The influence of lifestyle on demographic responses to climate change : the Alpine marmot as a case study

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The influence of lifestyle on demographic responses to climate change: the Alpine marmot as a case study

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Abstract

Understanding populations' response to environmental variation is a central issue of ecology, and has become a compelling goal in the last years due to climate change. In this broad context we could expect some species-specific ecological characteristics known to influence life history traits, such as lifestyle, to shape the demography of populations in variable environments as well as structure between-species differences in response to environmental change. Yet, the influence of species' lifestyle on population demographic responses to environmental variation is still poorly understood. During my PhD, I tried to fill this gap primarily through the analysis of an extensive data set of an Alpine marmot (*Marmota marmota*) population in the Alps. Alpine marmots present a particular lifestyle. Individuals live in family groups of variable size, typically composed of one dominant breeding pair, of sexually mature and immature subordinates and of pups of the year. Half the year, they hibernate together in burrows and practise cooperative breeding with male subordinates acting as helpers for the pups, increasing their survival probability during hibernation. I first investigated how the marmot's lifestyle (hibernation and sociality) mediated the effects of weather fluctuations on age-specific survival variation. I found that juvenile survival strongly decreased over the years because of inter-related effects of harsher winter weather conditions and social factors (i.e., decrease in helpers' presence). In a second step, I studied the adaptive value of cooperative breeding in this Alpine marmot population, and showed that the positive influence of helpers' presence on juvenile survival was vanishing with climate change. The Alpine marmot population is currently decreasing accordingly. However, in parallel to the latter changes, I found a better access to dominance for subordinate individuals over the years, compensating in part this decrease, and highlighting a complex influence of sociality on marmot response to climate change. Finally, I compared the demography of the Alpine marmot population with that of an Alpine chamois (*Rupicapra rupicapra*) population, subjected to similar weather conditions in the Alps. I was able to show that the difference in lifestyle and reproductive tactic between these species shaped their demographic responses to environmental variation, providing them with different resistance to current environmental change.

Key words: Lifestyle; Life history traits; Environmental variation; Population growth rate; Cooperative breeding; Sociality ; Hibernation; *Marmota marmota*; *Rupicapra rupicapra;* Climate change

Résumé

Comprendre la réponse des populations aux variations environnementales est un défi central en écologie et est devenu un enjeu indéniable ces dernières années avec le changement climatique. Dans ce contexte, nous pouvons nous attendre à ce que certaines caractéristiques écologiques propres aux espèces, comme le mode de vie, qui ont évolué en réponse à des contraintes environnementales et qui influencent les traits d'histoire de vie des espèces, puissent façonner la démographie des populations en environnement variable. Pourtant, cette influence du mode de vie sur la réponse démographique des populations demeure encore mal comprise. J'ai essayé de combler cette lacune au cours de ma thèse, principalement par l'analyse d'un jeu de données exceptionnel obtenu grâce à un suivi à long terme d'une population de marmottes alpines (*Marmota marmota*) dans les Alpes Françaises. La marmotte alpine présente un mode de vie très particulier. Les individus vivent au sein de groupes familiaux de taille variable, généralement composés d'un couple de dominants reproducteurs, de subordonnés et de juvéniles. Ils hibernent durant la moitié de l'année, et pratiquent l'élevage coopératif ; les subordonnés mâles participent activement à la survie des jeunes durant l'hibernation, et sont alors appelés *helpers*. J'ai d'abord étudié comment le mode de vie de la marmotte (qui allie hibernation et socialité) a influencé les effets des fluctuations météorologiques sur les variations de survie de chaque classe d'âge. Les résultats ont alors révélé une forte diminution de la survie des juvéniles au fil des ans, et cela du fait d'effets interactifs entre facteurs environnementaux (i.e., hivers de plus en plus rudes) et sociaux (i.e., diminution de la présence des helpers). Dans un deuxième temps, j'ai étudié la valeur adaptative de l'élevage coopératif au sein de cette population de marmottes alpines et j'ai pu montrer que les effets bénéfiques de la présence des helpers sur la survie des juvéniles tendaient à disparaître du fait du changement climatique. En conséquence de cela, la population de marmottes alpines semble être actuellement en déclin. Cependant, l'impact du changement climatique semble avoir été en partie limité par une plus grande probabilité d'accéder à la dominance pour les subordonnés au cours des dernières années, ce qui démontre une influence complexe de la socialité sur la réponse de cette espèce. Enfin, j'ai comparé la démographie de la population de marmottes alpines avec celle d'une population de chamois (*Rupicapra rupicapra*) soumise à des variations météorologiques similaires dans les Alpes. J'ai été en mesure de montrer que le mode de vie et la stratégie de reproduction de ces espèces ont façonné différemment leurs réponses démographiques aux variations environnementales, et ainsi au changement climatique.

Mots clés: Mode de vie ; Traits d'histoire de vie ; Variation environnementale ; Taux d'accroissement des populations; Élevage coopératif; Socialité ; Hibernation ; *Marmota marmota* ; *Rupicapra rupicapra* ; Changement climatique.

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Chapter 1

Introduction

1.1. Understanding the relationship between the environment and organisms: the central issue of ecology

1.1.1. A historical questioning

For a long time, biologists have been interested in understanding relationships linking species to their environment. This concern joins the very definition of ecology, which refers to “the study of the relations between animals and their environment, both animate and inanimate” (King and Russell 1909). While this term has been firstly coined by Haeckel (1876), ecology has a more ancient origin in essence, being amongst others related to natural history and to first naturalistic observations of animals and plants, such as those made by the ancient Greek philosopher Aristotle. For a long time, this relationship was highly simplified and suffered from critical gaps, the overall natural world being considered as static and unchanging. Species were viewed as being in harmony, perfectly adapted to their environment. As a result prevailing thoughts at that time failed to give explanation to the wide diversity of living organisms on earth and especially to explain why similar habitats or landscapes could host completely different plant and animal species all around the world (Benson 2000). Advances regarding these ecological issues have been made thanks to Charles Darwin's work, that he presented in its book “On the Origin of Species” in 1859. Darwin understood that relationships between species and their environment were dynamical and historical, the diversity of life on earth being the outcome of a process he called evolution by natural selection (Darwin 1859). Considering populations composed of numerous individuals, they all show differences in the expression of their phenotypic traits such as in their morphology, physiology or behaviour, which confer them with different ability to reproduce and survive in their environment. As a result, individuals which are the most adapted to environment will more broadly participate to reproduction and to the succeeding generations, giving them many of the same “best adapted” characteristics as theirs. This process then repeats over generations, so that each trait is continuously challenged by new ones or new changes in environmental conditions. Over the long

term this may lead to adaptation, and to speciation at a longer temporal scale. The overall diversity of organisms' life is then the reflection of years and years of evolution under multiple and diverse selection pressures.

1.1.2. Selection pressures: toward the influence of environmental factors

"Species are produced because there is an environmental opportunity and genetic wherewithal to make them possible"

Dobzhansky (1973)

In his seminal paper, (Dobzhansky 1973) proposed to grasp the tremendous diversity of organisms in the light of evolution, highlighting a direct causal link with environmental characteristics. By observing the diversity of species' way of living and interacting with their environment, as well as the variety of inhabited habitats, he proposed that organisms' diversification occurred along with availability of ecological niches and challenges imposed by sequential environmental changes. Speaking of "environmental opportunity", he directly positioned environment at the centre of the evolutionary process, identifying it as the main constituent of selection pressures shaping species evolution. This could include physical characteristics, such as change in weather conditions, in vegetation cover or other abiotic factors that define species habitats. It could also include change in biotic factors (interactions with other species) which directly govern ecological niche occupancy, trophic interactions and between-species competition.

Therole of these selection pressures on evolutionary change is hard to quantify in part because they can operate at different geographical and temporal scales (Barnosky 2001; Benton 2009). More importantly, in the same way as identifying environmental selection pressures should inform about species-environment relationships, depicted the way species interact with their living environment inform on active selection pressures. And, focusing on small temporal scale, this relationship is way more complex that it seems, so that overall environmental factors (biotic or abiotic) with which species interact can not be seen

as independent from one another. Consider as an example a trophic chain linking a predator to its preys, which themselves rely on plant resource. Complex direct or indirect interactions exist between this predator and the other parts of the chain, and all of it can furthermore be limited by external environmental conditions such as weather conditions. Variation in each of these components can thus have repercussions on others, from individuals to species through populations; and this overall interaction could hence be viewed as an integral part of selection pressures.

Identifying key environmental factors driving species diversity is thus challenging and a main way to approach this issue would be first to understand how species deal with environmental variability. This then requires more specific case studies to get insights in mechanisms behind evolution of species' life characteristics. Considerable advances regarding this issue have been reached in the last years along with the development of life history theory (Stearns 1976), a field of study dedicated to the evolution of the biological characteristics that describes species' life, better known as life history traits.

1.1.3. Life history theory: keys to understand this relationship

Life history theory

Living organisms, from plants or bacteria to animals, display a tremendous diversity of life characteristics that is readily noticeable. This goes from differences in body size, such as between huge elephants or whales and small insects or microscopic protists, to the way organisms reproduce and survive across ages. We may compare for instance corals, which can reproduce asexually or sexually and produce million of eggs at each reproductive event, to the blue whale, which only give birth to one offspring every two to three years. A huge diversity of lifespan also exists across organisms, such as observed between the short-lived flies, which can live for up to around 30 days, and the long-lived seabirds, as the albatross, which can live for more than 60 years. All these biological characteristics defining the species' life refers to life history traits. These traits describe the overall species life history and directly relate to survival and reproduction of organisms, such as age at maturity,

number and size of offspring, growth, reproductive success, age-specific mortality, or lifespan (Stearns 1992).

Fisher (1930) gave an important contribution in understanding why such variations in life histories exist, proposing a mathematical basis to study Darwin's evolutionary theory. Natural selection can be seen as selecting for traits that maximise the individual fitness, which is the contribution of an individual to the successive generations in a given environment, in such a way that the frequency of this trait in the population tend to increase over time. Thus, for natural selection to occur on a given life history trait, the latter must: have a heritable basis, present between-individual variation in its expression, be related to the individual fitness (Darwin 1859). Disentangling relationships between life history traits and fitness should thus inform about evolutionary process of life histories and species-environment relationships.

Another milestone in the development of life history theory was brought by the principle of allocation developed by Cody (1966). This important principle states that only a limited amount of resource is available for an individual, which must then allocate this energy optimally between its growth, maintenance (survival) and reproduction in order to maximise its fitness (Stearns 1992). Life history traits are thus not independent from each other but co-vary with each-others, their variations being constrained by the subsequent trade-offs stemming from this energy allocation, i.e. the fitness benefit from a change in one trait is associated to a cost from a change in another (Stearns 1989). The scope of natural selection is therefore constrained within a restricted amount of possible trait combinations. This coordinated evolution of life history traits, better known as life-history strategies (Stearns 1976), can greatly differ between species and populations and be seen as different responses to environmental selective pressures.

Life histories and the environment

Understanding relationships between life history strategies and the environment is thus an important point in ecology. Cole (1954) suggested that life history strategies can be regarded as adaptive, contributing to the fitness of an individual, and be

investigated by approaching their effects on the "average individual fitness", measured as the intrinsic growth rate of the population, *r* (originally termed the Malthusian parameter of population increase by Fisher 1930). The effect of natural selection could thus be approached at a population scale since population growth rate directly relies on life histories.

From this population level approach, emerged a predictive model to explain the evolution of life history in relation with the environment: the r-and K-selection theory. MacArthur and Wilson (1967) characterised two kinds of selection relying on environmental conditions to which individuals are subjected. On a first hand, the so-called "*r-selection*", which refers to density-independent conditions in unstable environments, where selection should select for traits allowing a high productivity and a maximisation of the intrinsic rate of increase (*r*). On the other hand the "*K-selection*", which operates under density-dependent conditions in stable environments, where selection should rather select for traits allowing for high competitive abilities, and thus act toward an increase of the carrying capacity (*K*). Different life history strategies being expected according to the different selective environmental pressures.

The r- and K-selection theory is in line with works of (Dobzhansky 1950) who proposed that latitudinal differences observed in species diversity, from temperate environments to tropics, should be explained by differences in the way natural selection shapes life histories, viewing also density-dependent selection as the major evolutionary process. However, several criticisms can be made to this theory, whose main one being that it oversimplifies the process of natural selection (Wilbur et al. 1974; Reznick et al. 2002). First, other environmental factors than density-dependence can be identified as potential selective pressures for life histories, such as resource availability, predation, weather conditions and environmental fluctuation (Wilbur et al. 1974; Law 1979; Reznick et al. 2002). Any variation in these environmental factors may affect mortality and reproduction rates in a population, acting to varying degrees according to individual's age. Patterns of evolution of life history should thus mainly depend on which age group are subjected to selection in age structured populations (Promislow and Harvey 1990; Reznick et al. 2002). Second, the kind of selection to which populations are

subjected is not fixed but change over time according to variations in selective pressures and population dynamics. Overall, understanding how species' life histories are influenced by the environment may require a demographic investigation of how variations in these factors influence age-specific birth and death rates in populations, and whether they act separately, conjointly, or as factors of density-dependent regulation (Gadgil and Bossert 1970; Michod 1979; Law 1979; Reznick et al. 2002). A typical example illustrating the importance of environmental variation while considering age-specific mortality in the evolution of life history was brought from the extensive work of Cole (1954) on the evolution of semelparity and iteroparity. These two reproductive tactics oppose species whose individuals reproduce only once over a short lifetime (semelparity) and species whose individuals reproduce several times (iteroparity). Cole raised a paradox: he found that iteroparity appeared as the least effective strategy in maximising the intrinsic population growth rate, thus asking why iteroparity is so widespread among species. An explanation for this was later demonstrated with respect to environmental variation, which was not previously considered: iteroparity should be selected as an optimal reproductive tactic in environments causing wide variations in juvenile survival and thus in reproductive success, while semelparity should be the optimal strategy in environments generating high or variable adult mortality (Murphy 1968; Charnov and Schaffer 1973; Schaffer 1974a).

Finally, when asking the general question on how individuals face environmental variation, a first step would be to understand which types of temporal variation individuals may be exposed and constraints that the latter implies.

1.2. The environment: temporal variations and constraints

1.2.1. The different types of temporal variations

Environmental variation can be defined along two main axes: space and time. At first, a focus in ecology has been on understanding how spatial variation in environments influenced species distribution, since these impacts were more readily detectable and directly observable. The other complementary part of environmental variation, i.e. temporal variation, on which we will mainly focus, plays an important role in ecology and evolution. Its influence on individuals is however more difficult to grasp directly, as it requires long-term monitoring of both populations and of the environmental conditions they encounter.

Likewise, properly defining the timescale of observation is also all the more important as this will condition the type of temporal variation in environmental factors that can be captured. Indeed, considering a time-series of an environmental factor, such as mean temperature or precipitation over several decades (see Fig. 1.1); such time-series can possibly be decomposed in several different patterns of environmental variations, occurring on different time-scales (Fig. 1.1, Wolkovich et al. 2014):

- *the trend*, which reveals the magnitude and direction of the long-term global change in environmental factor. It is expressed on long time steps, such as several years or decades;

- *cycles,* which refers to periodic variations in environmental factor on a smaller time-step than the trend. They can be expressed on a more or less short timescale, since it might refer to decadal cycles, such as observed for climatic events or to within-year variations, such as illustrated by among seasons variations;

- *the "noise",* which refers to all underlying environmental variability and constitutes the truly unpredictable component of environmental variation (i.e. the environmental stochasticity). It is hiding beneath previous levels of variation, such as daily, monthly or annually (between-year) variations in environmental conditions.

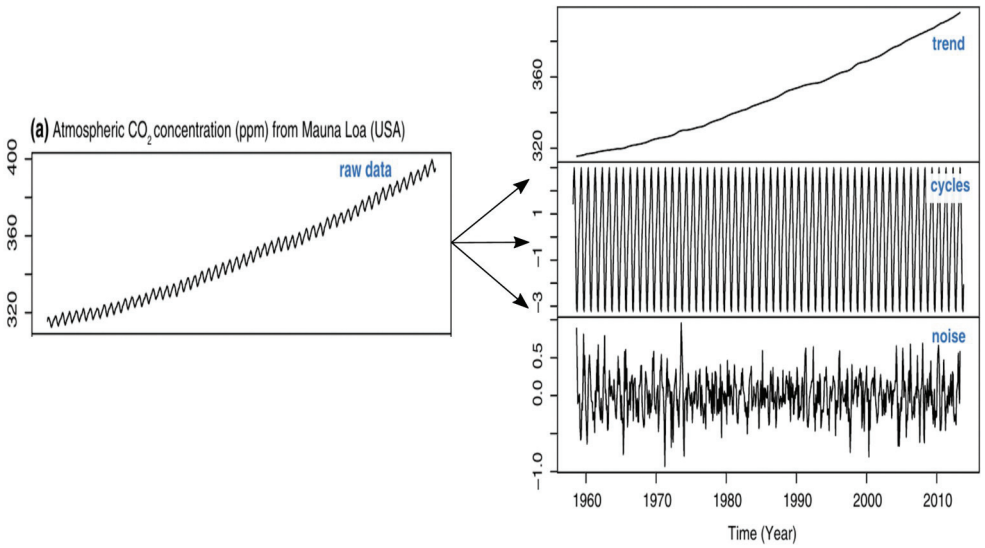

Figure 1.1. Decomposition of a time-series in different environmental temporal variation: long-term trend, regular cycles, and remaining "noise" (from Wolkovich et al. 2014).

These levels of environmental variation are also important as they can all impact population fluctuations and life history traits evolution, by imposing several different constraints on individuals. Let us take the example of a continuous change or modification of habitat characteristics at a given location. This may represent a direct threat for individuals inhabiting this habitat which may depend on specific food resources or on shelters provided so far by this changing environment. Individuals may not be adapted anymore to the environment with which they interact, which may impact population demography and persistence.

Let us also consider seasonality, a central feature of many habitats, which brings other types of constraints to individuals. Seasons are generally defined from variation in the availability in resources (e.g. food, water) or in predation pressure, which are generally the reflect of weather variation that occurs throughout the year (e.g. temperature, rainfall). Accordingly, the annual life cycle of many species can be divided into two distinct environmental periods: a "growing season" (e.g. the summer in temperate areas), during which individuals may achieve energy gains; and a "non-growing season", (e.g. the winter in temperate areas), when individuals face energy loss (Fretwell 1972). As a consequence, seasonality puts constraints on

fat and energy storage to sustain harsh seasons, and on the timing of growth and breeding, and may thus directly constrain survival and fecundity patterns (Boyce 1979; Conover 1992).

Environmental stochasticity represents however unpredictable and random variations in time, resource availability, weather conditions or in habitats availability. These fluctuations are very constraining for species, especially as those can hardly anticipate and adjust their resource allocation, like their reproductive allocation according to upcoming environmental conditions. Consequently, individuals incur more or less important year to year variations regarding their probability to survive and to successfully reproduce, which in turn contributes in reducing their long term fitness on average (Philippi and Seger 1989). This random temporal variations can put constraints on individual life cycles, as for instance on the apportionment of the reproduction throughout the life as to minimise such costs. We will also see that these variations have substantially contributed in shaping life history strategies as a response.

As it will be developed in next parts, species and populations can respond to these variations in different ways, adapting particular life history strategies or lifestyle for instance. Beyond that, unpredictable environments appear to be challenging for individuals. Environmental predictability directly depends on the intensity of environmental variability, but can also depend on the repeatability and regularity of environmental cycles. This has been well presented by (Colwell 1974), who showed that predictability can be separated in two components, (i) the constancy, which is the inverse of the between-year environmental variability, and (ii) the contingency, which refers to seasonality and thus the degree of repetition of environmental change within each year. Perfect predictability can then be met from perfect contingency, perfect constancy, or from particular combinations of the two (Colwell 1974).

Overall environmental predictability should be equally considered when studying the influence of environmental conditions on populations. It can especially allow defining environmental harshness for populations, even more than mean conditions in some cases. Highly seasonal habitats, such as mountainous or Arctic

environments, present predictable environmental variation over each year with seasonal changes in external conditions. These habitats are generally viewed as sharply constrained and limiting for species, displaying what could be regarded as extreme living conditions, such as short growing seasons and long severe winters for instance (Martin 2001; Beniston 2006). However, resident species are generally well adapted to these variations, which attests for long-term evolutionary process (Martin 2001). Thus, more than environmental conditions, environmental unpredictability (including between-year variations and deviations from contingency) can more severely impact population demography and life history traits of these species. This is well illustrated by Yoccoz and Ims (1999)'s study realised on two vole species from different locations; the European snow vole (*Chionomys nivalis*) in the French Alps, and the sibling vole (*Microtus levis*) at Svalbard. While these environments display similar seasonality patterns, considering the length of their breeding season, they nevertheless differ in terms of environmental variability; between-year variability is much larger in winter at Svalbard, which results in unstable and less insulating snow layer than in European Alps. Being an important determinant of small mammals survival and reproduction, such differences in the stability and predictability of snow cover between Svalbard and the Alps induced different demography and life history strategies for the two species. On one hand, sibling voles, inhabiting the highly variable environment, exhibit large inter-annual population fluctuations, with fast life history strategies favouring recolonisation, while on the other hand, snow voles display stable population sizes with slower life history strategies, lower reproduction and higher survival rates (Yoccoz and Ims 1999).

Overall the way each type of environmental variation can constrain individuals and populations has been fairly defined, showing that each level of variation matters and might sometimes act in complex interaction with each other. However, more unknowns remain on understanding how it impacts individuals and populations, and to fully grasp the way species deploy their responses to these variations.

1.2.2. Climate change: what are the implications ?

It should be noted that these different patterns of environmental variation, as environmental stochasticity, are generally not fixed (i.e. stationary, over time) but are perpetually changing along ecological times instead (Wolkovich et al. 2014). At the moment, species are precisely faced with a global non-stationary process with climate change, which disrupts overall environmental variation, impacting a wide range of environmental factors, at an increasing rate.

Patterns of climate change and weather variations have been highly studied for the last decades (IPCC 2013), revealing that each level of temporal environmental variation is concerned with these changes. Overall, as we know, trends are globally moving towards warmer temperatures, while in parallel polar ice sheets and spring snow covers in the Northern Hemisphere are decreasing in extent since the mid-19th century (IPCC 2013). However, beyond these global observations, trends in weather conditions, as patterns of temperature increase and precipitation, can greatly vary locally according to the location and season (Boer et al. 2000; Räisänen 2002; Giorgi et al. 2004). For instance, average temperature increase appears to be greater over high latitudes and altitudes of the Northern Hemisphere, and to be mostly important in winter than in the other seasons with regional exceptions (Salinger 2005). Similarly, mean precipitation has been observed to increase highly in North America while on the contrary it is decreasing in the northern sub-tropics, resulting in drought periods (Salinger 2005). In Europe, mean precipitations are expected to increase in winter over all but the southern parts, while to globally substantially reduce in summer (Giorgi et al. 2004; Rowell 2005). Individuals are now faced with long-term trends in environmental conditions, which, as we previously saw, can provide detrimental constraints for their persistence. Moreover, these changes occur at unprecedented speed which can question the ability of individuals and populations to sustain them.

Underneath these trends, the climate has also been presenting significant changes in its variability in the last decades that have been well observed over a wide range of environmental factors. For instance, increase in precipitation variability, with greater drought or heavy rainfall events, have been observed in the

last decades in different regions (Räisänen 2002; Salinger 2005). Similarly, higher occurrence of drier conditions in winter have been recorded in central and southern Europe while wet anomalies have been observed over Scandinavia (Hurrell 1995). Again, these changes appear to be structured by locations and seasons. In Europe for instance, inter-annual variance of both temperature and precipitations are mainly expected to increase in summer, and to only poorly change in other seasons (Giorgi et al. 2004; Rowell 2005). Individuals are thus faced with an increasingly variable world, which as approached earlier, may translate to increased variability in survival or reproduction for individuals, and have strong repercussions as well on individuals' fitness and on the stochastic population growth rate.

Moreover, both change in mean and variance in weather parameters may ultimately lead to an increase in extreme event frequencies and intensity (see Fig. 1.2). Greater extremes of dryness, heavy rainfall, and more drought and flooding events have been observed since the mid 20th century, and are expected to substantially increase in the following decades (Easterling et al. 2000; Salinger 2005; IPCC 2013). When combined, these two changes may be especially detrimental for individuals, since they can lead to environmental conditions which may go beyond any feasible adaptation or tolerance of species.

At last, these changes in weather conditions should also have direct and indirect impacts on animals, as they impact contingency of environmental variation, disrupting timing of seasons but also plant phenology. A change in the phenology of plants has been largely observed in last years, as a consequence of warmer springs and winters (Menzel and Fabian 1999; Schwartz et al. 2006). In temperate areas for instance, spring events (e.g. bud-break, flowering) started earlier in later years, resulting in an overall lengthening of the growing season in mid and northern latitudes (Menzel and Fabian 1999; Schwartz et al. 2006; Menzel et al. 2006). Seasonality patterns can overall be disrupted according to increased inter-annual variability in weather parameters, as could also be the contrast between the different seasonal environmental conditions. In this context, we might expect that the environmental pressures to which individuals are submitted in seasonal environment would remain the same, (e.g., constraints on the timing of reproduction, and on energy storage) but that they might be either amplified or relaxed. The main

challenge for individuals would then be to succeed in tracking these phenological changes, adapting their life event timing accordingly, to avoid any cost on reproductive success or survival.

Climate change is inherently environmental variation, but this human-induced phenomenon is however exceptional because of the rapidity and intensity of the changes that occur over a relatively short timescale. Species are now interacting with changing environments and a great challenge emerged in last years as to predict and understand how populations and species have been impacted by these environmental variations. Such purpose directly joins the issue of understanding how populations and species deal with environmental variations. Hence, seeing differently, from the rapid changes and responses that climate change induces on relatively observable timescale, this current context can also be viewed as providing a study framework to understand better how individuals and populations respond to variations in their environment. On one hand, this context of climate change has already allowed to confirm past theories in this search, while on the other hand, it brings other issues, such as better understanding which factors structure species response to environmental variation and explain differences in sensitivity to increasing changes.

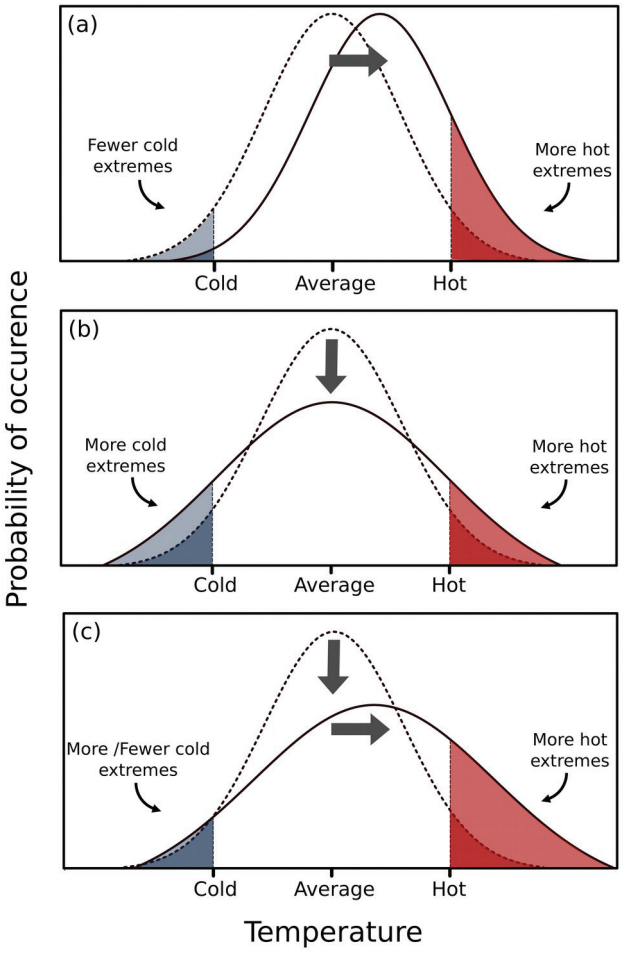

Figure 1.2. The plausible pathways of climate change on weather variables: the temperature as an example. Current climatic trends involve both increasing mean temperatures and climatic variability, with extreme events becoming more frequent.

1.3. Individual, populations and species' responses to environmental variation.

Let us make a short point on the different mechanisms through which species and populations can express adaptive responses to environmental change. Facing environmental variations and underlying constraints, individuals can either (i) tolerate or respond to these variability and adapt to changes, or (ii) be unable to respond and adapt, then directly or indirectly experiencing their effects on life history traits and population dynamics for instance. Adaptation can be regarded at different timescales and then reflect different underlying mechanisms, from evolutionary responses, over a more or less long term (macroevolution vs. microevolution), to phenotypic plasticity, over shorter terms.

