has acted via changes in resource availability affecting the ability of individuals to acquire resources and grow. There is still debate over the importance of different drivers of change in body size, particularly the relative contributions of phenotypic plasticity and genetic change. Here, I investigate long-term body mass declines in juvenile Alpine chamois. Body masses of both sexes have consistently declined within three neighbouring populations. Making use of the long-term data set on body masses, I model the effects of temperature, population density and vegetation productivity on inter-annual mass variation. Despite changes in population density during the study period, warmer temperatures during the growing season appear to be the primary driver of mass declines. There is no evidence that the timing or productivity of resources have been altered during this period. The models suggest that juvenile mass is most strongly affected by temperatures experienced by their mothers prior to and during gestation and lactation, emphasising the importance of lagged effects on juvenile condition. I propose that warmer temperatures have affected the activity budgets of female chamois, limiting the amount of time they can spend foraging and acquiring resources for their offspring. Thus, my novel proposal is that climate change may not only drive body size change indirectly via effects on resource availability, but also by directly affecting the ability of individuals to acquire these resources.

5.2 Introduction

Climate and environmental change have impacted species in a variety of ways, from altering their spatial distributions (e.g. Hickling et al. 2006, Parmesan and Yohe 2003, Perry et al. 2005) to changing the timing of their annual events (e.g. Hoye et al. 2007, Menzel et al. 2006, Thackeray et al. 2010). Recently, focus has broadened to include the impacts of climate change on life-history traits and subsequently on population processes (Ozgul et al. 2010, Pelletier et al. 2007). Specifically, there is evidence that responses to climate change include widespread body size changes, particularly declines, which could have pronounced negative impacts on the functioning and productivity of ecosystems (Gardner et al. 2011, Sheridan and Bickford 2011). Body size declines driven by climate change have been recorded in the past, for instance in large ungulates during the Pleistocene, and may have led to the extinction of some species (Guthrie 2003).

Several direct and indirect drivers of body size declines in recent decades have been proposed. Firstly, in some taxa, higher metabolic rates are predicted in warmer environments (Bickford et al. 2010) and might lead to decreased body size, unless individuals can increase their rate of food intake (Sheridan and Bickford 2011). Secondly, in line with Bergmann’s rule (Bergmann 1847), it can be beneficial to be smaller (and thus have a larger surface area to volume ratio) in warmer environments, due to a reduced need for heat conservation and a greater need for heat loss (Mayr 1956). Intraspecific trends between body size and both latitude (Ashton et al. 2000) and temperature (Freckleton et al. 2003) have been observed, providing some support for ‘Bergmann clines’. In spite of these proposed mechanisms for direct effects, the majority of studies have implicated an indirect link between climate and resource availability as the most likely driver of body size change (Gardner et al. 2011). Climate and environmental change can alter the timing, quality and quantity of resources, limiting the rate at which individuals acquire resources (e.g. Husby et al. 2011, Ozgul et al. 2009). In general, most evidence to date suggests that phenotypic plasticity, rather than microevolution, is responsible for changes in size in response to a warming climate (Husby et al. 2011, Teplitsky et al. 2008).

In ungulates, body mass is an important indicator of fitness (Clutton-Brock et al. 1985, Gaillard, Festa-Bianchet, Delorme, et al. 2000) and can respond rapidly to environmental change (Ozgul et al. 2009). High body mass is commonly related to high reproductive success (e.g. Stewart et al. 2005) and survival (e.g. Loison, Langvatn, et al. 1999). As such, changes in body mass can have important effects on population dynamics (Gaillard, Festa-Bianchet, Delorme, et al. 2000, Ozgul et al. 2009). There is some evidence of direct climate effects on ungulate body mass, particularly in seasonal environments, and these effects could be altered in a changing climate. For instance snow cover and depth, which have seen decreases over the past few decades in some areas (e.g. Laternser and Schneebeli 2003), affect the costs of locomotion in some species, limiting their ability to forage (Parker et al. 1984). In alpine species, high temperatures in spring and summer can cause heat-stress (Grignolio et al. 2004), reducing the time individuals can spend foraging (Aublet et al. 2009). As a result I propose that, in alpine areas, which have been strongly affected by climate warming (Luterbacher et al. 2004), reductions in time spent foraging due to higher thermoregulatory costs could lead to reduced body size in some species. Climate change is predicted to drive similar changes in temperature-dependent activity budgets in other taxa (Sinervo et al. 2010).

The indirect link between climate, resources and ungulate body mass is well studied and could be strongly influenced by climate change (e.g. Pettorelli, Weladji, et al. 2005, Pettorelli et al. 2007). Climate during spring and summer is thought to have the strongest effect on body condition due to its influence on the quality and phenology of vegetation (Mitchell et al. 1976). Climate change has already affected the growing conditions at these times; earlier springs are being recorded in many areas (Linderholm 2006) and have been linked to higher juvenile body mass in ungulates due to longer growing-seasons and higher vegetation quality (Garel et al. 2011, Pettorelli, Weladji, et al. 2005). However, warmer springs can have negative impacts on body mass as higher temperatures can lead to faster rates of vegetation ‘green-up’ and, thus, a shorter period of access to nutrient-rich emergent vegetation associated with early spring (Crawley 1983, Pettorelli et al. 2007). Non-climatic drivers can also influence ungulate body mass; negative density effects on mass are common in ungulates (e.g. Mysterud, Yoccoz, et al. 2001, Stewart et al. 2005, Toigo et al. 2006). These effects generally operate through increased intraspecific competition at higher population densities resulting in lower per-capita food intake (Skogland 1985).

The body condition of juvenile ungulates has been shown to be particularly responsive to environmental variation (Kjellander et al. 2006, Pettorelli et al. 2007, Toigo et al. 2006). This is largely due to the fact that juveniles invest highly in growth, and not in reproduction, meaning that their body condition is very sensitive to the availability of resources. Juvenile phenotypic quality is thought to be strongly influenced by lagged environmental effects, particularly by the conditions during gestation and lactation (Oftedal 1984). As such, lagged climatic drivers (Cote and Festa-Bianchet 2001, Weladji and Holand 2003), affecting the availability of resources to mothers and their ability to obtain these resources, as well as lagged population density (Bonenfant et al. 2002, Kjellander et al. 2006), affecting competition for resources, can be strong predictors of juvenile body mass. Experiencing poor environmental conditions in youth could suppress growth rates and result in smaller body size at maturity (Ozgul et al. 2009).

Here, I report pronounced long-term declines in the body mass of juveniles in three neighbouring populations of Alpine chamois in the Italian Alps (Fig. 5.1). These populations have grown significantly over the past 30 years as hunting has become more strictly controlled (Fig. 5.2a). During the same period, the climate has warmed markedly (Fig. 5.2b). I investigate potential causes of the observed mass declines, seeking to tease apart the relative contributions of changes in density and temperature, as well as other putative drivers such as vegetation quality and phenology. Furthermore, I am interested in whether drivers act directly on juveniles or via lagged effects on their mothers.

5.3 Materials and methods

5.3.1 Body mass data

Body mass data were used on 10,455 yearling (≈1.5 year old) Alpine chamois (5,762 males and 4,693 females), excluding data collected prior to 1979, which were limited. Using a previous model of seasonal body mass change (chapter 3; Mason et al. 2011), yearly estimates of juvenile body mass were produced, standardised to day 300 of the year (27th October). Body mass was estimated after the growing-season because body condition at this time will have been influenced by the spring and summer environment, which is thought to have a strong influence on ungulate body mass (Oftedal 1984).

Within each site, and for each sex, there was a clear downward trend in body mass over time (Fig. 5.1). Due to the non-stationary nature of the data, the body mass time series were detrended by fitting straight lines and calculating residuals. However, detrending can remove long-term fluctuations related to environmental change trends (Jonzen et al. 2002, Wu et al. 2007), which are of primary interest to us. As a result, I modelled both raw body mass data, to examine drivers of long-term trends, and body mass residuals, to examine drivers of deviations from the long-term trend (i.e. years in which mean body mass was particularly high or low).

5.3.2 Climatic and demographic data

To investigate density-dependence, site-specific population density estimates were used from censuses performed in September every year between 1981 and 2009 (with the exception of 1990 and 1991; official data of Adamello Brenta Nature Park, Trento Province, Italy). It was assumed that density estimates in September would reflect the population density over the preceding growing season. To investigate a possible direct thermoregulatory link between climate and body mass, I calculated yearly site-specific estimates of mean growing season temperature between 1982-2007 using data from high-altitude local weather stations located in each of the three study sites (Forecasts and Organization Office, Civil Protection and Infrastructures Department, Trento Province, Italy).

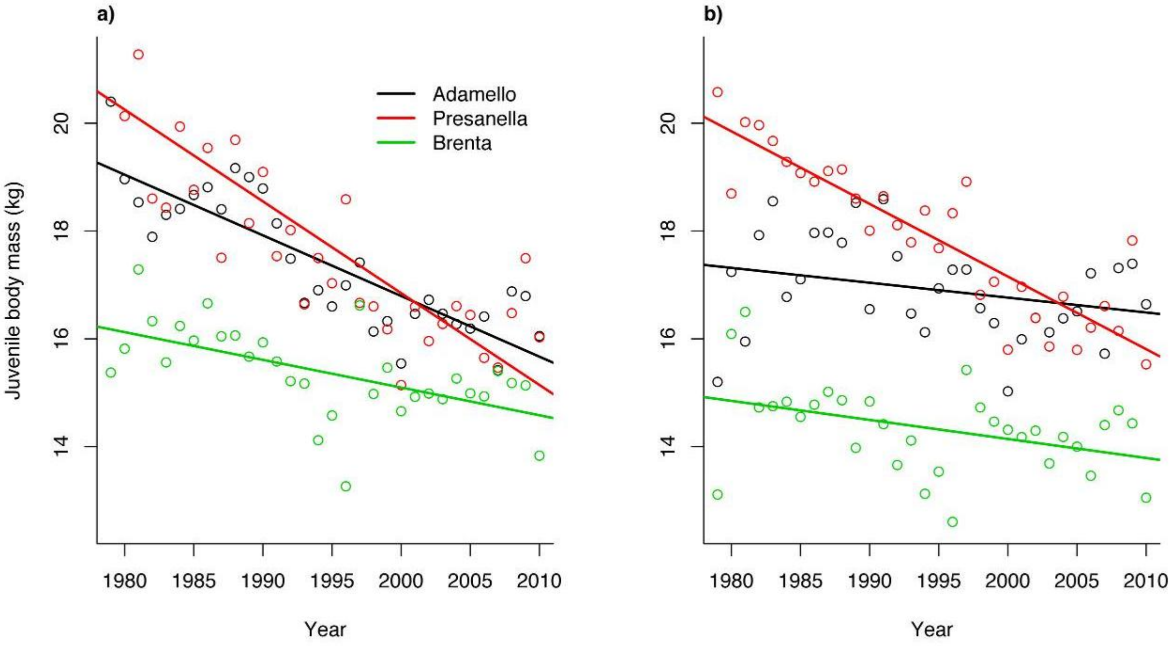

Figure 5.1 Long-term temporal trends in **a)** male and **b)** female juvenile body mass in the three study sites between 1979 and 2010. Points are yearly mass data and straight lines are fitted trends.

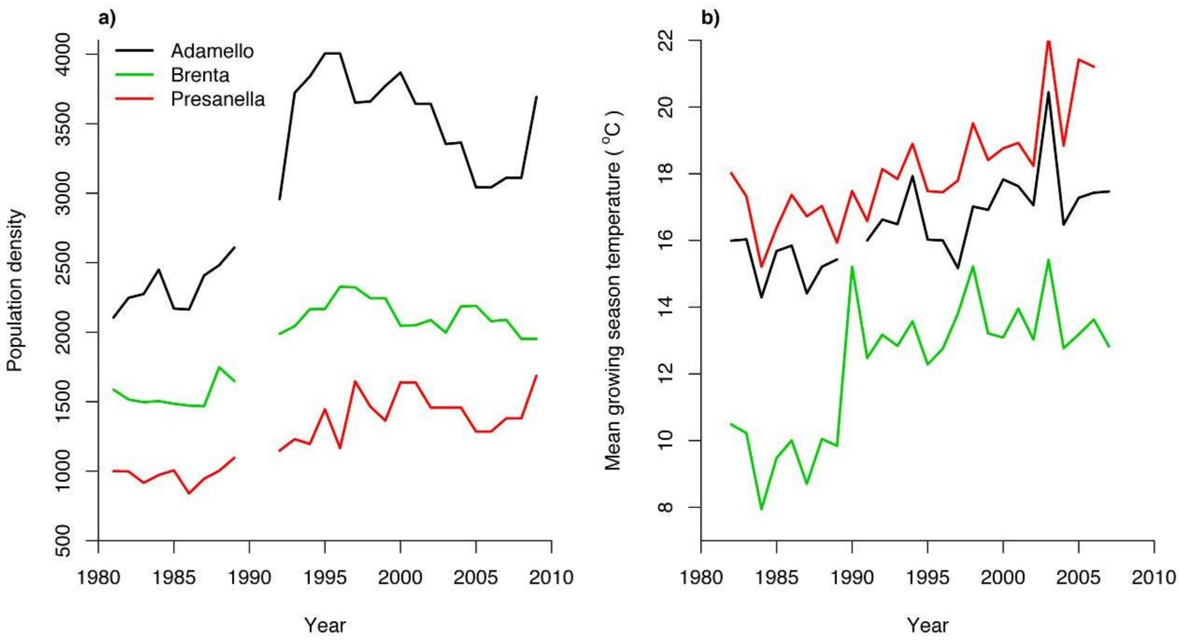

Figure 5.2 Long-term variation in **a)** population density, between 1981 and 2009, and **b)** mean growing season daily maximum temperature, between 1982 and 2007, in the three study sites. Gaps show years with missing data.

To investigate the effect of vegetation productivity and phenology on mass, NDVI (normalised difference vegetation index) data were used, processed by the Global Inventory Modelling and Mapping Studies group (GIMMS; Pettorelli, Vik, et al. 2005, Tucker et al. 2005). These data are global at a 0.07 degree resolution (8km by 8km) and are available at bimonthly intervals between 1982 and 2006 (thus slightly restricting the yearly data range). As each of the three sites covered a number of NDVI pixels, the mean NDVI of all pixels contained (or partially contained) within a given site were calculated, weighted by the area of each pixel contained within the site. Previous studies have implicated a number of characteristics of annual NDVI variation as being important to ungulate body condition (e.g. Pettorelli, Weladji, et al. 2005, Pettorelli et al. 2007). Here, I seek to derive these metrics in a standardised fashion, despite inherent noise in NDVI estimates caused by factors such as cloud cover, water, snow or shadow (Pettorelli, Vik, et al. 2005). Specifically, annual NDVI variation was characterised using the following functional form:

$$\overline{p}(s,y,t) = \alpha_{s,y} + (\beta_{s,y} - \alpha_{s,y}) * \exp\left(- \left| \frac{t - t^*}{\sigma_{s,y}} \right|^{z_{s,y}} \right),$$

where $\overline{p}(s,y,t)$ is predicted NDVI at time-period t in site s and year y, $\alpha_{s,y}$ and $\beta_{s,y}$ are minimum and maximum NDVI respectively in site s and year y, $\sigma_{s,y}$ is a parameter related to the width of the function and $z_{s,y}$ is a parameter describing the shape of the function. Variation in NDVI data, p(s,y,t), about the predicted mean was beta distributed. Thus, the likelihood of the model parameters, $\boldsymbol{\theta}_{s,y}$, given the data, parameterised by $\overline{p}(s,y,t)$ and the dispersion coefficient $\phi_{s,y}$, is

$$L(\theta_{s,y}) = \prod_t \frac{\Gamma(a_{s,y,t} + b_{s,y,t})}{\Gamma(a_{s,y,t})\Gamma(b_{s,y,t})} p_{s,y,t}{}^{a_{s,y,t}-1}(1-p_{s,y,t})^{b_{s,y,t}-1},$$

where Γ(x) is the complete gamma function, $a_{s,y,t} = \overline{p}_{s,y,t} / \phi_{s,y}$ and $b_{s,y,t} = (1-\overline{p}_{s,y,t}) / \phi_{s,y}$. The most parsimonious fit was identified using Akaike's information Criterion (AIC) (Burnham and Anderson 2002, Richards 2008).

Using fitted NDVI relationships from each year, four NDVI metrics were calculated relating to vegetation productivity and phenology which have been shown to be important, either to juvenile alpine chamois specifically or to other ungulate species (Garel et al. 2011, Pettorelli, Vik, et al. 2005). Maximum rate of spring green-up ($\mathrm{NDVI}_{\mathrm{rate}}$) was calculated as the maximum first derivative of $\overline{p}_{s,y}(t)$ (i.e. the maximum rate of NDVI increase). The duration of the growing season ($\mathrm{NDVI}_{\mathrm{duration}}$) was calculated as the length of time between the maximum second derivative of $\overline{p}_{s,y}(t)$ (the start date of the growing season; when the rate of NDVI increase is increasing at its maximum rate) and the minimum second derivative of $\overline{p}_{s,y}(t)$ (the end date of the growing season; when the rate of NDVI increase is decreasing at its minimum rate). Maximum NDVI ($\mathrm{NDVI}_{\mathrm{max}}$) was calculated as the maximum value of $\overline{p}_{s,y}(t)$ and total growing-season NDVI (INDVI) as the integral of $\overline{p}_{s,y}(t)$ within the bounds of the growing season. An illustration of the calculation of these metrics can be seen in Figure 5.3.

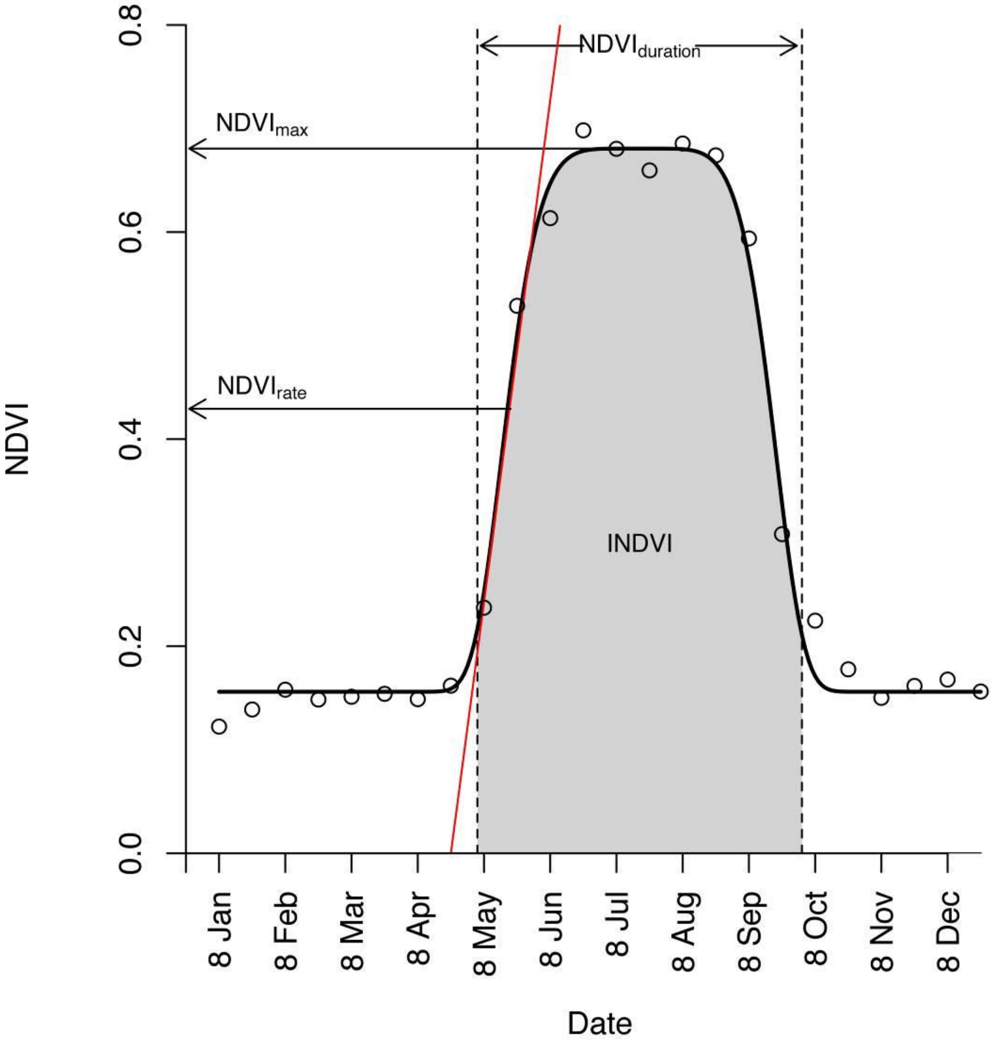

Figure 5.3 An example of seasonal variation in NDVI, from Adamello in 1993, illustrating how NDVI metrics were calculated. Data points show NDVI estimates from each two-week time period. The curve is the fitted NDVI relationship. Vertical dashed lines show the start and end dates of the growing season (the maximum and minimum second derivatives of the curve), from which $NDVI_{duration}$ is calculated. The red line is a tangent to the curve at the point of maximum slope (the maximum first derivative of the curve); $NDVI_{rate}$. The shaded area is the integral of the fitted curve within the bounds of the growing season; INDVI. $NDVI_{max}$ is the maximum NDVI value of the fitted curve.