Overall, species' life histories and life characteristics are generally the reflect of macroevolution which occurred on a large evolutionary timescale, such as thousands of years being the result of long term adaptive process in close relationship with environmental selection pressure. This process thus involves genetic variability in heritable fitness-related traits and then results in change in genetic composition of a population. Evidence for micro-evolution (evolutionary adaptation over short timescales) especially emerged in the last years along with studies investigating species and population's response to fast ongoing climate change (see Reale et al. 2003; Bradshaw and Holzapfel 2006; Menzel et al. 2006).

An adaptive response can also arise without a change in the genetic composition of a population, being achieved through the existence and expression of a variety of phenotypes for a given genotype under different environmental conditions (Via and Lande 1985). This response then relies on phenotypic plasticity which may in some case allow individuals to maintain fairly constant fitness in the new environment. Plastic response can be expressed at different levels, such as within or across individuals in a population, within a year or throughout the individual lifespan (Visser 2008), and can then provide almost immediate adaptation to changes.

An adaptive response to environmental change can result from both these

mechanisms for a phenotypic trait subjected to natural selection. The scope of the response will however not be the same depending on the mechanism involved; while plasticity proved to be very effective to deal with short-term and/or unpredictable environmental variation, providing rapid adaptation, it should only poorly allow populations to cope with long-term changes in the environment. Adaptation by evolution on the other hand appears as more viable for populations undergoing long-term changes in environmental factors (Lande and Shannon 1996), such as induced by climate change. Phenotypic plasticity however often appears as an important and common response in species to cope with variation in the environment (Merilä 2012) and it can also be subject to selection. Genetic variation for plasticity has been indeed demonstrated (Nussey et al. 2005), which can lead to the expression of different level of plasticity for a given heritable life history traits between individuals in a population. In highly variable environments, selection pressure could select for higher degree in plasticity. Such selection on the strength of phenotypic plasticity has been evidenced in a great tit (*Parus Major*) population to cope with mismatch between breeding dates of birds and the increasing variable availability of caterpillars, on which chicks feed on (Nussey et al. 2005). Such genetic adaptation brings other perspectives with regards to the ability of species to cope with fairly long-term environmental variation, especially if phenotypic plasticity reaches high levels and have similar directional effect with evolution (Berteaux et al. 2004; Visser 2008).

Most of the adaptive responses to environmental variation originate from these different mechanisms. A main challenge for ecologists is then to depict from which mechanism a response originates, since each may provide different quality of response according to the types of environmental changes individuals have to cope with. However, another major challenge is also to have a comprehensive understanding of the overall responses that are expressed in relation to the different types of environmental variation. Various strategies and adaptations are already known to confer fitness benefits when facing environmental variability. Determining how and whether they truly evolved as a response to environmental variation appears more complex. In the next parts, I propose to give an overview of main

current knowledge on this issue according to each type of environmental variation, and see what remains to be investigated.

1.3.1. Response to long-term directional changes in environmental conditions

Long-term trends in environmental conditions can beyond a certain threshold create local mismatches between the biology, requirements and tolerance of individuals and their living environment. To deal with such detrimental changes, individuals can either move and track favourable environmental conditions or succeed in adapting to the new ones. Several illustrations of a selection toward these last responses can especially be provided in the context of climate change which typically includes long-term directional trends in weather conditions.

Move and track favourable conditions

A response to a detrimental change in environmental factors can be for individuals to move and escape poor environmental conditions to limit fitness repercussions. Such an answer should not be without any effect on population dynamics as it can bring a new dynamic in the extinction/colonisation processes of populations. Several examples of species' range shift as a response to the recent changing trends in weather conditions corroborate this expectation for subsequent impacts on populations. Northern range expansion of several species of birds have been reported in North America (Johnson 1994) and Europe (Thomas and Lennon 1999; Berteaux et al. 2004) and relate to environmental trends. Higher overall temperatures appear responsible for these large colonisation trends as it allows the cooler margin of temperature species range to be extended northward, thus the sequential establishments of new populations (high temperature being especially favourable for breeding success of birds). Several species of butterflies, which are also sensitive to temperature, demonstrate similar responses to higher temperatures in Europe with a northern expansion of their range boundaries (Parmesan et al. 1999).

Furthermore, other than moving in latitude, individuals can also present

elevational migration because of continuous change in environmental conditions. This has been highlighted in the last years for both mountainous plants and animal populations (Hughes 2000). Significant upward shifts of both mountainous forest trees and the floristic vegetation have been reported in mountains of Europe and North America in the last decades because of increased mean temperatures in higher elevation (e.g. Walther et al. 2005; Lenoir et al. 2008; Kelly and Goulden 2008). However, extinction risk increased at lower-level elevation because of stressful drier conditions (Lenoir et al. 2008; Kelly and Goulden 2008). Similar elevational range expansion have been also highlighted in some small mammal species in North America, such as for the pocket mouse or the California vole, supposedly in response to higher temperatures as well (Moritz et al. 2008). However, opposite change in the distribution of small mammals have also been observed in the same region with the expansion to lower-elevation of some shrew species (Moritz et al. 2008).

Adapt to changes

Adaptation is another option in coping with continuous change in the environment. Change in mean environmental conditions can directly alter selection pressures acting on populations, and induce changes in life history traits. Change in phenotypic traits cane be especially expected as a response to such environmental change.

Here again, the actual context of climate change provides an interesting framework to investigate such adaptive response to environmental trends. Recently, a widely observed change in a phenotypic trait has been seen as one of the major adaptive response to climate change: a large decline in body size observed across many organisms which has been related to the global increase of temperatures that occurred in the last decades (Gardner et al. 2011; Sheridan and Bickford 2011). This hypothesis is mainly based on theoretical expectation regarding the influence of temperature on metabolic rates and body size of individuals. Ectothermic species are predicted to display higher metabolic rates in warmer environments, which involve additional energetic costs that can lead to reduced energy allocation to growth for

the benefit of survival and/or reproduction. Following this mechanism, higher temperatures should thus select for smaller individuals. This has been proposed, amongst others, to explain the observed trend for smaller body size in amphibians and reptile species in last decades (Bickford et al. 2010; Sheridan and Bickford 2011).

For endothermic species, as birds and mammals, the observed shrinking in body size have been interpreted in line with the Bergmann's rule (Bergmann 1847), which predicts a negative relationship between temperature and body size. Larger body size should be selected in colder environments as it should enhance heat conservation (because of a lower ratio of surface area to body volume, Lindstedt and Boyce 1985; Millar and Hickling 1990), while a decrease in body size should be adaptive when facing high temperature as it should allow a better heat dissipation (Blackburn et al. 1999). According to this theory, the observed decline in body size is to be seen as an adaptive, microevolutionary response to warmer environmental conditions (Gardner et al. 2011; Sheridan and Bickford 2011).

A recent review however suggest that this phenotypic change should be the result of phenotypic plasticity and could be a non-adaptive response to change in several environmental factors, such as temperature or resource availability and quality (Teplitsky and Millien 2014). This is well illustrated by Ozgul et al. (2009)'s study that shows that declining size of the Soay sheep (*Ovis aries*) is a plastic response to both changes in winter conditions and extended growing season that enable the survival of slow-growing individuals, and density-dependence, which negatively influenced lamb growth. Amongst birds, the decrease in body size of the red billed gulls (*Larus novaehollandiae scopulinus*) (Gienapp et al. 2008) and great tits (*Parus major*) (Husby et al. 2011) have also been related to plasticity. Being indirectly related to increased temperature, as the result of deteriorating habitat quality or of reduced prey availability. Opposite trends has also been evidenced regarding body size in the last years for several species. As for the Eurasian Otter (*Lutra lutra*) in Sweden, whose temporal increase in body size have been related to both a decrease in energy expenditure because of higher temperatures and an increase in food availability from longer growing season (Yom-Tov et al. 2010). The Yellow-bellied marmot (*Marmota flaviventris*) similarly displays larger body masses

over time, benefiting from a longer growing season (Ozgul et al. 2010), which also appears to be an indirect effect of an increase in mean annual temperature which allows for a shorter duration of ice cover.

Limiting factors in these responses

Overall, different responses are expressed between species facing trends in environmental conditions. On one side this might reflect differential changes in environmental conditions according to population locations. On the other side, we might ask whether some factors structure species responses to this environmental variation and drive to these differences.

Some ecological factors can already be highlighted as limiting the first response, which is to escape poor environmental conditions, such as the capacity for individuals of a given species to move and/or travel long distances, or the availability of good surrounding living conditions. For instance, polar organisms, such as polar bears or penguins, ice-obligate species, are highly specialised to their habitat and in the same time are already at the extreme limit of their distribution. Mountaintop species are faced with the same limitation. As a result, range contraction have been already observed for these species (Parmesan and Yohe 2003; Parmesan 2006), reflecting local population extinctions. Such species have only one option left to cope with these trends, which will certainly be to adapt, through phenotypic plasticity as a first step or through evolution. Here again, we may wonder if this is achievable, given the high speed at which the changes occur, and the strong specialisation of these species for their habitat

We can also suspect evolutionary adaptation to be constrained in some cases. It might for instance be limited for species with low adaptive potential (Hoffmann and Sgrò 2011). Similarly, we might expect species displaying populations with low turn-over of individuals to be less resilient to continuous and rapid change in their environmental conditions (Gamelon et al. 2014). The generation time, an index of species' position along the “slow-fast continuum” (Gaillard et al. 2005), is inversely related to the maximum annual growth rate of species (Niel and Lebreton 2005; Lebreton 2006). Thus, because of a low maximum

growth rate, long-lived species might recover more slowly from any external perturbation and be more sensitive to global change (Lebreton 2011). This so-called "malediction of long-lived species" (Lebreton 2006, 2011) is well evidenced by the higher risk of extinction that long-lived and larger species are experiencing compared to species of smaller body size and longevity (Cardillo 2003, 2005) .

1.3.2. Responses to seasonality

Seasonality puts important constraints on individuals regarding fat and energy storage and on the scheduling of growth and breeding (Boyce 1979; Conover 1992). Generally individuals have to sustain food scarcity and thermoregulatory costs to survive the non-growing season and successfully reproduce afterwards. Similarly, there is a need for reproduction to occur sufficiently early in the growing season to maximise reproductive success; to allow offspring to grow and acquire a sufficient body mass to sustain the following winter period. As a result seasonality also appears as an important selective force shaping life histories. Behavioural, physiological, phenotypic and phenological adaptations are amongst some of the responses that evolved over long timescale to cope with these constraints.

Adaptive responses to cope with the harsh seasons

Different strategies can be observed among organisms to cope with this predictable seasonal resource depression and the weather severity of the non-growing season.

First, such as for coping with detrimental environmental living conditions, individuals can move to avoid the "harsh" season and minimize any repercussion on fitness. Various organisms living in seasonal environment indeed display seasonal migration. This goes from long-distance migration, such as performed by some birds, marine mammals and some bats, to medium-distance or altitudinal migration, as observed for some mammals in African plains or for some mountainous animals. Seasonal migration allows to live in relatively "constant" environment for individuals as it may regulate resources availability all along the year (Alerstam et al. 2003).

Other adaptations have been supposed to evolve to sustain this critical period, as certain energy saving strategies implying reduced metabolism such as diapause, torpor and hibernation for instance (Lyman et al. 1982). These different forms of animal dormancy allow to substantially save energy, to survive the period of food shortage and then be able to reproduce during the breeding period. They involve different underlying mechanisms. Diapause, which is often displayed in insects, implies a genetic basis but no decrease in body temperature for the organism in addition to reduced metabolic rate. Hibernation, which is mainly performed by mammals as bats and rodents, implies prolonged or several bouts of torpor over months (Geiser and Ruf 1995; Geiser 1998). These strategies allow to survive with limited or without food for more or less long periods but also to sustain severe external environmental conditions (Turbill et al. 2011; Ruf et al. 2012). Moreover, by reducing energy requirements, they also allow to reduce the time animals spend foraging and thus predation risk. Similarly, hibernation usually involve the use of shelters, such as burrows, which can also limit the exposure to detrimental environmental conditions (Turbill et al. 2011).

Lastly, with regards to hibernation, it also involves an energy storage strategy to sustain prolonged torpor, even through food storage or through the accumulation of fat reserves (Humphries et al. 2003). That brings us with another response that organisms display to cope with seasonality: seasonal variation in body mass. Such variation is widespread in vertebrates and is often considered an adaptive response to seasonality and to periods of food shortages (e.g. Prestrud and Nilssen 1992). Body mass and fat reserves are important determinant of fasting endurance, plastic individuals with high body mass are expected to be selected in seasonal environment, surviving winter and achieving good reproduction (Pelletier et al. 2007). Similarly, a selection for fast growth and large body size individuals has also been suggested in seasonal environments (see Lindstedt and Boyce 1985 on mammals; (Conover 1992) on fishes; (Ashton 2002) on birds). As larger body size should allow for better fasting endurance and heat conservation (Lindstedt and Boyce 1985; (Millar and Hickling 1990).

Responses to phenological constraints

Seasonal environments put important constraints on the timing of breeding and growth. As seen previously, it generally induces a need for individuals to grow and acquire sufficient fat reserves during the growing season, to sustain the upcoming food-shortage period, and then reproduce successfully. However, breeding period generally appears to be restricted to only a short time-window over the growing season. The latter being characterised by temporal variation in resource abundance and quality. In temperate areas, it can be decomposed in: a vegetation growing period in early spring, which provides individuals with high-quality nutrients; a peak in vegetation abundance in summer; and a decrease in both vegetation quality and quantity (Pettorelli et al. 2005b, 2007). There is only a short time-period left to attempt breeding in suitable environmental conditions, given the energy requirement it entails for females, and to ensure reproduction and offspring fitness. Indeed, offspring fitness typically peaks early in the season (Perrins 1970; Varpe et al. 2007; Verhulst and Nilsson 2008) while reproductive success generally declines throughout the growing season (Hatchwell 1991; Rowe et al. 1994). This temporal declines can be related to the decrease in food availability and quality at the end of season together with predation pressure (Perrins 1970; Hatchwell 1991). Even though it can also be related to temporal difference in breeder quality in some cases (Verhulst and Nilsson 2008; Plard et al. 2014a). There is a strong selection pressure on the phenology of life events in species inhabiting seasonal environment, which present a highly constrained life cycle accordingly.

Seasonal environments induce strong selection against late or too early breeding and date of birth, rather selecting for the timing of reproduction to match phenology of the vegetation. This can be observed in great tits (*Parus major*) which start reproducing before the food peak to synchronise food demand of chicks with the peak in caterpillars abundance to maximise offspring fitness (Perrins 1965; Verboven et al. 2001). It can also be observed in large herbivores as roe deer (*Capreolus capreolus*) for which early synchrony in parturition is seen as adaptive to match the spring vegetation flush and reduce the predation impact (Rutberg 1987; Plard et al. 2014b). This selective pressure on scheduling reproduction can also be

well evidenced with climate change, as several changes in the timing of breeding have been highlighted as a response to warmer temperature and earlier spring. Earlier breeding has been reported amongst several organisms, such as birds (e.g. Crick et al. 1997; Both et al. 2004), amphibians (e.g. Beebee 2002), or mammals (e.g. Coulson et al. 2003; Reale et al. 2003; Moyes et al. 2011). The adaptive value of these life history traits in seasonal environments can furthermore be illustrated in this context, if we now look at species which did not succeed in adapting their timing of breeding and date of birth to match new vegetation phenology. We then see that individuals generally undergo negative fitness effects, such as a decrease in offspring production or in offspring or breeder fitness (e.g. Thomas et al. 2001, amongst blue tits; Post and Forchhammer 2008, amongst caribou) mainly because of a mismatch between food abundance and breeders/offspring requirements, which can have detrimental effect for population demography (e.g. Plard et al. 2014a, amongst roe deer).

In the same way, arrival of migration and date of emergence, from hibernation or diapause, appear to be under similar selection since they directly drive the subsequent timing of reproduction and synchrony with vegetation phenology. This can also be highlighted with climate change, as a trend for earlier arrival of migratory species (e.g.Sokolov et al. 1998; Hüppop and Hüppop 2003, for change in spring migration timing amongst birds), but also earlier emergence from hibernation (e.g. Inouye et al. 2000, for yellow-bellied marmots; Sheriff et al. 2011, for the Arctic ground squirrel) have been reported in the northern hemisphere as a response to earlier spring in the last years. While, on the other hand, important population declines have been reported for migratory birds which have not changed their timing of spring arrival (Both et al. 2006; Møller et al. 2008).

At last, early breeding in the growing season generally requires sufficient body fat reserve at the end of the harsh season or to acquire it fast enough at the beginning of the growing season, which is challenging, especially for young individuals in high seasonal environments, as they only have little time to grow and accumulate fat reserve before the first breeding season. This can directly affect the age of maturity amongst some species, since both age and size of maturity are predicted to be delayed if an increase in growth allow for further higher reproductive

value (Stearns 1992). In that way, delayed or plastic age at maturity can be seen as an adaptive reproductive tactic in high seasonal environments (Drent and Daan 1980). This has been for instance suggested for the lizard *Sceloporus undulatu,* which presents delayed maturation according to decreasing length in its activity season (Adolph and Porter 1996), or for the brown bear (*Ursus arctos*), for which age at first reproduction increases with latitude and shorter growing season within its geographic range (Ferguson and McLoughlin 2000).

When directional change in the environment intersects seasonality patterns…

Species living in seasonal environments have evolved strategies to adapt these predictable changes in environmental conditions. Nowadays, seasonality patterns and contingency seem altered by global changes. As seen earlier, these changes influence selection pressures related to seasonality, particularly intensifying them, allowing to highlight the responses species display to them. For a given variation (e.g. earlier vegetation growth), some species seem not to display any response, or do not display similar responses while it was thought they have evolved same strategies to cope with seasonal environments. This raises questions and unknowns regarding the mechanisms which come into play in a species' response to seasonality.

Such disparity in responses can reveal differences in life history flexibility between species as to adapt phenology of life events. This can refer to differences in phenotypic plasticity, as the ability to change timing of breeding, but also physiological constraints which might limit flexibility in the duration of particular life events, or at last, this can highlight that some life strategies may be more advantageous than others in such changing environments. Let us take the example of the roe deer, whose populations currently undergo lower growth with decreasing recruitment because of earlier spring (Gaillard et al. 2013). In contrast with similar large herbivores as the red deer (*Cervus elaphus,* (Moyes et al. 2011), roe deer appears unable to advance the date of birth to match the vegetation phenology and maintain constant individual fitness (Plard et al. 2014a), highlighting a lack of phenotypic plasticity in the timing of birth for this species. This lack of plasticity has

been suggested to reflect the inability to reduce gestation length with increasing temperature in late winter, and thus to track this environmental cue (Plard et al. 2014a).

1.3.3. Response to stochastic environmental variations

Stochastic variations in environmental conditions are inherent to every environments, although being variable in intensity. As approached earlier, such unpredictable variation can have a detrimental influence on individual fitness. By generating variability in reproductive success and/or in survival probability across years, environmental variation increases the risk of failure for individuals in both reproduction and survival over their lifetime. An adaptive response to such environmental constraint would be to adopt strategies that maximise the individual fitness not necessarily by increasing mean vital rates but rather by decreasing temporal variance in them. This important tenet of adaptation in random environments has been well conceptualized through the bet-hedging strategy (Gillespie 1974; Slatkin 1974 ; Seger and Brockmann 1987), which originally says that in varying environments, higher individual fitness should be achieved by minimising temporal variation in reproductive success rather than maximising the annual reproductive success (Philippi and Seger 1989).

Reproductive tactics in variable environments

Iteroparity is a perfect illustration of a bet-hedging strategy. It can be seen as a risk-spreading strategy which evolved in random environments (Schaffer 1974b). Breeding several times at a low level throughout a long lifespan allows to spread over several occasions the risk for reproductive failure in an environment that generates high variability in reproductive success, and as a result allows to maximize the geometric mean fitness (Murphy 1968; Charnov and Schaffer 1973; Schaffer 1974b). Iteroparity has been at first seen to be especially selected in environment which generate variability in juvenile survival, while relatively greater variation in adult survival should select for more semelparity (Murphy 1968; Schaffer 1974b).

However, environmental variability can lead to both iteroparity or semelparity irrespective of the relative variability between age classes (Orzack and Tuljapurkar 1989). Different levels of variability should rather tend to favour a certain type of reproductive tactic than another, with iteroparity being overall a much more advantageous strategy in stochastic environments (Orzack and Tuljapurkar 1989; Benton and Grant 1999).

Delayed reproduction appears to provide similar benefits as iteroparity in uncertain environments, and understanding whether these two types of life history delay can evolve together as an adaptive response to environmental uncertainty has been investigated (Tuljapurkar and Wiener 2000; Wilbur and Rudolf 2006; Koons et al. 2008). It results that the evolution of delayed reproduction in iteroparous species should be favoured by environmental stochasticity in itself only under certain circumstances and level of stochasticity, as in the case where juvenile survival is higher than adult survival (Koons et al. 2008). Overall, delayed onset of reproduction can be viewed as adaptive in long-lived species or as a constraint, regardless of environmental stochasticity. Fecundity is frequently size- and age-dependent, especially in large, long-lived organisms, which can require time delay to acquire adequate state. Also, in long-lived iteroparous species, each event of reproduction has a cost for both future survival and subsequent breeding attempts, so delaying the first reproduction could be selected if it maximises overall reproduction throughout the lifespan (Harvey and Zammuto 1985).

Species' pace of life and environmental canalization

The way reproductive effort is distributed over time appears as one key component in species response to environmental stochasticity. Long-lived species typically display conservative strategies, favouring survival over reproduction; individuals generally avoid jeopardising their own survival at the expense of their offspring survival or future reproduction. In this case longevity is the key of individual fitness in uncertain environment. Short-lived species, on the opposite, display fast life history strategy, and allocate highly in first reproduction events over survival and future reproduction.

As a result, general patterns of variation in fitness components can be observed across species, traducing different responses to environmental variability both according to species life history strategies and across life history traits of a given species. Long-lived species indeed display lower and more variable reproduction (including fecundity and juvenile survival) compared to adult survival. This general pattern has been repeatedly reported empirically for both long-lived iteroparous mammals (Gaillard et al. 2000a) and birds (Saether and Bakke 2000). Conversely, short-lived species display high and less variable reproduction than survival, which generally appears highly variable (Gaillard and Yoccoz 2003). These patterns prove to be the reflect of environmental canalisation: a canalisation (against temporal variation) of fitness components with the greatest impact on fitness, and thus on the population growth rate, i.e. with higher elasticities and sensitivities (Pfister 1998; Gaillard and Yoccoz 2003). In long-lived iteroparous species, elasticity of the stochastic population growth rate to adult survival is considerably greater than for juvenile survival or reproduction. Adult survival has the greatest impact on the population growth rate, and displays the smallest temporal variation (Gaillard and Yoccoz 2003). Sensitivities provide some insights on the way natural selection act in random environment (Benton and Grant 1996). Here, this demonstrates strong selection pressures toward strategies that minimise temporal variation in adult survival in long-lived species, in line with the conservative tactic that they display. This can be illustrated empirically. Amongst ungulates, adult females have been shown to adopt a "prudent" or "risk-avoidance" strategy when resources are scarce, by reducing their allocation in offspring, such as maternal care, to favour their own gain in body mass (see Festa-Bianchet and Jorgenson 1998).

Overall, species pace of life appears to be playing a structuring role in the way species respond to random environmental variation. Patterns of sensitivities of the population growth rate to vital rates can indeed be observed according to generation time, with population growth rate of short-lived species being generally more sensitive to overall changes in fecundity rate, and population growth rate of long-lived species being rather more sensitive to changes in adult survival (see Fig. 1.3, Lebreton and Clobert 1991). Likewise, the action of natural selection on life history traits, as for environmental canalisation (the way each fitness component is

impacted by temporal variation), seems to vary across species according to the pace of life.

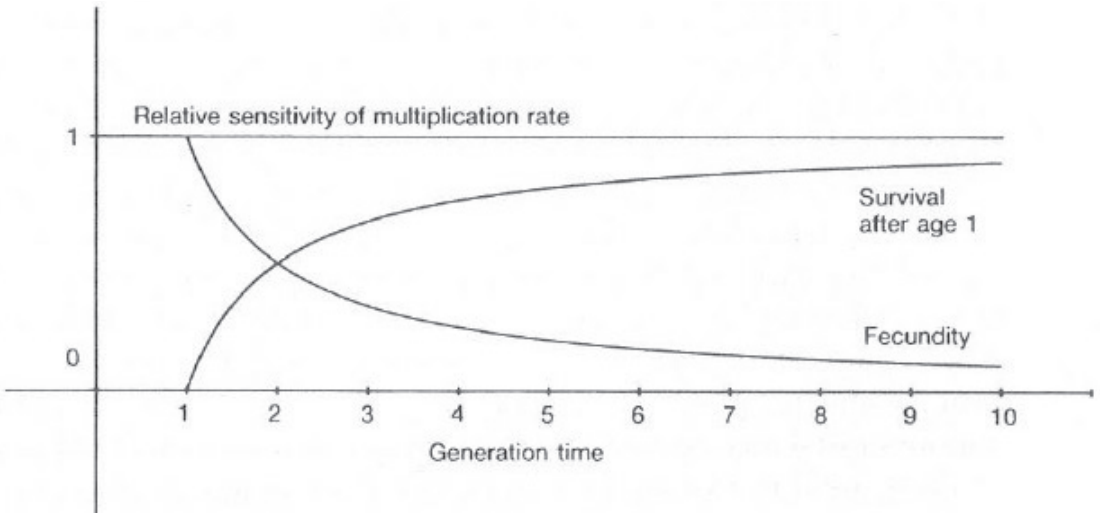

Figure 1.3. Relative sensitivity of the population growth rate to survival after 1st year and to fecundity, as functions of generation time (from Lebreton and Clobert 1991).

Which responses to more unpredictable environment?

Despite increasing knowledge on the topic, the way environmental stochasticity influences species life history remains poorly understood. Species have adapted a certain amount of environmental stochasticity, through different strategies, but we might suspect that their ability to deal with random environmental variation is limited, and that demographical consequences may occur if a threshold in the intensity of environmental stochasticity is exceeded. This can be observed empirically, looking for instance at the detrimental effect that higher frequency of extreme events induce on individual fitness, such as greater frequency of failure in reproduction, increased adult mortality, and the resulting population declines or extinctions (Parmesan et al. 2000; Jiguet et al. 2006; Moreno and Møller 2011).

"How will species deal with increasing environmental stochasticity?", "may some life history strategies be more efficient than others to cope with these changes?" are questions that can be asked. As we have seen the way individuals allocate resources between current and future survival and reproduction is

determinant in stochastic environments and will determine life history strategies adopted by species and the costs of reproduction that may be experienced (Hamel et al. 2010b). One main goal when dealing with increasing stochasticity should be the need for individuals to limit the fitness costs of reproduction of any kind. In that way, life history flexibility in the decision as to breed or not to breed should be important. Besides, plastic reproductive tactics have been identified as optimal and a major asset for species in highly variable environments (Bårdsen et al. 2011). Different reproductive tactics can be identified amongst long-lived species in unpredictable environments, traducing different energy allocation to reproduction. Some can be characterised as "risk prone reproductive tactic", which involves high investment in reproduction regardless of environmental conditions and should result in high reproductive output in good conditions while resulting in high survival costs when conditions are harsh. Another strategy corresponds to a "risk averse reproductive tactic", which as seen earlier, involves low investment in reproduction, with females being more prone to defer breeding to preserve their own survival. It can result in low reproductive gain afterwards but allows in return to maintain survival during harsh years. Overall, a selection towards risk averse strategy is expected to allow individuals to better deal with increasing stochasticity, buffering them against adverse conditions which is thus expected to be favoured in this context (Bårdsen et al. 2011).

Overall, species with low flexibility in their life histories appear as more threatened than other by increasing variable environmental conditions. This can be illustrated by the European shag (*Phalacrocorax aristotelis*, (Frederiksen et al. 2008) or the Antarctic fur seal (*Arctocephalus gazella,* (Forcada et al. 2008). These two species display reproductive tactics that are no longer viable with increasing variability. As a result, species' populations now experience a decrease in their stochastic population growth rate mainly because of increased variability in adult survival (Forcada et al. 2008; Frederiksen et al. 2008). In contrast with other Antarctic mammals and birds which present flexibility in the choice to reproduce or not, the Antarctic fur seal continues to reproduce despite critical environmental conditions. Furthermore, this species is an income breeder, and so individual body condition and the ability for females to sustain reproduction is very sensitive to

available resources. As a global result, survival of breeding females is more variable and much lower in the last year because of increased environmental stochasticity (Forcada et al. 2008). Low flexibility in this case has thus led to increased cost of reproduction for adults with detrimental effect on their performance.

At a more global scale, predictions have also be made regarding factors that should determine species sensitivity to increased environmental stochasticity. It has been shown that long-lived species should overall be more resistant to increasing variation in their environment than short-lived species (Morris et al. 2008; Sæther et al. 2013; Gamelon et al. 2014, 2016). An overall buffering effect of the generation time to environmental stochasticity was thus highlighted with the influence of stochastic changes on populations decreasing with the species' pace of life (Sæther et al. 2013).