5.3.3 Modelling variation in mass and mass residuals

To standardise the environmental predictors, they were z-transformed, within site, as follows: $x_{z,s,y} = (x_{s,y} - \overline{x_s}) / \sigma_s$, where $x_{s,y}$ is a predictor in year *y* and site *s*, $\overline{x}_s$ is the site-specific mean of that predictor and σ_s the site-specific standard deviation.

Logistic regression models were fitted separately to data from each site, using the following model structure:

$$\overline{m}_{s,y} = a_s + \frac{b_s}{(1 + e^{(\beta_{0,s} + \beta_{sex,s}.sex_{s,y} + \beta_{density,s}.density_{s,y} + \beta_{temp,s}.temp_{s,y} + \beta_{NDVI,s}.NDVI_{s,y})})}$$

where $\overline{m}_{s,y}$ is predicted juvenile mass in site *s* and year *y*, $\beta_{\text{sex,s}}$, $\beta_{\text{density,s}}$, $\beta_{\text{temp,s}}$ and $\beta_{\text{NDVI,s}}$ are model coefficients for sex, population density, temperature and NDVI, respectively, in site *s*. Similarly, variation in body mass residuals was modelled over time:

$$\overline{r}_{s,y} = a_s + \frac{b_s}{(1 + e^{(\beta_{0,s} + \beta_{sex,s}.sex_{s,y} + \beta_{density,s}.density_{s,y} + \beta_{temp,s}.temp_{s,y} + \beta_{NDVI,s}.NDVI_{s,y})})}$$

where $\overline{r}_s$ is predicted juvenile mass residual in site *s*. Both sexes were modelled together, using sex as a predictor. Models were fitted with all possible biologically meaningful combinations of population density, $\text{NDVI}_{\text{rate}}$, $\text{NDVI}_{\text{duration}}$, NDVI_{max}, INDVI, sex and temperature. Since the different NDVI metrics were frequently highly correlated, only one was allowed per model. To account for environmental effects on juvenile mass from previous years, density, temperature and NDVI data were used from three different years: year 1 (the year a cohort was conceived), year 2 (the year of a cohort's birth) and year 3 (the year a cohort was shot) (see Table 5.1). Since different lagged effects were often highly correlated for given predictors, data were only allowed from one year for each predictor per model. Given the temporal range of the predictors, and to use the same data in each model, data were used for the 19 years between 1984 and 2006, excluding 1990, 1991, 1992 and 1993. The data were normally distributed. In total 414 models were fitted for each site. The most parsimonious models were identified using AIC, considering models with a ΔAIC of ≤6 and lower than the ΔAIC of all simpler nested models (Richards 2008). A second stage of model selection allowed either separate parameter estimates for each sex or single parameter estimates for both sexes, assessing the parsimony of models with different combinations of these sex-specific and non-sex specific parameters (see Table 5.2). Statistical analyses were performed using R version 2.15.0 (R Development Core Team 2012).

Table 5.1 The timing of key events in the lives of a cohort of yearling chamois relative to the vegetation growing seasons in years 1, 2 and 3.

<table>
<tr><th>Year</th><th>Jan</th><th>Feb</th><th>Mar</th><th>Apr</th><th>May</th><th>Jun</th><th>Jul</th><th>Aug</th><th>Sep</th><th>Oct</th><th>Nov</th><th>Dec</th></tr>
<tr><td rowspan="2">1</td><td colspan="3"></td><td colspan="6">Vegetation growing season</td><td colspan="3"></td></tr>
<tr><td colspan="9"></td><td colspan="3">Cohort conceived</td></tr>
<tr><td rowspan="2">2</td><td colspan="3"></td><td colspan="6">Vegetation growing season</td><td colspan="3"></td></tr>
<tr><td colspan="4"></td><td colspan="2">Cohort born</td><td colspan="6"></td></tr>
<tr><td rowspan="2">3</td><td colspan="3"></td><td colspan="6">Vegetation growing season</td><td colspan="3"></td></tr>
<tr><td colspan="2">Cohort weaned</td><td colspan="7"></td><td colspan="3">Cohort shot</td></tr>
</table>

Table 5.2 The best models for each site and response variable. Shown are the most parsimonious combinations of sex and non-sex specific parameters.

Response	Site	Sex	a	b	β_0	β_{sex}	$\beta_{density}$	β_{temp}	β_{NDVI}	σ	K	LL	AIC
Body mass	Adamello	Males	x	x	x		x	x	x	x	10	-17.1	54.3
		Females		x				x	x				
Body mass	Presanella	Males Females	x	x	x	x	x	x	x	x	8	-27.3	70.5
Body mass	Brenta	Males	x	x	x			x	x	x	7	-30.2	74.3
		Females		x				x					
Residuals	Adamello	Males Females	x	x	x			x		x	5	-22.5	54.9
Residuals	Presanella	Males Females	x	x	x	x	x	x	x	x	7	-29.4	72.8
Residuals	Brenta	Males Females	x	x	x		x	x	x	x	7	-16.3	46.5

5.4 Results

Between 1979 and 2010, consistently across all three populations, juvenile chamois body masses decreased (Fig. 5.1 a & b). The extent of this decrease has varied considerably both among sexes and sites although, in all sites, decreases in male mass have been more pronounced than decreases in females. Decreases have been largest in Presanella (mean altitude, 2096m), where both sexes have been similarly affected (mass decreases estimated from linear trends: males, 25.8%, females, 20.9%). In Adamello (mean altitude, 1909m), male mass decreases have been high (18.2%) but female mass declines have been much lower (4.9%). In Brenta (mean altitude, 1607m), mass decreases have been lower than the other sites but similar in both sexes (males, 9.9%, females. 7.4%). During the same period, all three populations increased in size substantially, peaking in the mid 1990's before declining slightly in recent years (Fig. 5.2a). There have also been striking increases in growing season temperatures in all sites between 1982 and 2007 (Fig. 5.2b). In contrast there have been no pronounced long-term trends in the four NDVI metrics between 1982 and 2006, although growing seasons have tended to be longer and more productive over the past five years (Fig. 5.4).

Model selection shows that density, temperature and NDVI all play a role in describing long-term variation in juvenile body mass (Table 5.3). Within each site, the top model sets contain a number of closely competing models, consisting of different NDVI metrics and time-lags for density and temperature. There is some consistency however; the top model for each site always contains a temperature variable, as do the majority of all models. The top models in each site fit the data well, describing a high proportion of the variation in juvenile male and female body mass (Fig. 5.5). In both Adamello and Presanella, density, temperature and NDVI are present in the majority of models in top model sets. In Brenta, all top models feature one of density and temperature as well as an NDVI predictor. In all sites, there is evidence that predictors from the current year or either of the preceding years can explain a high degree of body mass variation (Table 5.3). However, the best models in both Adamello and Presanella contain density in year of conception (year 1) and temperature in year of birth (year 2), showing that these lagged density and temperature effects best explain the observed body mass variation. In Brenta, the top model contains temperature from year of conception but no density effect, suggesting that density is less important here (although it does feature in other models in the top model set). The evidence for NDVI effects is inconsistent among the top models, with a range of NDVI metrics from different lags appearing in the top model sets. There is only consistent evidence for a specific NDVI metric in Brenta, where total growing season NDVI (INDVI) in year of birth features in the best four models.

In contrast to the body mass models, the fit of residual models is very poor (Fig. 5.6). This suggests that, whilst long-term body mass trends can be explained, deviations from these trends cannot. Due to the poor fits of these models, they cannot be used to make predictions. However, there are some encouraging similarities with the body mass models: temperature in year of birth is in the top model in both Adamello and Presanella (Table 5.4), emphasising the importance of a lagged impact of growing season temperature on body mass in these sites.

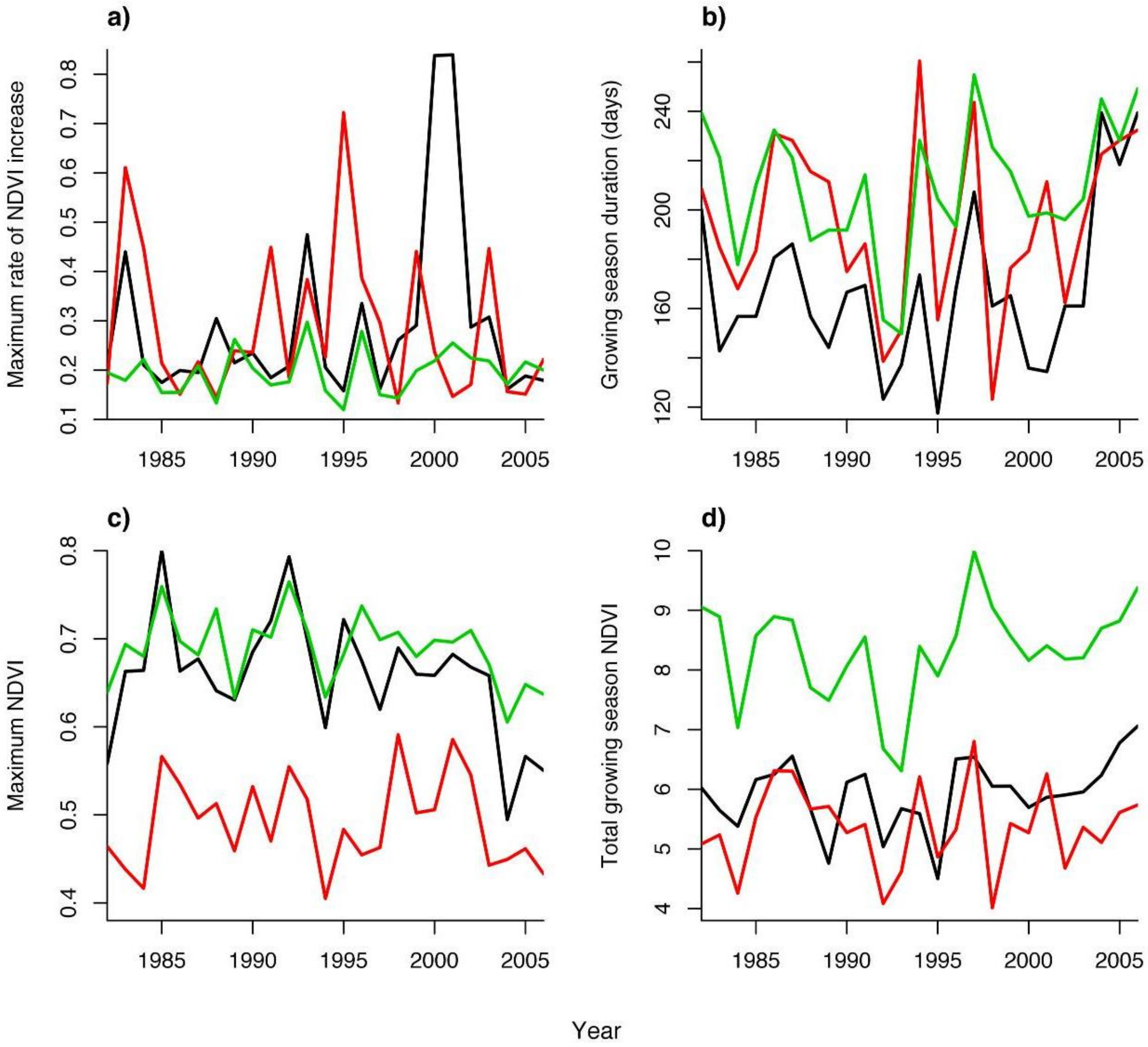

Figure 5.4 Long-term variation in **a)** maximum rate of NDVI increase ($NDVI_{rate}$), **b)** growing season duration ($NDVI_{duration}$), **c)** maximum NDVI ($NDVI_{max}$) and **d)** total growing season NDVI (INDVI) between 1982 and 2006 in Adamello (black), Presanella (red) and Brenta (green).

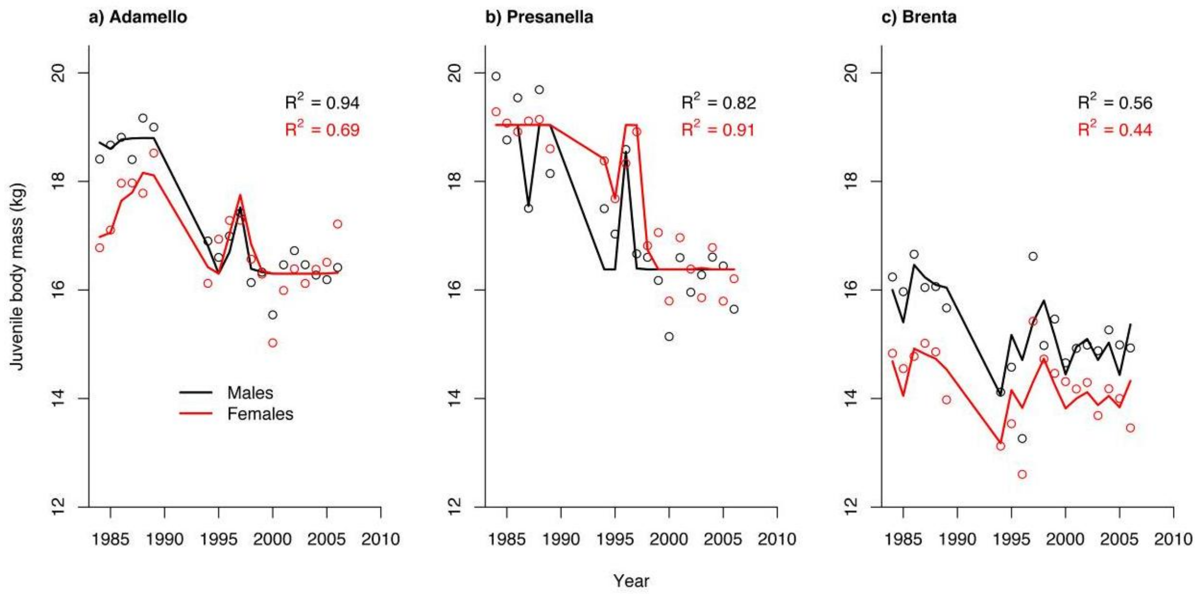

Figure 5.5 Fitted mass predictions of best models for males and females in the three study populations. Lines are predictions and points are mass data for years used in modelling (i.e. years for which there is no missing data for any predictor). R^2 values shown for each sex.

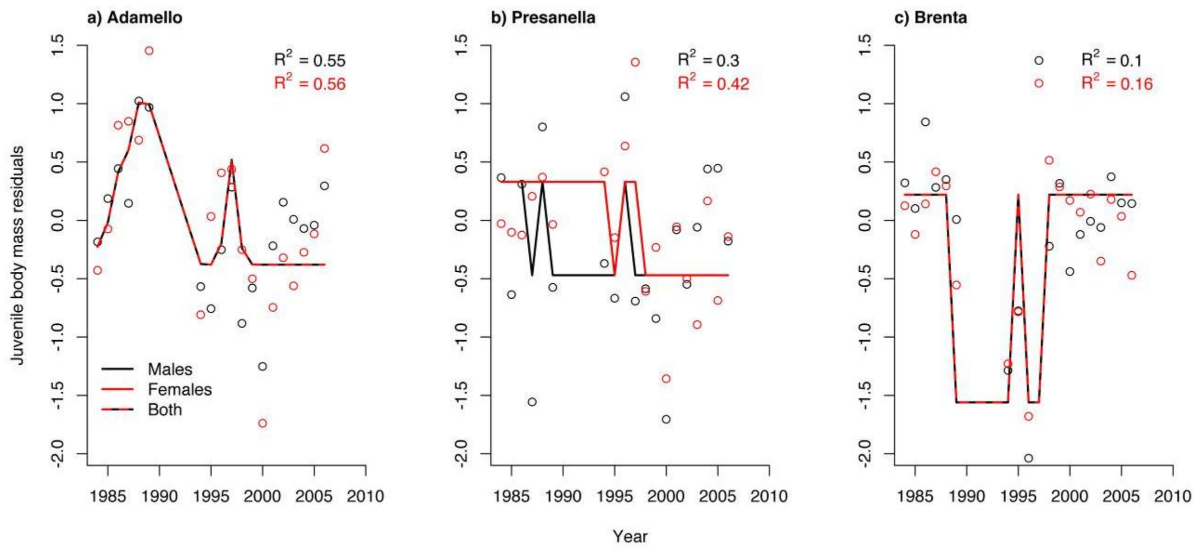

Figure 5.6 Fitted residual predictions of best models for males and females in the three study populations. Lines are predictions and points are residual data for years used in modelling (i.e. years for which there is no missing data for any predictor). R^2 values shown for each sex.

Table 5.3 Top model set for logistic regressions of body mass data in each site. Models shown have a ΔAIC that is ≤6 and lower than all simpler nested versions (Richards 2008). The number of parameters (K), log-likelihood (LL) and ΔAIC are shown for each model.

Site	Density	Temp	NDVI	K	LL	ΔAIC
Adamello	y1	y2	Rate.y1	8	-22.5	0.0
	y3	y2	Rate.y1	8	-22.9	0.8
	y2	y3	Peak.y1	8	-23.0	0.9
	y1	y1		7	-24.1	1.1
	y2		Peak.y1	7	-26.0	4.9
Presanella	y1	y2	Rate.y3	8	-27.3	0.0
	y3	y3	Duration.y3	8	-27.3	0.1
	y1	y3	Rate.y3	8	-27.5	0.4
	y3	y2	Rate.y2	8	-27.5	0.5
	y3	y3	INDVI.y3	8	-27.8	1.0
	y3	y2	Rate.y3	8	-27.8	1.1
	y1	y3	INDVI.y2	8	-28.4	2.3
	y1	y3	Duration.y3	8	-28.4	2.3
	y1	y3	Duration.y2	8	-28.6	2.7
	y1	y2	INDVI.y2	8	-28.8	3.2
	y2	y2	Rate.y3	8	-28.9	3.2
	y1	y2	Rate.y3	8	-28.9	3.3
	y1	y3	INDVI.y3	8	-29.0	3.4
	y2	y2	Duration.y2	8	-29.0	3.4
	y3	y2	Peak.y3	8	-29.0	3.4
	y1	y2	Duration.y2	8	-29.0	3.4
	y3	y3	Rate.y1	8	-29.0	3.5
	y3	y3	Rate.y2	8	-29.0	3.5
		y2	Rate.y3	7	-30.2	3.8
		y2	INDVI.y2	7	-30.4	4.4
		y2	Rate.y2	7	-31.1	5.6
Brenta		y1	INDVI.y2	7	-31.3	0.0
	y3		INDVI.y2	7	-32.2	1.8
	y1		INDVI.y2	7	-32.4	2.1
	y2		INDVI.y2	7	-32.8	2.9
	y3		INDVI.y3	7	-33.1	3.6
		y1	Rate.y3	7	-33.7	4.8
		y1	Rate.y2	7	-33.8	5.0
	y3		Rate.y3	7	-33.9	5.2
		y1	INDVI.y3	7	-33.9	5.2
		y2	INDVI.y2	7	-34.0	5.3
		y1	Duration.y3	7	-34.1	5.6
		y1	INDVI.y1	7	-34.2	5.7
		y3	INDVI.y3	7	-34.2	5.7
		y1	Duration.y2	7	-34.3	5.9
		y1	Rate.y1	7	-34.3	5.9
	y3		Duration.y3	7	-34.3	5.9
		y3	Duration.y3	7	-34.3	6.0

Table 5.4 Top model set for logistic regressions of body mass residual data in each site. Models shown have a ΔAIC that is ≤6 and lower than all simpler nested versions (Richards 2008). The number of parameters in each model (K), log-likelihoods (LL) and ΔAICs are shown.

Site	Density	Temp	NDVI	K	LL	ΔAIC
Adamello		y2	Rate.y1	7	-21.8	0.0
	y3	y3		7	-23.4	3.4
		y3	Peak.y1	7	-24.4	5.2
	y1		Rate.y2	7	-24.4	5.2
	y3		Rate.y1	7	-24.7	5.8
Presanella		y2	Duration.y2	7	-29.4	0.0
		y3	Duration.y3	7	-30.7	2.6
		y2	Rate.y3	7	-30.7	2.6
		y2	INDVI.y2	7	-30.7	2.6
	y1		Peak.y1	7	-30.7	2.6
		y1	Rate.y2	7	-31.0	3.3
			Peak.y1	6	-32.0	3.3
			INDVI.y1	6	-32.4	4.1
			Duration.y1	6	-32.4	4.1
Brenta	y3	y3	INDVI.y2	8	-15.9	0.0
	y3	y1	INDVI.y3	8	-18.7	5.5

The predictions of the best body mass models in each site can help to tease apart which predictors are driving body mass declines. Growing season temperature appears to be an important driver in all three sites, as shown clearly by the data and model predictions (Fig. 5.7). There are negative logistic relationships between temperature and mass in Adamello and Presanella with abrupt declines in mass at intermediate temperatures (Fig. 5.7 a-b). These predictions suggest that juvenile males and females born in warmer years weigh substantially less than those born in cooler years. In Brenta, the relationship between temperature and mass is also negative but more linear than in the other sites (Fig. 5.7 c) and suggests that juveniles weigh less if they were conceived in a warmer than average growing seasons.

Overall, it appears that early-life environmental conditions, during the first year or even prior to birth, can have the largest impact on juvenile body condition. The effect of density from the best models is generally weaker than temperature. There is only a strong density effect in Presanella, where females, but not males, that were conceived in high density years weigh less. There is no strong evidence for an effect of NDVI on mass change; the NDVI effects present in best models being weak and varying substantially among different sites.

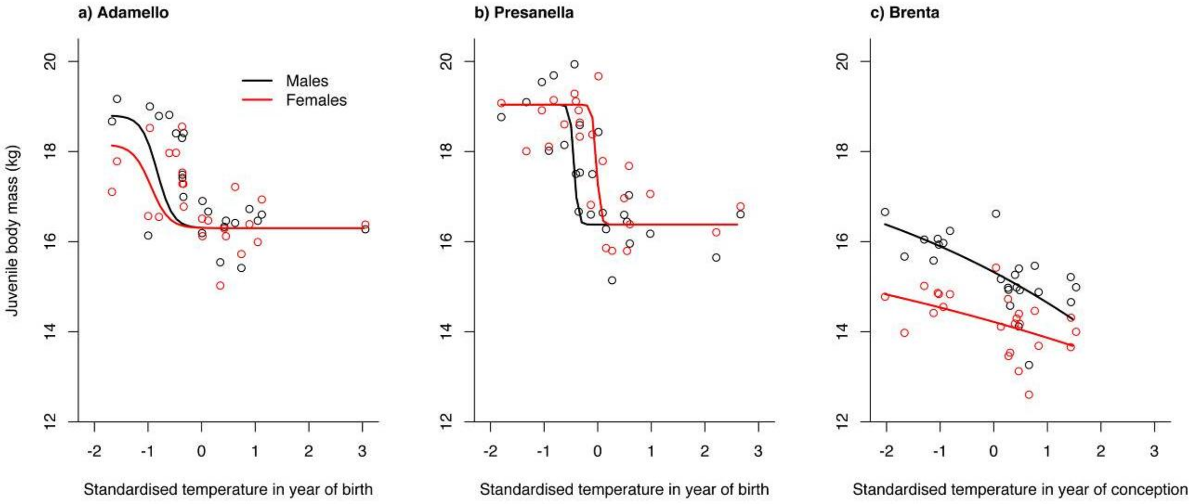

Figure 5.7 Predicted and observed variation in male and female juvenile body mass with z-transformed mean growing season daily maximum temperature in the three study populations. For Adamello and Presanella, mean growing season temperature is from the year of a cohort's birth, whilst for Brenta, it is from the year of a cohort's conception. Lines are predictions of the best model for each site, with other predictors set to mean values, and points are mass data from years used in modelling (those years for which there is no missing data for any predictor).

5.5 Discussion

Body mass models performed well in explaining long-term declines in juvenile body mass in all three study sites (Fig. 5.5). However, the poor fits of residual models show that deviations from the general trends (i.e. years in which juveniles are particularly heavy or particularly light) cannot be explained (Fig. 5.6). Mass declines appear to have been driven predominantly by increases in growing season temperatures; pronounced negative effects of growing season temperature are present in the best body mass models in all sites (Fig. 5.7). Previously, a negative effect of spring and summer temperatures has also been found on juvenile chamois horn length (Chirichella, Ciuti, Grignolio, et al. 2013), adding weight to this finding. The evidence for a negative effect of population density on mass, as a result of the observed population growth in the study area (Fig. 5.2b), is comparatively weak. There is little evidence of a strong effect of changing vegetation productivity or phenology on mass (Fig. 5.4).

The climate during spring and summer has warmed markedly during the study period (Fig. 2b). During this period, there has been no consistent change in either vegetation productivity or phenology (Fig. 4) and there is no relationship between temperature and any of the NDVI metrics. As such, it seems that temperature has not acted indirectly through effects on resource quality, but more likely directly on chamois behaviour or physiology. As such, this provides an interesting contrast to the majority of studies to date which have implicated changes in food abundance as the most likely cause of body size declines (Gardner et al. 2011). In this study system, it may be that changes in the ability of individuals to acquire resources, rather than changes to the availability of resources themselves have driven the observed mass declines. In a similar alpine ungulate, the ibex, temperatures above 15-16^{o}C result in heat discomfort in males, reducing the time they are able to spend foraging (Aublet et al. 2009). In ungulates, behaviours such as allocating less time to foraging, are thought to play a vital role in thermoregulation because they can be more energetically efficient than autonomic thermoregulation (Dussault et al. 2004, Maloney, Moss, Cartmell, et al. 2005). Higher daily temperatures during the growing season may have led to chamois spending more time resting and less time foraging than chamois in the past, reducing their ability to store energy reserves. Indeed, like many ungulates, chamois are known to reduce their feeding activity during the hottest period of the day (Christie 1964, Ruttimann et al. 2008).

From model selection there is evidence that the negative effect of temperature on juvenile mass is lagged (Table 5.3). This suggests that juvenile mass is primarily limited via effects on their mother's condition; temperature may limit the ability of breeding females to forage and store the resources necessary for gestation (year 1) and lactation (year 2) (see Table 5.1). The importance of lagged effects on juvenile condition has been highlighted in ungulates (e.g. Bonenfant et al. 2002, Cote and Festa-Bianchet 2001). However, that environmental conditions even prior to conception can be important, as is the case in Brenta, is surprising. Previous work on juvenile chamois has shown that environmental conditions during their second year of life, which influence the ability of juveniles to acquire resources directly, are also important (Chirichella, Ciuti, Grignolio, et al. 2013, Garel et al. 2011). For instance, in this study area, spring temperatures during the second year of life have been shown to have a pronounced negative influence on juvenile horn length (Chirichella, Ciuti, Grignolio, et al. 2013). My results are not in complete opposition to this: models containing temperature in the year that cohorts were shot (year 3) are still present in the top model sets for each site (Table 5.3), suggesting that environmental conditions in this year explain some variation in juvenile mass.

Population density has changed substantially during the study period (Fig. 2) and this appears to explain some variation in juvenile mass; a density effect is present in the majority of the top body mass models in Adamello and Presanella (Table 5.3). In each of these sites, density from the year a cohort were conceived is in the best model, showing that population densities experienced by mothers prior to conception could be influencing juvenile condition. However, the effects of density on body mass are much less pronounced and consistent across sites and sexes than temperature effects are. The only strong evidence for negative density-dependence is in Presanella females. This general absence of a strong negative density effect on mass is surprising, given that it has been detected in a wide range of ungulate species (Kjellander et al. 2006) and even specifically in juvenile chamois (Garel et al. 2011). It is possible that hunting regimes have maintained populations below their carrying capacities, limiting the effect of resource competition on mass. In either case, whilst model selection shows that density is important in explaining some inter-annual variation in body mass (Table 5.3), the evidence suggests that increasing growing season temperatures have had a stronger effect on juvenile mass than density. In Brenta, an effect of density is absent from the best body mass model altogether (Table 5.3), likely due to the fact that Brenta is a calcareous area, consisting of higher quality vegetation than the other sites (see chapter 3; Gensac 1990), and thus probably has a higher carrying capacity.

From model selection, there is good evidence that vegetation productivity and phenology are important in explaining some of the inter-annual variation in juvenile body mass; NDVI metrics feature in all but one of the models in top models sets (Table 5.3). However, there is a lack of consistency in which NDVI metrics are selected in different models, meaning that evidence is weak for specific NDVI effects. Only in Brenta, where the top four models contain a positive effect of INDVI from the year a cohort were conceived, is there strong evidence for a specific effect. This is consistent with previous work in this study area, which found that the ability of individuals to acquire resources in Brenta is much more variable than in the siliceous sites (Chirichella, Ciuti, Grignolio, et al. 2013). This is thought to be because the nutrient quality of calcareous vegetation is more strongly affected by climatic variation (Cavallero et al. 2007, Michalet et al. 2002). This importance of vegetation productivity on juvenile mass has previously been highlighted in ungulates (Pettorelli et al. 2006), including chamois (Garel et al. 2011). In Adamello and Presanella, there is a suggestion that rate of green-up is important to juvenile body mass, which agrees with previous work suggesting the importance of early spring conditions in this species (Table 5.3; Garel et al. 2011). However, the directions of the effects of rate of green-up in these sites are opposite; in Adamello the effect is negative and in Presanella it is positive. It remains possible, given that NDVI is only a proxy for vegetation productivity, that changes in vegetation quality and phenology have had more of an effect than suggested here. However, the available evidence shows little support for an indirect effect of changing resource availability or quality on body mass. Another potential driver of smaller juvenile body mass is that the timing of births could have changed, despite the lack of any pronounced shift in the timing of spring green-up. However, this is unlikely here because earlier, rather than later, births are more likely to occur in a warming climate and would be expected to result in increasing juvenile body mass over time (e.g. Ozgul et al. 2010).

Climate change appears to have directly influenced the body condition of chamois and could have significant impacts in the future. If temperatures continue to increase at the current rate, chamois may be forced to forage at higher temperatures, relying on autonomic rather than behavioural thermoregulation, unless they can move to higher altitudes. On hotter days, alpine ungulates tend to move to higher altitudes (Aublet et al. 2009, Grignolio et al. 2004), however, the potential to do this is obviously limited and will decrease further as the alpine climates continue to warm. High-altitude chamois populations appear to be ideal candidates to investigate the impacts of climate change using activity budget models, which have been applied in other taxa (Dunbar 1998, Willems and Hill 2009). By characterising the proportion of time individuals spend foraging in different climatic conditions, it may be possible to predict how their activity budgets will be affected in the future, assuming that populations remain within their current geographic ranges. This type of prediction could be used to inform conservation practice, particularly when addressing the feasibility of management strategies such as assisted migration.

The results suggest that climate change may not only drive body size change indirectly via effects on resource availability, but also by directly affecting the ability of individuals to acquire resources. However, there is currently much uncertainty in the importance of different drivers of size change (Sheridan and Bickford 2011), as well as a lack of understanding of the relative contributions of genetic change and phenotypic plasticity (Teplitsky et al. 2008). Furthermore, whilst declines in body size are most common, in some taxa there are examples of variable or even increasing body size trends (Gardner et al. 2011). Such variation and uncertainty make predicting how body sizes may change under future climate change very difficult. Correlational studies such this one are important in highlighting potential drivers of change, however an increasing focus on mechanism of change is required in order to robustly predict future responses. Reductions in body size are likely to have far-reaching effects on the functioning and productivity of ecosystems, particularly given the different ways in which different taxonomic groups and trophic levels are affected (Gardner et al. 2011, Sheridan and Bickford 2011).

Chapter 6

Climate, hunting and demographic variation in chamois

6.1 Abstract

To predict species' responses to climate change, it is necessary to establish the relationships between climatic variation and population dynamics. However, inferring such associations is not always possible due to a lack of reliable, long-term data on population changes. Here, I address this problem by combining data on three populations of Alpine chamois from different sources: intermittently collected census data, long-term annual harvest records and age-ratios, the latter inferred from observations in the field. In common with other studies on ungulates, there is strong evidence for age-specific survival rates, with separate survival estimates for kids (0.56-0.73), yearlings (0.73-0.95) and adults (0.95-1.00). I find evidence for an influence of both spring and winter climate on chamois population dynamics; specifically, there is a negative effect of temperature during spring and summer on fecundity and survival, and, surprisingly, a positive effect of snow depth on fecundity. In addition, there is evidence for a negative effect of population density on survival. Strikingly, adult natural mortality is extremely low in these populations, particularly in males. I propose that this pattern is driven directly by high hunting mortality, largely replacing natural mortality and resulting in shorter life-expectancies than in natural populations. To my knowledge, such a phenomenon has not been documented previously. These results highlight the value of integrating harvesting data into demographic studies, particularly for heavily managed populations. This study reveals that climate can still exert a considerable influence on population dynamics, despite very high levels of mortality from hunting. Ungulate harvesting plans will require careful adaptation in the future in response to the influence of temperature and precipitation changes in the alpine region.

6.2 Introduction

The importance of understanding the complex links between climatic and environmental variation and population dynamics is well understood (Gaillard et al. 2013). Future changes in temperature, precipitation, phenology and the frequency of extreme events are likely to influence the ability of individuals to acquire resources, survive and reproduce (Walther et al. 2002). Making robust, detailed predictions about how these changes will influence populations under climate change, whilst difficult, is vital for wildlife management in a changing climate. Effects of climate and environmental change on population processes are already evident in many species (Lane et al. 2012, Ozgul et al. 2010, Saether et al. 2000, Thompson and Ollason 2001). For instance, earlier springs have advanced emergence from hibernation of yellow-bellied marmots (*Marmota flaviventris*), increasing over-winter survival in adults and resulting in higher population growth rates (Ozgul et al. 2010). Interestingly, in another hibernating rodent, the Columbian ground squirrel (*Urocitellus columbianus*), increased snowstorms in late-winter have resulted in later emergence and population growth rates have subsequently decreased (Lane et al. 2012). These contrasting outcomes highlight the inherent difficulties in generalising future climate effects across study systems.

In order to make predictions, it is important to establish the relationship between climate and demographic parameters. Among mammals, ungulate populations are particularly well-studied in this respect (e.g. Gaillard et al. 1998, Saether 1997), making them good systems with which to investigate climate effects on demography. Ungulate population dynamics are generally characterised by high, consistent levels of adult survival but variable levels of recruitment, due to strong variation in juvenile survival and fecundity (Gaillard et al. 1998, Saether 1997). Whilst adult survival is considered to have the highest elasticity of ungulate demographic parameters, it is generally only strongly affected by extreme climatic events (e.g. Rughetti et al. 2011). Conversely, the survival of juveniles (and to some extent senescent individuals) is more susceptible to climatic and environmental variation due to their smaller energy reserves and higher metabolic demands (compared to prime-aged adults) (Hudson 1985, Solberg et al. 2001). Juvenile survival has been shown to be the strongest driver of variation in population growth rates (Gaillard et al. 1998, Gaillard, Festa-Bianchet, Yoccoz, et al. 2000). Fecundity can also be strongly influenced by climatic and environmental variation in ungulates, thus affecting recruitment (Saether 1997). The majority of previous studies on ungulate population dynamics have focused on the negative influence of harsh winter conditions on demographic parameters (e.g. Milner et al. 1999, Post and Stenseth 1999). Recently, however, focus has shifted towards the influence of spring conditions, particularly spring phenology (Gaillard et al. 2013). However, whilst the negative relationship between winter severity and survival rates is relatively consistent across ungulate study systems, highly variable effects of spring climate on recruitment have been reported (e.g. Helle and Kojola 2008, Pettorelli et al. 2007). Thus, whilst certain generalities can be made, other patterns remain specific to individual species and even populations.

Climate change may influence the demography of populations, resulting in a need to adapt management strategies (Hulme 2005). As such, it is important to study the effects of climate on heavily managed populations, in order to determine the combined influences of climate and management on population dynamics. For many ungulate populations, harvesting by humans represents a strong influence on population dynamics which must be incorporated into studies. Even controlled hunting can have strong and unpredictable impacts on population demography, ranging from disturbing age and sex-ratios (Milner-Gulland et al. 2003) to reducing vital rates such as fecundity (Solberg et al. 2002) and natural survival (Singer and Zeigenfuss 2002). Ungulate harvesting regimes are frequently male-biased, leading to female-biased sex ratios of as much as 0.95 in some populations (Noyes et al. 1996). In polygynous populations, males are seldom limiting; nevertheless, unchecked, male-biased harvesting can lead to reproductive collapse (Milner-Gulland et al. 2003). As such, the incorporation of males into population dynamics studies, the significance of which is now widely accepted (Mysterud et al. 2002), is particularly important in studies of harvested populations. Furthermore, since many harvested ungulate populations are carefully monitored, often by full population censuses, data on the abundances of different sex and age-classes are frequently available (e.g. Mysterud et al. 2007), from which dynamics and vital rates can be inferred.

Here, I study the influence of climatic and environmental variation on the population demography of a heavily harvested population of Alpine chamois, in order to establish the potential effects of climate change on a species of great cultural and economic importance. I combine long-term, yet intermittently collected, abundance data from population censuses with data on the sex and age-structure of annual culls and field data on age-ratios to model variation in abundance of different age-classes. Species, like Alpine ungulates, inhabiting harsh and variable environments are predicted to be strongly affected by climate and environmental change (Ozgul et al. 2010, Parmesan 2006). Interestingly, the influence of climate on population dynamics has been previously studied in several non-hunted populations of chamois, providing an interesting comparison to this study. In these studies, winter conditions have been shown to be important to survival in this species (Loison, Jullien, et al. 1999b, Willisch et al. 2012) whilst spring conditions have been shown to affect chamois body condition (Garel et al. 2011). Here, by investigating the parallel effects of hunting and climatic conditions, I hope to reveal how important climate change could be, to heavily managed populations, which are often of considerable economic and cultural importance.

6.3 Materials and methods

6.3.1 Census data

Since 1981, annual censuses have been performed each October by hunters and game-keepers in the study area, giving estimates of total population size. Unfortunately, these censuses do not provide data on the abundances of different age-classes and sexes. Since 1993 in Presanella, 1995 in Adamello, and 1996 in Brenta, comprehensive, age-structured censuses have been undertaken, generally biennially (official data of Adamello Brenta Nature Park, Trento Province, Italy). These censuses provide abundance estimates for kids (≈ 0.5 years), yearlings (≈ 1.5 years), adult males and adult females (≥ 2.5 years). Censuses are performed in September, prior to the annual cull. Using the age-structured census data, kid to adult female ratios (K:F; number of kids /number of adult females) were calculated as an estimate of female fecundity, for each year when such a census was performed Fig. 6.1). Using these estimates, mean K:F was calculated for each area, which were used as estimates of fecundity, F, in the population models. It is important to note that this is a composite parameter, incorporating early kid survival, during the first few months of life, as well as fecundity. The use of age-ratios, such as juvenile to female ratios, to infer demographic parameters, has received some criticism (Bonenfant et al. 2005, Caughley 1974). However, here age-ratios are used for populations living in an open habitat where variation in detectability of individuals is unlikely to be a source of bias (Harris et al. 2008).

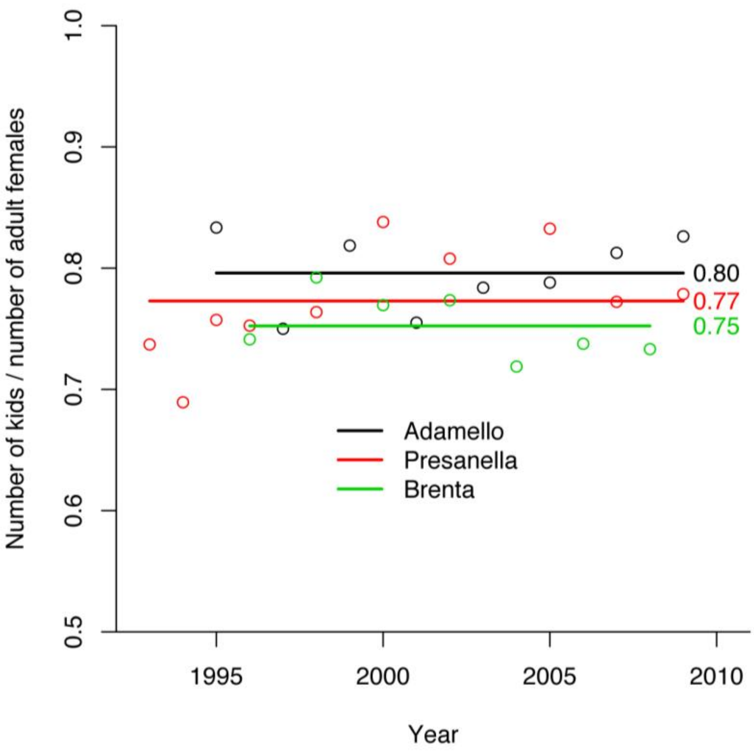

Fig. 6.1 Temporal variation in K:F from yearly censuses in the three study populations. Horizontal lines show mean values.