1.4. Which role of the species lifestyle in the response to environmental variation?

Globally we see that species responses to environmental variation appear idiosyncratic. Although general mechanisms of adaptation and strategies to cope with environmental variations have been well described among species, the response to changes in environmental variations appears as very specific to each species or populations. This shows us that it still remains challenging to understand mechanisms underlying responses of individuals to environmental variation and to predict them. Hence, and beyond the direction that the response takes, we see that this asks a general unanswered question: what are the overall factors which structure individuals responses to environmental variations?

We saw some factors have started to be identified, such as the generation time, whose structuring role reveals strong influence of species' life histories in the response and sensitivity of individuals to changes in environmental conditions. The environment plays an important role in the evolution of life history strategy, and in turn these co-evolved species-specific characteristics tend to determine the way individuals deal with environmental variations and thus the species sensitivity to any change in the environment. Similarly, it would be worth thinking that any factor that tend to influence species life histories in a way could also play a role in individuals' response to environmental variation, and that their effects should have to be explored in this context. In that respect, the lifestyle appears as a good avenue of investigation. The species' lifestyle is now well known to strongly shape species life histories and seems to play an important role in the adaptation of individuals to their environment. Accordingly and as we shall see, lifestyle is situated at the interface between the environment and population demography, and a structuring effect of this factor could thus be expected in the expression of the individual's response to environmental variation. Yet, still little is known on this topic.

1.4.1. Influence of the lifestyle on life histories

There is no one single definition of the lifestyle (e.g. Dobson 2007; Sibly and Brown 2007; Okie et al. 2013; Gaillard et al. 2016). Here, we will consider that species lifestyle can refer to the way of life that is shared between individuals of a species and which relies on the interrelation of ecological, physiological, behavioural or anatomical traits. Thus it shall for instance include species characteristics such as the foraging and living environment, as whether individuals display a fossorial, terrestrial, arboreal or aerial life, but also the flight capability, the type of diet or the social organisation of the species.

Recently, evidence for a strong influence of lifestyle over species' life histories was provided. Particular lifestyles seem to explain variations in life histories over the slow-fast continuum, after accounting for body mass and phylogeny, and thus to influence the species pace of life (Shattuck and Williams 2010; Healy et al. 2014; Williams and Shattuck 2015; Healy 2015). Here is some evidence for a structuring effect of the lifestyle on species life histories.

Flight capability and foraging environment

Particular lifestyles, such as the flight capability and the habitat type, have been shown to explain unexpected long lifespan across birds and mammals given their body mass (Shattuck and Williams 2010; Healy et al. 2014). Volant species, for instance, appear to live longer than non-volant species after correcting for the body size (Healy et al. 2014). This relationship, between the aerial life and longevity, was reported several times for birds (Lindstedt and Calder, 1981; Pomeroy 1990; Ricklefs 2010) but also amongst mammals, as for bats or for other gliding and flying mammals, which display higher longevity compared to similar-sized non-flying mammals (Austad and Fischer 1991; Holmes and Austad 1994). This increased longevity for flying species was generally attributed to their ability to escape more easily predation, unfavourable conditions or other environmentally-driven mortality (e.g. Pomeroy 1990; Holmes and Austad 1994; Healy et al. 2014). Similarly, arboreal mammals evolve higher longevity than terrestrial mammals for a given

body mass. It has been assumed arboreal environments also reduce individual mortality through providing similar protection against predation or bad environmental conditions (Shattuck and Williams 2010; Healy et al. 2014).

Hibernation and fossoriality

In the same framework, hibernation has been associated with increased survival rates among mammals (Wilkinson and South 2002; Turbill et al. 2011) and to slow life history strategies, with an overall co-evolution of traits such as delayed age at maturity, lower reproductive rate, and longer generation time (Turbill et al. 2011). The beneficial effect of hibernation on survival may ultimately be related to resistance to energetic constraints that torpor brings, as it allows individuals to better survive periods of food shortage and/or harsh weather conditions in seasonal environments (Humphries et al. 2003). However recent evidence suggests the beneficial effect of hibernation might be confounding with the effect of sheltering and predator avoidance (Liow et al. 2009; Turbill et al. 2011; Ruf et al. 2012). Hibernation generally involves individuals retirement in caveats or underground in burrows and also implies a substantial period of inactivity in these shelters throughout the year which protects from external threats and limits predation risk (eg. Bieber and Ruf 2009). Other processes, such as the beneficial effect of torpor on physiological ageing, seem also to come into play to explain the long lifespan of hibernating species (Ruf et al. 2012; Turbill et al. 2012).

Fossoriality may provide in itself the ability to escape predation. The way a fossorial lifestyle influences lifespan variation in mammals and birds has also been addressed by Healy et al. (2014) in its large comparative study. However, while Healy et al. (2014) found a positive effect of fossoriality on species lifespan, observed variations in lifespan in non-volant species turned out to be better explained by sociality, which was so far neglected in the comparative analysis (Williams and Shattuck 2015; Healy 2015). More precisely, eusocial species have shown to live longer than non-eusocial species for a given body size, so that the beneficial effect of sociality should mostly explain the extraordinary longevity of some subterranean species (Healy 2015).

One can thus face difficulties when addressing the influence of lifestyle on species' life histories. We see that species lifestyle can be defined by the co-evolution of several interrelated traits, whose effects can be more or less complex on individuals fitness, acting in same direction or not. It could then be hard to affiliate an observed fitness gain to a particular lifestyle trait and to disentangle the effect of each of them on life history traits. Moreover, the way each lifestyle reduces environmentally-driven mortality and thus limits the effect of environmental variations remains unclear. A buffering effect towards bad environmental conditions is often proposed as an explanation for decreased mortality, but is rarely identified in details, which reflects issues in identifying pathways through which the lifestyle benefits to species life history traits.

A focus on sociality

Sociality can be defined as the tendency of organisms to live in groups (Alexander 1974). Different levels of sociality are displayed across species. A sociality gradient can be drawn, where species range from solitary at the first end, to cooperative breeding and eusocial at the other extremity (Table 1.1, see (Silk 2007; Berger 2015). These sociality levels are then determined according to the social organisation (e.g. family structure), the social behaviours (e.g. alarm calls) or the reproductive tactics (e.g. communal breeding) that the species displays (Table 1.1).

As previously seen, a high degree of sociality was shown to increase species longevity. Sociality may have multiple effects on species life histories depending on the level of sociality that is displayed. More or less complex social lifestyles have been overall related to low annual mortality and long lifespans in numerous organisms, such as insects (Keller and Genoud 1997), birds (Wasser and Sherman 2010), or mammals (McNutt and Silk 2008). Here also, these lifestyles may allow reducing environmentally-driven mortality, in different ways. Group living can provide mutual protection against predators, as social groups generally display shared vigilance behaviours or alarm calling (Clutton-Brock et al. 1999). Similarly, the formation of colony may translate in shelters allowing to decrease the predation risks (Alexander 1974; Armitage 1981; Wasser and Sherman 2010). Group living

may also provide benefits regarding resources exploitation, allowing for the practice of social foraging or resource defence when food is sparse or ephemeral (Ebensperber 2001; Johnson et al. 2002), or allowing the provisioning of reproductive females by subordinates in eusocial species for instance (Keller and Genoud 1997).

Table 1.1. Classifications and definition of sociality levels (from Berger 2015).

Sociality levels			**Definition**
Solitary			- No interactions between adult individuals except for reproduction
Gregarious			- Group formation - No interactions between adults - Groups may last or exist only during mating season - Allo-parental care may occur
Colonial			- Group formation in pairs (sometimes for life) - Few interactions between pairs
Social group	Plural breeders	Absence of allo-parental care	- Group living - Cooperative interactions - Overlap of generations
		Allo-parental care	- Group living - Cooperative interactions - Overlap of generations - Allo-parental care
		Communal breeders	- Group living - Cooperative interactions - Overlap of generations - Synchronisation of reproduction and equally shared parental care
	Singular / cooperative breeders	Reversible	- Group living - Cooperative interactions - Overlap of generations - Reproduction monopolized by dominant individuals - Delayed dispersal and reproduction of subordinates - Allo-parental-care provided by subordinates
		Eusocial	- Group living - Labour division - Reproduction monopolized by one or few individuals - Subordinates are sterile cooperative breeding

Additional fitness benefits may be found in species practising allo-parental care. In these species, reproducing individuals may receive helps in rearing offspring from other reproducing conspecifics (e.g. amongst communal breeders) or from non-reproducing subordinates (e.g. the helpers, amongst cooperative breeders) and generally benefit from higher fitness as a result, with especially increased reproductive success (see Silk 2007 for a review on mammals). Amongst species practising cooperative breeding, the presence of helpers in family groups has indeed been shown to positively influence the reproductive success, allowing to increase offspring growth rates and survival (Allainé et al. 2000; Russell et al. 2002). This increase in reproductive success can be provided in different ways by helpers. Helpers can indeed offer protection against predators, participate in offspring feeding by practising allo-suckling (Knight et al. 1992; Russell et al. 2003a), or provide offspring with thermodynamic benefits, as especially observed for burrowing and hibernating species (Allainé et al. 2000; Allainé and Theuriau 2004). Furthermore, helpers can provide the reproducing individuals with other fitness benefits, as they can reduce maternal care by lightening the load of the reproductive cost (Crick 1992 on birds; Russell et al. 2003b on mammals) and thus indirectly enhance the body condition of mothers. This can in turn allow for reduced inter-breeding intervals and allow for higher breeding attempts and litter size (see Russell et al. 2003a). Similarly, through this help, the social breeders can save and allocate more energy to their maintenance, which allow them to display longer lifespan and higher lifetime-reproductive success (Crick 1992).

Hence, the way sociality impacts individual fitness may appear more complex than for other lifestyles. Especially as beneficial effects of sociality result from group living in itself, and will depend on the group composition and on interactions with conspecifics. Consequently, family group characteristics and conspecific behaviours, which overall define the social environment, may be considered as another level of variation, in the same way as the external environment, which can impact individual fitness and thus population dynamics. More, factors which make the social environment vary can indirectly play a role regarding the influence of sociality on individuals.

1.4.2. What is the relationship between species lifestyle and environmental variation?

Overall, certain lifestyles have a net influence on species life history traits, providing individuals with fitness benefits. We saw however that underlying mechanisms through which these beneficial effects occur may remain unclear in some point. It appears difficult to identify the relative influence of each lifestyle trait and the way they impact individual fitness. Moreover, while certain species lifestyles have been supposed to provide fitness benefits by offering protection from bad environmental conditions, it remains unclear how and to which extent the lifestyle come into play in the way species are impacted by environmental variations, which is our main issue here.

According to life history theory we might overall suspect a structuring role of the lifestyle in the response of individuals to environmental variations, determining especially species sensitivity to environmental variability. Lifestyle might indeed indirectly influence species sensitivity to environmental stochasticity through its influence on the generation time. We saw that a more or less slow pace of life can be expected according to species lifestyle, and also that species resistance to increased stochastic environmental variation depend on their pace of life (Morris et al. 2008; Tuljapurkar et al. 2009; Sæther et al. 2013). Through this, different resistance to random environmental variations should also be expected according to the species lifestyle. Long-lived species are predicted to be more resistant to high stochastic environmental variation than short-lived species, certainly because an adult stage is generally maintained in long-lived species populations which allows limiting variations in the population growth rate (Morris et al. 2008). This permanent adult stage is especially allowed in long-lived species through selection towards behaviours or strategies that buffer adult survival against temporal variation. Hence, in a similar way, lifestyles which allow for increased lifespan are often seen as providing an additional buffering effect on adult survival against environmental variation. We might suppose that species whose lifestyle contributes to increase the generation time, providing buffering effects on adult survival, should better resist and cope with stochastic environmental variations.

Beyond this expectation, a first step should however be to fill gaps in understanding how species lifestyle modulates the effects of environmental fluctuations, whether they are predictable or unpredictable variations, and understanding whether lifestyle acts through increasing mean vital rates and/or decreasing variance.

Some work has been performed as to understand the beneficial effect of certain lifestyles against environmental changes. As such, species displaying lifestyle characteristics such as hibernation, daily torpor or sheltering have shown to be at lower risk of extinction than similar-sized species in the context of climate change (Liow et al. 2009; Geiser and Turbill 2009). Such resistance to environmental variations has been attributed to the physiological and behavioural traits defining these particular lifestyles, which were suggested to provide individuals the ability to cope with both expected and unexpected environmental changes (Geiser and Turbill 2009). Originally, hibernation has been considered to be an adaptation allowing individuals to deal with seasonality and thus predictable harsh seasons (Humphries et al. 2003), while later it was also viewed as a way to avoid predation in small mammals (Bieber and Ruf 2009; Turbill et al. 2011). On the opposite, daily torpor has been mainly seen as an adaptation to cope with unpredictable daily fluctuation in weather conditions (Geiser 1998). Furthermore, sheltering, a correlation of both hibernation and torpor, may allow for the possibility of displaying a risk averse behaviour and to deal with the unexpected, with the opportunity to shelter for longer or shorter periods when environmental conditions are detrimental; caveats or burrows offering quite constant thermal conditions, and protection against predators. Everything suggests these lifestyles should buffer against both predictable and unpredictable environmental variations and increase individuals fitness through both increasing mean value of vital rates or decreasing their temporal variance.

The way lifestyles modulate the effects of environmental variation in shaping life history traits can also be asked for other lifestyles such as for cooperative breeding, a high level of sociality. While barely considered at first, relationships between cooperative breeding and environmental conditions have been increasingly studied

in the last years. This well reflects the progressive theories which emerged over years as to explain the evolution of cooperative breeding, and the relative place of the environment in them. Cooperative breeding started to be viewed as a response to environmental variation from the ecological constraint hypothesis (Emlen 1982a; Koenig et al. 1992; Hatchwell and Komdeur 2000) which predicts that harsh environmental conditions, whether it be weather conditions, predation or habitat saturation, may constrain dispersal and force young individuals to delay dispersal and stay in family groups. Cooperative behaviours are then seen as doing the best of the bad job of staying in the natal family group and skip reproduction, as helpers may benefit from indirect fitness gain by helping in rearing siblings (Russell and Hatchwell 2001). However, the way cooperative breeding influences the effect of environmental variation on individuals has been mainly discussed later in the last decades, during which several studies investigated the adaptive value of cooperative breeding, always in order to get insights in its evolution. It appears that helpers presence and cooperative behaviours might be promoted by years with more severe environmental conditions, and it seems to provide a higher beneficial effect on mean reproductive success in those years (Canário et al. 2004; Covas et al. 2008). Cooperative breeding should indirectly be a way to respond to bad environmental constraint. In recent years, large-scale studies highlighted that the distribution of cooperatively breeding birds was closely positively associated with highly variable habitats, suggesting cooperative breeding might be adaptive in random environments (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Cockburn and Russell 2011). Cooperative breeding was suggested as being a bet-hedging strategy, allowing to cope with random environmental variations, while helpers presence was shown to increase the reproductive success by also decreasing reproductive variance (Rubenstein 2011; Koenig and Walters 2015).

The role of environmental variation is still debated in understanding the evolution of cooperative breeding. By allowing a buffering of individual fitness against temporal environmental variation, this lifestyle might confer populations of cooperatively breeding species with resistance against strong environmental variation compared to other species. However, to date, this topic remains quite overlooked with only few studies performed on this issue, mainly on birds.

Furthermore, it would be interesting to explore this lifestyle influence in the current context of climate change, taking advantage of stochastic demography, to have a better understanding of the way lifestyle structures species response to environmental variation.

1.5. Aim of the thesis

This PhD thesis aims at better understanding the role of the species lifestyle in species response to environmental variation. Specifically, my thesis mainly focuses on investigating demographic response of an Alpine marmot (*Marmota marmota*) population to environmental temporal variation in the current context of climate change, seeking at understanding how the Alpine marmot lifestyle, which involves hibernation and cooperative breeding, modulates its response.

My thesis takes advantage of a long-term individual-based dataset on an Alpine marmot population in the French Alps, intensively monitored for around 26 years (*chapter 2*). This species appears as a well suited biological model regarding our issue. Alpine marmots live in highly seasonal mountainous environments and hibernate for six months throughout the year, which thus strongly constrain its annual life cycle. Then, this species is highly social. It lives in family groups of variable size, from 2 to 20 individuals, and practices cooperative breeding, with male subordinates acting as helpers for their siblings, through shared thermoregulation during hibernation, which increases juvenile survival as a result (Allainé et al. 2000; Allainé and Theuriau 2004). Thus, variability in the composition of social groups gives the possibility to capture the effects of cooperative breeding on fitness of relatives. The aim of this study finally proves to be to investigate the effects of these two lifestyle traits, hibernation and social-living, which both very likely evolved as a response to environmental constraints, on this species response to environmental variation. My thesis work has been divided into three parts.

In the first part (*chapter 3*), we investigated the effects of weather fluctuations on age-specific variations in survival of the Alpine marmot population, looking especially at the influence of the Alpine marmot lifestyle on these responses. We overall expected earlier springs to positively impact individuals survival as hibernation within burrows and social thermoregulation should prevent them from detrimental changes in the winter conditions. This chapter has been published in *Journal of Animal Ecology*.

The second part (*chapter 4*) then aimed at investigating the adaptive value of cooperative breeding in the Alpine marmot population regarding environmental variation. We especially asked at first whether the presence of helpers allowed not only to increase mean juvenile survival but also to decrease temporal variance in survival of this age-class. We secondly investigated the implication of such possible effects of cooperative breeding on the stochastic population growth rate, especially expecting a buffering influence of the latter against environmental variation. This chapter corresponds to a manuscript in progress.

In the third part (*chapter 5*), we asked whether differences in lifestyle and reproductive tactic might explain differences in the demography between Alpine marmot and Alpine chamois (*Rupicapra rupicapra*) populations. These two long-lived species share a similar position on the slow-fast continuum and should be subjected to similar environmental variation in the Alps. We nevertheless expected the way their vital rates were impacted by environmental variation and their overall population demography to differ between populations because of their different lifestyle and reproductive tactic. We especially expected a higher buffering of vital rates and as a result a higher buffering of the population growth rate for the Alpine marmot population compared with the Alpine chamois population. We also expected their difference in lifestyle to explain their difference of response to climate change. This chapter also corresponds to a manuscript in progress.

Finally, I conclude this thesis manuscript by providing a synthesis and perspectives regarding the main results obtained throughout these studies. Moreover, I generally discuss their implications regarding the understanding of mechanisms underlying species responses to environmental variation (*chapter 6*).

Chapter 2

Material & Methods

2.1. The Alpine marmot

2.1.1. The genus *Marmota*

The genus *Marmota* (Order: Rodentia, Family: Sciuridae, see Fig. 2.1) comprises fifteen species (Brandler and Lyapunova 2009; Steppan et al. 2011), which are all restricted to the Northern hemisphere (Fig. 2.2).

Marmots have a recent origin, as their lineage has rapidly diversified for about 10 million years, with the earliest known fossil marmot (*M. minor*) being dated from the late Miocene (Thomas and Martin 1993; Steppan et al. 2011). They have originated in North America, and reached Eurasia then in late Pliocene (Steppan et al. 2011), and all contemporary species evolved afterwards during the Pleistocene (2.5-0.01Ma). Two major speciation events have been highlighted: a first one in Western North America, which resulted in the subgenus *Petromarmota*, grouping the majority of the Western North American species, and a second one in Central Asia, resulting in the subgenus *Marmota* (see Fig. 2.2, Armitage 2014).

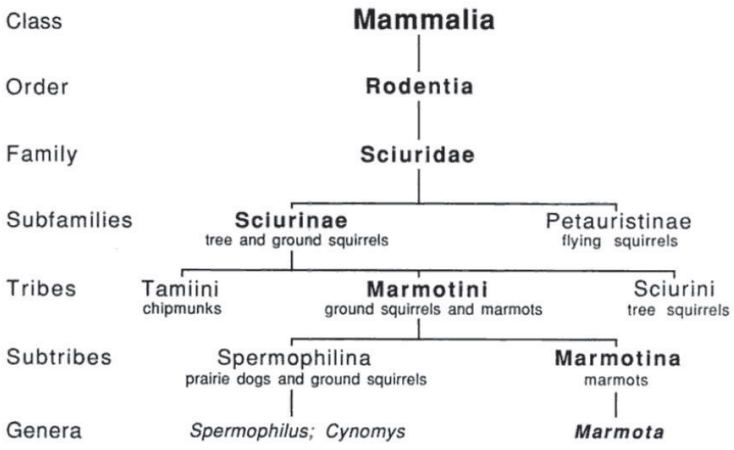

Figure 2.1. Genealogy of marmots (from Barash 1989).

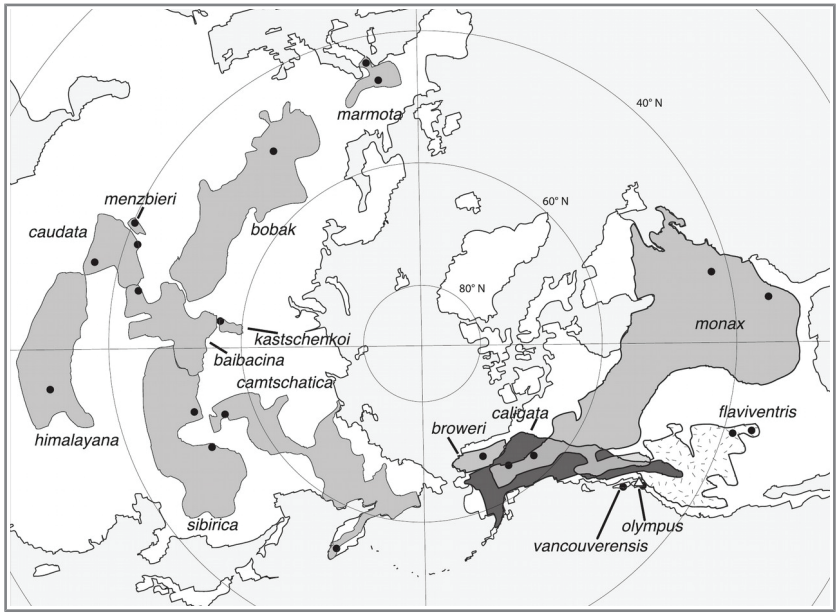

Figure 2.2. Polar view showing the overall distribution of the 15 species of the genus *Marmota* in the Northern Hemisphere (from Steppan et al. 2011).

The woodchuck *(M. monax*) appears as the most primitive living marmot (Brandler and Lyapunova 2009). It is presumed to have split off from the ancestral marmot and remained in North America while its "sister group" the subgenus *Marmota* diversified in Europe and Asia (Armitage 2014).

Overall, marmots evolved in cool and moist habitats in North America or in the periglacial environments of Eurasia, while their distributions suffered from important changes with overall warming and progress of the forest at the end of the last glaciation, which restricted them to high latitudes and altitudes (Armitage 2007, 2014, Fig. 2.2). Nowadays, they all inhabit open habitats such as steppes in Eurasia, mountain meadows in subalpine or alpine areas, at generally high elevations, except for the woodchuck, which is restricted to low elevations and inhabits both meadows and woodlands (Armitage 2000; 2014).

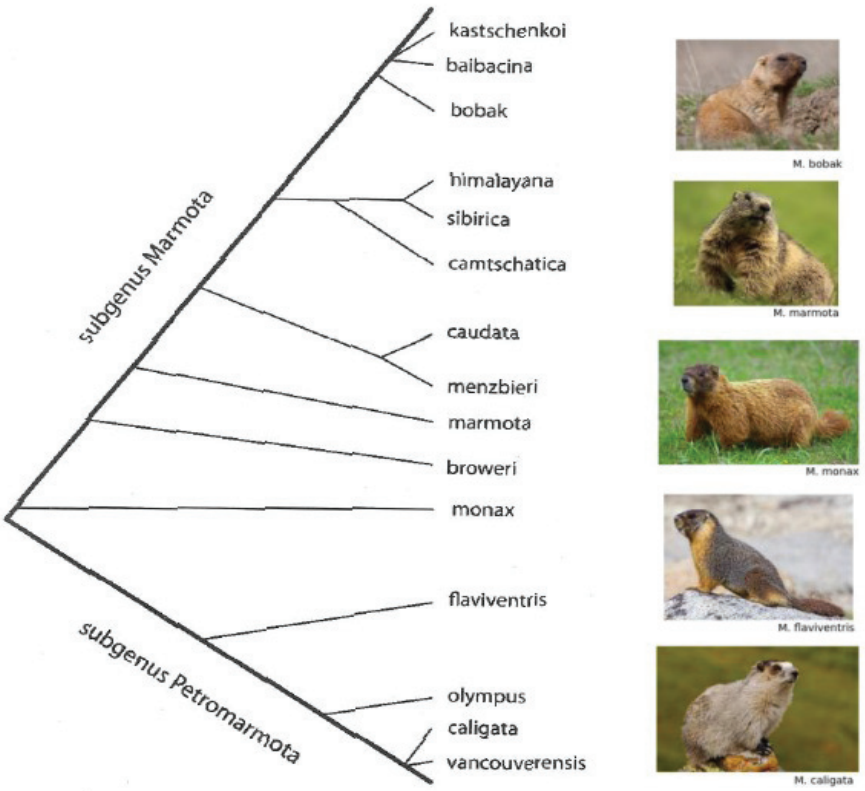

Figure 2.3. Phylogeny of the genus *Marmota*. The two heavy axes represent two major clades and the thin lines identify the species groups. The position of the thin lines along the major axes indicates the relative time of species diversification (from Armitage 2014), and marmot illustrations, as examples.

The fifteen marmot species present several ecological similarities: they are all diurnal, territorial, burrow-dwelling, herbivorous, eat a variety of forbs and grasses, and have a comparable morphology (with phenotypic differences, Fig. 2.3, Armitage 2014). Because they evolved in harsh environments, characterised by a marked seasonality with cold winters and short and warm growing seasons (Armitage 2007), marmots share common strong adaptive ecological features. First, they display large body size, being the largest genus of the *Marmotini* tribe, and secondly, they all display hibernation as an energy-saving strategy (Armitage 2014). Both these features allow them to cope with the adverse long and cold winters, during which resources are no longer available (Armitage 2007) The success of hibernation highly depends on the amount of energy stored by hibernators to sustain fasting and the energetic cost of thermoregulation (Humphries et al. 2003). As marmots do not store food resources within burrows, all their available energy resides in the fat reserves

that they accumulated before hibernation. Their large body size can be seen as adaptive accordingly; larger sizes allow to accumulate more fat and to reach higher body mass, as well as to use the stored fat more slowly (Armitage 1981; Armitage and Blumstein 2002; Armitage 2007). Overall, large variation in the length of hibernation exists between marmot species (Table 2.1), ranging from 4.5 months (e.g. *M. monax*) for the shortest to around 8 months (e.g. *M. menzbieri*, *M. camtschatica*) at most. Hibernation length is directly related to the length of the growing season which vary greatly according to species distribution, with shorter growing seasons in high altitudes and latitudes (Armitage and Blumstein 2002).

Finally, the particularity of the *Marmota* genus is that marmot species evolved a large diversity of social systems (Blumstein and Armitage 1999; Allainé 2000; Armitage 2007), ranging from the solitary woodchuck, to the highly social, cooperative breeding Alpine marmot (*Marmota marmota)* (Table 2.1). This diversity in the degree of sociality has been rapidly attributed to differences in the harshness of marmots environments, and especially to the length of the growing season, as sociality level seems to increase with both altitude and latitude and thus the shortness of the growing season (Barash 1974, Table 2.1). Winter is a main source of mortality for marmots (Arnold 1990a, 1993b). Likewise, a short growing season is strongly constraining for individuals: the shorter this season is, the less time they have to acquire sufficient body mass to sustain energy depletion of thermoregulation during hibernation. This is especially true for juveniles and young individuals which might not be able to sustain the cost of hibernation because of their small body size. As a first step, short growing seasons should hence have selected for delayed maturity and natal dispersal in marmots, and the retention of young individuals within family groups (Armitage 1999; Blumstein and Armitage 1999). In a second step, harsher environments, with long and colder winters, might have resulted in the formation of extended family groups, and the need for joint hibernation. A high level of sociality including a high reproductive skew and cooperative breeding might then allow maximising social thermoregulation, increasing juvenile survival, and should overall benefit to the members of the family group (Blumstein and Armitage 1999; Allainé 2000).

Table 2.1. Sociality, habitat characteristics and life history traits of species of the *Marmota* genus.