6.3.2 Field data

Between May 2011 and August 2012, abundance data were collected for different age-classes within valleys in two areas of the study region: Val Nambrone in Presanella and Val d'Ambiez in Brenta. In total, 41 surveys were performed in Presanella and 34 in Brenta. Chamois were observed on the morning of each survey day, between 6am and 10am, when they are most active (Pachlatko and Nievergelt 1985), from distances of 70 to 1000m using binoculars and a spotting scope. All visible chamois were recorded and classified as kids, yearlings, adult males or adult females, based on body size and horn length and shape (Knaus and Schröder 1983). This is possible in this species due to minimal overlap between age-classes in terms of size and horn-length and clear differences in horn morphology between adult males and females. Using these data, it was possible to calculate an estimate of kid survival, S_k, over the winter of 2011/2012. As in alpine ungulates in general, mortalities in this species are thought to occur predominantly during winter (Loison, Festa-Bianchet, et al. 1999). As such, an index of over-winter kid survival should broadly relate to annual kid survival. This estimate was calculated by comparing mean observed K:F in 2011, weighted by the sample size observed on a given survey, to the weighted mean observed ratio of yearlings to adult females (Y:F) in 2012 (i.e. the same cohort of juveniles; kids become classified as yearlings on 1st May of their second calendar year), as follows (Fig. 6.2):

$$\bar{S}_k(s) = \frac{\sum\left[K : F_{2011}(s,d).n_{2011}(s,d)\right] \Big/ \sum n_{2011(s,d)}}{\sum\left[Y : F_{2012}(s,d).n_{2011}(s,d)\right] \Big/ \sum n_{2012(s,d)}}$$

where $K{:}F_{2011}$(s,d) is K:F in a given site, *s*, on day *d* in 2011 and n_{2011} (s,d) is the total number of individuals observed on the same day. Similarly, $Y{:}F_{2012}$(s,d) is Y:F in a given site, *s*, on day *d* in 2012 and n_{2012} (s,d) is the total number of individuals observed on the same day. This method does not account for adult female over-winter survival; however, due to the high, stable nature of adult survival rates in most ungulate populations, variation in adult female survival has been shown to be a suitable denominator in this metric in other ungulates, not masking variation in juvenile survival (Harris et al. 2008). Unfortunately it was not possible to conduct field observations in Adamello, so there are no field estimates of S_k for this site.

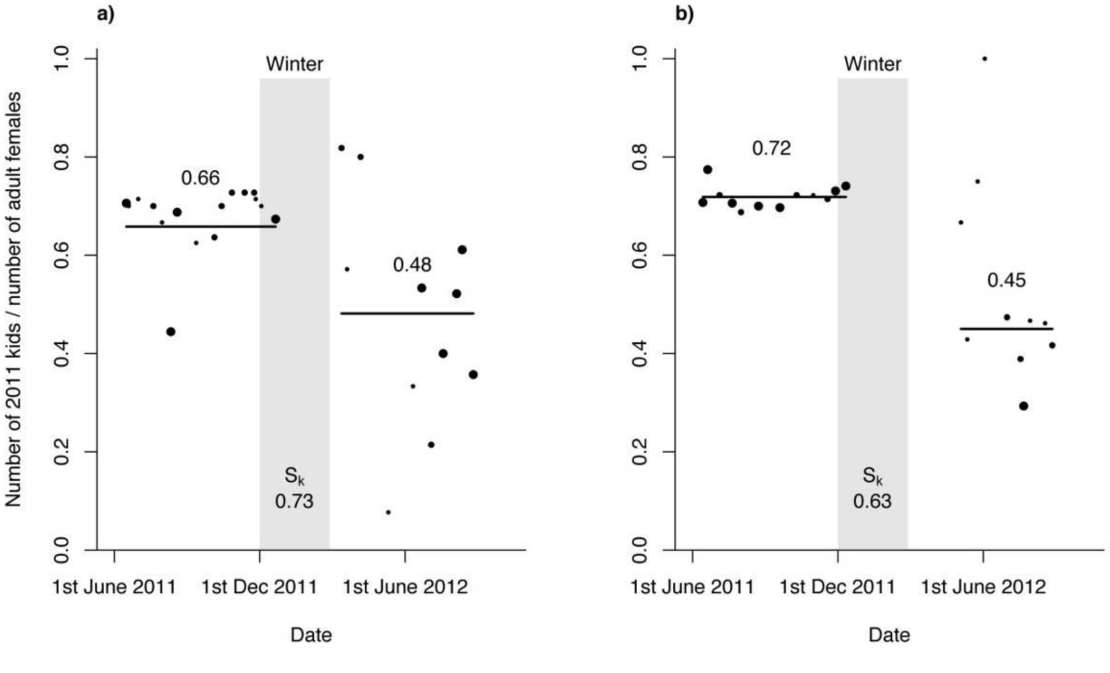

Fig. 6.2 Temporal variation in the observed ratio between kids born in 2011 and adult females before and after winter 2011/12 in **a)** Presanella and **b)** Brenta. Data points represent individual survey days and the sizes of these points signify the number of individuals observed during each survey. Horizontal lines are weighted mean ratio values before and after winter. Estimates of over-winter kid survival, S_k, derived from these values (as described above) are shown. Shaded grey areas show the approximate duration of winter (1st December – 1st March).

6.3.3 Climate and environmental data

Four climatic and environmental variables were identified that are likely to influence chamois population dynamics: maximum rate of spring green-up (derived from NDVI data, see chapter 5), mean growing season temperature (see chapter 5), population density (total population size from annual non age-structured census) and mean winter snow depth (calculated from local weather station data; Forecasts and Organization Office, Civil Protection and Infrastructures Department, Trento Province, Italy). Rate of green-up, population density and snow depth have all been previously demonstrated to be important for ungulate survival and fecundity (Helle and Kojola 2008, Pettorelli et al. 2007, Willisch et al. 2012). Similarly, results from chapter 5 highlighted the importance of growing season temperature to body condition in these chamois populations.

6.3.4 The population dynamics model

A model of chamois population dynamics was created, using age-structured census data and annual cull data (as described in chapter 2), also incorporating census estimates of fecundity, *F*, and field estimates of kid survival, S_k. Initial exploration of the data suggested contrasting demographic parameters among the three sites; as such, different parameter values for each site were considered. Initially, a model of site and age-specific survival and fecundity was created, consisting of up to five parameters which were constant across years: kid survival, S_k; yearling survival, S_y; adult female survival, S_f; adult male survival, S_m and adult female fecundity, *F*. Using these parameters it was possible to model the abundances of kids, yearlings, adult females and adult males. The number of kids, n_k, in year t+1 and site s, was calculated as

$$n_k(s,t+1) = \left(\left(n_f(s,t) - c_f(s,t)\right).S_f\right).F$$

where n_f is the number of adult females, c_f the number of females culled, S_f adult female survival and *F* adult female fecundity. The number of yearlings, n_y, was

$$n_y(s,t+1) = n_k(s,t).S_k$$

where n_k is the number of kids and S_k is kid survival. The number of adult females, n_f, was

$$n_f(s,t+1) = \left(\left(n_f(s,t) - c_f(s,t)\right).S_f\right) + \left(\left(\frac{n_y(s,t)}{2} - c_{yf}(s,t)\right).S_y\right)$$

where c_f is the number of females culled, S_f adult female survival, n_y the number of yearlings, c_{yf} the number of female yearlings culled and S_y yearling survival. Here, it is assumed that the sex ratio of yearlings prior to the cull is roughly 1:1 (this is the case in another chamois population; Corlatti 2007). The number of adult males, n_m, was

$$n_m(s,t+1) = \left(\left(n_m(s,t) - c_m(s,t)\right).S_f\right) + \left(\left(\frac{n_y(s,t)}{2} - c_{ym}(s,t)\right).S_y\right)$$

where c_m is the number of males culled, S_m adult male survival, n_y the number of yearlings, c_{ym} the number of male yearlings culled and S_y yearling survival. n_k, n_y, n_f and n_m were simulated for every year after the first age-structured census was performed in each site, using the abundance estimates from this census as the initial values of n_k, n_y, n_f and n_m. For every year after the initial year, abundances were simulated based on the predictions from the previous year rather than resetting the simulations using the observed abundances from the census. For each site, 20 different models were considered, each with a different, ecologically sensible combination of age and sex-specific demographic parameters, some of which were optimised and some of which were fixed estimates from field and census data, as shown in Table 6.1. During model fitting, data were only considered from years in which full age-structured censuses were performed. It was assumed that the variation in the abundance data in site s about the modelled mean is normally-distributed with variance $\sigma_{s.}$ Thus, the log-likelihood of the model parameters in site s, denoted $\boldsymbol{\theta}_s$, given all the data, was given by

$$LL(\theta_s) = \sum_a \sum_t \left(-\frac{1}{2}\ln(2\pi) - \ln(\sigma_s) + \frac{1}{2}\left(\frac{\bar{n}_a(s,t) - n_a(s,t)}{\sigma_s}\right)^2 \right)$$

where $\bar{n}_a(s,t)$ and $n_a(s,t)$ are the predicted and observed abundances of age-class a in site s and year t. For each site, the most parsimonious model was identified using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002).

Having established the most parsimonious models with parameter estimates fixed across years, models were then considered in which demographic parameters were allowed to vary with the four climatic and environmental variables. To establish climatic and environmental impacts on demographic parameters at a management-relevant spatial scale, the same environmental effects were fitted across all three sites. Variation in demographic parameters was modelled using the logistic function, combined with the logit function to bound parameters between 0 and 1. The value of a given demographic parameter p in site s and year t was calculated as follows

$$p_{s,t} = \frac{\exp \lambda_{s,t}}{1 + \exp \lambda_{s,t}}$$

where

$$\lambda_{s,t} = \ln\left(\frac{\overline{p}_s}{1 - \overline{p}_s}\right) + \beta.E_{s,t},$$

$\overline{p}_s$ is the mean value of a demographic parameter in site *s*, β is an area-wide linear effect on a given environmental predictor and $E_{s,t}$ is the value of a environmental predictor in site *s* and year *t*. Survival rates (S_k, S_y, S_f and S_m) and adult female fecundity (*F*) were allowed to vary linearly with $\lambda_{s,t}$ calculated from each of the four climatic and environmental variables. In total, 720 models were considered, each with a different combination of the six environmental predictors. The log-likelihood of the model parameters, denoted $\boldsymbol{\theta}$, given all the data, was given by

$$LL(\theta) = \sum_s \sum_a \sum_t \left(-\frac{1}{2}\ln(2\pi) - \ln(\sigma_s) + \frac{1}{2}\left(\frac{\overline{n}_a(s,t) - n_a(s,t)}{\sigma_s}\right)^2 \right)$$

where $\overline{n}_a(s,t)$ and $n_a(s,t)$ are the predicted and observed abundances of age-class *a* in site *s* and year *t*. The most parsimonious models were identified using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002, Richards 2008). Statistical analyses were performed using R version 2.15.3 (R Development Core Team 2012).

Table 6.1 A summary of the 20 different model types considered per site in the fixed annual parameter models. x indicates optimised parameters, * indicates fixed S_k estimates from field data and † indicates fixed F estimates from census data. K is the total number of optimised parameters per model.

<table>
<tr><th>Model</th><th>S_k</th><th>S_y</th><th>S_f</th><th>S_m</th><th>F</th><th>K</th></tr>
<tr><td>1</td><td>*</td><td></td><td>x</td><td></td><td>†</td><td>1</td></tr>
<tr><td>2</td><td colspan="2">*</td><td colspan="2">x</td><td>†</td><td>1</td></tr>
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6.4 Results

For the simplest models, with constant demographic parameter values across years, the most parsimonious models in all sites provide strong evidence for the presence of age-specific survival rates (Table 6.2). In Presanella and Brenta, the most parsimonious model contains kid survival estimated from field data. In Adamello, where there was no field estimate of kid survival, this parameter appears to be lower than in the other two sites. In all three sites, the most parsimonious model contains adult female fecundity estimated from censuses.

Table 6.2 Demographic parameter estimates from most parsimonious model in each site. S_k is kid survival, S_y is yearling survival, S_f is adult female survival, S_m is adult male survival and F is adult female fecundity. * indicates survival estimates derived from field K:F values and † indicates fecundity estimates derived from census K:F values. Mean and standard deviation (σ) of parameter values across sites are shown.

	Adamello	**Presanella**	**Brenta**	**Mean**	$\boldsymbol{\sigma}$
S_k	0.56	0.73*	0.63*	0.64	0.09
S_y	0.95		0.77	0.82	0.12
S_f		1.00	0.95	0.97	0.03
S_m			1.00	0.98	0.03
F	$0.80^{\dagger}$	$0.77^{\dagger}$	$0.75^{\dagger}$	0.77	0.03

In one case, Brenta, there is evidence for sex specific survival, with adult male survival being higher than adult female survival. In all sites, predicted adult survival rates are very high, suggesting that natural mortality rates (i.e. mortality not from hunting) are extremely low in these populations. Strikingly, when mean age-specific mortality rates inferred from the best models (i.e. mortality from natural causes, as the annual cull is included in the model) are compared to the mean proportion of each age-class culled each year, there are strong differences in the relative contributions of these sources of mortality among age-classes (Fig. 6.3). Whilst kid mortality is solely due to natural processes, a large proportion of yearlings are culled each year, which in two of the sites (Adamello and Brenta) results in mortality from the cull being higher than natural mortality in this age-class. Due to this heavy harvesting regime, and generally high natural mortality, as much as 57% of this age-class (in Presanella) can die each year. In adults, the cull accounts for an even greater proportion of mortality, for instance, for males in Brenta, the models predict that over 99.9% of mortality is due to the annual cull.

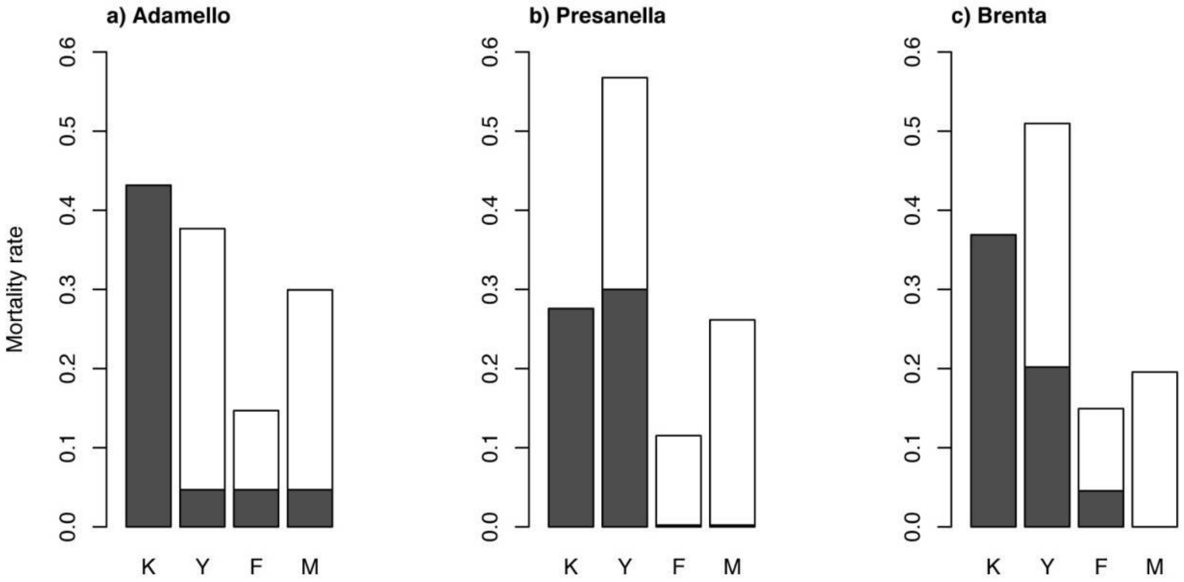

Fig. 6.3 The mean relative contributions of the annual cull (white bars) and natural mortality (grey bars; inferred from predicted survival rates from the best model) to annual mortality rates in kids (K), yearlings (Y), adult females (F) and adult males (M) in the three study populations.

Models allowing demographic parameters to vary with climatic and environmental conditions capture the general, long-term, population trends in the three study sites (Fig. 6.4). There is strong evidence for the impact of climatic and environmental variation on demographic parameters; the null model, without climate effects, performs considerably worse than the best models (Table 6.3, Fig. 6.5). There is strong evidence for negative effects of population density and mean growing season temperature on survival. There is slightly weaker evidence for a negative effect of growing season temperature and a positive effect of mean winter snow depth on female fecundity.

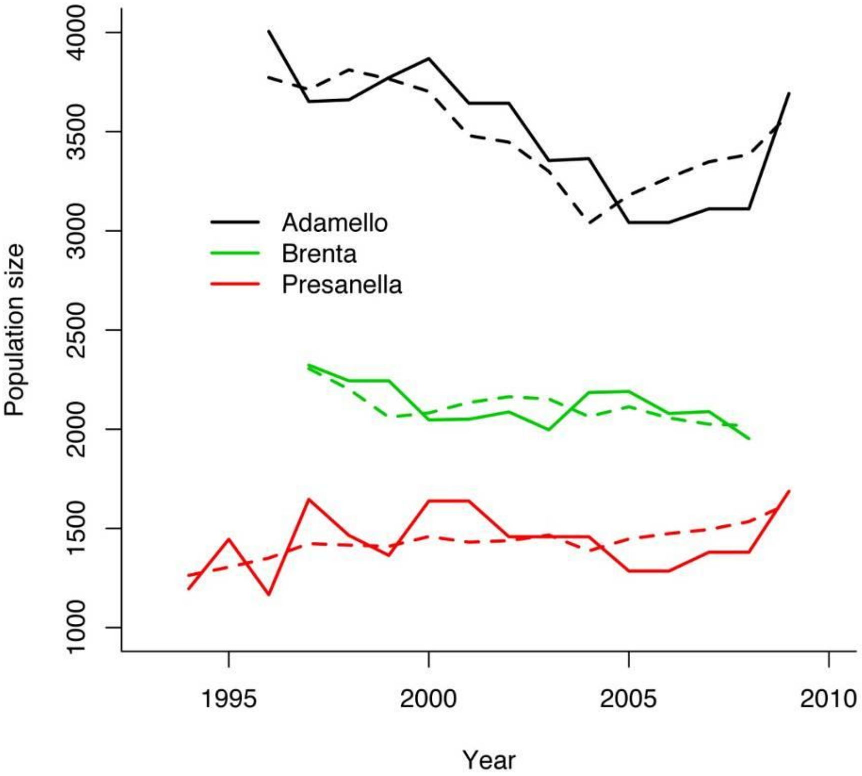

Fig. 6.4 Annual variation in observed (solid lines) and predicted (dashed lines) population sizes in the three study areas. Observed population size is from the annual non-age structured census. Predicted population size is produced using the most parsimonious model incorporating environmental variation across all sites (see Table 6.3).

Table 6.3 Model selection results from population models fitted with different combinations of environmental predictors (maximum rate of spring green-up (Rate), population density (Density), mean growing season temperature (Temp) and mean winter snow depth (Snow)) across all three sites. Standardised coefficient values are shown for each environmental predictor. Maximum log-likelihoods (LL) are shown for each site, as well as across all sites, alongside K (the total number of optimised parameters in a model) and ΔAIC values. Only the most parsimonious models (those with a ΔAIC value that is ≤6 and lower than all simpler nested versions (see Richards 2008)) and the null model (model 5) are displayed.

				Model		
		1	**2**	**3**	**4**	**5 (null)**
Fecundity	**Rate**					
	Density					
	Temp	-0.12		-0.11		
	Snow	0.18	0.17			
Survival	**Rate**					
	Density	-0.16	-0.16	-0.14	-0.14	
	Temp	-0.19	-0.21	-0.19	-0.20	
	Snow					
Adamello	**LL**	-160.8	-161.7	-160.6	-161.6	-162.6
Presanella	**LL**	-191.6	-192.0	-193.3	-193.7	-196.9
Brenta	**LL**	-121.8	-121.7	-122.6	-122.2	-125.1
	K	13	12	12	11	9
All	**LL**	-474.2	-475.4	-476.5	-477.5	-484.6
	ΔAIC	0.0	0.4	2.4	2.5	12.8

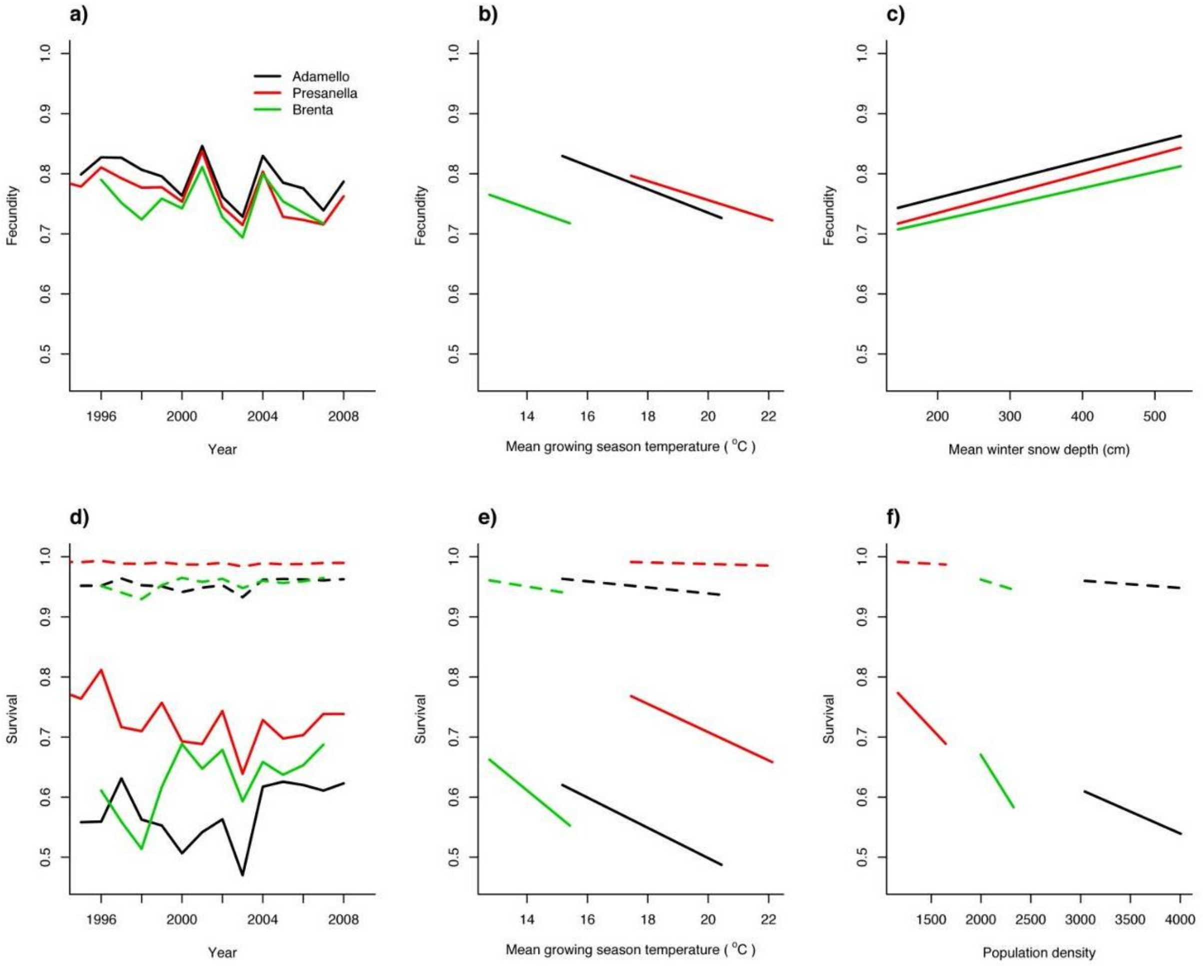

Fig. 6.5 Variation in demographic parameters with time (**a** & **d**) and climatic and environmental factors (**b**, **c**, **e** & **f**) in the three study populations. Top panels show variation in fitted adult female fecundity, *F*, with **a)** time, **b)** mean growing season temperature and **c)** mean winter snow depth. Lower panels show predicted kid survival, S_k (solid lines) and adult female survival, S_f (dashed lines) with **d)** time, **e)** mean growing season temperature and **f)** population density. The most parsimonious model (see Table 6.3) was used to calculate fitted values.

6.5 Discussion

This analysis reveals intriguing effects of both climate and hunting on chamois population dynamics. In contrast to juvenile age-classes, there is extremely low natural mortality in adults, virtually zero in some populations (Fig. 6.3). I propose that this phenomenon could be driven by high hunting mortality, which appears largely to replace natural mortality in some of the populations. Climate also exerts an influence on demography; survival, particularly in juveniles, is negatively affected by both growing season temperature and population density (Fig. 6.5 d-f). The fecundity of adult females is also influenced negatively by growing season temperature, but is higher following winters with deeper snow (Fig. 6.5 a-c). I will now discuss these findings in greater detail, particularly referring to potential consequences of climate change on the demography of harvested species such as chamois.

In common with most mammals (Caughley 1966), there is strong evidence for age-specific patterns of survival. In ungulates, young individuals tend to have lower survival rates due to smaller energy reserves, higher metabolic requirements and a higher sensitivity to environmental fluctuations (e.g. Jorgenson et al. 1997, Loison, Festa-Bianchet, et al. 1999). Here, in general, juvenile survival is considerably lower than adult survival (Table 6.2). In stark contrast, adult survival rates (ignoring mortality due to harvesting) in these populations appear to be extremely high (at least 0.95). Indeed, the vast majority of adult mortality results from the annual cull, particularly in Presanella and Brenta (Fig. 6.3). In Brenta, there is evidence for sex-specific adult survival, with male survival being higher than female survival (Table 6.2). This might appear surprising, given the high allocation of energy to reproduction by males prior to winter (see chapters 3 and 4). However, there is recent evidence suggesting that high reproductive effort does not necessarily result in high mortality in male ungulates (Lemaître and Gaillard 2013). One potential explanation for the higher survival of males than females in Brenta relates to the previous finding that males have a slower pace of life in this site, gradually increasing reproductive effort across life (chapter 3; Mason et al. 2011). A lower hunting pressure on males in Brenta (mean proportion of adult males harvested per year (from census years): Adamello, 32.3 ± 1.5%; Presanella, 29.5 ± 2%; Brenta, 25.2 ± 1.6%), and a more balanced cull between the sexes, could be driving this life-history strategy and high male natural survival in this area.

Hunting could also be driving the observed patterns of low natural mortality (in both sexes) directly rather than indirectly via effects on life-histories. Natural mortality rates in adult ungulates are generally low, on average 0.12 in males and 0.07 in females (Toigo and Gaillard 2003), however natural adult mortality in these populations is particularly low: between 0.05 and ≈0 in males and females. I propose that this might is caused by high hunting pressure on yearlings and adults, reducing the probability of mortality due to natural causes. Mean life-expectancies in these populations are very short; 3.3-3.7 years in males and 5.7-6.1 years in females (see chapter 3). These are considerably shorter than estimates from another, non-hunted, chamois population where males and females live on average 6.8 years and 7 years, respectively (Bocci et al. 2010). By reducing natural life-expectancies so dramatically, hunting may be largely replacing natural mortality in the study populations. To my knowledge, such a phenomenon has not been reported previously. In fact, there is some evidence, from both males and female ungulates, that high hunting mortality can lead to heightened natural mortality due to higher investment in reproduction early in life (Singer and Zeigenfuss 2002, Toigo et al. 2008). An alternative explanation for the observed patterns is that high harvesting intensity could result in reduced natural mortality due to the removal of lower quality individuals from these populations. However, the potential for hunters to select high quality individuals is limited in this study area, as previously discussed (see chapter 2).

The estimates of juvenile survival are broadly consistent with those found by longitudinal studies of chamois, or slightly higher than in these unhunted populations (e.g. mean kid survival: Adamello, 0.56; Presanella, 0.73; Brenta, 0.63; Loison et al. 1994, 0.58 , Willisch et al. 2012, 0.52). Similarly, estimates of fecundity, which vary on average between 0.75 and 0.8 (see Fig. 6.1), are in line with estimates from studies on other chamois populations, where rates have been found to vary between 0.71 and 0.86 (Corlatti 2007, Levet et al. 1995). The results provide support for the use of juvenile to female ratios to infer juvenile survival and adult female fecundity: estimates of kid survival and adult female fecundity derived from kid to female ratios were selected in the most parsimonious models in all cases where they were available (Table 6.2). Previously, the use of age-ratios to infer demographic parameters has been criticised because, in certain species, the visibility of juvenile ungulates can vary seasonally, resulting in misleading estimates of survival and fecundity (Bonenfant et al. 2005). However, if applied in suitable habitats and at sensible times of the year, age-ratios can still be an important tool for determining productivity and juvenile survival in ungulate populations. In these populations of chamois, each spring adult females and kids form large, visible groups, grazing on areas of high-altitude grassland. This means that, once the birthing season has finished at the start of June, these groups can be easily surveyed. Similarly at this time of year, yearlings are visible and easily recognisable, allowing the survival rate of a given cohort to be estimated. In further support of these K:F estimates, K:F remained constant prior to winter 2011, suggesting the detectability of kids did not change during this period (see Fig. 6.2). This is unless there was a concurrent increase in detectability and decrease in kid numbers, the former of which is unlikely given that chamois groups are already occupying open habitat at this time.

There was strong evidence for effects of climatic and environmental factors on survival and fecundity (Table 6.3, Fig. 6.5). Interestingly, the results suggest an important effect of both spring/summer and winter climatic conditions on chamois population dynamics. When demographic parameters were allowed to vary with climatic and environmental predictors, all four models in the top model set contained negative effects of mean growing season temperature and population density on survival. The model predicts kid survival to be much more variable with climate than the survival of older age-classes is (Fig. 6.5). This is consistent with the general pattern of variable juvenile survival but constant adult survival in large herbivores (Gaillard et al. 1998). There is also evidence, albeit weaker, for an influence of climate on fecundity; the most parsimonious model contains a negative effect of growing season temperature and a positive effect of winter snow depth on fecundity. The presence of a negative effect of temperature during spring and summer on both survival and fecundity is intriguing given that I have previously found a negative relationship between temperature at this time and body mass in juveniles in these populations (see chapter 5). Previously, I hypothesised that in warmer growing seasons individuals might spend less time foraging due to higher thermoregulatory costs, limiting their ability to acquire resources to allocate to growth and thermoregulation (see chapter 5). In several northern ungulates, positive relationships have been found between body condition and both fecundity (Saether and Haagenrud 1983, Sand 1996) and survival (Berube et al. 1999, Loison, Langvatn, et al. 1999). The same could be true here: in warmer years, individuals may be smaller and have less resources to allocate to reproduction and to over-winter survival.

Survival also appears to be negatively affected by population density, a common finding for ungulate species (e.g. Festa-Bianchet et al. 2003, Fowler 1981, Portier et al. 1998). At higher population densities, higher levels of intra-specific competition can lead to a reduction in per-capita food intake and, thus, fewer resources for individuals to devote to thermoregulation during winter (Skogland 1985). Again, I have previously highlighted a negative link between population density and body mass in these populations, adding weight to these findings (see chapter 5). Surprisingly, and in contrast to previous studies (Loison, Jullien, et al. 1999b, Willisch et al. 2012), there was no evidence for a negative effect of winter snow depth on survival in chamois. Intriguingly, though, results suggest a positive effect of snow depth on fecundity (Table 6.3). In other ungulates, deeper snow is thought to influence survival and fecundity negatively, due to higher locomotion costs and difficulty in accessing forage (Jacobson et al. 2004, Post and Stenseth 1999). However, in these populations of chamois, a species which is well adapted to locomotion in deep snow due to having an inter-digital membrane which spreads their body weight over a larger surface area (Couturier 1958), this does not appear to be the case. Furthermore, following snowy winters, spring foraging conditions may be improved due to a longer and more variable snowmelt, resulting in greater spatial variability in the timing of emergence of nutrient-rich vegetation (Crawley 1983, Jacobson et al. 2004, Mysterud, Langvatn, et al. 2001, Post and Stenseth 1999). Indeed, slower rates of green-up during spring have been shown to affect body mass positively in other ungulate species (Pettorelli et al. 2007); this could have a positive effect on fecundity. However in these study populations, evidence for such an effect on body mass is weak and ambiguous (see chapter 5).

This study highlights the potential impacts of changing climatic conditions during different seasons on chamois population dynamics. Most importantly, high temperatures during spring and summer appear to influence both survival and fecundity negatively in this species, possibly mediated by effects on body condition. Given that I have already identified striking body mass declines in these populations, which are correlated with growing season temperatures (see chapter 5), the potential for impacts of climate change on chamois population dynamics appears high. In the European Alps, both temperatures during spring and summer and levels of precipitation during winter are predicted to increase significantly in the future (Beniston et al. 1995). As such, wildlife managers in this region will need to monitor carefully how this climate change influences variation in demographic parameters. This will be particularly important in heavily harvested populations where it may be necessary to adjust levels of hunting pressure as survival and fecundity rates are altered in the future.

Chapter 7

Climate change, inter-specific interactions and the foraging behaviour of female chamois

7.1 Abstract

The underlying behavioural mechanisms of climate-driven ecological change are poorly understood. Interactions with other species can strongly influence behaviours, particularly at fine temporal and spatial scales, and can significantly ameliorate or exacerbate climate-driven effects. To date, the effect of inter-specific interactions on behaviour has been overlooked in projecting potential responses of species to climate change. Here, I investigate the relative influences of ambient temperature and an interaction with domestic sheep (*Ovis aries*) on the summer foraging behaviour of an alpine ungulate, the chamois. Using data on female chamois activity budgets and daily patterns of altitudinal migration by chamois groups, variation in these behaviours was modelled in relation to temperature and the presence of sheep. There was evidence for a moderate time-independent effect of temperature: chamois forage less and migrate further upslope when it is hotter. Strikingly, chamois behaviour was strongly disturbed by the presence of sheep, pushing their mean daily altitudinal range 82-110m upslope. Across the European Alps, this range-shift would correspond to a dramatic 83% decrease in the availability of suitable foraging habitat. This is considerably more pronounced than the 7-38m mean upslope shift in altitude use predicted in response to a mean 5°C summer temperature increase, the most extreme 2100 climate scenario for the region. These results highlight an important role of inter-specific interactions in determining the realised niche of species in mountainous environments. Modelling range-shift responses to climate change without considering the influence of biotic interactions on behaviour is likely to result in spurious projections, particularly at small spatial scales. These findings also highlight that controlling certain species, in this case the careful management of livestock, could be an important strategy for mitigating the impacts of climate change on threatened species affected adversely by competition or disturbance. Additionally, this study reveals that upslope migration could be less important for montane species affected by climate change than previously thought; changes to activity budgets could also play an important role. It appears that, without long-term behavioural adaptation, montane species may be unable to track the upslope movement of their thermal niches under future climate change.

7.2 Introduction

Climate change has caused well-documented changes to the distribution (e.g. Hickling et al. 2006, Perry et al. 2005), phenology (e.g. Menzel et al. 2006, Thackeray et al. 2010), morphology (e.g. Gardner et al. 2011, Sheridan and Bickford 2011) and demography (e.g. Ozgul et al. 2010, Thompson and Ollason 2001) of populations. However, in many cases, little is known about the nature of the behavioural changes underlying these responses. Many animals display diurnal behavioural rhythms strongly entrained to environmental cues, such as variation in light intensity and ambient temperature, which are important in controlling the energy balance of a species (Aschoff 1979). In order to make detailed predictions about how species will respond to climate change, it is important to understand the effect of a warming climate on such behavioural patterns. Models linking behavioural routines and climate are uncommon (Dunbar 1998, Dunbar and Shi 2012, Korstjens et al. 2010) and to date have been focused on single species, not accounting for inter-specific interactions, which can explain the absence of species from large portions of their fundamental niche (Connell 1961, Davis, Lawton, et al. 1998, Silander and Antonovics 1982).

Predicting how behavioural patterns will be altered in the future is difficult because there may be long-term behavioural adaptation to climate and environmental change, through phenotypic plasticity (Przybylo et al. 2001) or microevolution (Reale et al. 2003), which are not evident in current conditions. Ultimately, to predict how populations adapt to a changing climate requires long-term observational data (e.g. Clutton-Brock and Pemberton 2004) or experimental studies (e.g. Ayrinhac et al. 2004). However, for most populations, long-term behavioural data are not available and, for many, experimentation is not feasible. In such cases, studies of the current relationship between behaviour and climate can shed light on the plasticity of a species' behavioural response to climatic variation and this has been used to predict future behavioural change (Dunbar 1998, Korstjens et al. 2010, Lehmann et al. 2008). However, it is unclear how short-term patterns of behavioural variation will translate into long-term change. Techniques that predict future temporal change in ecological traits based on spatial patterns of ecological variation are similarly limited; spatial variation may not translate into temporal change (e.g. Lawler et al. 2006, Thuiller 2004). Nevertheless, such approaches have been used to infer whether phenotypic plasticity alone is sufficient for populations to remain in equilibrium with climate (Phillimore et al. 2010). Studies conducted over short time-scales could also be applied to this end, identifying whether a different mechanism of long-term adaptation, such as microevolution, will be required for populations to keep track with climate change.

In endotherms, temperature has been shown to exert a strong influence over the timing and allocation of reserves to vital behaviours such as foraging, resting and moving between habitat patches (Dunbar 1992b, Korstjens et al. 2010). In many species, individuals adjust their behavioural patterns depending on ambient temperature as a form of behavioural thermoregulation, which is generally thought to be less energetically expensive than autonomic thermoregulation (Dussault et al. 2004, Maloney, Moss, Cartmell, et al. 2005). Behavioural thermoregulation can entail reducing activity during the hottest parts of the day (Aublet et al. 2009), moving to cooler areas such as higher altitudes (Aublet et al. 2009) or areas in shade (Wolf 2000), or actively performing heat-dissipation behaviours, such as wing spreading in birds (du Plessis et al. 2012). Performing such behaviours can lead to a reduction in foraging efficiency (du Plessis et al. 2012). The ability of species to forage effectively in a changing climate, acquiring sufficient resources for growth and survival, will be crucial to the persistence of populations in the future. Reductions in body size in response to a changing climate, which have been observed across a range of taxa, have largely been attributed to changes in the availability and quality of resources (Gardner et al. 2011). However, reductions in the ability of animals to forage effectively may also influence body condition (see chapter 5), which in turn could affect fecundity and population dynamics (Ozgul et al. 2009, Ozgul et al. 2010).

Measuring the activity budgets of species, how much time they allocate to different behaviours, can be useful for establishing how species moderate their behaviours in different climates. Activity budget models have been shown to predict the distributions of species, by identifying the climatic conditions in which they are able to devote enough time to performing vital activities such as foraging and resting (Korstjens et al. 2010, Lehmann et al. 2008). In environments where activity budgets are limited by climate, for example if there is a negative effect of high temperatures on foraging, models can be used to predict the responses of species to climate change (e.g. Dunbar 1998). Linking these models to incorporate other aspects of behavioural thermoregulation, such as daily migratory patterns, would improve our understanding of the relationship between behaviour and temperature, allowing us to make more accurate predictions about behavioural responses to climate change. This can be explored in mountainous environments, where many species undergo daily migration to higher altitudes at the hottest part of the day, during spring and summer (e.g. Aublet et al. 2009). Long-term altitudinal range shifts have already been recorded in many species, driven by temperature increases (Chen et al. 2011). Understanding the influence temperature exerts over daily migration patterns, as well as activity budgets, could help us understand how long-term temperature increases might affect the altitudinal ranges used by species in the future.

Behavioural routines can be influenced by a range of non-climate factors, including the availability of resources (e.g. Lehmann et al. 2008), population density (e.g. Mobaek et al. 2008) and interactions with other species (e.g. Wauters et al. 2001). Such factors need to be considered when making predictions under climate change. Inter-specific interactions, in particular, exert an important influence on range-shifts under climate change (Araujo and Luoto 2007, Suttle et al. 2007, Van der Putten et al. 2010). For tightly linked species, for example insects and host plants, the effect of biotic interactions can be stronger than climate effects on populations (Araujo and Luoto 2007) and can even reverse the effects of climate change (Suttle et al. 2007). However, the role of generalistic interactions has been overlooked. Inter-specific interactions may prove particularly important in mountainous environments, as climate change pushes populations upslope into an ever diminishing area of habitat (Chen et al. 2011), potentially bringing different species into competition. For instance, in guilds of mountain ungulates, where there is often a high degree of dietary overlap among species (Bertolino et al. 2009), upslope migration due to climate change could result in a higher degree of range overlap than in the present and an increase in competition for resources. Indeed, competitive exclusions among mountain ungulate species are thought to have caused local extinctions in the past (Mishra et al. 2006). If competitive interactions exclude populations from parts of their fundamental niche, ignoring them would lead to significant errors in future projections of spatial ranges, particularly at small spatial scales.

Here, I study the effects of temperature and inter-specific interactions on the diurnal foraging behaviour of Alpine chamois during the summer. I evaluate the roles of different behaviours: activity budgets and altitudinal migration. Ungulates typically show pronounced levels of behavioural thermoregulation, devoting more time to resting and rumination, and less time to foraging, during the hottest part of the day (Green and Bear 1990, Shi et al. 2003). When temperatures get too high, these rhythms can even be interrupted altogether; in chamois, normal feeding behaviour ceases at temperatures of 28-32^{o}C (Hamr and Czakert 1986). In mountainous environments, ungulates also behaviourally regulate their temperature during summer by migrating to higher altitudes during the middle of the day (Aublet et al. 2009). There is some evidence that chamois behaviour can be affected by other ungulate species; for example, introduced mouflon are thought to have displaced chamois in some areas of the Pyrenees (Gonzalez 1987). Furthermore, Alpine chamois actively avoid other ungulate species, moving to sheltered areas if mouflon or domestic sheep are present (Chirichella, Ciuti and Apollonio 2013). I investigate how variation in temperature and the presence of domestic sheep (*Ovis aries*) influence chamois activity budgets and altitudinal migration, using structural equation modelling (SEM) to investigate the interplay between temperature, inter-specific interactions, altitude use and time spent foraging. Using these relationships, I make inferences about the potential influence of climate change on chamois behaviour and the relevance of biotic interactions.