Marmot species	Sociality[1]		Habitat harshness		Life history traits[4]	
	Social organization	Sociality	Length of hibernation[2]	Elevation (m a.s.l.)[3]	Age at dispersal	Age at maturity
M. monax	Solitary	Solitary	4.5	close to 0	< 1	1
M. flaviventris	Female matrilines	Social group without allo-parental care	7.5	2,800 - 3,000	1	2
M. vancouverensis	Restricted families*	Social group with allo-parental care	7.0	700 - 1,400	2	3
M. olympus			7.5	>1,400	2	3
M. caligata			7.5	> 1,600	2	3
M. marmota	Extended families*	Cooperative breeders	6.5	1,000 - 3,000	≥ 3	2
M. baibacina			7.0	~ 3,000	2	2
M. bobak			7.7	-	≥ 3	3
M. sibirica			6.6	up to 3,800	≥ 3	2
M. caudata			7.6	4,100 - 4,300	≥ 3	> 3
M. camtschatica			8.2	up to 1,900	-	-

1. Blumstein and Armitage 1999; Allainé 2000, Schwartz et al. 1998; **2.** Armitage 2014; **3.** Armitage 2000, Patil et al. 2013; **4.** Armitage 2007, 2014

2.1.2. The Alpine marmot, *Marmota marmota*

Habitat type and diet

The Alpine marmot's natural geographic distribution encompasses both the Alps and the Carpathian Mountains where a sub-species has been described (*M. marmota latirostris*). It was successfully introduced in the Pyrenees between 1948 and 1988 from different Alpine populations (see Appendix I). Other introductions occurred in the Massif Central (France), in the Black Forest (Germany) and in the Apennines (Italy) (Fig. 2.4).

The Alpine marmot's habitat usually involves Alpine and sub-Alpine grasslands between 1000 and 3000 m asl. in altitude (Allainé et al. 1994; López et al. 2010). Alpine marmots live in a territory whose boundaries generally vary little from year to year and which includes a main burrow, side burrows and latrines. The main burrow consists of several interconnected rooms, with several exits to the outside. Secondary burrows consist in small excavations with only a single exit that mainly serve as refuges against predators.

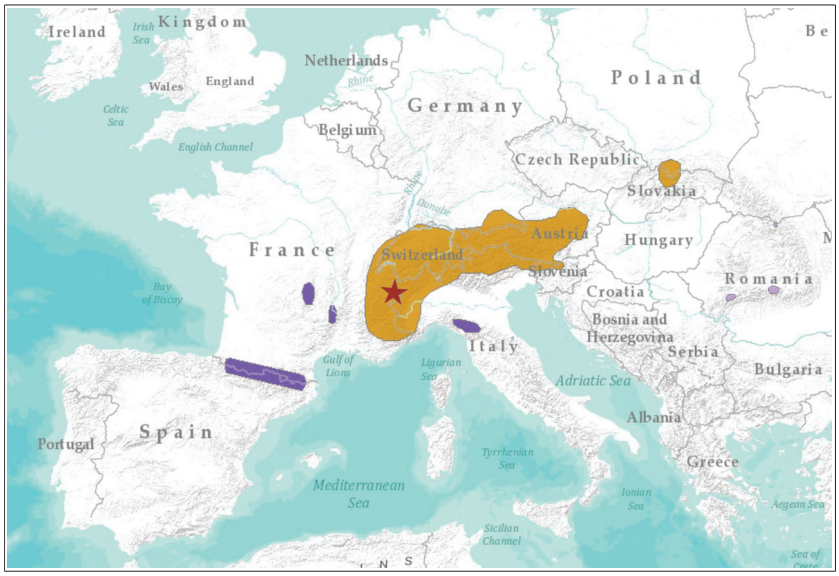

Figure 2.4. Contemporaneous distribution of the alpine marmot. Natural populations are represented in yellow, reintroduced populations in light purple and introduced populations in dark purple. The red star indicates the location of the monitored population of Alpine marmots in La Grande Sassière Natural Reserve. Image from http://www.iucnredlist.org.

Alpine marmots are herbivorous (Bertolino et al. 2009) and sometimes insectivorous. Their diet can be very diversified and depend on the phenological development of plants and the nutritional requirements of the individuals. Rare cases of carnivory and/or cannibalism have been also reported in this species (Ferrari et al. 2012, S. Pardonnet, personal communication)

Morphology

Alpine marmots are characterised by a brown coat, with orange markings on the back and with beige to orange on the belly, a brown muzzle, with a white band, between the nose and the eyes, and small ears (Fig. 2.5). They display short legs and a bushy brown tail with a black tip. Alpine marmots do not display any sexual dimorphism. They grow until the age of three and once adult measure between 45 and 68 cm without the tail. Their body mass vary strongly throughout the year, being on average close to 2.2 kg (for adults) at the emergence from hibernation in mid-April and around 6.5 kg at the entry of hibernation in mid-October (Körtner and Heldmaier 1995).

Figure 2.5. Alpine marmots (a pup on the left, an adult male on the right) from La Grande Sassière population (French Alps). Photo credit: Marie-Léa Travert.

Species life cycle

The Alpine marmot is a long-lived species whose average lifespan is around 7 years, and a maximum lifespan of 16 years old has been observed in our population. Alpine marmots reach sexual maturity at only two years old. From this age onward, individuals can either attempt accessing dominance and start reproducing or stay as

subordinate in the natal family group. As a result the mean age of first reproduction is generally delayed from 3 years old (Fig. 2.1).

The annual life cycle of the species is strongly constrained by hibernation, and can be split into two nearly equal periods: the active period (from mid-April to mid-October) and hibernation, a period of inactivity (from mid-April to mid-October, Fig. 2.6). From the emergence of hibernation begins a race against time for the Alpine marmot, in order to reproduce and to guarantee their future survival and reproduction by storing sufficient fat reserve. Females are receptive only for a short period of one day. Reproduction occurs a few weeks after emergence and females give birth from 1 to 7 pups after a gestation period of 30 days (Hacklander and Arnold 1999). Females can only give birth to one litter per year given the shortness of the active period. The altricial youngs are entirely dependent on their mother at birth and stay in the burrow during 40 days thereafter, being nursed by their mother. Once weaned they emerge from the burrow between mid-June and mid-July, weighting around 350g and they start feeding on plants. A bias in sex-ratio at emergence toward males is observed in the studied population (Allainé 2004). The rest of the active season is dedicated to foraging until hibernation.

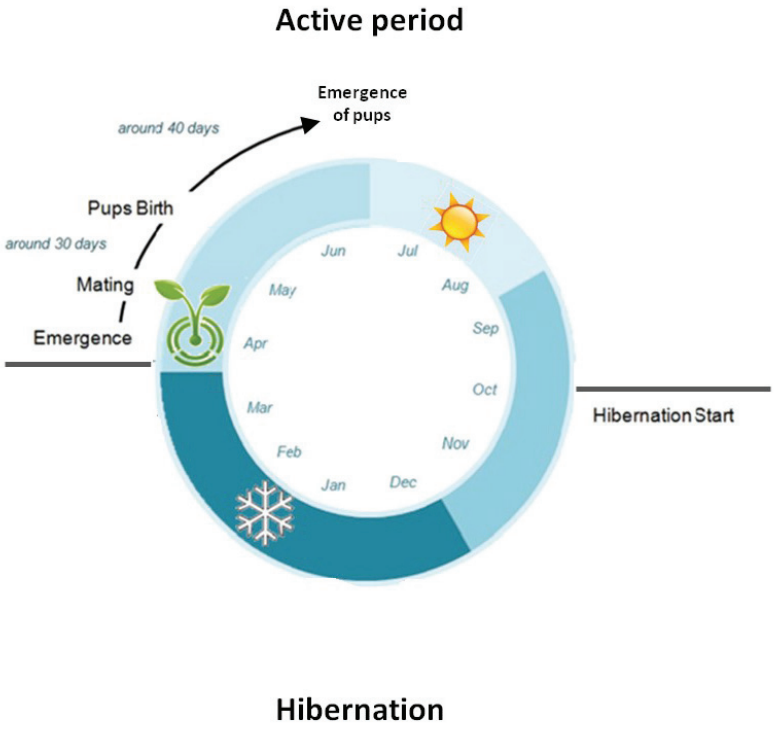

Figure 2.6. Annual life-cycle of the Alpine marmot.

A hibernating species

The length of hibernation varies by a few days between families and depending on altitude. All members of the family group hibernate together in a chamber of the burrow, called *hibernaculum* (Körtner and Heldmaier 1995). Hibernation is characterised by a succession of several torpor bouts of varying length throughout time, interrupted regularly by synchronised euthermic phases (awakening phases, see Fig. 2.7). During these torpor bouts, both oxygen consumption and body temperature decrease, jointly with an important slowdown of the metabolic rate (Arnold 1993a). Overall, torpor allows a substantial reduction in energy requirements, which in turn can provide direct fitness benefits, as it increases the chance of surviving the winter and to reproduce afterwards in the following spring (Humphries et al. 2003).

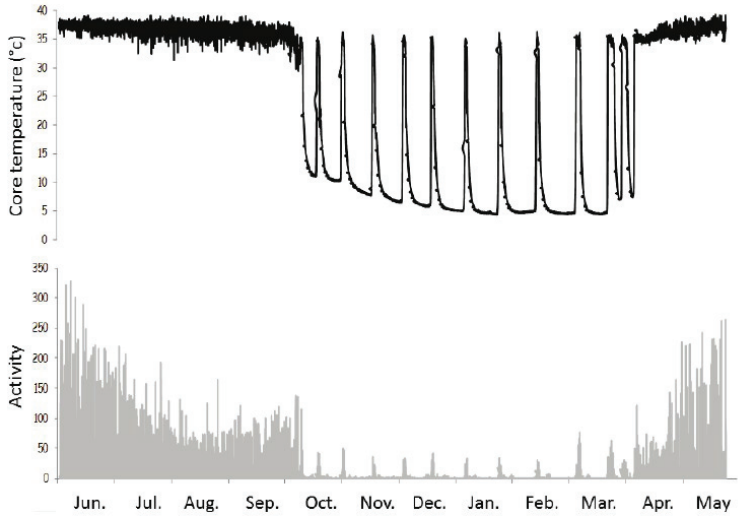

Figure 2.7. Body temperature and activity profiles of an adult male Alpine marmot from La Grande Sassière population within a year (provided by Benjamin Rey).

During the euthermic periods (these phases of activity last between 24 and 50 hours) the body temperature is around 38°C, the cardiac rhythm is at 180-200 beats per minute. During torpor, body temperature can decrease until a minimum of 5°C, while the cardiac rhythm decreases to 28-38 beats (Arnold 1988). Although euthermia periods represent less than 10% of the hibernation length, they are

responsible for 85% of the energetic expenditure during the hibernation period (Arnold 1988). These periods are physiologically necessary for the survival of individual, but are very costly. Between-individual synchronisation in the timing of euthermic phases and huddling with the other members of the groups allow to reduce this cost.

A social species practising cooperative breeding

Alpine marmots live in family groups of 2 to 20 individuals (Allainé 2000). Family groups are composed of a dominant couple; sexually mature (2 years and older) and immature (younger than 2 years old) subordinates of both sexes; and pups of the year (Allainé et al. 2000). Affiliative interactions can be observed between all individuals of the same social group (Perrin et al. 1993), although less frequent with the dominant male. Antagonistic interactions can be observed as well, especially between dominants and subordinates of the same sex.

Alpine marmots are socially monogamous. In each family group, only the dominant couple reproduces, while reproduction of subordinates is physiologically suppressed in both sexes by aggressive behaviours (Hackländer et al. 2003). Intra-sexual competition between dominants and subordinates leads to high rates of stress hormones (e.g. corticosteroids), which in turn leads to low levels of testosterone and progesterone in subordinate males and females, respectively (Arnold and Dittami 1997; Hackländer et al. 2003). However, while subordinate females experience almost a complete reproductive suppression, some subordinate males might access reproduction through extra-pair copulations (Goossens et al. 1998; Cohas et al. 2006) .

The dominance is in average reached slightly above 3 years old for both sexes (Lardy et al. 2012). Access to dominance for subordinates is generally made either by dispersing and evicting a dominant of the same sex from its territory, by inheriting or dislodging a parent from the natal territory, or by occupying a vacant dominant position (Arnold 1990b, 1993a). Two dispersal period can be defined, with the main occurring just after hibernation and before reproduction, and the second in early summer (Magnolon 1999). Dispersal can be a risky strategy, as in case of

failure in reaching the dominance status, the subordinate becomes a floater and might be forced to hibernate alone, facing a very high risk of mortality (Magnolon 1999; Stephens et al. 2002). Likewise, dominant individuals which loose their territory also have very high mortality rates (Lardy et al. 2011). However, once dominance is reached, individuals of both sexes may stay dominant and reproduce for one to several consecutive reproductive years, gaining high fitness benefits, until being evicted by another individual or dying (Lardy et al. 2011). The probability to successfully monopolise reproduction and the dominance tenure of dominant males decrease with the number of subordinate males present in the family group (Allainé and Theuriau 2004; Lardy et al. 2012). Similarly, the probability for dominant females to lose dominance increases with the number of female subordinates in the family group (Lardy et al. 2013), which indicates high levels of intra-sexual competition in the Alpine marmot.

Finally, both dominants and subordinates also benefit from group living. Subordinates of both sexes play a central role on anti-predator alarm, on play-fights with the youngs, and on maintenance of the burrow (Lardy et al. 2011). More importantly, Alpine marmots are cooperative breeders (Blumstein and Armitage 1999), and the presence of male subordinates is associated with increased survival rates of juveniles (Allainé et al. 2000; Allainé and Theuriau 2004). Sexually immature and mature subordinate males are considered to be helpers (Arnold 1990b, 1993b). Male subordinates actively participate in social thermoregulation (sensu Arnold 1993b) by warming the family hibernaculum. For each euthermia periods, subordinate males wake up earlier and stay longer active than the other members of the groups, thus dissipating more heat and warming the burrows (Arnold 1988, 1993a). They also arouse and rewarm earlier at the end of hibernation, allowing a passive rewarming of the pups and to arouse from hibernation with less cost (Arnold 1988). As result pup survival is highly correlated to the number of subordinate males present in the family group during their first hibernation (Allainé and Theuriau 2004). However, this also means costs for subordinate males in terms of body mass loss (Arnold 1990a, 1993b). This allowed nonetheless seeing that subordinate males adjust their investment in thermoregulation according to their relatedness to the pups. Helpers hibernating with full-siblings lose more weight than subordinate

males that were not related to the pups (Arnold 1993b), which indicates indirect fitness benefits should be a driver of this active helping behaviour. On the contrary, the presence of subordinate females has a negative impact on juvenile survival during winter and probably compete with juveniles for heat during hibernation (as suggested by Allainé and Theuriau 2004), and thus do not benefit to dominants.

2.2. Study sites and population monitoring

2.2.1. La Grande Sassière Natural Reserve

All data were collected from a wild population of Alpine marmots located in La Grande Sassière Natural Reserve located in the French Alps, close to the Italian border (Fig. 2.4, 45°29′N, 6°59′E). This natural reserve is managed by the Vanoise National Park in the Haute Tarentaise valley (Tignes, Savoie). The altitude in this area ranges from 1850 to 3747m a.s.l.. The weather conditions are typical of an Alpine climate, with marked seasonality, low average temperatures, strong daily and annual variation in temperature and marked precipitation which falls mainly in the form of snow over the year. The vegetation is strongly diversified and is composed of alpine and sub-alpine grass types and hosts a profusion of flowers in late spring, early summer. The fauna includes numerous emblematic species of the Alps such as the Alpine chamois (*Rupicapra rupicapra*), the Alpine ibex (*Capra ibex*), the bearded vulture (*Gypaetus barbatus*), as well as predators of the Alpine marmot, such as the red fox (*Vulpex vulpex*), or the golden eagle (*Aquila chrysaetos*). The intensity of predation pressure could not be assessed since predation is almost never observed. However, the rarity of predation events observed despite the relatively intense observation pressure tends to indicate that predation only plays a minor role in shaping the Grande Sassière population dynamics (field observation).

Figure 2.8. Central view of La Grande Sassière natural reserve.

The study area only represents a portion of La Grande Sassière natural reserve. It is located on the relatively low part of the reserve, at 2,340m a.s.l. (45°29'N, 6°59E). All the monitored family territories are distributed in an area of approximately 1.5 km long and 500m wide, located roughly at the same altitude, and are North or South oriented (Fig. 2.8, 2.9). Overall, the sun exposure, as well as the size of the home-range are good indicators of the territory quality for Alpine marmots (Allainé et al. 1994). For instance, snow-melt on the north-facing slopes tend to start later than on the south-facing slopes, which may lead to later access to food resources during the early active period (Vuren and Armitage 1991). From 1990 to 2016, 25 families were intensively followed by capture-mark-recapture protocol, providing 26 years of monitoring data. Even if the boundaries of a territory do not vary drastically between years, a cartography of marmot territories is defined and actualized each year (Fig. 2.9).

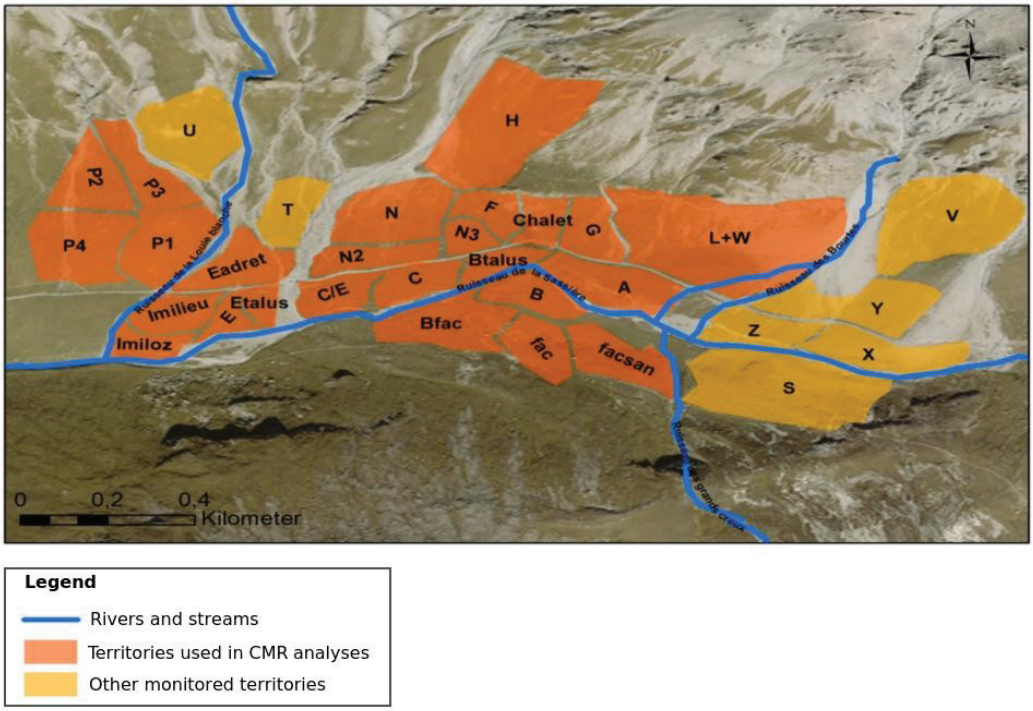

Figure 2.9. Distribution of the different Alpine marmot family territories, monitored by capture-mark-recapture protocols at La Grande Sassière, French Alps. Orange territories are followed intensively since 1990-1993 and were used in our survival analyses. Yellow territories are only followed since 2013.

2.2.2. Data collection procedure

Marmot trapping and handling

Individuals are monitored each year from mid-April to mid-July by a capture-mark-recapture protocol. Individuals are captured using two-door live traps baited with dandelions (*Taraxacum densleonis,* Fig. 2.10). Between one and four traps are placed near the entrance of the main burrows of each territory to easily assign captured individuals to their family group. During the pups emergence period (from the 15th of June to the 15th July), each territory and burrow is scrutinised to determine the date of the emergence of pups. Then juveniles are counted, captured by hand or by small two-door live traps within few days of their emergence, and are subsequently marked with both transponders and ear-tags. Almost all juveniles are captured within the three days following their emergence from the burrow.

Once captured, individuals are tranquillised with Zolétil 100 (0.1 mL/kg) by

intramuscular injection. Individuals are then sexed based on the ano-genital distance, aged from their size (up to three years), and weighed. Morphological characteristics (presence of visible testis for males, developed teats for females, development of scent glands for both sexes) are used to confirm dominance status determined from observation (see behavioural observations section below). All marmots captured for the first time are individually marked with a transponder chip (model ID100, 0.9 cm long, <0.1 cm in diameter, Trovan Ltd, www.Trovan.com, Identifikationssysteme, Metternicher Straße 4, 53919 Weilerswist, Germany) injected under the skin of the neck for permanent individual recognition, and with one metal tags (1 cm x 3 mm) at their ear for visual identification of sex (right side for females and left side for males). Dominants are additionally tagged with a family-specific coloured plastic tag on the opposite ear.

Figure 2.10. Adult male in front of two-door live trap baited with dandelion.

Additional handlings are done including morphological measurements (e.g. tibia length, body length without tail); skin biopsies, hair and blood samples, for genetic analyses; and anal, jugal and buccal glands secretion samples, for chemical analyses. Faecal samples are also collected immediately after the capture of a given individual for parasitology analyses. Microsatellite genotyping of all captured individuals allowed parentage analyses to be run to precisely determine kinship among individuals from a family group. Because all pups from the study area are captured at emergence, the parentage analyses also allowed us to determine with certainty individuals that successfully reproduced each year.

Behavioural observations

Behavioural observations are additionally conducted on a daily basis throughout the field season to determine group sizes and compositions. For each group, the number of adults, two years old, yearlings and pups of each sex are counted thanks to ear marks and the use of 10x50 binoculars and 20x60 telescopes. Scent-marking and antagonistic behaviours are also reported, allowing us to categorise individuals as subordinates or dominants (Bel et al. 1999). Observations are always done outside of the focal marmot territory at a distance from 80 to 200m to avoid disturbing marmots.

Chapter 3

Socially-mediated effects of climate change decrease survival of hibernating Alpine marmots

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Abstract

In the context of global change, an increasing challenge is to understand the interaction between weather variables and life histories. Species-specific life histories should condition the way climate influences population dynamics, particularly those that are associated with environmental constraints, such as lifestyles like hibernation and sociality. However, the influence of lifestyle in the response of organisms to climate change remains poorly understood. Based on a 23-year longitudinal study of the Alpine marmot, we investigated how their lifestyle, characterized by a long hibernation and a high degree of sociality, interacts with the ongoing climate change to shape temporal variation in age-specific survival. As generally reported in other hibernating species, we expected survival of Alpine marmots to be affected by the continuous lengthening of the growing season of plants more than by changes in winter conditions. We found, however, that Alpine marmots displayed lower juvenile survival over time. Colder winters associated with a thinner snow layer lowered juvenile survival, which in turn was associated with a decrease in the relative number of helpers in groups in the following years, and therefore lowered the chances of over-winter survival of juveniles born in the most recent years. Our results provide evidence that constraints on life history traits associated with hibernation and sociality caused juvenile survival to decrease over time, which might prevent Alpine marmots coping successfully with climate change.

Key-words: French Alps, global warming, lifestyle, *Marmota marmota,* path analysis, sociality, winter conditions

3.1. Introduction

In the context of global climate change (IPCC 2013), an increasing challenge in ecological research is to understand the role of weather variables in shaping life history traits and their effects on population growth rates (Merilä 2012). Across species, some general patterns of life history variation have emerged, such as the strong structuring effect of age and sex in the responses of demographic rates to environmental variation in vertebrate populations (Jorgenson et al. 1997; Gaillard et al. 2000b; Coulson 2001). For instance, in long-lived iteroparous species like large herbivores (Gaillard et al. 2000b; Coulson 2001) or seabirds (Jenouvrier et al. 2005; Oro et al. 2010), juveniles are more susceptible to changes in environmental conditions than adults (Gaillard and Yoccoz 2003).

Among-species differences in lifestyle should potentially influence both demography and life history trait responses to climate change. Indeed, species having a lifestyle (sensu Harvey and Purvis 1991) that buffers individuals' life history traits against harsh environmental conditions generally benefit from a longer lifespan than expected based on their body mass (Healy et al. 2014). For instance, aerial, arboreal, or fossorial lifestyles, that allow individuals to escape from predation, are associated with increased longevity in birds and mammals (Shattuck and Williams 2010; Healy et al. 2014). Likewise, hibernation directly affects energy allocation, the central process of life history strategies (Cody 1966; Stearns 1992), by allowing individuals to save energy during seasons of food shortage and to protect themselves from predators. This results in an increase in survival for hibernating species, compared to similar-sized but non-hibernating species (Wilkinson and South 2002; Turbill et al. 2011). Similarly, sociality may be selected in strongly limiting environments by providing higher access to food resources, reducing predation risk, and lowering the costs of thermoregulation during hibernation (Alexander 1974; Arnold 1990a; Boyles et al. 2008). Overall, these lifestyles confer advantages to individuals that increase longevity and improve survival (see Keller and Genoud 1997 for an example on social insects, Wasser and Sherman 2010 on social birds, and Williams and Shattuck 2015 on a social mammal).

Lifestyles that evolved in response to climatic constraints should shape the way species are influenced by climate change. In temperate areas, climate change can impact animal populations in two ways: (*i*) directly *via* changes in the weather conditions during winter, acting on the energy demands of animals, or (*ii*) indirectly *via* changes in weather conditions in spring and summer (vegetation growth), acting on the availability and quality of food resources, which ultimately determine the amount of fat reserves needed to sustain winter conditions. Those direct and indirect effects may act together or against one another on life histories. For hibernating species, which are sheltered from adverse winter conditions and mostly rely on fat reserves accumulated during their active period to survive hibernation (Lyman et al. 1982; Humphries et al. 2004), climate change should mainly influence demographic rates indirectly through changes during the growing season. An overview of studies investigating the responses of hibernating species to climate change suggests that the indirect effects through variation in resource availability and quality, whether positive or negative, are generally observed (Table 3.1.a,b). However, the population dynamics of some hibernating species depend on winter harshness, as shown by the decreased litter size with decreasing snow cover reported in Alpine marmots (*Marmota marmota*) Tafani et al. 2013; Table 3.1.b), suggesting heterogeneous responses of hibernating species to climate change.

The effect of sociality on species life histories is mainly mediated by the size or the composition of the social group (see Emlen and Wrege 1991 and Paquet et al. 2015, for examples on social birds; Hodge et al. 2008 and Lardy et al. 2015 for examples on mammals). For instance, in the cooperatively breeding meerkats (*Suricata suricatta*), female reproductive success increases with group size (Hodge et al. 2008)and juvenile survival is higher in the presence of helpers which participate in feeding pups (Clutton-Brock 2001). The responses of social species to climate change could, hence, depend in part on the influence of climate on the social group structure. Generally, climate change affects reproductive parameters and therefore population recruitment (Table 3.1.b,c). Environmental variability may change the size and/or the composition of social groups with some delay because newly recruited individuals will be helpers in the following years (see Bateman et al. 2013). Hence, environmental variability may impact the composition of social

groups and could influence the population dynamics of social species by altering social factors associated with an improved reproduction. Up until now, the role of sociality on population dynamics of social species has only been assessed by investigating the effects of sociality and climate separately (Russell et al. 2002; Patil et al. 2013). However, a comprehensive approach linking weather variation to social effects on demographic rates would improve our understanding of the role of lifestyle in the response of social species to climate change.

Marmots are particularly interesting biological models with which to assess the role of the lifestyle in population response to climate change, because they are hibernating species and display various degrees of sociality directly related with the climatic constraints of their environments (Barash 1974; Armitage 1999). The observed variation in the degree of sociality across species of marmots seems to be linked to the harshness of the environment such as a short growing season, and increases with both altitude and latitude (Barash 1974; Armitage 1999; Blumstein and Armitage 1999). The Alpine marmot lives at high elevation with harsh winters and lies at one extreme of the social gradient, being the most social marmot species (Blumstein and Armitage 1999; Allainé 2000). Alpine marmots hibernate in extended family groups with one dominant breeding pair and subordinates (Arnold 1990b; Perrin et al. 1993), and display cooperative breeding (Solomon and French 1997; Blumstein and Armitage 1999). Accordingly, Alpine marmots present delayed dispersal from the family group, the reproductive suppression of female subordinates, while male subordinates carry part of the breeding costs through social thermoregulation directed towards offspring to which they are related during hibernation, while female subordinates do not (Arnold 1993a; Allainé et al. 2000; Allainé and Theuriau 2004).

Using a 23 year-long monitoring of an Alpine marmot population in the French Alps, we aimed to assess how the species' lifestyle (hibernation and sociality) interacted with weather variation in shaping age-specific survival patterns by testing the three following expectations. (1) Being a long-lived species (Cohas et al. 2007a), annual survival rates of Alpine marmots should be strongly structured by individual age and social status. We thus expected juveniles to be more sensitive to fluctuations

in weather conditions than older individuals because the population growth rate of long-lived species is less sensitive to juvenile than to adult survival (Gaillard et al. 2000b; Gaillard and Yoccoz 2003). (2) We expected survival of the Alpine marmot to be influenced by both summer and winter conditions because weather variation can affect the survival of individuals directly, through changes in the energy requirement during winter, and indirectly, through the availability and quality of resources (Table 3.1). While yellow-bellied marmots (*Marmota flaviventris*) benefit from earlier springs to achieve improved body condition before hibernation (Ozgul et al. 2010), Alpine marmots suffer from harsh winter conditions by showing decreased litter size in response to colder winters with thinner snowpack (Tafani et al. 2013). Hence, we expected opposing direct and indirect effects of weather variation on Alpine marmot survival, with marmots of all age classes benefiting from earlier springs and longer access to food resources with negative impact of colder winters. However, as generally observed for hibernating species (Table 3.1), we expected the influence of indirect effects to be stronger than that of direct effects and the consequences of climate change on demographic rates of Alpine marmots to be positive overall. Finally (3), we expected climate change to have a delayed "socially-mediated" effect on juvenile survival by modifying the social structure of groups. We recently reported that climate change is currently inducing a decrease in litter size in our study population (Tafani et al. 2013), which could reduce the number of helpers present in the groups during hibernation two years later. Being a cooperative breeder, the juvenile survival of Alpine marmots increases with the number of helpers in the family group during hibernation (Allainé et al. 2000; Allainé and Theuriau 2004). Consequently, this long-term decrease in litter size (Tafani et al. 2013) could contribute to a further decrease in juvenile survival.