7.3 Materials and methods

7.3.1 Study area

The study area is Lauson, located in Cogne valley, Gran Paradiso National Park, Italy (GPNP; 45°34' N, 7°18' E) (Fig. 7.1). The area contains a population of approximately 200 alpine chamois. The summer altitudinal range of chamois here is between 1,600m and 3,200m above sea level, with groups of females and kids generally occurring from 2,500m upwards. Above the tree-line (at approximately 2,200m), the area is characterised by alpine meadows, open rock faces, moraines and scree slopes. Chamois in GPNP are protected from hunting and have few natural predators.

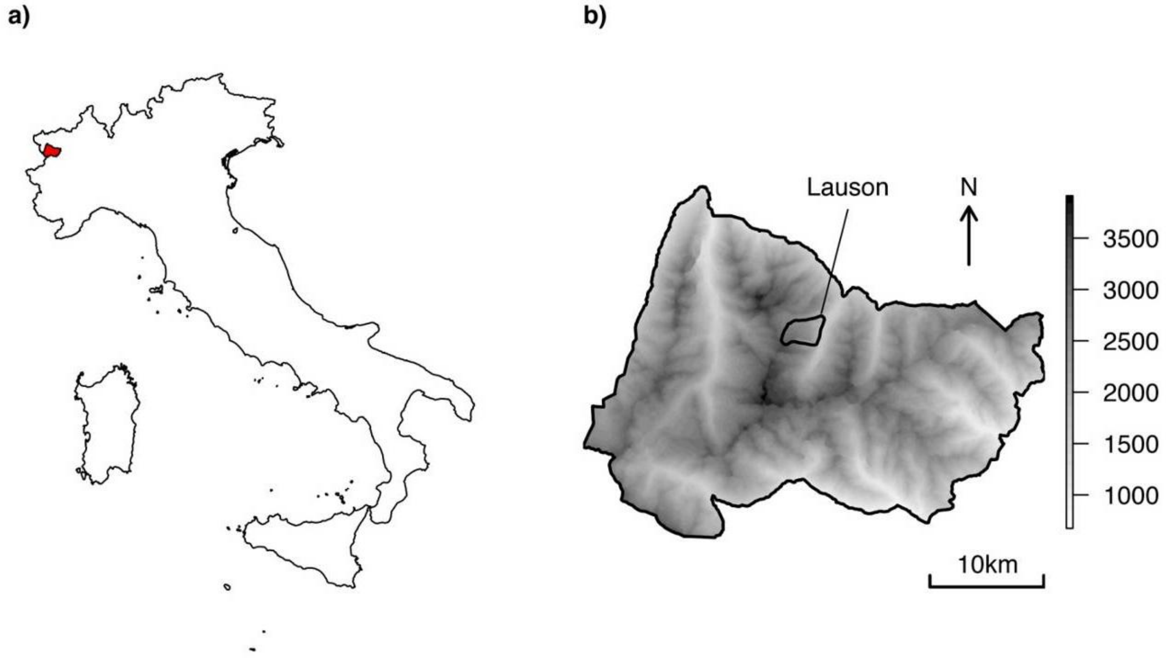

Figure 7.1 Map of **a)** Italy, indicating the location of GPNP in red, and **b)** GPNP, displaying the location of the study area, Lauson. Shading indicates altitude in metres.

7.3.2 Data collection

A population of unmarked individuals (mean group size, 21.6 ± 0.3), predominantly females and kids, was monitored between the 29th June and the 25th July 2012. The study was conducted over this period to coincide with the introduction of livestock into the area, occurring approximately halfway through the study. On the 12th July, a flock of roughly 100 domestic sheep, intermittently associated with shepherds and sheep-dogs, was introduced to the lower altitudes of the valley (approximately 2,250-2,400m) and remained there throughout the rest of the study period. This created two treatment periods over which to investigate the effect of inter-specific interactions: sheep-absent (13 days) and sheep-present (14 days). The study was constrained to this period in order to reduce the potential of seasonal variation in behaviour, climate and resource availability between the two treatments.

Chamois were observed across a range of different times each day, between 6am and 8.30pm, from distances of 30 to 300m using binoculars and a spotting scope. At five minute intervals, instantaneous scan samples (Altmann 1974) were performed and the activities of all visible individuals were recorded. Activities were classified as resting, standing, moving, foraging and 'other' (drinking, salt-licking, urinating and defecating). In total, 914 scans were performed during 78 observation hours. Simultaneously with each scan sample, the local air temperature ($Temp_{local}$) was recorded using two Gemini TinyTalk TK-0014 data-loggers placed near to the location of the observed group. One of these was wrapped in foil and placed in the shade, to reduce the effect of direct solar radiation (hereafter 'screened temperature') and one was exposed to direct solar radiation (hereafter 'unscreened temperature'). Screened and unscreened temperatures were recorded to provide insight into the relative roles of ambient temperature and solar radiation in thermoregulation. Both are thought to play a role in mammalian heat exchange (Porter et al. 2000), however their relative importance is likely to vary among different species and environments. Screened temperature data were also recorded from a fixed altitude location in the study area at 2,700m ($Temp_{fixed}$), which could be related to daily variation in chamois altitude usage. The mean altitude of the group's location at each time interval was located on a 1:25,000 map of the study area.

7.3.3 Statistical analysis

Mean activity budgets were determined for adult females, adult males, yearlings and kids by calculating the proportion of all observations of individuals partaking in each activity across the whole study period (Fig. 7.2). For adult females (2 years and older), the sex- and age-class for which there were most data, I investigated variation in time spent foraging and altitude use.

SEMs were applied, using the 'lavaan' package in R (Rosseel 2012), to model the interplay between foraging behaviour, altitude use, temperature, time of day and an interaction with sheep. SEM is a multivariate modelling approach which allows for collinearity among predictors. Models were fitted to examine the effects of up to 14 predictors on three response variables: altitude, local temperature and time spent foraging (see Fig. 7.3). Time of day was converted to minutes and so varied between 390 (6.10am) and 1,230 (8.30pm). Mean time spent foraging by all adult females in each scan sample was calculated, and assigned a weight based on the number of individuals observed. Time spent foraging was bounded between 0 and 1 and was z-transformed to remove this truncation. Based on *a priori* expectations and some preliminary data exploration, quadratic effects of time of day on all three response variables were allowed. All other predictors had linear effects.

Models were considered with all ecologically sensible combinations of predictors. Models were considered using either screened or unscreened temperature as the local temperature variable ($\mathrm{Temp}_{\mathrm{local}}$). In total, 1,321 different models were fitted. To assess model performance the root mean square of error approximation (RMSEA) was used, a commonly applied goodness-of-fit test for assessing SEMs (Chen et al. 2008). In SEM, model fit is determined by comparing the observed variable covariance matrix to the modelled covariance matrix. Models were considered with non-significant RMSEA p-values, i.e. where the observed and modelled covariance matrices did not differ significantly, as acceptable. Next, of these models, the most parsimonious ones were identified using AIC, considering models with a ΔAIC of ≤ 6 and lower than the ΔAIC of all simpler nested models as most parsimonious (Richards 2008).

In order to make projections into the future, future temperature change was simulated by increasing the fixed-altitude temperature observations ($\mathrm{Temp}_{\mathrm{fixed}}$) by 5°C, the most extreme mean temperature increase during summer predicted for the region by 2100 (IPCC 2007). For all other predictors the data observed during the study were used. Predictions of future time spent foraging and altitude use were made using the most parsimonious model (Table 7.1). To estimate uncertainty in future predictions, this model was fitted to 1000 bootstrapped replicates of the data to determine 95% confidence intervals (Efron and Tibshirani 1991).

Next, the area of available foraging habitat was calculated for the summer altitudinal ranges predicted by the most parsimonious model, both in the present and for 2100. Unfortunately, fine-scale predictions of changes to the distribution or productivity of forage vegetation as a result of climate change do not exist, so it was assumed that land-cover did not change between the present and 2100. The area of available foraging habitat was estimated using the Corine land-cover 2006 data-set at 100m resolution (EEA 2010b) and digital elevation data at 90m resolution from the Shuttle Radar Topography Mission (Jarvis et al. 2008). Altitudinal ranges were defined by the upper and lower bounds of confidence intervals of predicted altitude use, across all times of day. Predictions were made across the entire range of the species, which encompasses the whole of the European Alps (Shackleton 1997). For the altitudinal ranges predicted by the model, the predominant land-cover classes present are bare rock, glaciers/perpetual snow, natural grassland and sparsely vegetated areas. Potential foraging habitat was defined as the area covered by either natural grassland or sparse vegetation. Statistical analyses were performed using R version 2.15.3

(R Development Core Team 2012).

7.4 Results

Adult male, adult female and yearling chamois display very similar activity budgets (Fig. 7.2), spending 48-52% of their time foraging, 27-33% resting, 11-13% standing, 5-9% walking and the remainder of their time in other behaviours. In contrast, kids spend considerably less time foraging (23%) and more time resting (53%).

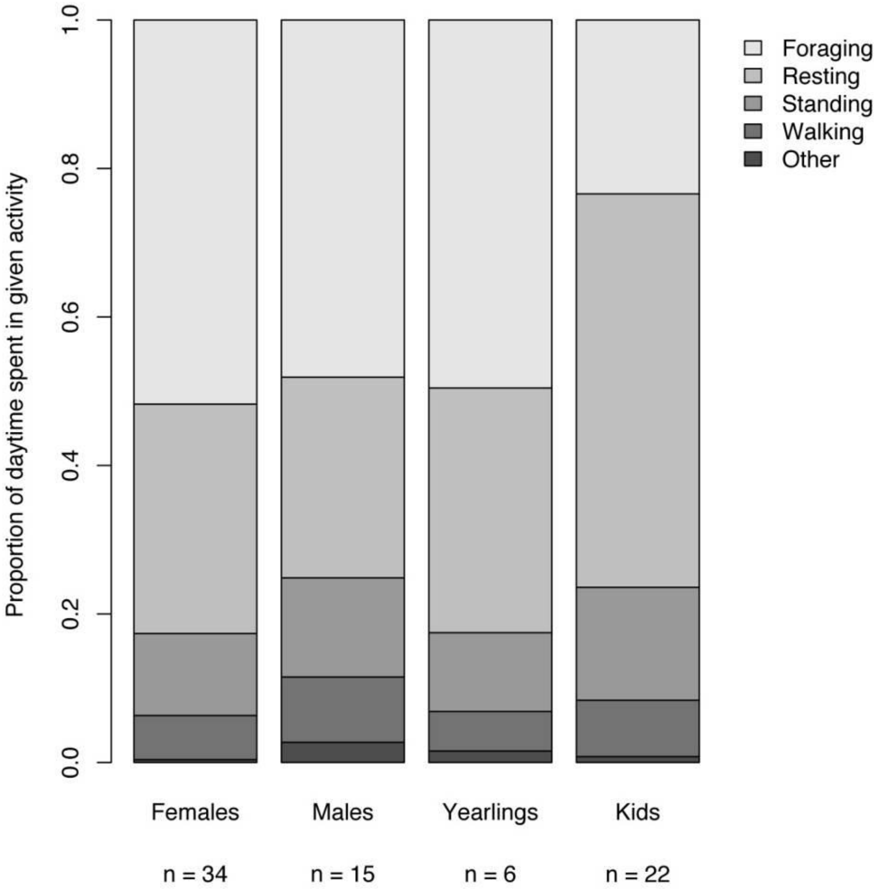

Figure 7.2 The average activity budgets of different sex- and age-classes. Estimates of sample size (n) are the maximum number of individuals in a given sex- and age-class recorded in a single scan-sample.

Table 7.1 Most parsimonious model. R^2 values, number of model parameters (K) and RMSEA ± 95% confidence intervals are shown. Coefficient values are standardised. The response variables are altitude use (Altitude), local temperature ($\text{Temp}_{\text{local}}$) and time spent foraging (Foraging).

Response	Altitude	$\text{Temp}_{\text{local}}$	Foraging
Time of day	1.9	2.6	-2.2
Time of day^2	-1.8	-2.8	2.2
Sheep	1.3		
$\text{Temp}_{\text{fixed}}$	0.2	0.4	
$\text{Temp}_{\text{local}}$			-0.3
Altitude		-0.1	0.1
Group size			
R^2	0.60	0.47	0.31
K		32	
RMSEA	0.077 (0.046-0.111)		

One model outperformed all others; there were no simpler nested versions within 6 ΔAIC (see Table 7.1, Fig. 7.3). This model fitted the observed data well, as shown by a non-significant RMSEA value (Table 7.1). R^2 values for each response variable are relatively low, particularly for time spent foraging (Table 7.1); however, this is unsurprising due to the high variability between individual samples in the response variables, particularly time spent foraging. The model performs well in predicting variation in mean time spent foraging (Fig. 7.4 a-b) and mean altitude use (Fig. 7.4 c-d), both with time of day and temperature.

There is strong evidence for a quadratic effect of time of day on female chamois foraging behaviour (Table 7.1, Fig. 7.4 a & c). Females spent a high proportion of their time foraging early in the morning, this proportion decreases to its lowest point in the middle of the day before increasing again to high levels in the evening (Fig. 7.4a). Similarly, chamois groups showed a strong diurnal pattern of altitudinal variation, moving from lower altitudes in the morning to high altitudes in the middle of the day and descending to lower altitudes again in the evening (Fig. 7.4c). There is also strong evidence for an effect of temperature on both time spent foraging and altitude use (Table 7.1, Fig. 7.4 b & d). At higher temperatures, females spent less time foraging and moved to higher altitudes. Interestingly, unscreened temperature was a better predictor of foraging behaviour than screened temperature, being the local temperature variable ($\text{Temp}_{\text{local}}$) selected in the best model to explain variation in time spent foraging. There is no evidence for an effect of group size on activity budgets, suggesting an absence of pronounced density dependent effects (Table 7.1).

Strikingly, the presence of sheep shifted the mean altitudinal range used by chamois strongly upwards, with chamois migrating on average a further 82-110m upslope in the presence of sheep (Fig. 7.4 c & d, Fig. 7.5a). Across the European Alps, this upward shift would result in an 83% decrease in the area of suitable foraging habitat. In contrast, the potential effect of increasing temperature due to climate change is much weaker (Fig. 7.5a), shifting their altitudinal range only 7-38m upslope on average. This shift in range would result in only a slight decrease, 8%, in the available area of foraging habitat. Similarly, the potential effect of future 5^{o}C temperature increase on activity budgets is relatively modest, reducing the proportion of time spent foraging by a maximum of 10%.

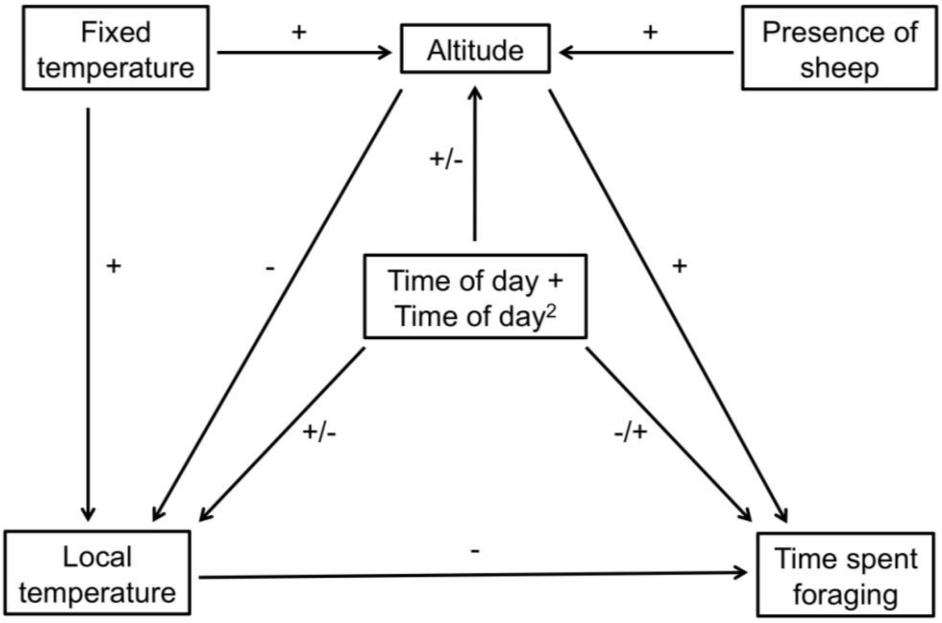

Figure 7.3 Path diagram showing the most parsimonious SEM. Arrows indicate hypothesised causal pathways, from predictors to response variables. '+' and '-' indicate directions of effects.

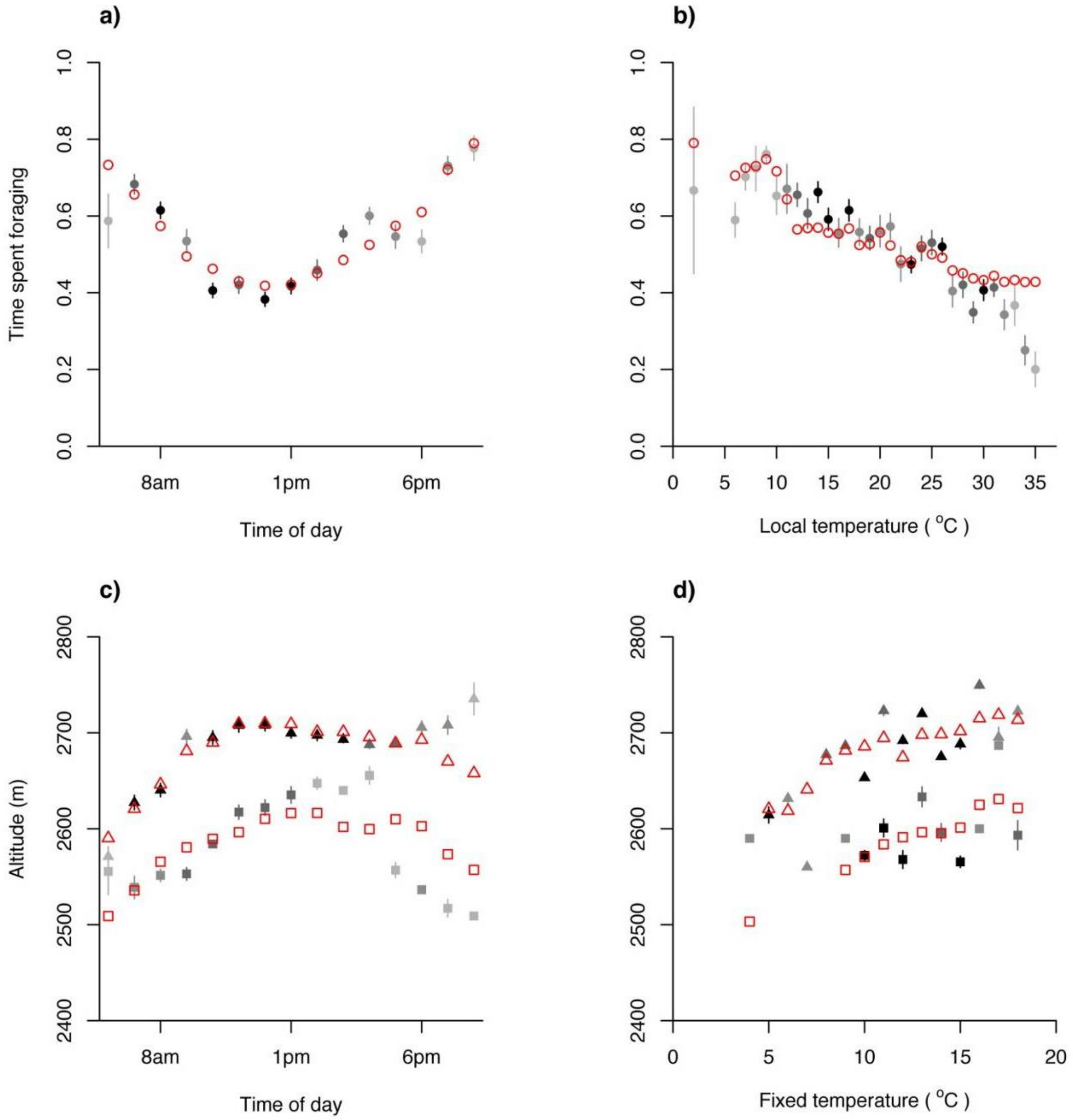

Figure 7.4 Variation in observed (grey/black filled symbols) and predicted (red, empty symbols) weighted mean time spent foraging (**a**-**b**) and altitude use (**c**-**d**). Means were calculated across all scan samples within hourly or one-degree bands, and were weighted by the number of individuals recorded per scan sample. In **a)** and **b)**, means were calculated across the whole study period. In **c)** and **d)**, means were calculated separately for when sheep were present (triangles) and when sheep were absent (squares). Darker filled symbols indicate observed means calculated from a higher number of scan samples. Lines show standard errors of observed data.