Table 3.1. Effects of climate variables on the life-history traits of medium-sized mammals according to three different lifestyles: mammals that (a) hibernate and are solitary, (b) hibernate and live socially, and (c) live socially without hibernating.

Species	Weather variable	Life-history Traits	Effect	References
a) Hibernating species				
Rodentia				
Arctic ground squirrel *(Urocitellus parryii)*	Early springs (advanced snow-melt)	Emergence date, breeding date	+	Sheriff et al. 2011
Golden-mantled ground squirrel (*Callospermophilus lateralis)*	Prolonged summer rainfall (reduced food access)	Juvenile survival, reproductive rates	-	Kneip et al. 2011
Edible dormouse (*Glis glis*)	Early springs (increased temperature, seed productivity)	Emergence date, population abundance	+	Adamík and Král 2008 Kager and Fietz 2009
Common hamster (*Cricetus cricetus*)	Late springs (delayed snow-melt)	Reproductive output	-	Hufnagl et al. 2011
Carnivora				
Raccoon dog (*Nyctereutes procyonoides)*	Mild springs (high temperatures, low snow-depth)	Fat deposition	+	Melis et al. 2010
b) Social hibernating species				
Rodentia				
Columbian ground squirrel (*Urocitellus columbianus*)	Late springs (delayed snow-melt)	Emergence date, individual annual fitness	-	Lane et al. 2012
Yellow-bellied marmot (*Marmota flaviventris*)	Warmer spring temperatures (advanced snow-melt and food availability)	Emergence date, body mass, adult survival rate	+	Schwartz and Armitage 2005, Ozgul et al. 2010
		Reproductive success	+	Maldonado-Chaparro et al. 2015

Alpine marmot (*Marmota marmota*)	Winter severity (thinner snow layer)	Litter size	-	Tafani et al. 2013
Hoary marmot (*Marmota caligata*)	Thin snowpack in winter	Overwinter survival	-	Patil et al. 2013
		Average fecundity	-	Patil et al. 2015
Chiroptera				
Little brown myotis (*Myotis lucifugus*)	Summer dryness	Breeding and survival probability	-	Frick et al. 2010
	Winter temperatures			Humphries et al. 2002
		Over-winter survival	-	
Nothern bat species (x6)	Summer dryness	Reproductive success	-	Adams 2010
c) Social species				
Chiroptera				
Flying foxes (*Pteropus spp.*)	High temperature extremes	Survival rates	-	Welbergen et al. 2008
Carnivora				
Meerkat (*Suricata suricatta*)	Dryness of current and previous years	Reproductive success, recruitment, group size	-	Russell et al. 2002 Bateman et al. 2013
Eurasian badger (*Meles meles*)	Mild winter	Population abundance	+	Macdonald and Newman 2002
Lagomorpha				
European rabbit (*Oryctolagus cuniculus*)	High spring precipitation	Population abundance	-	Rödel and Dekker 2012 Rödel et al. 2005
	Low winter temperature	Body mass loss, delayed onset of reproduction	-	
European hare (*Lepus europaeus*)	High summer/autumn precipitation	Population abundance	-	Rödel and Dekker 2012

3.2. Materials and Methods

3.2.1. Study species and population

Alpine marmots are cooperative breeders, territorial and socially monogamous (Allainé 2000). They live in family groups of up to 20 individuals (Arnold 1990a), composed of a dominant breeding pair, sexually mature subordinates of at least two-years of age, immature yearlings and juveniles (Arnold 1990a; Perrin et al. 1993). Dominant individuals monopolize reproduction and inhibit reproduction of male and female subordinates through aggressive behaviour (Arnold and Dittami 1997; Hackländer et al. 2003). Mating occurs shortly after the end of hibernation in mid-April. Gestation lasts 30 days followed by 40 days of lactation inside a natal burrow, and pups emerge and are weaned between mid-June and mid-July. Members of a family group hibernate in the same burrow from mid-October to mid-April (Arnold 1988). Subordinate males are involved in social thermoregulation during hibernation (Arnold 1993c) and act as helpers by improving juvenile overwinter survival (Arnold 1988, 1993a; Allainé et al. 2000; Allainé and Theuriau 2004). Subordinates of both sexes start to disperse once they reach the age of two years (Arnold 1990b; Magnolon 1999) and themselves become dominant in due course.

The study population is located in La Grande Sassière Nature Reserve (French Alps, 45°29'N, 6°59E) at 2,300 m a.s.l.. From 1990 to 2013, individuals were monitored by a capture-mark-recapture protocol. Marmots were trapped each year from mid-April to mid-July. Once captured, individuals were tranquillized and individually marked for permanent identification. All captured individuals were sexed and aged, and classified into three categories on the basis of their body size: juveniles (i.e., young of the year), yearlings (i.e., born in the previous year), and adults (i.e., two years of age). Social status was assessed by scrotal and teat development for males and females, respectively. We included data collected on 1,172 individuals captured between 1990 and 2013 in our analyses (see Appendix 3.1 for additional information about the study design and protocols).

3.2.2. Climate and weather covariates

In the first instance we used the winter North Atlantic Oscillation index (NAO, (Hurrell 1995) as an index of global change to assess whether Alpine marmots responded to the global signature of climate change. This assessment was preliminary only because the NAO is a poor index of the proximal causes of ecological variation (Hallett et al. 2004). We then used local weather indices to identify particular mechanisms by which weather variation influences the survival of Alpine marmots.

Given the timing of captures in the field, we defined annual survival of the Alpine marmot as the proportion of individuals that survive between spring at year *t* and the following spring at year *t+1*. We focused on four weather variables with potential impact on marmot annual survival based on three key periods of the Alpine marmot's annual life cycle when environmental conditions are critical (see Appendix 3.2 for details about the choice and description of the weather variables): (*i*) during the active season, at year *t,* when marmots are storing fat reserves to survive the next hibernation; (*ii*) during hibernation, between years *t* and *t+1,* when marmots have to maintain sufficiently high body temperatures while the burrow temperature decreases (Arnold et al. 1991); and (*iii*) at emergence from hibernation the next spring of year *t+1*, when marmots rely exclusively on their remaining body fat to cope with adverse environmental conditions.

The Normalized Difference Vegetation Index (noted NDVI,Pettorelli et al. 2005b) is a proxy for primary production (Pettorelli et al. 2005a). We used the NDVI measured from April 15th to May 1st to assess the timing of snowmelt and thereby the time during which marmots have access to food resources. High NDVI values indicate early snowmelt and access to food resources for marmots (i.e. early spring), and a longer vegetation growth. The vegetation onset indeed correlates well with snowmelt in mountain environments (Pettorelli et al. 2007). At year *t*, $NDVI_t$ may drive over-winter survival during the coming hibernation. We also considered NDVI at year *t+1* to match marmots' emergence from their burrows (noted $NDVI_{t+1}$) and to test whether environmental conditions at emergence from hibernation after a 6 months fast, affected marmot survival between *t* and *t+1*.

The Bagnouls-Gaussen Index (noted BGI_t, Gaillard et al. 1997 is a commonly used drought index for temperate areas (see Garel et al. 2004 and Toïgo et al. 2006) which we used as a proxy of food availability and quality in summer of year *t*. We calculated BGI_t values from July 1st to August 31st to match periods during which marmots, especially pups who just emerged, actively feed before hibernation. Droughts can be a strongly limiting factor of primary production in temperate areas (see Mysterud et al. 2008). Low BGI_t values are associated with hot and dry summers, which means less forage for marmots and potentially low over-winter survival.

Lastly, we defined a winter weather variable, WIN_t, to assess environmental conditions during marmot hibernation between years *t* and *t+1*. Hibernation is a critical period for marmots (Arnold 1990a), when weather conditions such as extreme temperatures and thin snow cover strongly decrease hibernaculum temperature and marmot body mass (see Tafani et al. 2013), and thus potentially influence survival. Our WIN_t variable is an index of winter harshness that combines temperature and snow precipitation from December 1st to March 31st. Low values of the winter index correspond to cold dry winters with little snow cover.

We searched for a signature of climate change by testing for temporal trends in the weather variables using linear models and quantified the correlation among our predictive variables using Pearson correlations (Appendix 3.3).

3.2.3. Social structure of groups

To investigate the effect of climate change on juvenile survival, through yearly changes in the number of subordinate males (helpers), we computed an index of group composition calculated as the proportion of families that had at least one helper during hibernation between years *t* and *t+1* (HELP). We did not have access to the actual number of helpers during hibernation, but our index is a good proxy of the beneficial effect of social thermoregulation on juvenile survival (Allainé et al. 2000). We used Generalized Linear Models (GLM) with a binomial distribution and a logit link function to test for a temporal trend in the proportion of families with

helpers.

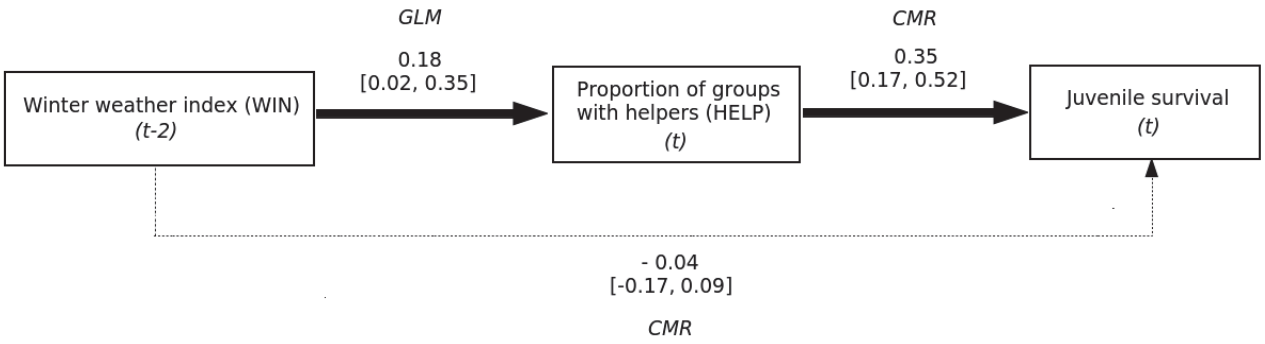

Figure 3.1. Path diagram showing the two putative effects of winter weather conditions at year t-2, acting on juvenile survival at year t, in the Alpine marmots of La Grande Sassière, France. Path coefficients are given with their associated 95% confidence intervals (95% CI). Solid lines indicate statistically supported effects (95% CI excludes 0), and thin lines non-statistically supported effects (95% CI include 0).

3.2.4. Modelling annual survival of marmots

We defined annual survival of Alpine marmots at year *t* as the probability of surviving (designated Φ_t) between springs from year *t* to *t+1*. We used multi-state capture-recapture models (MS-CR, Lebreton *et al*. 2009, see (Cohas et al. 2007a) for an application to Alpine marmots) to investigate patterns of annual survival. MS-CR models, which make it possible to differentiate survival between subordinate (*s*) and dominant (*D*) individuals (Cohas et al. 2007a), are based on a transition matrix with different probabilities of switching from one status to another (Ψ), and associated vectors of transition from time *t* to time *t+1* corresponding to survival (Φ) and capture (*p*) probabilities for each social status (see formula 1).

$$\begin{matrix} \Psi^{ss} & 1-\Psi^{ss} \\ 1-\Psi^{DD} & \Psi^{DD} \end{matrix} \begin{matrix} \Phi^{s}_{t} & p^{s}_{t} \\ \Phi^{D}_{t} & p^{D}_{t} \end{matrix} \quad (1)$$

where p_t^a is the probability for an individual of status *a* to be captured at year *t*; Φ_t^a is the probability that an individual of status *a* in year *t* survives to year *t+1* and does not permanently emigrate from the study area (apparent survival); and Ψ_t^{ab} is the

probability that an individual of status *a* in year *t* is of status *b* in year *t+1,* after it survived or did not permanently emigrate between *t* and *t+1*. As dominant individuals never return to subordinate status (Arnold 1993a), we fixed the probability of remaining dominant (Ψ^{DD}) as 1. Hence, the probability of staying subordinate (Ψ^{ss}) was the only transition parameter estimated. Moreover, marmots cannot access dominant status before reaching sexual maturity, which generally occurs from age three onwards (Farand et al. 2002; Cohas et al. 2007a). However, a few individuals became dominant at the age of two (N=34). We therefore fixed the probability of becoming dominant to 0 for individuals younger than two years.

We considered social status, sex, age class and time effects and their interactions on all capture, survival and state transition probabilities. Hence, the most general model was: *p(status*sex*ageclass*time) Φ(status*sex*ageclass*time) Ψ(sex*ageclass*time)*, with age-classes corresponding to juvenile *[from 0 to 1 year-old]*, yearling *[from 1 to 2 years-old]*, and adult *[from 2 years-old]* classes. We first tested whether the full time-dependent model fitted adequately our data with respect to the three hypotheses listed by Burnham et al. (1987). There are several assumptions for MS-CR models to be valid such as the equal probability for individuals to be recaptured at a given year, or all individuals having the same probability of surviving to time *t+1*, immediately after being marked. We could test whether our data complied with these assumptions with goodness-of-fit-tests (GOF tests, (Pradel et al. 2003) implemented in the program U-CARE (Choquet et al. 2005). Then, starting from the general model, we reduced the number of parameters by considering only biological hypotheses based on our field experience and previous studies (Arnold 1993a; Farand et al. 2002; Allainé and Theuriau 2004) and selected the most parsimonious nested model as the baseline model, from which subsequent survival analyses were performed. This selection was done successively for capture, survival, and then state transition probabilities using the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002).

3.2.5. Direct and indirect effects of climate on survival

We tested the effects of environmental variables on survival separately for each age-class and social status. We first used the selected baseline MS-CR model to test for a temporal trend in survival by including year as a continuous covariate. To investigate whether variation in survival was related to global climate change, we regressed survival on the NAO index, by replacing the temporal trend with the NAO covariate. We examined potential proximal mechanisms by which weather variation could impact survival by quantifying the relative influence of the active vegetation period and of winter. We tested for the effects of spring and summer at *t,* of winter between *t* and *t+1*, and spring at *t+1* by including the four corresponding weather variables *(*$NDVI_t$, BGI_t, WIN_t and $NDVI_{t+1}$) as covariates to the baseline MS-CR model.

We also performed these analyses using "de-trended" covariates for age or social classes with temporal trends by adding year as a continuous covariate to account for the trend in survival (Appendix 3.4) because spurious correlations may occur when both survival and climatic covariates show temporal trends (Grosbois et al. 2008).

We used AICc to assess the effect of both large-scale climate and local weather variables on survival, and to select the combination of covariates that best explained the annual survival variation of each group. We then assessed the effect size of each combination of climatic covariates on variation in survival using an analysis of deviance (ANODEV; Skalski et al. 1993). The corresponding R^2 statistic quantifies how much the weather covariates accounted for the observed temporal variation in average annual survival.

3.2.6. Socially-mediated effect of climate on juvenile survival

We hypothesized that climate change can influence juvenile survival by modifying the social composition of groups during hibernation. We expected the decrease in litter size reported in the population in response to a thinner snow cover (Tafani et al. 2013) at year *t* to result in a lower number of helpers present in the population

two years later, and thus to a decrease in juvenile survival in those subsequent years. To test this hypothesis we performed a path analysis (Shipley 2009) where the effect of the winter index (WIN) at *t-2* on juvenile survival at year *t* was mediated through a lagged effect on the number of helpers at year *t* (Fig. 3.1). We estimated the path coefficients in two steps. We first used a binomial GLM to test for the delayed effect of the winter index at year *t-2* on the proportion of groups with helpers in the population during hibernation at year *t*. We then used MS-CR models to test for the immediate effect of the proportion of groups with helpers on juvenile survival. Finally, path coefficients of the direct effect of the winter weather index at *t-2* on juvenile survival at *t* was calculated with MS-CR models, after accounting for the effect of the social factor. The significance of the path coefficients was assessed by investigating whether the confidence interval at 95% of the estimated coefficients included zero or not (Shipley 2009). We also tested for first-order interaction between the proportion of groups with helpers at time *t* and the weather covariates at time *t*.

All statistical analyses were performed using R version 3.1.0 (R Development Core Team 2011) and all MS-CR analyses were conducted using MARK (White and Burnham 1999) and the package RMark 2.1.7 (Laake and Rexstad 2008). All weather and social covariates were standardized (i.e. with a mean of 0 and sd of 1) for the survival analysis. Parameter estimates are given as mean ± SE and on the logit scale for analyses using MS-CR or GLM models.

3.3. Results

3.3.1. Temporal trends in environmental and social variables

Temporal variation in climatic and weather indices revealed trends in the environmental conditions at La Grande Sassière over the 23 years of study. The winter index decreased by 0.07±0.03 per year from 1990 to 2013 ($r^2 = 0.21$, *P-value* = 0.02; Fig. 3.2.a) and correlated with the NAO ($r^2 = 0.59$, *P-value* < 0.01), which also decreased over time ($\beta = -0.17 \pm 0.06$, $r^2 = 0.22$, *P-value* < 0.01), pointing to a

locally expressed signature of climate change. Hence, the harshness of winters at La Grande Sassière increased over years, with colder temperatures that favored frost rather than snow. No temporal trends occurred in spring and summer weather indices related to the growing season (NDVI, $\beta = 0.02 \pm 0.03$, $r^2 = 0.02$; BGI, $\beta = 0.02 \pm 0.03$, $r^2 = 0.02$, Fig. 3.2.b,c). We also found a negative temporal trend in the proportion of families with helpers during hibernation. Over the past 23 years, the proportion of groups with helpers decreased from 80% in 1990 to 46% in 2013 on average ($\beta = -0.05 \pm 0.02$, $r^2 = 0.42$, *P-value* < 0.01, N = 375; Fig. 3.2.d). Thus, a marked change in the group structure of marmots occurred at La Grande Sassière over the period, with fewer groups having helpers during hibernation.

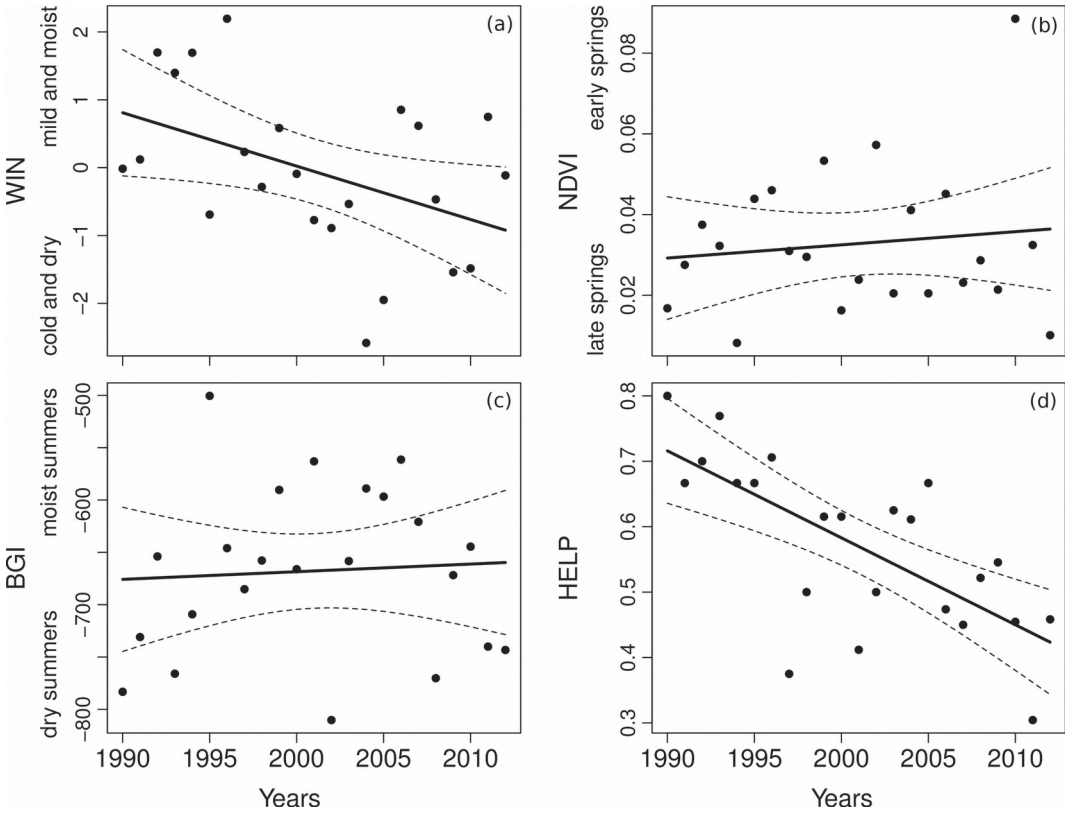

Figure 3.2. Yearly variations between 1990 and 2012 in (a) the winter weather index (WIN), (b) the spring weather index (NDVI), (c) the summer weather index (BGI), and in (d) the social index (HELP), at La Grande Sassière, France. Solid lines represent the predictions of the linear effect of time and dashed lines their associated confidence intervals (± 95% CI).

3.3.2. Selection of the reference MS-CR model

The two components of the GOF tests, testing for trap-dependence and transience, were not statistically significant when accounting for the age structure of the population, suggesting that the full age- and time-dependent model satisfactorily fitted marmot survival data (see Appendix 3.5 for details). The model with additive effects of age and time was the most parsimonious for capture probabilities (Appendix 3.6, Table S3.6.a). The probability for an individual to be captured increased throughout the study period from 0.76±0.07 to 0.92±0.03, and decreased with age from 0.91±0.02 at one year-old to 0.66±0.02 for older individuals. The variables selected for survival were the effects of social status, age and time (Appendix 3.6, Table S3.6.b). We did not find any evidence of between-sex differences in survival (β = -0.08±0.09, for the male vs. female difference). As expected, survival increased with age, from 0.59±0.08 in juveniles to 0.80±0.12 in yearlings, and was then markedly higher for dominant adult marmots than for subordinates (0.81±0.10 vs. 0.52±0.15, respectively). Finally, survival varied from year to year for each age and social class (Fig. 3.3). The selected model for state transition probabilities only included an age-class effect on the probability of becoming dominant (Appendix 3.6, Table S3.6.c), which markedly increased with age, from 0.07±0.02 at two years of age to an average of 0.45±0.03 in older individuals.

3.3.3. Effects of climate, weather and social factors on alpine marmot survival

We detected a temporal trend in survival of juveniles only, which decreased from 0.85±0.16 in 1990 to 0.42±0.07 in 2013 (β = -0.06±0.01, R^2 = 0.39, Fig. 3.3.a). We could not detect any trend over time in survival of other age-classes (yearlings: β = -0.04±0.03, R^2 = 0.11, Fig. 3.3.b; dominant adults: β = -0.02±0.02, R^2 = 0.06, Fig. 3d; subordinate adults: β = 0.01±0.02, R^2 = 0.002, Fig. 3.3.c).

In accordance with our first expectation, juvenile survival increased with NAO (β = 0.35±0.08, R^2 = 0.34), reflecting a strong response of juveniles to climate

change, while no effect of NAO was detected on survival in any other age-class (yearlings: $\beta = 0.10 \pm 0.14$, $R^2 = 0.02$; subordinates: $\beta = -0.01 \pm 0.11$, $R^2 < 0.01$; dominants: $\beta = 0.04 \pm 0.13$, $R^2 < 0.01$).

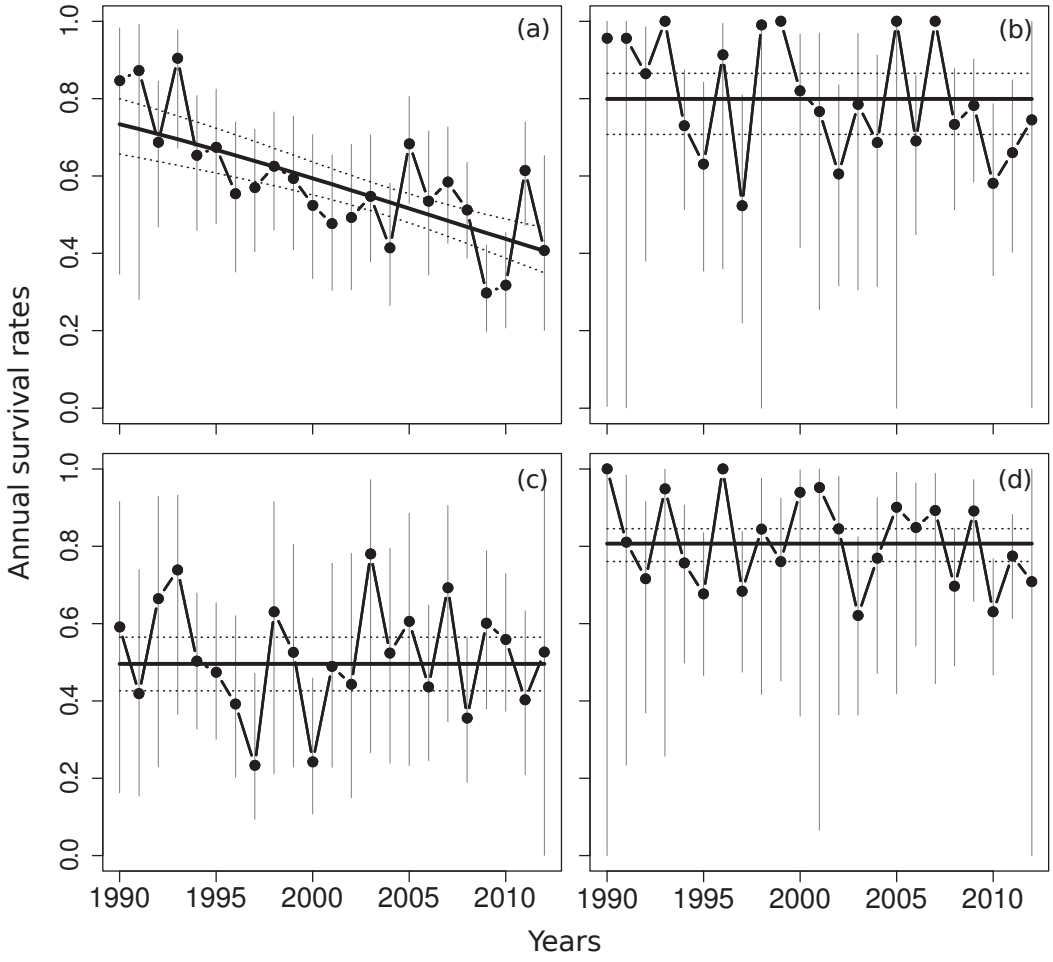

Figure 3.3. Annual estimates (± 95% CI, vertical segments) of age-specific survival of Alpine marmots in La Grande Sassière (France) from 1990 to 2012, estimated from the full-time dependent capture-mark-recapture model, and the corresponding time trends (± 95% CI, dashed lines) for (a) Juveniles, (b) yearlings, (c) subordinate adults and (d) dominant.

Among all the combinations of local weather and social variables we analyzed to explain the observed yearly variation in juvenile survival, only the interactive effects between the winter index and the proportion of families with helpers during hibernation were statistically significant (Table 3.2.a). The interactive effects

accounted for about 55% of the between-year variation observed in juvenile survival (Table 3.2.a). No effect of weather conditions during the active vegetation period was detected after controlling for this interactive effect, which runs counter to our expectations. The negative effects of harsh winters on juvenile survival appeared to be buffered by a high proportion of groups having helpers during hibernation (WIN_t, $\beta = 0.33 \pm 0.07$; $HELP_t$, $\beta = 0.35 \pm 0.09$; Interaction, $\beta = -0.29 \pm 0.09$, Fig. 3.4.a,b). Hence, through time, the detrimental effect of harsher winters on juvenile survival was reinforced by the simultaneous decrease in the proportion of groups with helpers.

The selected model for yearling survival only included the effect of the NDVI in April the year after hibernation ($NDVI_{t+1}$) (Table 3.2.b), which accounted for 14% of the total observed variation in annual survival (Table 3.2.b). Earlier snowmelt at emergence ($NDVI_{t+1}$) was detrimental for yearling survival ($\beta = -0.26 \pm 0.14$, Fig. 3.4.c).

Survival of subordinate adults was related to summer weather conditions before hibernation (Table 3.2.c) with the best model including the index of summer drought (BGI_t), accounting for 22% of the observed between-year variation (Table 3.2.c). However, subordinate adult survival tended to be positively influenced by hot and dry summers ($\beta = -0.21 \pm 0.11$, Fig. 3.4.d).

For dominant adults, the selected model included the BGI_t index, together with the additive effect of the $NDVI_{t+1}$ at the end of hibernation (Table 3.2.d). These effects accounted for 36% of the observed variation in adult survival of dominant marmots (Table 3.2.d). Unlike subordinates, dominant marmots suffered from dry summers ($\beta = 0.34 \pm 0.14$, Fig. 3.4.f) and, given the negative correlation between their survival and NDVI values ($\beta = -0.27 \pm 0.10$, Fig. 3.4.e), earlier springs were detrimental for dominant adults at the time of their emergence from burrows.

3.3.4. Climate change effect on juvenile survival through social composition of groups

We found little evidence for any effect of winter weather conditions at year *t-2* on juvenile survival at year *t*, after accounting for the effect of the proportion of groups

with helpers during hibernation (β = -0.04±0.07; Fig. 3.1). However, as expected, past winter conditions influenced juvenile survival through effects on social factors. The winter weather conditions at year *t-2* was associated with the proportion of groups with helpers during hibernation at year *t* (β = 0.18±0.08; Fig. 3.1), accounting for 27% of the observed variation between years in the proportion of groups with helpers. Harsher winters induced a decrease in the proportion of groups with helpers two years later, which in turn decreased juvenile survival (β = 0.35 ± 0.08; Fig. 3.1).

Overall, juvenile survival seems to be equally influenced by the proportion of groups with helpers and the winter conditions at year t. Hence, by accounting for 27% of the observed variation in the proportion of helpers at t, the delayed effect of winter conditions at year t-2, mediated by the social group structure at t, must be weaker than the direct effects of winter conditions at year t on juvenile survival.

Table 3.2. Model selection based on AICc of the five best weather models of the Alpine marmots survival, at La Grande Sassière, France: (a) Juveniles, (b) yearlings, (c) subordinate adults, (d) dominant adults. The constant (CST) and full-time model (T) models are presented. Four local climatic variables were tested on each age-class: the NDVI in April, before ($NDVI_t$) and after hibernation ($NDVI_{t+1}$), the BGI_t in summer before hibernation and the seasonal winter index WIN_t. One social covariate, the proportion of families having helpers during hibernation ($HELP_t$) was tested on juvenile survival. Covariates included in each model are marked with a + for additive effects and with the subscript * for interactive effects between the two concerned covariates. *k* = number of parameters, AICc = Akaike's Information Criterion, R^2 = proportion of annual survival variation accounted for by the entered covariates, computed with an analysis of deviance.

	CST	T	$NDVI_t$	BGI_t	WIN_t	$NDVI_{t+1}$	$HELP_t$	*k*	Deviance	AICc	Delta AICc	R^2
	+		.	.	.	.	.	*31*	***2782.13***	***4748.29***	**-**	**-**
a) Juveniles		+	.	.	.	.	.	*53*	*2718.13*	*4729.98*	-	-
			.	.	*	.	*	**34**	**2744.27**	**4716.60**	**0.00**	**0.59**
			.	+	*	.	*	35	2743.49	4717.88	1.28	0.60
			.	.	*	+	*	35	2743.78	4718.17	1.57	0.60
			+	.	*	.	*	35	2744.24	4718.64	2.04	0.59
			.	+	*	+	*	36	2743.34	4719.80	3.20	0.61
b) Yearlings		+	.	.	.	.		*50*	*2760.53*	*4766.09*	-	-
			.	.	.	+		**32**	**2779.02**	**4747.23**	**0.00**	**0.14**
			.	.	*	*		34	2777.30	4747.42	0.19	0.22
			.	+	.	+		33	2778.03	4748.30	1.07	0.19
			.	.	+	+		33	2778.37	4748.64	1.41	0.17
			+	.	.	+		33	2778.97	4749.24	2.01	0.15
c) Subordinates		+	.	.	.	.		*53*	*2764.01*	*4775.86*	-	-
			.	+	.	.		**32**	**2778.21**	**4746.42**	**0.00**	**0.22**
			+	+	.	.		33	2777.41	4747.68	1.26	0.26
			.	+	.	+		33	2777.80	4748.08	1.66	0.24
			.	+	+	.		33	2778.03	4748.30	1.88	0.23
			+	.	.	.		32	2780.50	4748.71	2.29	0.09

d) Dominants	+	.	.	.	.	*51*	*2755.32*	*4762.98*	-	-
		.	+	**.**	+	**33**	**2771.71**	**4741.98**	**0.00**	**0.39**
		.	*****	.	*****	34	2770.80	4743.13	1.15	0.42
		.	.	.	+	32	2777.62	4745.83	3.85	0.17
		.	+	.	.	32	2777.85	4746.07	4.09	0.16
		.	.	*****	*****	34	2774.11	4746.44	4.46	0.30

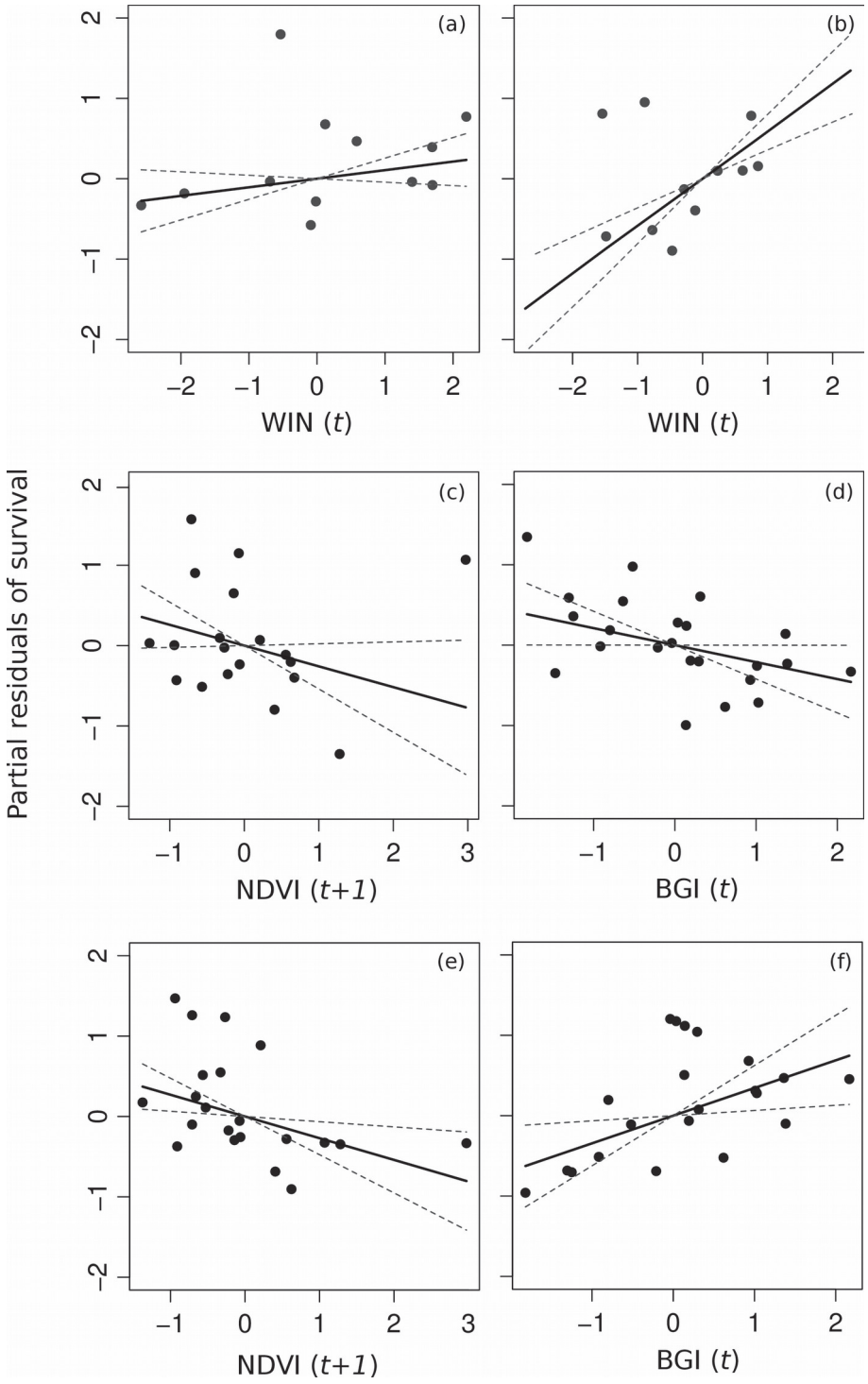

Figure 3.4. Variation in age-specific survival as a function of environmental covariates between 1990 and 2012 for the Alpine marmots of La Grande Sassière, France. Dots represent partial annual residuals of juvenile survival in relation to the standardized winter index (WIN) at year t (a) when a high proportion (more than 60%) and (b) when a low proportion (less than 60%) of groups have helpers in the population, (c) residuals of annual survival of yearlings in relation to the NDVI in April at year t+1, (d) residuals of annual survival of subordinate adults in relation to the BGI index in summer at year t, partial annual residuals of dominant adults in relation (e) to the NDVI in April at year t+1 after accounting for the effect of the BGI index, and (f) to the BGI index at year t after accounting for the effect of the NDVI in April at year t+1. Solid lines represent the model predictions and dashed lines their associated confidence intervals (± 95% CI).

3.4. Discussion

We found that changing climate is shaping the Alpine marmot population through effects on social and demographic structures. The main effect of climate change arises from immediate interactive effects of winter conditions and of the social structure of groups. Although of a limited magnitude, juvenile survival of marmots also decreased over time because of a delayed effect of colder and drier winters that reduces the relative number of helpers over the years. Those two socially mediated effects on juvenile survival provide a likely mechanism to account for the current negative influence of climate change on population dynamics of Alpine marmots.

3.4.1. Sociality matters

The two different effects of climate change we report on juvenile survival through the social composition of groups (Fig. 3.1) provide new evidence for socially mediated effects of weather conditions on demographic rates in a social species. Winters are known to be a major cause of mortality in juvenile marmots because of their lower body condition at the entrance in hibernation and their lower ability to thermoregulate (French 1990). Until now, there were evidences to show that social thermoregulation (Barash 1974; Armitage 1999) and the low energetic balance characterizing this species (Armitage et al. 2003) limited juvenile overwinter mortality. Juveniles might benefit from having helpers in their family group since subordinate males may warm them during hibernation by producing heat during periodic arousal (Allainé et al. 2000; Allainé and Theuriau 2004). Our results agreed with this assumption as the helper's presence during hibernation buffered the effect of winter weather conditions on juvenile survival. Furthermore, we showed that the observed decrease in the proportion of groups with helpers has amplified the negative effect of winters on juvenile survival. Colder winters with thinner snowpack reduced the insulation effect of snow and may have increased the energetic costs of hibernation when temperatures in burrows are very low (Tafani et al. 2013). Those energetic costs have been strengthened by a decrease in the

presence of helper presence and this has probably contributed to the decrease in juvenile survival during hibernation.

The temporal changes we report in the demographic structure of the Alpine marmot population have their origin in past winter weather conditions, thus revealing delayed effects of climate change on survival through social factors. This decrease over time in the presence of subordinate males in families has to be linked with the decrease in litter size observed in the studied population (Tafani et al. 2013), but also to a lower survival of juveniles from previous years, resulting later in a smaller number of two-year-old subordinate individuals. Hence, a negative looping effect of climate change on juvenile survival of marmots may currently be at work, in which a decrease in juvenile survival at a given year leads to a decrease in the survival of juveniles born in the subsequent years.

3.4.2. Thermal and resource-mediated effects of weather on alpine marmot survival

That spring conditions negatively influenced the survival of older marmots more than winter harshness contradicted our expectation. In mountains, NDVI measures the timing of the onset of vegetation and is directly related to the timing of spring snowmelt (Pettorelli et al. 2007). Our results indicate a negative influence of earlier snowmelt on survival of both yearling and dominant adults. For Alpine marmots, an earlier snowmelt means a thinner snowpack at the end of winter when animals are in their poorest condition and strongly sensitive to cold. A similar pattern also occurs in *Marmota caligata* (Patil et al. 2013).

The survival of dominant Alpine marmots was negatively affected by warm and dry summers, whereas the survival of subordinate marmots was positively influenced by summer drought, a conflicting and surprising result. The results on dominant adult marmots were in agreement with previous studies on other mammalian herbivores (Van Horne et al. 1997; Garel et al. 2004). By constraining the ability of Alpine marmots to thermoregulate efficiently, high temperatures reduce the time window in which they can forage in summer (Türk and Arnold 1988). In addition, high summer temperatures lead to an earlier senescence of the vegetation,

and thus forage of poor nutritional quality (Pettorelli et al. 2007), perhaps limiting fat storage.

For subordinate individuals, the positive effect of warm and dry summer conditions on survival could reflect a change in dispersal. We measured apparent survival, which cannot distinguish between death and permanent dispersal in open populations. Alpine marmots generally disperse from two-years-old onwards (Arnold 1990b; Magnolon 1999), between late April to July. Thus, given the condition-dependent dispersal events and the high constraints of drought periods, subordinate marmots might have delayed summer dispersal to increase their chance of surviving winter, resulting in a slight increase in apparent survival when summer conditions are unfavorable.

3.4.3. Comparison with other hibernating species

The increasingly critical role of the hibernation period over the years we reported for Alpine marmot survival sharply contrasts with what is generally reported for survival in other hibernating species, which are mainly influenced by weather variation during the growing season (Table 3.1). Such a discrepancy can be explained by between-site differences in local weather conditions, or by between-species differences in physiology. Indeed, hibernating species may be subjected to opposing environmental changes depending on their location, as illustrated by the comparison between the Arctic ground squirrel (*Urocitellus parryii)* and the Columbian ground squirrel (*U. columbianus).* The former benefited from earlier springs over time (Sheriff et al. 2011; Table 3.1.a) while the latter suffered from delayed springs (Lane et al. 2012; Table 3.1.a). In addition, some biological characteristics such as the ability to save energy efficiently during hibernation could shape the response of hibernating species to climate change. For instance, small-sized hibernating species with reduced fat reserve capacity, such as some bat species (Humphries et al. 2002; Rebelo et al. 2010), the pygmy-possum (*Burramys parvus*, Geiser and Körtner 2010) or the hazel dormouse (*Muscardinus avellanarius*, Pretzlaff and Dausmann 2012), are expected to suffer from an increase in winter harshness because of a dramatic increase in energy depletion during hibernation.

The critical effect of summer drought also emerged from our study, as it directly influenced body mass of marmots at the beginning of winter, making weather conditions at the end of hibernation important for survival. Hence, if summer temperatures keep on rising as predicted (**IPCC 2013**), the positive influence of hibernation reported so far on hibernating species might be strongly challenged by climate change. Hibernators would increasingly struggle to sustain the energetic cost of winter, in the same way as non-hibernating species, with summer drought affecting negatively both survival and body mass (Pettorelli et al. 2005c).

3.4.4. Conclusion

As a whole, the ability of the Alpine marmots to cope successfully with climate change appears to be undermined by constraints associated with hibernation and sociality. No demographic compensation occurred to counteract the negative time trends we report in juvenile survival (Fig. 3.2) and litter size (Tafani et al. 2013) in this population of Alpine marmots. As a consequence, the deterministic growth rate decreased from around 0.99 during the first period (1990-2000), to 0.96 in recent years (2001-2013), see Appendix 3.7 for the Leslie matrices analyzed), supporting the hypothesis of an overall negative impact of climate change on Alpine marmots. Finally, our results highlight the importance of the species' lifestyle in shaping population response to climate change. We therefore encourage a greater consideration of the lifestyle of species in the analyses of the impact of climate change on life history variation.

Appendix

Appendix 3.1. Additional information on the study design, monitoring protocol and field data on the Alpine marmot population

Appendix 3.2 Additional information about the choice of weather variables

Appendix 3.3 Correlation matrix between the different climatic and weather covariates

Appendix 3.4 Complementary analyses using "de-trended" weather covariates for juvenile survival

Appendix 3.5 GOF tests details

Appendix 3.6 Selection of the baseline model for MS-CR analysis

Appendix 3.7 Leslie matrices used to compute the deterministic growth rates of the Alpine marmot population

Appendix 3.1. Additional information on the study design, monitoring protocol and field data on the Alpine marmot population

Study design

The Alpine marmot population is located in La Grande Sassière Nature Reserve (French Alps, 45°29'N, 6°59E) at 2,300m a.s.l. All the monitored family territories are distributed in an area of approximately 1.5 km long and 500 m wide, located roughly at the same altitude, and are North or South oriented (see Fig. S3.1). 25 families were intensively followed from 1990-1993 to 2013 by capture-mark-recapture protocol (Fig. S3.1), providing 23 years of monitoring data.

Data collection procedure

From 1990 to 2013, marmots were trapped each year from mid-April to mid-July using two-door, live-capture traps baited with dandelion (*Taraxacum densleonis*). Between one and four traps were placed near the entrance of the main burrows of each family group to assign with certainty trapped individuals to their family. Once captured, individuals were tranquillized with Zolétil 100 (0.1 $mL.Kg^{-1}$) and individually marked with a numbered ear tag (1 cm x 3 mm) and a transponder (model ID100, Trovan$^{(TM)}$, Germany) for permanent identification. All captured individuals were sexed using anogenital distance and aged based on their body size up to 3 years of age. Social status was assessed by scrotal and teat development for males and females, respectively. Almost all juveniles were captured within 3 days following their first emergence (emergence period from June 15th to July 15th).

Field data

Around 135 individuals (N_{min}=36, N_{max}=195) were captured/recaptured each year. In total 1,172 individuals were marked among the 25 intensively followed families, from 1990 to 2013. Among those individuals, 918 (78%) were firstly captured at the juvenile stage, 121 (10%) were marked as juveniles and 133 (10%) entered the dataset as adults (2 years and more). At last, around 54.7% of the marked individuals were male.

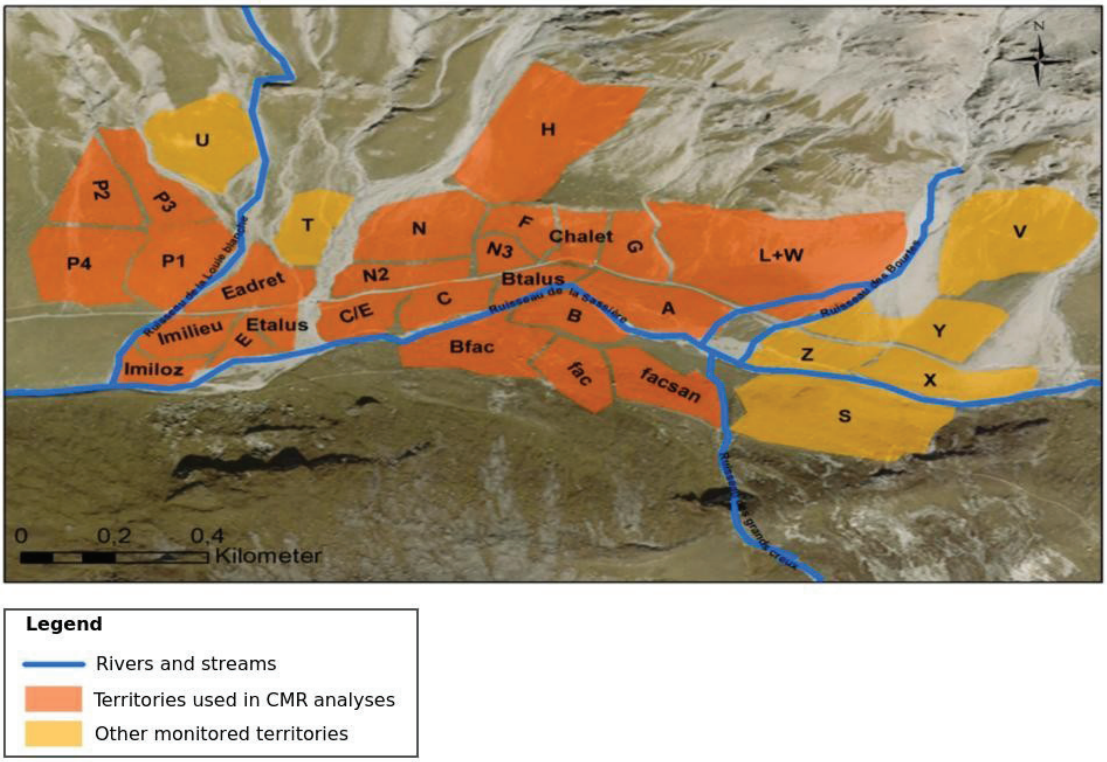

Figure S3.1. Distribution of the different Alpine marmot family territories, monitored by capture-mark-recapture protocols at La Grande Sassière, French Alps. The orange territories are followed intensively since 1990-1993 and were used in our survival analyses. The yellow territories are only followed since 2013.

Appendix 3.2. Additional information about the choice of weather variables

Given the timing of captures in the field, we defined annual survival of the Alpine marmot as the proportion of individual that survive between spring at year *t* and the following spring at year *t+1*. We chose and defined relevant weather variables accordingly.

We considered four weather variables with a potential influence on the energy budget of the Alpine marmots over a year. The annual life cycle of the Alpine marmot is characterized by three key periods, critical for marmot survival (see Fig. S3.2): **1)** the active season, time of energy acquisition, when marmots accumulate fat reserves before hibernating; **2)** the hibernation period, time of energy expenditure, when marmot sustain stressful thermal conditions and fast; and **3)** the end of hibernation, when marmots are more or less impaired by their fat reserve depletion and sensitive to environmental conditions. The four weather variables are representative of one of the three time periods, hence matching with key events of the Alpine marmot's life-cycle (Fig. S3.2).

1) NDVIt & BGIt: food availability and quality during the active season

During the active season (at year *t*, from mid April to early October, Fig. S3.2), marmots forage continuously to accumulate fat reserves to survive the 6-months of hibernation (Körtner and Heldmaier 1995). Consequently, both the timing of the snowmelt in spring that define the start of the growing season of plants (Ozgul et al. 2010; Sheriff et al. 2011; Lane et al. 2012), and the availability and quality of food resource in summer (Frick et al. 2010; Kneip et al. 2011), will influence the amount of stored energy in autumn right before hibernation. Because marmots rely solely on their fat reserve during hibernation, it is critical for their over-winter survival.

We thus assessed the timing of the snowmelt with the Normalized Differential Vegetation Index (NDVI) at year *t*, a remote sensing proxy of primary production (Pettorelli et al. 2005b; Hamel et al. 2009). The vegetation onset indeed correlates well with snowmelt in mountainous environments (Pettorelli et al. 2007). An early snowmelt is associated with a longer growing season and larger body mass

of marmots before the next hibernation, which may increase their survival (Ozgul et al. 2010). We calculated NDVI values from April 15th to May 1st to match marmots' emergence from their burrow at year *t* (Fig. S3.2). Those index values were extracted from the NOAA/NASA with a 8x8 km resolution (AVHRR) from 1990 to 2000 and a 1x1 km resolution (MODIS) from 2001 to 2013. High NDVI values indicate early snowmelt and access to food resources for marmots, that is early springs.

The summer is another key period of the growing season during which weather conditions matter. In temperate and dry areas, summer drought is a limiting factor for plant growth and quality, which provide the necessary energy resources for animal's fattening before winter (Toïgo et al. 2006; Mysterud et al. 2008). To quantify food resource availability and quantity in summer, we computed the Bagnoul-Gaussen Index (BGI, see Gaillard et al. 1997 for the calculation) at year *t*. The BGI is a meaningful drought index in temperate areas (see Garel et al. 2004 for an application on mouflon and Toïgo et al. 2006 on roe deer).

2) WINt: a proxy of within-burrow temperature during hibernation

Hibernation, occurring early October to mid April, between year *t* and *t+1* (Fig. S3.2), is another critical period for the marmots (Arnold 1990a) life cycle. During hibernation individuals have to sustain a long fast while keeping their body temperature above 5°C. Below this threshold temperature, fat reserves are depleted at a much higher rate (Arnold et al. 1991), which may strongly jeopardize their survival. We have previously shown that the temperature within the burrow dropped well below 5°C during cold winter with less snowpack (from December to March). Consequently, litter sizes were smaller and female Alpine marmots were lighter at emergence the following spring (Tafani et al. 2013). We thus characterized the environmental conditions during hibernation with a winter harshness index using outside air temperature and snow depth measured from December 1st and March 31st (WINt, see Fig. S3.2).

To keep the number of variables to a minimum, WIN_t combined air temperature and snow depth. We defined WIN_t as the residuals from the orthogonal

regression between the monthly average air temperature and snow depth. Low values of the winter index corresponds to cold and dry harsh winters, which are detrimental for hibernating marmots.

3) $NDVI_{t+1}$: environmental conditions at emergence after 6 months of fast

At vernal emergence (mid-April of year *t+1*), environmental conditions such as early snowmelt may impact marmot survival rates after hibernation, as previously shown on other marmot species (Schwartz and Armitage 2005; Patil et al. 2013), or the marmot litter size (Tafani et al. 2013). We thus also used the NDVI values derived in the second half of April, but at year *t+1,* to test whether snowmelt and the correlated vegetation onset affect marmot survival at the end of hibernation.

All the local weather variables that we used to compute the weather indices (air temperature, precipitation, snow depth) were recorded daily from the Météo France weather stations of Tignes (73296400) and Val d'Isère (73304404), located 5 km away from the study site.

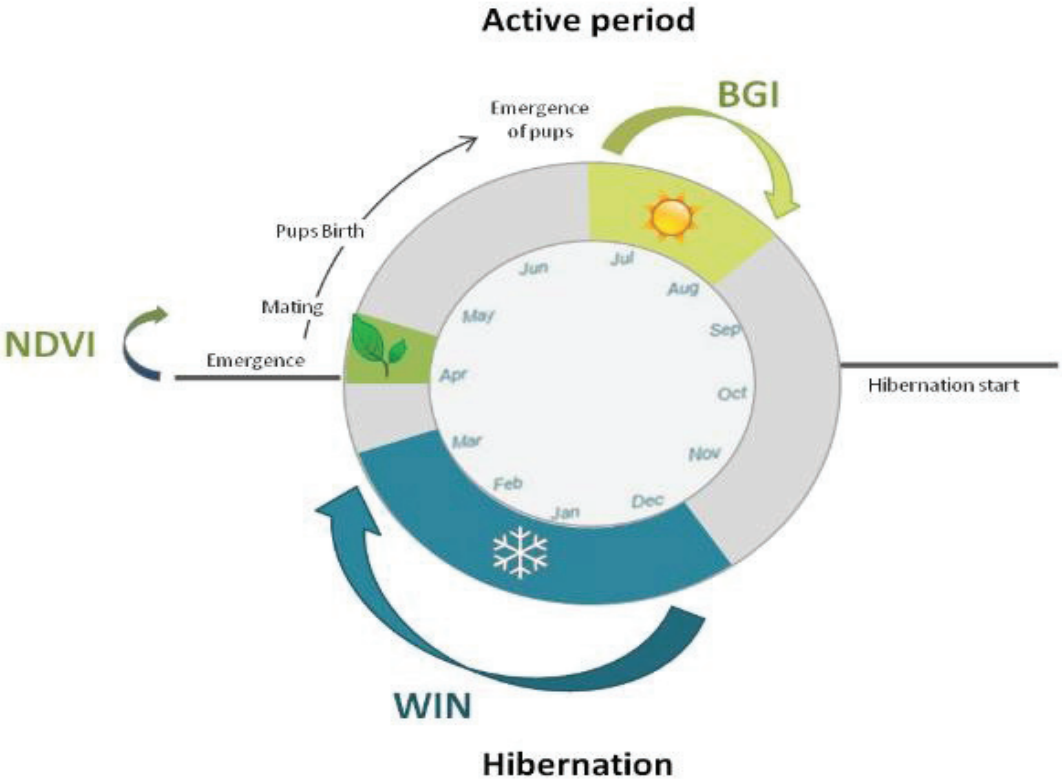

Figure S3.2. Annual life-cycle of the Alpine marmot with the four climate variables defined according to the three key periods of the marmot life-cycle: before hibernation ($NDVI_t$, BGI_t), during hibernation (WIN_t), and at emergence from hibernation ($NDVI_{t+1}$).

Appendix 3.3. Correlation matrix between the different climatic and weather covariates

Table S3.3. Pearson correlation coefficients among climate and weather indices in the site of La grande Sassière and their associated p-values. Only a statistically significant positive correlation was found between the global scale NAO index and the local winter weather index WIN.