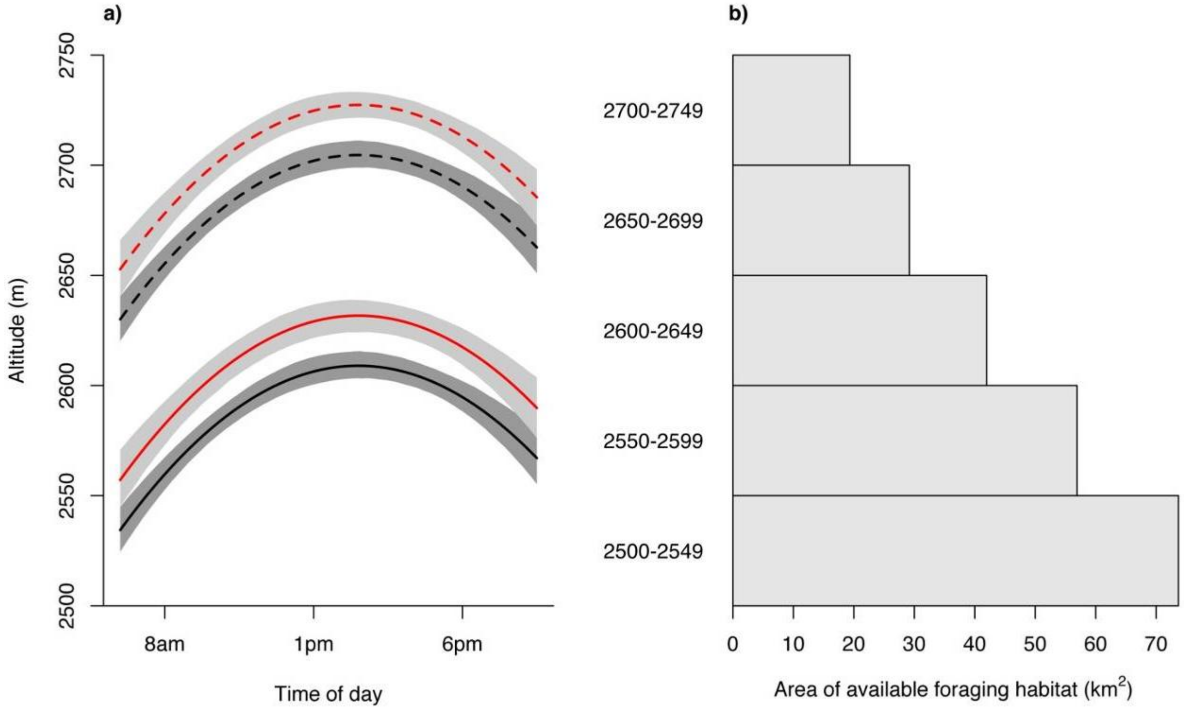

Figure 7.5 a) Predicted mean daily variation in altitude use in the presence (dashed lines) and absence of sheep (solid lines), both in the present climate (black lines) and a 5°C warmer climate (red lines). Predictions were made using the most parsimonious model, and using mean values for all predictors other than time of day. Grey shaded areas are 95% confidence intervals (Efron and Tibshirani 1991). **b)** Variation in available foraging habitat (see text for details), across the European Alps, in different 50m altitudinal bands, across the entire summer altitudinal range of this population.

7.5 Discussion

Temperature strongly influenced chamois behaviour, including both how much time they spend foraging and the range of altitudes they use. However, there was a pronounced effect of an interaction with sheep on their altitudinal range, dwarfing the influence of temperature on altitudinal migration. These findings highlight the profound influence biotic interactions can exert on species' distributions and underline the importance of characterising realised rather than fundamental niches when making range-shift projections, particularly at small spatial scales. In addition, this work reveals the complexity that can arise from the coexistence of different behavioural responses to climatic variation. Results suggest that chamois respond to variation in temperature by adjusting the amount of time they spend in different behaviours, as well as migrating to different altitudes.

A limiting effect of temperature on foraging behaviour has been observed in a range of species (e.g. Aublet et al. 2009, Dunbar 1992a, Gaston 2010). Another alpine ungulate, the ibex, responds similarly to temperature, moving to higher altitudes and allocating less time to foraging on hotter days (Aublet et al. 2009). In ibex, both time spent foraging and altitudinal migration were affected by air temperature and, to a lesser extent, solar radiation. Temperature also exerted a direct influence over chamois behaviour (Table 7.1, Fig. 7.4 b & d); when it was hotter, regardless of time of day, chamois allocated less time to foraging and moved to higher altitudes. Unscreened temperature explained more variation in time spent foraging than screened temperature did, suggesting that solar radiation is important in this species. The absorption of solar radiation is thought to play a key role in the heat balance of endotherms such as mammals and birds due to the presence of insulatory layers of fur or feathers (Porter et al. 2000). This study shows that the absorption of solar radiation could be an important cue in controlling patterns of behavioural thermoregulation.

Unfortunately, because we did not record unscreened temperature across a range of altitudes, it was not possible to examine the relative importance of solar radiation and air temperature on chamois altitudinal migration patterns. Nonetheless, that screened $\text{Temp}_{\text{fixed}}$ was a good predictor of chamois altitude use (Table 7.1, Fig. 7.4d) suggests that air temperature played a role in influencing altitudinal migration. However this effect was relatively modest: the model suggests that, after controlling for time of day during the study period, chamois moved an average of 7m upslope per 1^{o}C increase in air temperature (see Fig. 7.4). In contrast, during the summer, male ibex move approximately 25m upslope per 1^{o}C increase in air temperature (although this is not controlling for time of day) (Aublet et al. 2009). Whilst this disparity is striking, it reflects the fact that ibex are particularly stenothermic (adapted to a narrow range of temperatures) (Aublet et al. 2009, Grignolio et al. 2004), whereas chamois populations are eurythermic, being found across a wide altitudinal range in the Alps (500 to 3,100m) (Shackleton 1997, Spitzenberger et al. 2001). The limiting effect of temperature on activity budgets, contributing to a portion of their behavioural thermoregulation, may reduce the need for altitudinal migration in chamois. To my knowledge, relative contributions of different behaviours to thermoregulation have not been previously explored.

The presence of sheep did not affect chamois activity budgets but had a much stronger effect on altitudinal migration than temperature did (Table 7.1, Fig. 7.4a, 7.5a). Strikingly, after the introduction of sheep into the study area, chamois moved on average 96m upslope, moving to an entirely novel altitudinal range. It is likely that, due to the presence of young kids during spring and summer, adult female chamois are sensitive to potential sources of disturbance, leading them to take refuge at higher altitudes. Whilst there is frequently considerable overlap among ranges of wild ungulate species (Harris and Miller 1995, Hibert et al. 2010), the presence of livestock species can cause displacement of ungulates. In mountainous areas, wild ungulates may move to higher altitudes when disturbed, which can result in dietary changes and even bring them into competition with other wild species (Hibert et al. 2010, Shrestha and Wegge 2008a, b). However, to my knowledge, such a pronounced effect on a population's altitudinal range has not been documented previously. Some authors have suggested that range displacements are generally caused by the presence of humans and other animals associated with livestock (Bagchi et al. 2004), however range displacements can also occur where livestock are not attended by humans or guardian species (Shrestha and Wegge 2008a, b). In this study area, where sheep were periodically associated with shepherds, dogs and donkeys, it is unclear which species was the driver of upslope migration in chamois. No direct interactions were observed between chamois and sheep, or their associated guardian species at any point during the study. Regardless, this study highlights the strong influence that inter-specific interactions, as well as human activities, can exert on species distributions. This threat could be reduced, and the potential impacts of climate change ameliorated, by the appropriate management of the species responsible for negatively affecting vulnerable populations. This is particularly applicable in study systems where an inter-specific interaction has restricted the range of a relatively eurythermic species and where control of the responsible species' distribution is feasible, as is the case here with livestock.

In the most extreme climate change scenario for the region, a 5°C increase in mean temperature, the model predicts an increase of 7-38m in the mean summer altitudinal range of chamois; this is a modest change compared to the 82-110m effect of disturbance by sheep. Assuming an average 0.6°C/100m lapse rate (the rate of temperature change with increasing elevation) in the Alps during summer (Kirchner et al. 2013), if the climate warmed by 5^{o}C chamois would have to move approximately 830m upslope in order to remain in their current thermal niche. This suggests that chamois will lag behind climate change in the future, if they respond to long-term climate change in the same way that they respond to intra-annual climatic variation. Indeed, such patterns are emerging from long-term studies on a variety of taxonomic groups: altitudinal range-shifts appear to be lagging behind climate change (Chen et al. 2011). For example, in a community of tropical moth species, whilst altitudinal ranges have shifted on average 67m upslope in response to temperature increases, their thermal niche has shifted 127m upwards (Chen et al. 2009). In some areas, such lags could be explained by a lack of suitable or accessible habitat at higher elevations (Chen et al. 2011). Indeed, in the European Alps, suitable foraging habitat starts to become more limited at higher elevations (Fig. 7.5b). This is also the case in this study area where there is currently no suitable foraging habitat 830m upslope. The ability of herbivores living in mountainous regions to track climate change will greatly depend on the potential of plants to migrate upslope. In the European Alps, there is at least cause for some optimism on this score, with alpine plant species moving to higher elevations in response to climate change over both short (Erschbamer et al. 2009) and long time-scales (Lenoir et al. 2008).

The model also predicts that chamois would spend as much as 10% less time foraging in a 5^{o}C warmer climate. Such a change would undoubtedly have a considerable negative impact on the ability of individuals to acquire sufficient resources for growth and reproduction. However, in the future, ungulates might adapt how they perform behaviours, for instance by adjusting the timing of foraging bouts. They might allocate more time to foraging in the early hours and at night, when it is cooler, and further reduce the time spent active during the middle of the day. Such behavioural adaptation could reduce the need for upslope migration in a warming mountainous climate, if resources are scarcer at higher altitudes. This could be particularly beneficial given that locomotion is the most energetically expensive aspect of ungulate activity budgets, particularly in mountain environments (Fancy and White 1985). In general, this study shows that altitudinal migration does not play the primary role in behavioural thermoregulation in this species, due to considerable plasticity in activity budgets. However, it remains to be seen how this intra-annual pattern of behavioural variation translates into long-term behavioural adaptation in this species. In the absence of a different, long-term mechanism of adaptation, this study suggests that chamois will not track the upslope movement of its thermal niche.

In summary, variation in temperature exerts an influence over diurnal behavioural patterns of alpine chamois but some of these behaviours can be more strongly affected by the presence of other species. This finding highlights that accounting for inter-specific interactions is essential in understanding the impacts of climatic variation on species. Ignoring biotic interactions could lead to projections of climate change impacts very different to what might eventuate. This work also proposes a novel means by which to adapt management of susceptible species to cope with climate change, namely that controlling competitors of species with particularly divergent fundamental and realised niches could ameliorate climate impacts.

Chapter 8

General discussion

8.1 Synthesis

In this thesis, I investigated the influence of climate on the life-history, demography and behaviour of Alpine chamois, with the aim of expanding our knowledge of the variety of effects that climate and environmental change can have on the ecology of a given species. This work has illustrated some of the myriad influences that climatic variation can exert, highlighting that future climate change impacts on species are likely to be complex and varied. Climatic and environmental variation had striking effects on reproductive strategies, body condition, population dynamics, behavioural patterns and spatial ranges of chamois. My work underlines the significance of life-history and demographic responses to climate change, which in some cases can affect populations more strongly than range-shifts. Furthermore, this project illustrates the importance of considering the influences of anthropogenic and biotic factors in studies of climate change impacts on ecology. This project has also provided valuable new insights into the ecology of this common, but relatively understudied, species and has highlighted the mechanisms that underlie the susceptibility of alpine species to climate change.

The findings of this project have implications at a range of scales. I will now discuss these in light of five issues of increasing scope:

1. New insights into chamois ecology
2. Alpine ungulate conservation
3. The value of transversal and harvesting data
4. The spatial scale of ecological variation
5. The influence of climate on ecology

8.1.1 New insights into chamois ecology

This work has contributed significantly to our knowledge of chamois ecology, information on which was previously limited to an anecdotal literature (Couturier 1938, Knaus and Schröder 1983, Kramer 1969). There has been much recent discussion about the extent to which chamois are polygynous, despite being near monomorphic for most of the year and often showing equal mortality in males and females (Bocci et al. 2010, Corlatti et al. 2011, Gonzalez and Crampe 2001, Rughetti and Fiesta-Bianchet 2011). Chapter 3 (Mason et al. 2011) revealed a substantial somatic cost of reproduction, with males losing as much as 30% of their mass during the breeding season. However, surprisingly, there does not appear to be a survival cost of this behaviour; my findings from chapter 5 suggest that male and female survival is generally equal, as in other populations

(Bocci et al. 2010, Gonzalez and Crampe 2001). It has been suggested that this might be because the chamois mating strategy is less risky than in other polygynous ungulates (Corlatti et al. 2011). Indeed, recent evidence shows that male-male competition in chamois generally takes the form of indirect rather than direct aggressive behaviour, reducing the risk of injury-related mortality from physical contests (Corlatti et al. 2013). Also, an emphasis on indirect behaviours could limit the selection pressure for large body size and long horns, explaining the moderate degree of sexual dimorphism in this species. Findings from chapter 3 further hint at a conservative life-history tactic: in two of the study populations there appears to be a threshold body mass at which males will cease rutting, perhaps improving their chances of surviving the winter.

This project has also revealed some intriguing patterns of body mass variation across small geographic scales which are yet to be fully explained. In chapter 3, I found that males and females across all age-classes weigh considerably less in the calcareous region of the Trento study area, Brenta, than in the siliceous areas. Males and females weigh on average 7-8% and 12-13% less in the calcareous area than in the two siliceous areas, despite calcareous vegetation being more nutrient rich than siliceous vegetation (Gensac 1990). This is particularly surprising given that juvenile chamois from calcareous regions of this study have horns which are on average 2-7% longer than those from siliceous regions (Chirichella, Ciuti, Grignolio, et al. 2013). In chapter 3, I proposed that there might be less pressure to be large in calcareous areas because they are lower elevation and thus winters are probably not as harsh. Further investigation is required to provide support for this suggestion.

One of my findings, that young male chamois reproduce later in the breeding season (chapter 4; Mason et al. 2012), has received substantial support from two new studies on male ungulate reproductive strategies. Corlatti et al. (2013) found that subordinate male chamois, unable to hold territories during the peak of the rut, dramatically increase their frequency of mating behaviours late in the season. By contrast, young reindeer (*Rangifer tarandus*) have been shown to allocate high reproductive effort early in the rut, avoiding intense competition later on (Tennenhouse et al. 2012). The first of these findings confirms the presence of a late breeding strategy in subordinate chamois, whilst the second adds substantial weight to our proposal that this type of competition-avoidance tactic could be a general phenomenon in subordinate ungulates.

8.1.2 Alpine ungulate conservation

A number of findings in this thesis raise issues that could have important implications for the management of alpine ungulates. For instance, the observed striking declines in body mass (chapter 5), could have pronounced knock-on effects on population dynamics. If, as theorised in chapter 5, these trends were driven by warmer temperatures affecting the ability of chamois to forage, further disruptions to climate in the highly seasonal and sensitive alpine environment could have profound effects on the persistence of alpine populations. The results from chapter 6 suggest that high spring and summer temperatures negatively affect both population fecundity and survival, which could be due to decreases in body mass. Positive relationships between condition and both fecundity (Saether and Haagenrud 1983, Sand 1996) and survival (Berube et al. 1999, Loison, Langvatn, et al. 1999) have been recorded in other ungulates. Further work is needed to uncover whether temperature change could be influencing foraging behaviour, and to project what the implications are for population dynamics. However, this project illustrates that predicted summer temperature increases in alpine areas (IPCC 2007) could have negative impacts on the productivity and persistence of alpine ungulate populations.

The results from chapter 7, which uncovered the relative effects of temperature and inter-specific interactions on chamois foraging behaviour, could be of particular importance to the management of alpine ungulates. This work showed that whilst chamois activity budgets were strongly influenced by temperature during summer, disturbance by domestic sheep played a more significant role in controlling their altitudinal range. At fine spatial scales, relevant to local management strategies, studies will need to consider interactions with livestock, as well as with other wild ungulates, in order to make accurate predictions of range shifts and to manage populations appropriately. Such studies could determine potential for assisted migration, as well as suitable release sites, in light of the distribution of livestock species. This finding also highlights that controlling certain species, in this case livestock, could be a feasible management strategy, possibly ameliorating the impacts of climate change on vulnerable populations. Controlling the spatial and temporal distribution of livestock, which are often grazed on alpine pastures during summer, could reduce the magnitude of upslope range-shifts due to disturbance, maximising the area of foraging habitat available to alpine ungulates. This could be applicable for other mountain ungulates, for instance in the Himalaya there can be competition between wild ungulates and livestock due to considerable spatial and dietary overlap (Shrestha and Wegge 2008a, b). The regulation of certain species could be a general management strategy to reduce the adverse impact of biotic interactions on threatened populations in a changing climate.

8.1.3 The value of transversal and harvesting data

Throughout this study, I have used transversal data, from hunting records and population censuses, to reveal interesting patterns of ecological variation at the population level. The use of such datasets has been criticised because they cannot account for heterogeneity among individuals (Nussey et al. 2008). Furthermore, the role of transversal studies in current ecological research has been questioned as they often lack information on the life-history stage, age-class or dominance of different individuals (Clutton-Brock and Sheldon 2010). However, this work has demonstrated that transversal data can make a considerable contribution to ecology, for instance revealing population-scale life-history tactics (chapters 3-5), temporal trends in population demography (chapter 6) and the influence of climatic variation on populations (chapters 5-6). Used in conjunction with long-term longitudinal data on ecological variation among individuals (e.g. Ozgul et al. 2009), they might be of even greater value in the future and could be used to inform the management of populations experiencing climate change.

Data from harvesting proved particularly useful in this study, enabling the investigation of the body condition and demography of different subsets of populations. Harvest data can also be used to uncover the influences that hunting can exert on populations, although this can be difficult if data on hunter selection and effort is lacking. Regardless, a range of consequences of hunting on ungulate ecology have previously been identified using transversal data, ranging from changes in reproductive traits to alterations in demography (e.g. Coltman et al. 2003). In chapter 6, I revealed striking mortality patterns in adult chamois: mortality due to hunting is high whereas natural mortality is very low, even for an adult ungulate. High hunting pressures on yearling and adult age-classes appears to result in hunting mortality largely replacing natural mortality. Such a pattern is intriguing and illustrates an example of harvesting and climate simultaneously influencing different demographic parameters (in this case climate affects fecundity and largely juvenile survival). Future analyses incorporating harvest data and focusing on how alterations in harvesting strategy might mitigate negative influences of climate change on populations could be of much importance to the future management of harvested species.

8.1.4 The spatial scale of ecological variation

In chapter 3 (Mason et al. 2011), I uncovered that striking life-history variation can exist among closely neighbouring populations of a given species. Among three neighbouring populations, I found that males timed reproduction very differently across their lives and had very different life-expectancies, perhaps as a result (although cause and effect is very difficult to establish with transversal data; see Section 8.1.3). Additionally, considerable variation in body mass was evident among these sites. Whilst I was unable to test directly for a link between climate and life-history strategies, due to the small sample size of populations, it is likely that climatic and environmental variation is responsible for the observed plasticity (see discussion in chapter 3).

Environmentally driven variation in life-history traits, such as age of first reproduction, among populations is well-documented (Ergon et al. 2001, Lam and Calow 1989, Miaud et al. 1999). However, for entire life-history strategies to vary among proximal populations, as with the apparent continuum between terminal investment and reproductive restraint across these populations, is quite surprising. Such variation is generally overlooked, with most studies considering site-effects in terms of different values for life-history traits, such as age at first reproduction, but not allowing for the potential of entirely different life-history strategies to exist in different populations (e.g. De Block and Stoks 2004, Ergon et al. 2001, Monk 1985).

There is much recent evidence of inter-population variation in demography and life-history (e.g. Devenish-Nelson et al. 2012, Nevoux et al. 2010, Nilsen et al. 2009, Servanty et al. 2011). Despite this, frequently studies assume populations are only superficially different, just fitting population-specific intercepts (e.g. Devereux et al. 2008, Hewison et al. 2005, Thirgood et al. 2000). Not assessing the most parsimonious scale at which to analyse ecological variation could produce spurious results and inform misguided management decisions (Caro et al. 2005, Devenish-Nelson et al. 2012, Johnson et al. 2010). To my knowledge, there is not currently an accepted systematic protocol for examining the spatial scale of ecological variation for data aggregated from different populations. The most parsimonious model in an analysis could consist entirely of population-specific parameters, as is the case in chapter 3, or a combination of population-specific and global parameters, as is the case in chapter 6. Assessing the parsimony of aggregating and disaggregating parameter values across populations is crucial in revealing the true spatial scale of ecological variation. The results of this thesis suggest that different management strategies may be necessary across even neighbouring populations. Analyses focussing on, rather than accounting for, intra-specific variation in life-history could be of much value in the future.