	NDVI(t)	***BGI(t)***	***WIN(t)***	***HELP(t)***	***NDVI(t+1)***
NAO(t)	0.12	0.11	0.60*	0.08	0.09
	p=0.60	*p*=0.62	*p*=0.003	*p*=0.73	*p*=0.67
NDVI(t)		0.18	0.27	-0.31	-0.25
		p=0.40	*p*=0.21	*p*=0.16	*p*=0.25
BGI(t)			0.11	-0.19	0.32
			p=0.61	*p*=0.39	*p*=0.14
WIN(t)				0.19	-0.13
				p=0.39	*p*=0.55
HELP(t)					-0.15
					p=0.49

Appendix 3.4. Complementary analyses using "de-trended" weather covariates for juvenile survival

Table S3.4. Model selection of the effect of weather indices on juvenile survival of the Alpine marmot population at La Grande Sassière, France. The constant (constant), full-time, with time as a discrete factor (time), and trend, with time as continuous factor, (Time) models are presented. Four local weather variables were tested on juvenile survival: the NDVI in April, before *(t)* and after hibernation (*t+1*), the BGI in summer before hibernation and the seasonal winter index WIN, and one social covariate, the proportion of families having helpers during hibernation, HELP. Both the WIN and HELP indices were de-trended for the analyses, which is indicated by the "D_" prefix, and the added continuous time effect is represented with the "*Time*" term. K = number of parameters, Dev = Deviance, AICc = Akaike's Information Criterion, R^2 = proportion of annual survival variation accounted for by the selected covariates, computed with the analysis of deviance, and Beta±SE = coefficients of the relationship between weather covariates and juvenile survival, with their associated standard errors.

Models	K	AICc	Dev	R^2	Beta ± SE
Φjuv ~ constant	*31*	*4748.29*	*2782.13*	-	-
Φjuv ~ time	*53*	*4729.98*	*2718.13*	-	-
Φjuv ~ Time	*32*	*4722.23*	*2754.02*	-	-
***Φjuv ~ Time* + D_WIN (t)**	**35**	**4713.05**	**2738.65**	**0.43**	**0.23 ± 0.08**
+ D_HELP (t)	**…**	**…**	**…**	**…**	**0.03 ± 0.11**
+ D_WIN (t) : D_HELP (t)	**…**	**…**	**…**	**…**	**-0.37 ± 0.12**
Φjuv ~ Time + D_WIN (t)	36	4714.32	2737.86	0.45	0.22 ± 0.08
+ D_HELP (t)	…	…	…	…	0.04 ± 0.11
+ D_WIN (t) : D_HELP (t)	…	…	…	…	-0.36 ± 0.12
+ BGI (t)	…	…	…	…	0.07 ± 0.08
Φjuv ~ Time + D_WIN (t)	36	4714.65	2738.19	0.44	0.25 ± 0.08
+ D_HELP (t)	…	…	…	…	0.02 ± 0.11
+ D_WIN (t) : D_HELP (t)	…	…	…	…	-0.36 ± 0.12
+ NDVI (t+1)	…	…	…	…	-0.05 ± 0.07
Φjuv ~ Time + D_WIN (t)	36	4714.94	2738.48	0.43	0.10 ± 0.08
+ BGI (t)	…	…	…	…	0.12 ± 0.08
+ D_WIN (t) : BGI (t)	…	…	…	…	-0.16 ± 0.08
+ NDVI (t)	…	…	…	…	0.18 ± 0.08
Φjuv ~ Time + D_WIN (t)	36	4715.04	2738.58	0.43	0.21 ± 0.10
+ D_HELP (t)	…	…	…	…	0.04 ± 0.11
+ D_WIN (t) : D_HELP (t)	…	…	…	…	-0.35 ± 0.16
+ NDVI (t)	…	…	…	…	0.03 ± 0.12

Appendix 3.5. GOF tests details

We referred to the Cormack-Jolly-Seber (CJS) as the general model to realize the Goodness-of-fit (GOF) tests, as it allows for time-dependence in recapture and survival probabilities (Lebreton et al. 1992). The overall GOF test was significant (χ^2=180.71, df=82, p-value<0.001), with the 2.Ct test revealing trap-dependence (χ^2=60.64, df=22, p-value<0.001) and the 3.Sr test highlighting transient effects occurred in the Alpine marmot population (χ^2=32.15, df=21, p-value<0.001). However, those results might be due to an age stratification of both survival and recapture probabilities. Juvenile alpine marmots have lower survival rates between their first capture at *t* and recapture at *t+1,* than older individuals, as in many other mammals. As well, the recapture probability might decrease with ages, individuals being less prone to be recaptured along their lifetime (trap shyness). To see if the significance of the GOF tests were induced by an age stratification in our data, we performed another GOF test with a new dataset, where the first occasions of capture at the juvenile age were retrieved from the capture history. With this new dataset, the overall GOF test was not significant (χ^2=75.18, df=82, p-value=0.69), and no trap-dependence (2.Ct; χ^2=17.52, df=21, p-value=0.45) and transient effects (3.Sr; χ^2=11.37, df=22, p-value=0.97) were found anymore. Hence, the full time-dependent model adequately fit our data when the age structure of the population was taken into account in the general model.

Appendix 3.6. Selection of the baseline model for MS-CR analysis

Table S3.6. Modeling of capture (*p*), survival (*Φ)* and state transition probabilities (*Ψ)* for the Alpine marmots of La Grande Sassière, France. The constant, age-class, full-time and the five best explanatory models based on AICc for (a) capture, (b) survival, and (c) state transition probabilities. The subscripts *status, age-class, sex, time* stand respectively for an effect of the social status (subordinate or dominant), age-class (categorical variable including juvenile [from 0 to 1 year-old], yearling [from 1 to 2 years of age], and adults [from 2 years-old] classes), sex, and time (year) effect. The subscript * indicates interactive effects. K= number of parameters; AICc= Akake Information Criterion corrected for small sample size; wi= weight of the AICc.

Models	K	Deviance	AIC_c	wi
a) Capture model				
p ~ ageclass+sex+time	55	2718.24	4734.29	0.43
p ~ ageclass+time	**54**	**2721.05**	**4735.01**	**0.30**
p ~ status + ageclass + sex + time	56	2718.03	4736.18	0.16
*p ~ ageclass * sex + time*	57	2716.93	4737.18	0.10
*p ~ ageclass * time+ sex*	85	2662.58	4742.54	0.01
p ~ ageclass	33	2841.01	4811.28	0
p ~ time	52	2808.67	4818.43	0
p ~ constant	31	2916.46	4882.62	0
b) Survival model				
Φ ~ status*ageclass+ time	**52**	**2724.27**	**4734.02**	**0.63**
*Φ ~ status*ageclass+ time + sex*	53	2723.36	4735.22	0.33
*Φ ~ status*ageclass* sex + time*	56	2722.15	4740.31	0.03
*Φ ~ status*ageclass*	31	2782.14	4748.29	<0.01
*Φ ~ status*ageclass+ sex*	32	2781.25	4749.46	<0.01
Φ ~ time	49	2878.02	4881.50	0
Φ ~ ageclass	30	2874.11	4838.21	0
Φ ~ constant	28	2939.66	4899.66	0
c) State transition model				
*Ψ ~ ageclass * sex*	55	2718.70	4734.75	0.37
Ψ ~ ageclass + sex	54	2721.05	4735.00	0.33
Ψ ~ ageclass	**53**	**2723.36**	**4735.22**	**0.29**
*Ψ ~ ageclass * sex + time*	77	2684.24	4746.99	<0.01
Ψ ~ ageclass + time	75	2689.16	4747.62	<0.01
Ψ ~ constant	53	2821.22	4833.08	0
Ψ ~ time	75	2791.30	4849.76	0

Appendix 3.7. Leslie matrices used to compute the deterministic growth rates of the Alpine marmot population

Table S3.7a. Abbreviations used in the population matrix and the corresponding averaged estimates used to derive the deterministic growth rate of the Alpine marmot population according two periods: from 1990 to 2000 and from 2001-2013.

Demographic parameters		**Mean estimates used in the Leslie matrix**	
Abbreviations	*Meanings*	*From 1990 to 2000*	*From 2001 to 2013*
S0	Survival probability of juveniles, from 0 to 1 year	0.682	0.490
S1	Survival probability of yearlings, from 1 to 2 years	0.852	0.743
S2	Survival probability of subordinates from 2 to 5 years	0.489	0.529
S3	Survival probability of prime-aged dominants, from 2 to 8 year	0.844	0.829
S4	Survival probability of senescent dominants, from 8 to 14 years	0.626	0.626
F1	Annual number of female offspring produced at birth by 2 years-old females	2*0.25*0.45	2*0.25*0.45
F2	Annual number of female offspring produced at birth by prime-aged females of 3 to 10 years	4.08*0.67*0.45	3.76*0.70*0.45
F3	Annual number of female offspring produced at birth by senescent females of 10 to 15 years	3.32*0.67*0.45	3.32*0.70*0.45
T1	State transition probability, from 1 to 2 years	0.077	0.061
T2	State transition probability, from 2 years to 4 years	0.315	0.540

Table S3.7b. The Leslie matrix and the corresponding demographic parameters used in demographical analyses on the Alpine marmot population.

t+1 \ *t*	JUV	YEAR	SUB2	SUB3	SUB4	SUB5	DOM2	DOM3	DOM4	DOM5	DOM6	DOM7	DOM8	DOM9	DOM10	DOM11	DOM12	DOM13	DOM14	DOM15	DOM16
JUV	0	S1*T1*F1	S2*T2*F2	S2*T2*F2	S2*T2*F2	0	S3*F2	S3*F2	S3*F2	S3*F2	S3*F2	S3*F2	S4*F2	S4*F3	S4*F3	S4*F3	S4*F3	S4*F3	S4*F3	S4*F3	0
YEAR	S0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB2	0	S1*(1-T1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB3	0	0	S2*(1-T2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB4	0	0	0	S2*(1-T2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB5	0	0	0	0	S2*(1-T2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM2	0	S1*T1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM3	0	0	S2*T2	0	0	0	S3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM4	0	0	0	S2*T2	0	0	0	S3	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM5	0	0	0	0	S2*T2	0	0	0	S3	0	0	0	0	0	0	0	0	0	0	0	0
DOM6	0	0	0	0	0	0	0	0	0	S3	0	0	0	0	0	0	0	0	0	0	0
DOM7	0	0	0	0	0	0	0	0	0	0	S3	0	0	0	0	0	0	0	0	0	0
DOM8	0	0	0	0	0	0	0	0	0	0	0	S3	0	0	0	0	0	0	0	0	0
DOM9	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0	0	0	0	0	0	0
DOM10	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0	0	0	0	0	0
DOM11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0	0	0	0	0
DOM12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0	0	0	0
DOM13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0	0	0
DOM14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0	0
DOM15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0	0
DOM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S4	0

Table S3.7c. The two Leslie matrices used to compute the deterministic growth rate of the Alpine marmot population according two periods: A) from 1990 to 2000, and B) from 2001 to2013.

A)

	JUV	YEAR	SUB2	SUB3	SUB4	SUB5	DOM2	DOM3	DOM4	DOM5	DOM6	DOM7	DOM8	DOM9	DOM10	DOM11	DOM12	DOM13	DOM14	DOM15	DOM16
JUV	0	0.015	0.189	0.189	0.189	0	1.038	1.038	1.038	1.038	1.038	1.038	0.770	0.626	0.626	0.626	0.626	0.626	0.626	0.626	0
YEAR	0.682	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB2	0	0.786	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB3	0	0	0.335	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB4	0	0	0	0.335	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB5	0	0	0	0	0.335	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM2	0	0.065	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM3	0	0	0.154	0	0	0	0.844	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM4	0	0	0	0.154	0	0	0	0.844	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM5	0	0	0	0	0.154	0	0	0	0.844	0	0	0	0	0	0	0	0	0	0	0	0
DOM6	0	0	0	0	0	0	0	0	0	0.844	0	0	0	0	0	0	0	0	0	0	0
DOM7	0	0	0	0	0	0	0	0	0	0	0.844	0	0	0	0	0	0	0	0	0	0
DOM8	0	0	0	0	0	0	0	0	0	0	0	0.844	0	0	0	0	0	0	0	0	0
DOM9	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0	0	0	0
DOM10	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0	0	0
DOM11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0	0
DOM12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0
DOM13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0
DOM14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0
DOM15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0
DOM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0

B)

	JUV	YEAR	SUB2	SUB3	SUB4	SUB5	DOM2	DOM3	DOM4	DOM5	DOM6	DOM7	DOM8	DOM9	DOM10	DOM11	DOM12	DOM13	DOM14	DOM15	DOM16
JUV	0	0.010	0.338	0.338	0.338	0	0.982	0.982	0.982	0.982	0.982	0.982	0.741	0.655	0.655	0.655	0.655	0.655	0.655	0.655	0
YEAR	0.490	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB2	0	0.698	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB3	0	0	0.243	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB4	0	0	0	0.243	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB5	0	0	0	0	0.243	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM2	0	0.045	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM3	0	0	0.285	0	0	0	0.829	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM4	0	0	0	0.285	0	0	0	0.829	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM5	0	0	0	0	0.285	0	0	0	0.829	0	0	0	0	0	0	0	0	0	0	0	0
DOM6	0	0	0	0	0	0	0	0	0	0.829	0	0	0	0	0	0	0	0	0	0	0
DOM7	0	0	0	0	0	0	0	0	0	0	0.829	0	0	0	0	0	0	0	0	0	0
DOM8	0	0	0	0	0	0	0	0	0	0	0	0.829	0	0	0	0	0	0	0	0	0
DOM9	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0	0	0	0
DOM10	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0	0	0
DOM11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0	0
DOM12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0	0
DOM13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0	0
DOM14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0	0
DOM15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0	0
DOM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.626	0

Chapter 4

Decreasing adaptive value of cooperative breeding with climate change in Alpine marmots

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In preparation

Abstract

The role of environmental variation in influencing the evolution of cooperative breeding has been repeatedly debated over time. Recent studies envision cooperative breeding as a response to environmental variability, involving a bet-hedging strategy that allows reducing fecundity variance in highly variable environments. Such findings may have strong implications at the population level, but whether this social system can buffer population demography against environmental variation remains unknown. Here, using a 23 years-long data set, we aimed at assessing the adaptive value of cooperative breeding in a population of the socially hibernating Alpine marmot (*Marmota marmota*), currently facing a rapidly changing environment. As expected, the presence of helpers increased mean juvenile survival while decreasing its temporal variance. However, mean juvenile survival mainly decreased over years in family groups with helpers, which suggests that the fitness benefits of helping for both juveniles and helpers are reduced in presence of the climate change. The long-run stochastic population growth rate was negatively impacted, through both decreased mean and increased variance of annual growth rates. However, this negative impact was partly counterbalanced by a higher access to dominance and increased reproduction by subordinates in the most recent years. We conclude that climate change might be currently disrupting selection pressures that have promoted cooperative breeding in the Alpine marmot until now, leading to release the dispersal costs of subordinates and to decrease fitness benefits of helping behaviour. Overall, our results also highlight the need for detailed demographic analyses to better understand the evolution of social behaviour.

Key-words: cooperative breeding; environmental variability; ecological constraints; *Marmota marmota;* climate change; stochastic demography

4.1. Introduction

Identifying factors driving the evolution of cooperative breeding is a major challenge facing evolutionary ecologists for decades. Current approaches to study the evolution of cooperative breeding are generally based on a cost/benefit ratio involving both delayed dispersal and reproduction by independent offspring that allows structuring the population into kin groups, and helping behaviour by independent offspring within their family group (Emlen 1982a; Stacey and Ligon 1991; Koenig et al. 1992). The role of environmental variation for shaping these decision-making behaviours has been repeatedly debated within this framework.

The "ecological constraint hypothesis" identifies the environment as a major determinant of cooperative breeding (Emlen 1982a, b). This hypothesis emphasize the role of dispersal costs by stating that severe environmental constraints should directly limit the possibility of independent offspring to settle in a new territory and reproduce successfully (Emlen 1982a; Hatchwell and Komdeur 2000). Dispersal should be limited by environmental harshness in highly variable and unpredictable environments, and by habitat saturation in stable and predictable environments (Emlen 1982b; Koenig et al. 1992). Individuals that skip reproduction and stay within their family group should thus get fitness benefit from refraining a risky dispersal and helping their siblings to increase the reproductive success of their relatives, which leads to increase their own inclusive fitness (Hamilton 1964a, b; Russell and Hatchwell 2001). Cooperative breeding is mostly viewed as a "best of the bad job" behavioural tactic in that case. By contrast, other hypotheses put greater emphasis on the importance of the fitness benefits helpers may gain by staying in the family and helping relatives to explain the evolution of cooperative breeding (i.e. the "benefits of philopatry hypothesis", Stacey and Ligon 1991). The role of the environment in that context has been also included through the "life history hypothesis" (Arnold and Owens 1998), which proposes that cooperative breeding co-evolved with life history traits and is an inherent part of the life history strategy of a given species. Thus, cooperative breeding is associated with a slow pace of life and mostly occurs in species displaying low adult mortality and small clutch size in birds (Arnold and Owens 1998). Such a slow life history generates a low family

turnover and ultimately a saturation of the habitat, which limits the access to reproduction for newly independent offspring (Arnold and Owens 1998). Finally, delaying the onset of reproduction could also be adaptive in long-lived species, as it may allow to maximise the individual lifetime reproductive success, so that delayed reproduction and dispersal could also be viewed as an adaptive life history decision in cooperative breeding species which allows the formation and the cohesion of families (Covas and Griesser 2007). Numerous factors have thus been proposed to explain the evolution of cooperative breeding, which should be determined by both ecological and life-history factors (Hatchwell and Komdeur 2000; Covas and Griesser 2007).

Recently, a comparative study in birds has suggested that cooperative breeding should have mainly evolved in response to temporal environmental variability and unpredictability based on the observation that, at a large geographical scale, cooperatively breeding bird species do occur in arid regions with high between-year variability in rainfall (see Rubenstein and Lovette 2007 on African starlings, Sturnidae; Jetz and Rubenstein 2011 on 95% of the world's birds; but see Gonzalez et al. 2013). Cooperative breeding has thus been proposed to correspond to a bet-hedging strategy (sensu Slatkin 1974) that allows maximizing the long-term average reproductive success by decreasing its temporal variance when facing a mixture of poor and good environmental conditions (Cockburn and Russell 2011). In several species, the presence of helpers in family groups is more frequent under unfavourable environmental conditions (e.g. Emlen 1982a on the white-fronted bee-eater, *Merops bullockoides*; Canário et al. 2004 on the Azure-winged Magpie, *Cyanopica cyanus*) while the fitness benefits of helping in terms of increased reproductive success is more pronounced under adverse breeding conditions (e.g. Magrath 2001 on white-browed scrubwren, *Sericornis frontalis*; Covas et al. 2008 on the sociable weaver, *Philetairus socius*). These empirical studies highlight the crucial role of the environment in the decision to delay dispersal and to help, and suggest that cooperative breeding could have a buffering effect against environmental variation in reproductive success by limiting the negative impacts of poor environmental conditions.

The beneficial effect that the presence of helpers in a family group may

have on the reproductive success of the breeding pair has been extensively reported for many cooperative species, including mammals (e.g. Clutton-Brock 2001), birds (e.g. Mumme 1992), and insects (e.g. Salomon and Lubin 2007). Investigating the adaptive value of cooperative breeding is especially relevant to identify reliably the factors and circumstances that promote its evolution. However, these beneficial effects have mostly been investigated on the mean reproductive success of breeders, and have rarely addressed the variance in reproductive success. A recent study on the superb starling *(Lamprotornis superbus),* however, provides a notable exception by showing that the variance in reproductive success declined with increasing group size, while group size directly increased with temporal environmental variation during the pre-breeding season (Rubenstein 2011). These findings support the view that bet-hedging provides an evolutionary mechanism of the helping behaviour in variable environments. However, the intensity of the buffering effect of cooperative breeding on the variation in reproductive success remains equivocal and mostly limited to birds. The few other studies that investigated the influence of the helper presence either found no support (Reed and Walters 1996**,** on the red-cockaded woodpecker, *Leuconotopicus borealis*) or showed that the fitness benefit of having helpers only showed up in poor environmental conditions (Koenig and Walters 2015, on the acorn woodpecker, *Melanerpes formicivorus*).

The buffering effect of cooperative breeding on vital rates may have strong implications for population dynamics in variable environments. In this context, cooperative breeding could dampen the negative impact of environmental variation on the long-run stochastic population growth rate. Populations including individuals displaying cooperative breeding should thus be less sensitive to increasingly harsh and variable environmental conditions expected to occur with the ongoing climate change (Räisänen 2002; Giorgi et al. 2004) than populations without any cooperative breeders. However, to the best of our knowledge, no study has yet looked for assessing the relative contribution of the beneficial effects of cooperative breeding on population demography.

Here, we aimed to fill this knowledge gap by assessing how the individual fitness benefits of cooperative breeding in terms of reproductive success impact the long-run population growth rate in variable environments, especially when facing

increasingly changing environmental conditions. We used the Alpine marmot (*Marmota marmota*) as a study model, for which a detailed individual-based long-term monitoring (23 years) was available in a French Alps population. The marmots (genus *Marmota*) display a broad range of sociality levels whose evolution has been linked to the harshness of the mountainous environments, characterized by short growing seasons and yearly variable weather conditions (Barash 1974; Armitage 1999). The Alpine marmot is a socially hibernating species that displays cooperative breeding (Solomon and French 1997; Blumstein and Armitage 1999). This marmot hibernates in extended family groups composed of typically one dominant breeding pair, subordinates and pups of the year (Arnold 1990a; Perrin et al. 1993). Recently independent offspring generally delay their dispersal from the natal family group beyond two years of age. Female subordinates do not reproduce, and subordinate males act as helpers for juveniles (Arnold 1993b; Allainé et al. 2000; Allainé and Theuriau 2004). These latter actively warm up offspring to which they are related during hibernation (in winter) through social thermoregulation, which results in higher mean offspring survival (Allainé et al. 2000; Allainé and Theuriau 2004).

Overall, we expected that the presence of helpers should limit the impact of environmental variation on population demography by reducing temporal variance in offspring survival. Alpine marmot populations are structured in family groups of various compositions, which allow comparing reproductive success of breeders between groups with and without helpers. We therefore expected that (i) juveniles in family groups with helpers should display both higher mean survival and lower temporal variance in survival than juveniles in groups without helpers. Then, we expected that (ii) the survival of juveniles hibernating with helpers should contribute to increase the long-run stochastic growth rate of the population more than the survival of juveniles hibernating without helpers. The expected positive effect of helper presence should result in both an increase in the mean annual population growth rate and a decrease in the variance of annual growth rates. Finally, recent climate change resulted in increasingly harsher winters in our study site in recent years, which slowed down the Alpine marmot population demography through both decreased litter size and decreased juvenile survival (Tafani et al. 2013; Rézouki et al. 2016). In this context, we expected cooperative breeding to buffer the population

growth rate of Alpine marmots against the negative impact of climate change. More specifically, we expected that (iii) the decrease in juvenile survival should be dampened for juveniles that hibernate in family groups with helpers. Consequently, the survival of juveniles with helpers should have a less negative impact on the population growth rate than the survival of juveniles without helpers.

4.2. Material and methods

4.2.1. Study species

Alpine marmots are social, territorial and hibernating rodents that have been classified as cooperative breeders (Blumstein and Armitage 1999; Allainé 2000). They live in family groups of up to 20 individuals composed of a dominant breeding pair, sexually mature subordinates aged at least two years, immature yearlings and juveniles (Arnold 1990b; Perrin et al. 1993). Sexual maturity occurs at two-years of age but many individuals delay dispersal to acquire reproduction one or more years later, stay in their family group as subordinates, and generally do not reproduce before three years of age (Arnold 1990a; Magnolon 1999). Subordinates are reproductively suppressed by the dominant individual of the same sex, either completely for subordinate females (Hackländer et al. 2003)or only partially for subordinate males, as some males manage to escape reproductive suppression (Arnold 1990b; Cohas et al. 2007b).

Alpine marmots hibernate with their family group members from mid-October to mid-April (Arnold 1988). The mating occurs shortly after emergence in April and the pups emerge from mid-June to mid-July after 30 days of gestation followed by 40 days of lactation inside the natal burrow. Subordinate males actively heat the family hibernaculum through social thermoregulation during winters (Arnold 1990b, 1993b, a), which leads to increase juvenile survival during their first hibernation (Allainé et al. 2000; Allainé and Theuriau 2004) and to provide breeders with immediate fitness benefits while enduring themselves costs in terms of body mass loss (Arnold 1990b, 1993b, a).

4.2.2. Study site and protocol

All data were collected in a wild population of Alpine marmots located in La Grande Sassière Nature Reserve (French Alps, 45°29'N, 6°59E). Individuals were monitored each year from mid-April to mid-July using a capture-mark-recapture protocol from 1990 to 2013. Once trapped, marmots were tranquillized with Zolétil 100 (0.1 mL/kg), individually marked for permanent identification, sexed, and weighed. Based on their body size, individuals were aged according to three categories: juveniles (i.e., young of the year), yearlings (i.e., born in the previous year and thus slightly older than 1 year of age), and adults (i.e., $\geq$ 2 years of age).

Dominant animals (i.e. reproductive individuals) were categorized using scrotal and teat development for males and females, respectively. The number of weaned offspring per dominant female was assessed through capture and intensive observations at emergence from the natal burrow from June to mid-July. The mother-pup parentage was then confirmed by genetic analyses (Cohas et al. 2007b).

4.2.3. Estimation of vital rates

Survival rates

We used multi-state Capture-Mark-Recapture models (MS-CR, Lebreton et al. 2009) to estimate age- and state-dependent annual survival rates (see Table 4.1 for definition) of Alpine marmots from 1990 to 2013, based on data collected on 1,172 individuals. Mean annual survival rates were estimated following the same procedure as described in Rézouki et al. (2016**)** (Appendix 4.1) using the RMark 2.1.7 package (Laake and Rexstad 2008), derived from the MARK software (White and Burnham 1999), available within the R environment (Development Core Team 2011). Based on previous analyses on alpine marmots survival (Rézouki et al. 2016; Berger et al. 2016), we estimated specific survival rates along five age- and stage-classes, accounting for the dominance status of individuals: juveniles, yearlings, subordinate individuals (from 2 to 5 years of age), dominant prime-aged individuals

(from 2 to 7 years of age) and dominant senescent individuals (from 8 to 16 years of age) (see Table 4.1). Upper limit of subordinate survival rates have been fixed to 5 years of age since no older subordinate has been ever found in our study population. Beyond this age, subordinates may either become dominant, or fail in acceding a territory and presumably die. The onset of actuarial senescence of dominant individuals was fixed based on a previous detailed study on age-specific survival in the Alpine marmot (Berger et al. 2016).

We tested the influence of cooperative breeding on juvenile survival by testing first an interactive effect between the presence of cooperative breeding and the presence of helpers on juvenile survival, by including helpers' presence as an individual covariate (Appendix 4.1). Then, to test for an influence of the presence of helpers on temporal variation of juvenile survival, we included either an additive or an interactive effect of time on survival of both categories of juveniles (Appendix 4.1). Model selection was performed using the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002).

To investigate whether the presence of helpers influenced the amount of temporal variation in juvenile survival, we performed a post-hoc calculation of the corresponding temporal variance. It is important to distinguish the process variance from the sampling variance when making inference based on temporal variation in population parameters (Link and Nichols 1994; Gaillard et al. 1998; Loison et al. 2002). To do this, temporal variance in a given survival was estimated by fitting a random effect of time on the focal annual survival estimates using multi-level linear mixed models from the metafor package in R (Viechtbauer 2010). Those models allow fitting similar or different random effects of time on an age-specific series of survival estimates (here juvenile survival) according to a fixed factor (here the presence or not of helpers), and therefore to test for a difference in the amount of temporal variance among groups. This difference was tested from a model comparison using AICc (Burnham and Anderson 2002). Temporal variance of the other survival rates were similarly estimated using post-hoc calculations, except for the senescent individuals because of both the scarcity of data and their very low contribution to the variation in population growth rate. We thus set the senescent stage survival rates constant over time and fixed their variance to 0 (as done in

similar analyses, see e.g. Gaillard et al. 2013).

Reproductive parameters

We fitted generalized linear mixed-effect models (GLMER) with a Poisson distribution to estimate the mean annual litter size from 225 litters produced by 74 females captured from 1990 to 2013. The mother identity was included as a random effect to account for repeated measurements of the same individuals, and the aspect of the territory as a fixed factor to test for a potential confounding effect of territory quality. Mean litter size was estimated in three age-classes, included in the model as a three-level fixed factor and including two year-old individuals, prime-aged individuals (i.e. from 3 to 9 years of age), and senescent individuals (i.e. from 10 years of age onwards). The onset of senescence in reproductive rates was fixed based on a previous study investigating the reproductive senescence in our Alpine marmot population (Berger et al. 2015b).

We assumed the reproductive parameters to be constant over time for both the two years old and the senescent dominant females because the low number of females in these age-classes (N = 4 and N = 28, respectively) did not allow generating reliable annual estimates of reproduction. On the other hand, we estimated mean annual reproductive parameters for the prime-aged females by including an interactive effect of time. Finally, the temporal variance of this stage-specific reproductive rate was estimated by fitting a random effect of time in the GLMER model.