8.1.5 The influence of climate on ecology

This work highlights the important, sometimes dominant, influence that climate exerts over many aspects of a species' ecology. For chamois, I have found evidence that temperature during spring and summer is particularly important, negatively affecting body condition (chapter 5), fecundity, survival (chapter 6) and aspects of their foraging behaviour (chapter 7). This suggests that future increases in temperature could negatively influence these populations in a variety of ways. Also, I have found some evidence that these effects could be tightly linked. In chapter 5, I proposed that long-term declines in body mass could have resulted from individuals being unable to spend as much time foraging during spring and summer due to temperature increases. I found evidence to support this during fieldwork: in chapter 7, I showed that chamois reduce the time they spend foraging when it is hotter during summer, perhaps limiting their ability to acquire resources. Furthermore, reduced fecundity and survival rates in warmer conditions, as found in chapter 6, could be linked to poor body condition, as previously discussed.

Despite these apparent links between ecology and climate, this work has also highlighted the difficulty in establishing a link between climatic and environmental variation and fine-scale temporal variation in life-history traits and demography. This is best illustrated in chapter 5, where models linking long-term body mass trends with climate performed well but it was not possible to identify robust explanatory models for inter-annual mass variation. Similarly, in chapter 6, models could capture general trends in long-term population size but not fine-scale deviations. Such patterns are likely to be symptomatic of messy ecological datasets as well as the difficulties in identifying appropriate climatic and environmental variables, particularly if short-term climate events or fine-scale phenological linkages are driving ecological processes. These results highlight the need for an increasing focus on the influence of short-term variation in weather (as employed in chapter 7 to investigate behavioural variation), rather than long-term climate data, to reveal the causes of fine-scale deviations in population dynamics. Ultimately, studies investigating the link between demography and the timing and severity of local weather events will provide the most insight into the mechanisms of climate-driven demographic variability (Hallett et al. 2004).

I have also found that climate is not always a dominant force and that, at times, its influence on certain facets of ecology can be overshadowed by biotic factors (although this could change if climate effects are viewed in combination). Previously, it has been demonstrated that interactions between tightly linked species, such as parasites and their hosts, can have stronger effects than climate on spatial distributions, even at continental scales (Araujo and Luoto 2007, Suttle et al. 2007). In chapter 7, I showed that, at small spatial scales, even generalistic interactions can dwarf the influence of climate on range. During summer, disturbance due to domestic sheep forced chamois considerably further upslope than did higher temperatures. This demonstrates the need to consider inter-specific interactions, even for species without tightly linked life-histories, when modelling species' responses to climate change. Furthermore, it shows that human activities, which are often overlooked in understanding species-climate relationships, can have a pronounced effect on species' ranges at fine spatial scales.

8.2 Future work

The findings from chapter 7 highlight how little is known about how species' behaviours will be altered in the future, particularly the link between short-term behavioural variation and long-term responses to climate and environmental change. For instance, in alpine ungulates, populations shift their altitudinal ranges at a variety of different time-scales, from daily to seasonal shifts. However it is unclear how this variation will translate to long-term change.

I found that, during summer, whilst chamois show daily migratory patterns in response to temperature variation, this does not allow them to remain in the same thermal niche. Individuals moved on average only 7m upslope per 1^{o}C increase in temperature, despite a lapse rate in the Alps of 0.6^{o}C per 100m increase in altitude. This suggests that chamois may be able to maintain a wide thermal niche through autonomic thermoregulation. However, they are also likely to use other forms of behavioural thermoregulation, such as reducing the time they spend foraging during hot weather, as observed in chapter 7. In addition, other behaviours such as seeking shade from the sun and shelter from the wind could be employed. Future work that links factors such as temperature, solar radiation and wind speed with behavioural patterns, also considering physiological factors such as fur characteristics, could reveal further insight into how animals control their environmental conditions. The utilisation of different micro-climates could be an important tactic in mountainous environments where variable topography can create a range of slopes with different levels of solar radiation and shelter.

Remote data recording could be employed to study alpine ungulate temperature budgets; fitting data-loggers to individuals would reveal how behavioural thermoregulation affects the heat budgets of individuals relative to temperatures in the environment. There have been some advances using miniature black globe thermometers, which account for factors such as wind speed and solar radiation, attached to collared ungulates to examine the influence of behavioural thermoregulation on thermal budgets (Hetem et al. 2007, Hetem et al. 2011, Hetem et al. 2012). See Figure 8.1 for examples of temperature and behavioural recordings from blue wildebeest (*Connochaetes taurinus*) and impala (*Aepyceros melampus*). Utilising such methods with alpine ungulates could demonstrate the relative contributions of activity budgets, micro-climate selection and altitudinal migration to behavioural thermoregulation. The use of data-loggers which measure activity (e.g. Wilson et al. 2008) would also shed light on whether increased night-time activity might be a tactic to avoid high temperatures on hot days.

The extent to which daily patterns of behavioural thermoregulation will contribute to long-term behavioural change in response to climate change is unknown. However, some insight could be gained from studying captive populations, which will be constrained in performing certain behaviours. For instance, captive alpine ungulates, which are present in a number of zoos throughout the European Alps, are limited to a narrow altitudinal range, reducing their ability to thermoregulate through altitudinal migration. This could have considerable impacts on their heat budgets and behavioural routines. Comparing the behaviour of wild and captive alpine ungulates could reveal the importance of range shifts between different elevations and could, ultimately, shed light on the plight of stranded mountainous populations, which are unable to access higher altitudes. The ability of montane populations to adapt behaviourally to climate change could be crucial to their persistence.

8.3 Conclusion

This study illustrates the complexity of ecological responses to climate and environmental change. This complexity makes it extremely difficult to predict how populations will be influenced by future climate change. Modelling techniques that project only areas of suitable future range, such as species distribution models, are clearly inadequate to make robust predictions that encompass all of the ecological changes that are likely to result from climate change. In particular, such models enable no inferences about the effect of climate change on behaviour, physiology, demography, dynamics, biotic interactions or anthropogenic factors. This project presents a case-study in which climate has a strong influence on factors such as body mass, survival and fecundity but a relatively weak effect on distribution. Importantly, this illustrates that distributional change should not always be the dominant focus of studies. An increasing focus is needed on the interplay between different types of ecological change (e.g. Keith et al. 2008, Ozgul et al. 2010, Willems and Hill 2009), considering both climatic and non-climatic drivers of change. Case-studies on individual species and populations could help reveal the importance of different types of ecological change in order to identify general patterns. Furthermore, such studies could directly inform the management of populations.

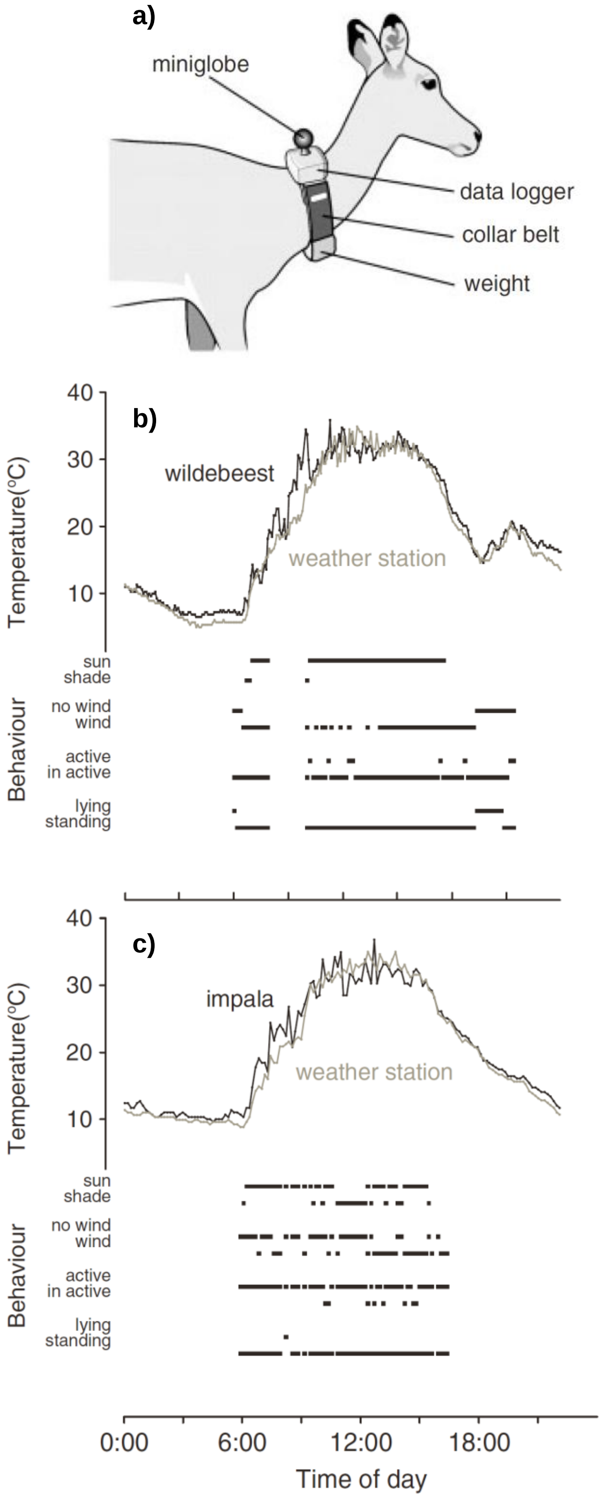

Figure 8.1 a) miniature globe thermometer attached to impala collar and temporal variation in temperature of thermometers fitted to **b)** wildebeest and **c)** impala with weather station temperature. Also displayed is temporal variation in behaviour, shade and wind. From Hetem et al. (2007).

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Table A1 Model selection results from cubic spline model fitted to male chamois body mass data. Models are distinguished by the functional forms of α_0 and β_0. Specifically, α_0 and β_0 were allowed to be constant across years (α_0; β_0), vary linearly with year ($\alpha_0(y)$; $\beta_0(y)$), quadratically with year ($\alpha_0(y^2)$; $\beta_0(y^2)$) or linearly with population density ($\alpha_0(d)$; $\beta_0(d)$). Sites were either treated separately (denoted by S) or site-effects were ignored. Maximum log-likelihoods (LL) and ΔAICs are shown for each site. Maximum log-likelihoods (LL) and ΔAICs are shown for each site. The most parsimonious models for each site are highlighted in bold (i.e. have a ΔAIC value that is ≤6 and lower than all simpler nested versions). K is the number of parameters in each model.

Model	K	LL	AIC	ΔAIC
M($\alpha_0(y^2),\beta_0(y^2)$,S)	**51**	**-16998.1**	**34098.2**	**0.0**
M($\alpha_0(y),\beta_0(y^2)$,S)	**48**	**-17002.8**	**34101.5**	**3.4**
M($\alpha_0(y^2),\beta_0(y)$,S)	**48**	**-17003.3**	**34102.7**	**4.5**
M($\alpha_0(y),\beta_0(y)$,S)	45	-17008.6	34107.2	9.0
M($\alpha_0(y^2),\beta_0(d)$,S)	48	-17010.3	34116.7	18.5
M($\alpha_0(y),\beta_0(d)$,S)	45	-17014.2	34118.3	20.1
M($\alpha_0(y^2),\beta_0$,S)	45	-17019.1	34128.2	30.1
M($\alpha_0(d),\beta_0(d)$,S)	45	-17022.3	34134.5	36.3
M($\alpha_0(y),\beta_0$,S)	42	-17024.2	34132.5	34.3
M($\alpha_0(d),\beta_0(y^2)$,S)	48	-17025.6	34147.1	48.9
M($\alpha_0(d),\beta_0(y)$,S)	45	-17031.8	34153.6	55.4
M($\alpha_0(d),\beta_0$,S)	42	-17041.6	34167.2	69.0
M($\alpha_0,\beta_0(y^2)$,S)	45	-17060.1	34210.3	112.1
M($\alpha_0,\beta_0(y)$,S)	42	-17081.1	34246.3	148.1
M($\alpha_0,\beta_0(d)$,S)	42	-17086.5	34257.0	158.8
M(α_0,β_0,S)	39	-17124.3	34326.7	228.5
M($\alpha_0(y),\beta_0(y)$)	15	-18889	37808.5	3710.3
M($\alpha_0(y^2),\beta_0(y)$)	16	-18889	37810.1	3711.9
M($\alpha_0(y),\beta_0(y^2)$)	16	-18889	37810.3	3712.1
M($\alpha_0(y^2),\beta_0(y^2)$)	17	-18889	37812.1	3713.9
M($\alpha_0(y),\beta_0$)	14	-18893	37814.6	3716.4
M($\alpha_0(y),\beta_0(d)$)	15	-18893	37815.5	3717.3
M($\alpha_0(y^2),\beta_0$)	15	-18893	37816.6	3718.4
M($\alpha_0(y^2),\beta_0(d)$)	16	-18892	37816.7	3718.5
M($\alpha_0(d),\beta_0(y)$)	15	-18918	37865.2	3767.0
M($\alpha_0(d),\beta_0(y^2)$)	16	-18917	37866.3	3768.1
M($\alpha_0(d),\beta_0(d)$)	15	-18921	37871.6	3773.4
M($\alpha_0,\beta_0(y^2)$)	15	-18937	37904.5	3806.3
M($\alpha_0,\beta_0(y)$)	14	-18939	37905.2	3807.0
M($\alpha_0(d),\beta_0$)	14	-18941	37910	3811.9
M($\alpha_0,\beta_0(d)$)	14	-18973	37973.3	3875.1
M(α_0,β_0)	13	-18975	37976.3	3878.1

Table A2 Model selection results from cubic spline model fitted to female chamois body mass data. Models are distinguished by the functional forms of α_0 and β_0. Specifically, α_0 and β_0 were allowed to be constant across years (α_0; β_0), vary linearly with year (α_0(y); β_0(y)), quadratically with year ($\alpha_0(y^2)$; $\beta_0(y^2)$) or linearly with population density (α_0(d); β_0(d)). Sites were either treated separately (denoted by S) or site-effects were ignored. Maximum log-likelihoods (LL) and ΔAICs are shown for each site. Maximum log-likelihoods (LL) and ΔAICs are shown for each site. The most parsimonious models for each site are highlighted in bold (i.e. have a ΔAIC value that is ≤6 and lower than all simpler nested versions). K is the number of parameters in each model.

Model	K	LL	AIC	ΔAIC
$M(\alpha_0(y^2),\beta_0(y),S)$	**48**	**-15186.8**	**30469.6**	**0.0**
$M(\alpha_0(y^2),\beta_0(y^2),S)$	51	-15186.4	30474.9	5.3
$M(\alpha_0(y),\beta_0(y^2),S)$	48	-15194.0	30484.0	14.4
$M(\alpha_0(y),\beta_0(y),S)$	45	-15197.5	30485.0	15.4
$M(\alpha_0(d),\beta_0(y^2),S)$	48	-15195.8	30487.6	18.1
$M(\alpha_0(y^2),\beta_0(d),S)$	48	-15197.6	30491.2	21.6
$M(\alpha_0(y),\beta_0(d),S)$	45	-15202.1	30494.2	24.7
$M(\alpha_0(y^2),\beta_0,S)$	45	-15205.2	30500.4	30.9
$M(\alpha_0(y),\beta_0,S)$	42	-15211.1	30506.2	36.7
$M(\alpha_0,\beta_0(y^2),S)$	45	-15210.2	30510.5	40.9
$M(\alpha_0(d),\beta_0(y),S)$	45	-15216.0	30522.0	52.4
$M(\alpha_0(d),\beta_0(d),S)$	45	-15226.2	30542.5	72.9
$M(\alpha_0,\beta_0(y),S)$	42	-15229.3	30542.5	72.9
$M(\alpha_0(d),\beta_0,S)$	42	-15236.3	30556.5	86.9
$M(\alpha_0,\beta_0(d),S)$	42	-15260.9	30605.7	136.1
$M(\alpha_0,\beta_0,S)$	39	-15282.4	30642.8	173.3
$M(\alpha_0(y^2),\beta_0(y))$	16	-17151.9	34335.9	3866.3
$M(\alpha_0(y^2),\beta_0(y^2))$	17	-17152.0	34338.0	3868.4
$M(\alpha_0(y^2),\beta_0(d))$	16	-17153.6	34339.3	3869.7
$M(\alpha_0(y),\beta_0(y^2))$	16	-17154.6	34341.3	3871.7
$M(\alpha_0,\beta_0(y^2))$	15	-17161.1	34352.2	3882.6
$M(\alpha_0(y),\beta_0(d))$	15	-17161.3	34352.6	3883.0
$M(\alpha_0(y^2),\beta_0)$	15	-17161.7	34353.4	3883.8
$M(\alpha_0(y),\beta_0)$	14	-17169.2	34366.5	3896.9
$M(\alpha_0(d),\beta_0)$	14	-17172.8	34373.6	3904.0
$M(\alpha_0,\beta_0(y))$	14	-17172.8	34373.6	3904.0
$M(\alpha_0(d),\beta_0(d))$	15	-17172.7	34375.4	3905.9
$M(\alpha_0(d),\beta_0(y))$	15	-17174.8	34379.5	3909.9
$M(\alpha_0(d),\beta_0(y^2))$	16	-17174.7	34381.3	3911.7
$M(\alpha_0(y),\beta_0(y))$	15	-17188.0	34406.0	3936.4
$M(\alpha_0,\beta_0(d))$	14	-17189.2	34406.4	3936.8
$M(\alpha_0,\beta_0)$	13	-17218.1	34462.1	3992.5

Appendix A1 Functional forms used to describe the relative rate of mass loss

The following are the five functional forms fitted for $F_A(s,t)$, which describes the baseline relative rate of mass change of age-class A individuals in site s on day t.

i) The constant function is given by

$$F_A(s,t) = c_{A,s}$$

where $c_{A,s}$ is a constant, A is age, s is site and t is day of year.

ii) The linear function is given by

$$F_A(s,t) = c_{A,s}\, p_{A,s}(t)$$

where $c_{A,s}$ is a constant describing the mean relative rate of mass change on day 252 of age A individuals in site s and

$$p_{A,s}(t) = 1 + \beta_{A,s}(t - 252)$$

iii) The quadratic function is given by

$$F_A(s,t) = c_{A,s}\, p_{A,s}(t)$$

where $c_{A,s}$ is a constant (as defined above) and

$$p_{A,s}(t) = 1 + \beta_{A,s,1}(t - 252) + \beta_{A,s,2}(t - 252)^2$$

iv) The cubic function is given by

$$F_A(s,t) = c_{A,s}\, p_{A,s}(t)$$

where $c_{A,s}$ is a constant and

$$p_{A,s}(t) = 1 + \beta_{A,s,1}(t - 252) + \beta_{A,s,2}(t - 252)^2 + \beta_{A,s,3}(t - 252)^3$$

v) The double cubic spline function is given by

$$F_A(s,t) = \begin{cases} c_{A,s}\, p_{A,s,0}(t), & if\ 252 \le t \le 30; \\ c_{A,s}\, p_{A,s,1}(t), & if\ 302 \le t \le 35, \end{cases}$$

where $c_{A,s}$ is a constant and

$$p_{A,s,i}(t) = \beta_{A,s,i,0} + \beta_{A,s,i,1}(t - t_i) + \beta_{A,s,i,2}(t - t_i)^2 + \beta_{A,s,i,3}(t - t_i)^3 ,$$

where t_i = 252+h_i and h = 49 days. The polynomial coefficients are calculated using

$$\beta_{A,s,i,0} = f_{A,s,i} ,$$
$$\beta_{A,s,i,1} = k_{A,s,i} ,$$
$$\beta_{A,s,i,2} = \frac{3}{h^2}(f_{A,s,i+1} - f_{A,s,i}) - \frac{1}{h}(k_{A,s,i+1} + 2k_{A,s,i}) ,$$
$$\beta_{A,s,i,3} = \frac{2}{h^3}(f_{A,s,i} - f_{A,s,i+1}) + \frac{1}{h^2}(k_{A,s,i+1} + k_{A,s,i}) .$$

The $f_{A,s,i}$ are the values of the polynomials at day t_i, and the $k_{A,s,i}$ are the slopes of the polynomials at t_i. Here these polynomials are normalised by setting $f_{A,s,0} = 1$, which sets $F_A(s,252) = c_{A,s}$. The unknowns are $k_{A,s,0}$, $k_{A,s,2}$, $f_{A,s,1}$, and $f_{A,s,2}$. The remaining slope, $k_{A,s,1}$, is calculated from these parameters using

$$k_{A,s,1} = \frac{1}{4}\left(3(f_{A,s,2} - f_{A,s,1}) - (k_{A,s,0} + k_{A,s,2})\right) .$$