4.2.4. Construction of demographic models

To investigate how the presence of helpers influenced the demography of the Alpine marmot population, we constructed a female-dominant post-breeding census and stage-structured population projection model (Caswell 2001), see the matrix in Appendix 4.2 and the life cycle graph on Fig. 4.1). According to the results of the CMR analysis, the juvenile stage has been split into two distinct categories: juveniles that hibernated with helpers vs. juveniles that hibernated without helpers.

The potential effect of the presence of helpers on the marmot demography was thus assessed by integrating these two juvenile stages and their associated survival rates in the population projection model (Fig. 4.1). We thus estimated a probability for juveniles to be in family groups with vs. without helpers during their first hibernation and included it in the model with the reproductive parameters (Fig. 4.1). This probability was estimated as the proportion of families observed with helpers in the population (parameter *H*, Table 4.1).

Variation in reproduction and survival rates were included in the projection model according to the different stages and age-classes that we considered (Table 4.1, Fig. 4.1). Lastly, age-specific probabilities of becoming dominant were introduced based on the selected capture-recapture model (see Appendix 4.1 for further details). The probability for subordinates to become dominant was lower between 1 and 2 years of age than from 2 years of age onwards.

Table 4.1. Abbreviations used when defining the life cycle and the population projection model notations for the Alpine marmots of La Grande Sassière (France).

Demographic parameters	
$s0_H$	Annual survival probability of juveniles (between 0 and 1 year of age) with helpers
$s0_{noH}$	Annual survival probability of juveniles (between 0 and 1 year of age) without helpers
s1	Annual survival probability of yearlings (from 1 to 2 years of age)
s2	Annual survival probability of subordinates (between 2 to 5 years of age)
s3	Annual survival probability of prime-aged dominants between (2 and 8 years of age)
s4	Annual survival probability of senescent dominants (between 8 and 16 years of age)
f1	Annual number of female offspring produced at birth by 2 years-old females
f2	Annual number of female offspring produced at birth by prime-aged females (between 3 and 10 years of age)
f3	Annual number of female offspring produced by senescent females (between 10 and 16 years of age)
H	Annual probability for juveniles to be in a family group with at least one helper
T1	Mean annual probability of transition between the subordinate and the dominant status for individuals between 1 and 2 years of age
T2	Mean annual probability of transition between the subordinate and the dominant status for individuals between 2 and 4 years of age

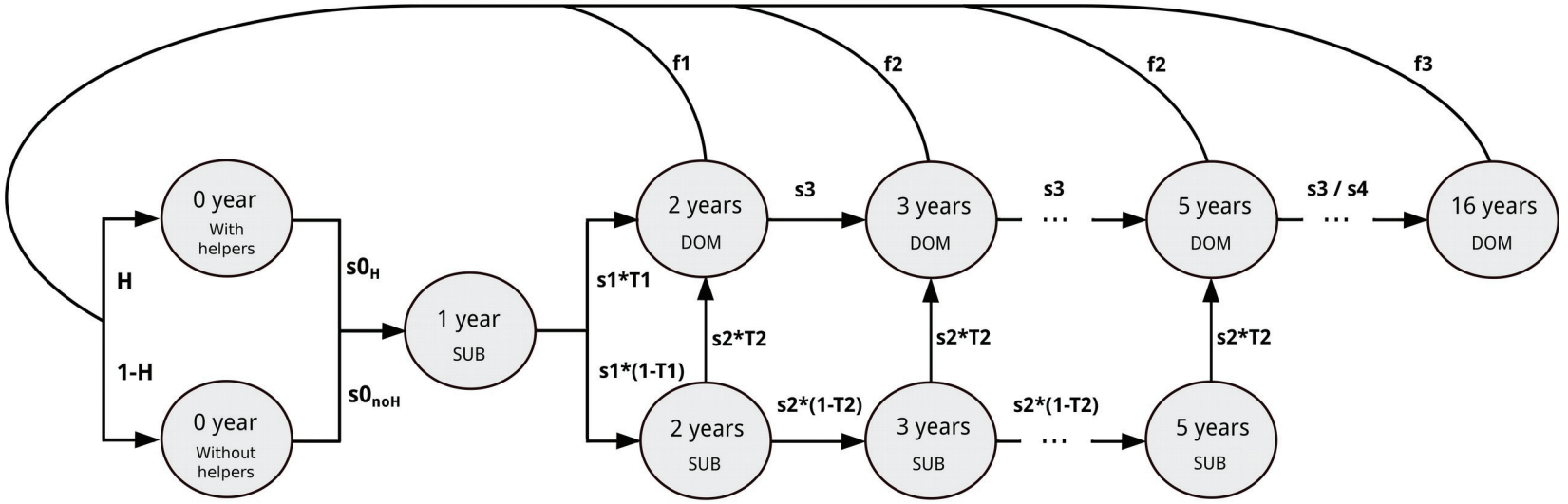

Figure 4.1. Life cycle graph of the Alpine marmot population used for modelling the population demography of La Grande Sassière (French Alps).

4.2.5. Demographic analysis

Two distinct demographic analyses were performed to test our two hypotheses regarding the influence of cooperative breeding on the population growth rate. First, to assess the overall effect of cooperative breeding on the stochastic population growth rate, we investigated at which extent the expected beneficial effects (in terms of both mean and variance in juvenile survival) of having helpers impact the mean and the variance of the population growth rate. Second, we assessed whether the presence of helpers contributed to the buffering of the stochastic population growth rate against climate change by investigating at which extent temporal changes in mean and variance of juvenile survival in family groups with and without helpers contributed to the observed temporal change in the population growth rate.

Effect of the presence of helpers on the Alpine marmot population growth rate

We estimated the stochastic population growth rate using both simulations (over 10,000 years) and the small noise approximation proposed by Tuljapurkar (1990). In this approximation, the stochastic population growth rate a could be written as a function of the intrinsic growth rate ($r = log\lambda 0$) minus the product of vital rates elasticities ($e$ij, $e$kl), coefficients of variation ($c$ij, $c$kl) and correlations (ρij,kl), between the elements ij and elements kl of the projection matrix, once assuming that serial temporal autocorrelations can be neglected (Tuljapurkar 1990; Horvitz et al. 1997, but see Tuljapurkar and Haridas 2006):

$$a^{(m)} = log\lambda_s^{(m)} \approx r^{(m)} - \frac{1}{2}\sum_{i,j}\sum_{k,l}\left\{e_{ij}e_{kl}c_{ij}c_{kl}\rho_{ij,kl}\right\}^{(m)}$$

The deterministic growth rate was estimated based on the mean annual matrix (Caswell 2001). We then performed a prospective analysis (sensu Caswell 2000) to assess the effect of a proportional change in the mean and the variance of juvenile survival with vs. without helpers on the stochastic population growth rate. We estimated the overall stochastic elasticity of juvenile survival (Ejuv^S), as well as its components, i.e. the elasticity with respect to the mean μjuv (Ejuv$^{S\mu}$) and the

elasticity with respect to the variance σjuv (Ejuv$^{S\sigma}$) of the juvenile survival, following Haridas and Tuljapurkar (2005).

We then examined the relative contribution of observed variation in survival rates to the annual variation in the population growth rate throughout the study period, using the approximation of variance proposed by Tuljapurkar (1990) and Horvitz et al. (1997), with a special focus on juvenile survival with vs. without helpers.

Effect of the presence of helpers on temporal demographic changes occurring in the Alpine marmot population

Lastly, to investigate whether the presence of helpers buffers the population growth rate against changing environmental conditions, we performed a stochastic life-table response experiment (SLTRE, Davison et al. 2013).

We divided our monitoring period into two time series of similar length, representative of different weather conditions, one from 1990 to 2000 and the other from 2001 to 2013 (see Gaillard et al. 2013 for a similar approach). Winter conditions were more favourable in the first period (i.e. mild and snowy) than during the second (i.e., colder temperatures, favouring frost but not snow; Appendix 4.3, Rézouki et al. 2016). This typology allowed us to capture the impact of climate change on the marmot demography by investigating the extent to which the stochastic population growth rate differed between the two periods and thus between the different environmental conditions. The stochastic LTRE analysis then allowed comparing among contributions of the mean, the variance, the correlation and the elasticity of the vital rates to the change of stochastic population growth rate between periods. We especially compared the contribution of differences in both the mean and the variance of juvenile survival, between juveniles with and without helpers, to the observed differences in population growth rate between periods. More details regarding the performed SLTRE analysis are provided in the Appendix 4.3.

4.3. Results

4.3.1. Effect of the presence of helpers on juvenile survival

As expected, model selection of CMR models revealed an influence of the presence of helpers on the overall mean juvenile survival (see Appendix 4.1), in line with previous studies (Allainé et al. 2000; Allainé and Theuriau 2004). Juvenile survival rates varied differently depending on whether they hibernated with or without helpers (i.e. the two-way interaction between year and the presence of helpers was retained in the selected model, Appendix 4.1). Juveniles hibernating with helpers survived better (0.66 ± 0.10) than did juveniles hibernating without helpers (0.49 ± 0.14). However, contrary to our expectation, the survival of juveniles that hibernated in the presence of helpers strongly decreased over time (β = -0.081 ± 0.037, Fig. 4.2), whereas the decrease in survival of juveniles without helpers was much weaker and not statistically significant (β = -0.029 ± 0.038, Fig.4.2). Thus, in most recent years juvenile survival was similar in groups with and without helpers (Fig. 4.2). Temporal variation in survival was slightly higher for juveniles without helpers (CV = 0.396, Fig. 4.3a) compared to juveniles with helpers (CV = 0.293, Fig. 4.3a). However, the overall year-to-year variation in juvenile survival was mainly due to the temporal trend observed in juveniles with helpers. When correcting for this trend, the coefficient of variation was much lower for juveniles with helpers than for juveniles without helpers ("de-trended" CV of 0.147 vs. 0.361, respectively). Relative to other demographic rates, juvenile survival was the most variable among years, with a coefficient of variation two times higher than that observed in other rates (all less than 0.15, Fig. 4.3a).

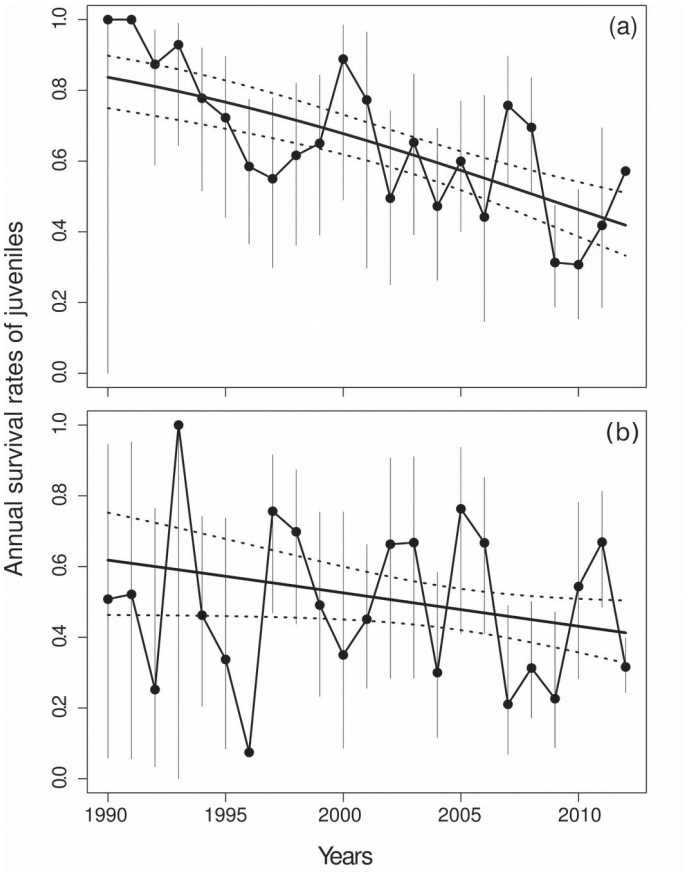

Figure 4.2. Annual estimates (± 95% CI, vertical grey segments) and the corresponding temporal trend (± 95% CI, dashed line) of juvenile survival from 1990 to 2013, for (a) juveniles that hibernated with at least one helper in their family group and (b) juveniles that hibernated without helpers, in the Alpine marmot population of La Grande Sassière (France).

4.3.2. Effect of the presence of helpers on the population growth rate

Elasticity analysis

The influence on the stochastic population growth rate of a proportional change in juvenile survival rates was stronger for juveniles with helpers than for juveniles without helpers ($E\text{juv}^{S}$ = 0.083 vs. $E\text{juv}^{S}$ = 0.051, respectively, Fig. 4.3b). For both categories of juveniles, the elasticity of the population growth rate was much higher for the mean ($E\text{juv}^{S\mu}$ = 0.085, with helpers; $E\text{juv}^{S\mu}$ = 0.052, without helpers) than for the variance ($E\text{juv}^{S\sigma}$ = -0.002, with helpers; $E\text{juv}^{S\sigma}$ = -0.0003, without helpers).

Elasticity with respect to either the mean or the variance of juvenile survival was stronger for juveniles with helpers, which should reflect the difference in survival mean and variance between these two categories of juveniles.

As expected, the prime-aged dominant stage survival had consistently the largest potential impact on the population growth rate, at least three times greater than the other parameters (Fig. 4.3b).

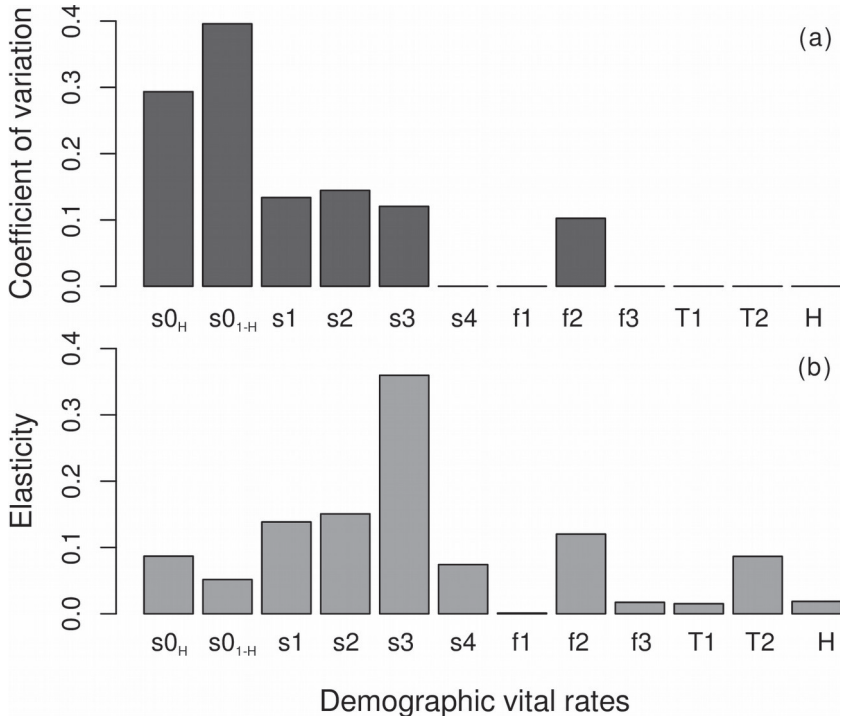

Figure 4.3. (a) Coefficient of variation measuring the temporal variation observed in each demographic parameter throughout the study period and (b) overall stochastic elasticity of the population growth rate to variation in each demographic parameter for the Alpine marmot population of La Grande Sassière (French Alps), monitored between 1990 and 2013.

Contribution of the mean and variance of juvenile survival to observed variation in the stochastic population growth rate

The deterministic population growth rate was of r = log(0.992) = -0.007. Stochastic variation slightly reduces this rate, which decreased it by about 0.003-0.004 ($a \approx$ log(0.989) $\approx$ -0.011 from the Tuljapurkar's small noise approximation and $a \approx$

log(0.988) ≈ -0.012, from simulations). Our Alpine marmot population is thus currently slowly decreasing.

We expected the presence of helpers to increase population growth rate through its beneficial influence on mean juvenile survival. This positive influence of cooperative breeding showed up when comparing models built by integrating only survival rates of juveniles with helpers (i.e., H = 1) or survival rates of juveniles without helpers (i.e., H = 0) in the population, leading to $a \approx \log(1.005) \approx 0.006$ and $a \approx \log(0.973) \approx -0.027$, respectively.

On the other hand and contrary to our expectation, the temporal variance in survival of juveniles with helpers contributed much more to the observed variation in population growth rate than did the variance in survival of the juveniles without helpers (relative contribution of 0.23 vs. 0.07, respectively, Fig. 4.4). However, this highest contribution was mainly due to the variation associated with the temporal trend, which accounted for almost 65% of the contribution of survival rates of juveniles with helpers. By contrast, temporal trend in survival rates of juveniles without helpers only accounted for about 15% of its contribution to the variance in the population growth rate (Fig. 4.4). Overall, the observed variation in the stochastic population growth rate was primarily due to temporal variation in the prime-aged dominant survival, which accounted for about 40% of the latter (Fig. 4.4).

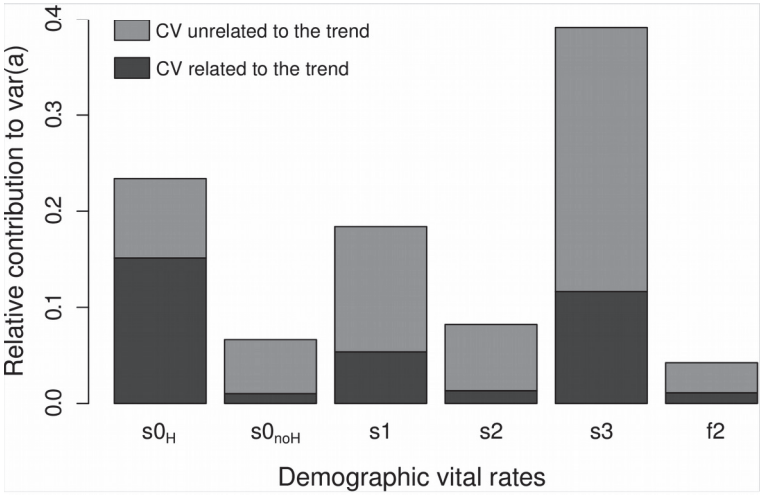

Figure 4.4. Relative contribution of demographic parameters (including the contribution of both variance and covariance) to the observed variation in the population growth rate of the Alpine marmot population in la Grande Sassière between 1990 and 2013.

4.3.3. Effect of the presence of helpers on the population demography within the climate change context

As expected based on the declining abundance of the marmot population, the stochastic population growth rate decreased from a = log(0.992) = -0.008 in the period between 1990 and 2000 to a = log(0.977) = -0.023 in the period between 2001 and 2013. As revealed by the stochastic LTRE analysis, this difference ($\Delta a \approx$ -0.015) was mostly due to differences in the mean vital rates (summed contribution of Δmean ≈ -0.0156, Fig. 4.5a). Differences in stochastic components of vital rates between the two periods was much less influential (summed contribution of ΔCV, Δcorrelation and Δelasticity ≈ -0.0003, Fig. 4.5b).

The marked decrease in the mean survival of juveniles with helpers ($s0_H$ = 0.78 ± 0.09 from 1990 to 2000 vs. s_{0H} = 0.54 ± 0.11 from 2001 to 2013) led this parameter to contribute the most to the observed decrease in the population growth rate over time (Δmean contribution of -0.035, Fig. 4.5a). On the contrary, the mean survival of juveniles without helpers remained quite constant over time ($s0_{noH}$ = 0.49

± 0.17 from 1990 to 2000 vs. $s0_{noH}$ = 0.48 ± 0.12 from 2001 to 2013) and had consequently only a negligible contribution to Δa (Δmean contribution of -0.001, Fig. 4.5a). Opposite changes in temporal variance of survival also occurred in the two juvenile categories. Whereas year-to-year variation in survival of juveniles with helpers increased between the two periods (CV = 0.185, from 1990 to 2001 vs. CV = 0.262 from 2001 to 2013) and slightly contributed to decrease the population growth rate (Fig. 4.5b), yearly variation in survival of juveniles without helpers tended to decrease between periods (CV = 0.455 from 1990 to 2001 vs. CV = 0.321 from 2001 to 2013), and had thereby opposite effect on the population growth rate (Fig. 4.5b). The influence of changes in the variance of vital rates on the stochastic population growth rate, however, was negligible.

Lastly, while between-period differences in mean juvenile and yearling survival generally contributed to decrease the population growth rate (Fig. 4.5a), a high increase in the probability of subordinates to become dominant from two years of age (T2 = 0.32 from 1990 to 2000 vs. T2 = 0.54 from 2001 to 2013) compensated those negative effects, which contributed to increase the population growth rate between the two periods (Δmean contribution of +0.047, Fig. 4.5a). This unexpected change accounts for the quite low demographic difference we found between the two periods, which we expected to be higher based on the, marked change in both survival and reproductive rates we previously identified (Tafani et al. 2013; Rézouki et al. 2016).

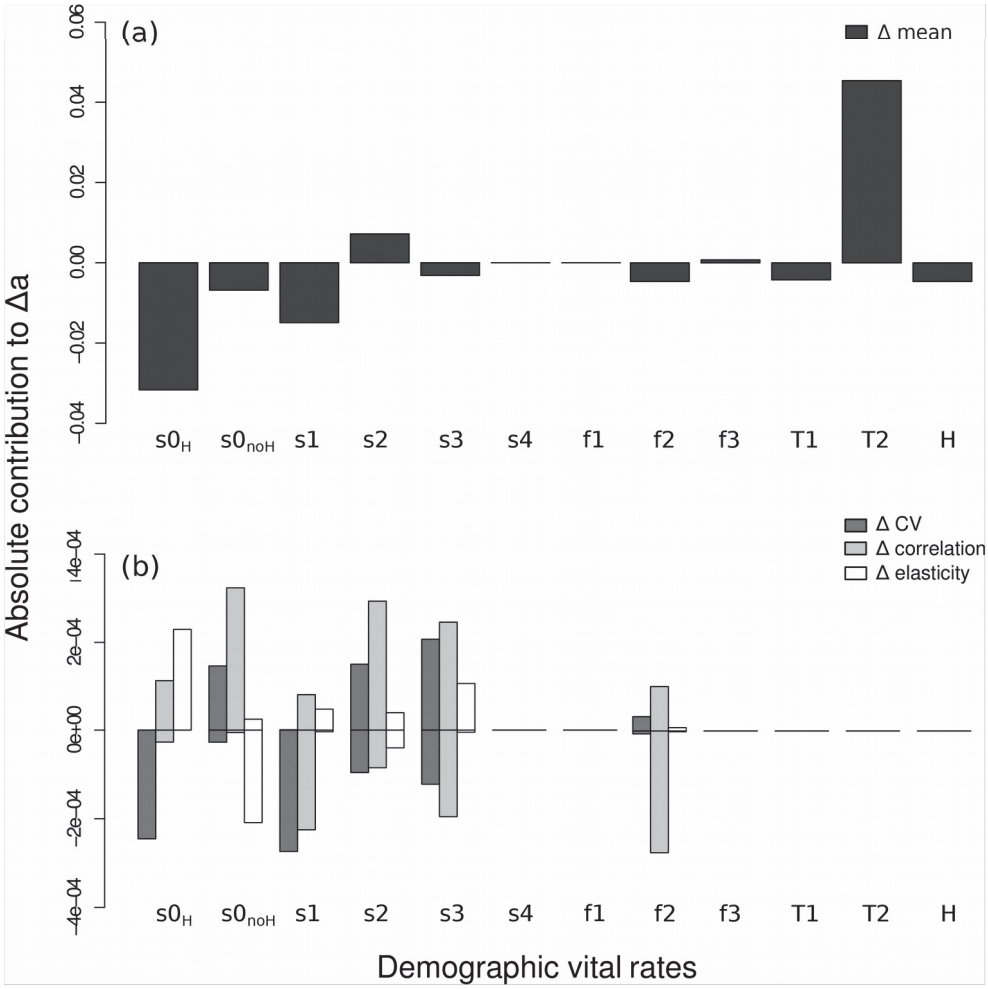

Figure 4.5. Decomposition of the difference in the stochastic population growth rate (Δa = -0.0155) between two consecutive time periods ($\Delta a = a^{P2} - a^{P1}$, with P_1 = 1990-2000 and P_2 = 2001-2013) in the Alpine marmot population of la Grande Sassière (France) using a stochastic LTRE analysis. (a) Contribution of the difference in mean vital rates (Δ *mean*), (b) contribution of the difference in the stochastic components of the vital rates, i.e., the difference in the coefficient of variation of vital rates (Δ *CV*), the difference in correlations between vital rates (Δ *correlation*) and the difference in elasticity of vital rates (Δ *elasticity*) between the two periods.

4.4. Discussion

The demographic analyses we performed revealed a strong adaptive value of cooperative breeding. However, the fitness benefits of the presence of helpers resulted mostly from increased mean juvenile survival. Fitness benefits of having helpers were mainly gained through responses to changes in the mean environmental conditions rather than through responses to the variance in environmental conditions in Alpine marmots. Furthermore, as mean environmental conditions changed in response to climate change in the Alps, the beneficial effects of cooperative behaviour were influenced by climate change. Contrary to our expectation, juvenile survival decreased much more over time in family groups with helpers than in groups without helpers, which explains the decrease we observed in the population growth rate throughout the study period. On the other hand, more subordinates apparently acceded to dominance in recent years, which impacted positively the population growth rate.

4.4.1. Adaptive value of cooperative breeding in Alpine marmots

Not only the presence of helpers during hibernation improves the mean juvenile survival in Alpine marmots, as reported in previous studies (Allainé et al. 2000; Allainé and Theuriau 2004), but it also reduces its year-to-year variation (Fig. 4.2, 4.3a). Temporal variation in juvenile survival has been previously associated with changes in the local weather, especially during winter (i.e., cold and dry vs. mild and snowy winters, Rézouki et al. 2016). Therefore, by warming juveniles during hibernation through heat production during periodic arousals (Arnold 1990b), helpers overall allow juveniles to resist the adverse winter conditions in mountains as well as to cope with yearly variation in winter harshness, which leads to buffer juvenile survival against weather fluctuations.

Overall, cooperative behaviour has a strong beneficial effect on the population growth rate of Alpine marmots and thereby on their individual fitness. The presence of helpers increased by up to 0.02 (i.e. almost 3%) the stochastic

population growth rate of the population we studied. However, such demographic benefits were only gained through increased mean juvenile survival. As expected (see e.g. Haridas and Tuljapurkar 2005; Tuljapurkar et al. 2009), changing the mean value definitely had a much higher potential impact on the population growth rate than changing in the same proportion the variance (i.e. an about fiftyfold difference for juvenile survival in our study). Additionally and contrary to our expectation, the variance in juvenile survival in groups with helpers contributed more than the variance in juvenile survival in groups without helpers to observed variation in the population growth rate (Fig. 4.4), although the latter was larger. Demographical analyses thus revealed an adaptive value of cooperative breeding through a response to the winter harshness rather than through a buffering effect on the response to variable environmental conditions, which is the opposite to what has been recently proposed in birds (Rubenstein and Lovette 2007; Rubenstein 2011).

4.4.2. Decreasing adaptive value with increasing climate change

Beneficial effects of cooperative breeding on individual fitness of Alpine marmot seem to vanish under the ongoing climate change. Contrary to our expectation, helpers do not buffer juvenile survival against current environmental conditions (Fig. 4.2). On the contrary, changes in both the mean and the variance of juvenile survival in the recent period negatively affected the population growth rate more strongly in family groups with helpers than in family without (Fig. 4.2). Both harsher winters and the lower proportion of groups with helpers (Rézouki et al. 2016) are likely to explain the observed decrease in overall juvenile survival. Climate change seems to have impacted juveniles in groups with helpers by decreasing both the number of helpers and their ability to help during hibernation. Indeed, the proportion of groups with helpers is an indicator of the total number of helpers present in the population and within family groups. A decrease in the number of helpers should be detrimental for the mean juvenile survival, especially if the social composition of groups is moving toward groups with only one helper, rather than groups with two helpers or more (Allainé and Theuriau 2004). In the meantime,

the increased frequency of colder winters with less snow, and thus a thinner insulation layers, might have increased energetic demands for marmots to sustain hibernation (Tafani et al. 2013; Rézouki et al. 2016) and thereby led social thermoregulation provided by helpers to be no longer beneficial for marmots in the most recent years (see Fig. 4.2).

The strong decrease in mean survival rates of juveniles with helpers mostly contributed to the observed decrease of the population growth rate over time (Fig. 4.5). However, the lower efficiency of cooperative breeding to dampen the negative effects of harsh environmental conditions in the period with marked climate change could have been more detrimental for population growth rate without the increased probability to become dominant that took place in the meantime. More than half of the negative effects of decreased survival and reproduction on the population growth rate were indeed compensated for by a higher access to dominance (Fig. 4.5). These parallel changes in demographic parameters provide the keys to understand the overall response of the Alpine marmot population to climate change and should not be considered as independent.

4.4.3. Towards a new selection pressure on cooperative breeding behaviour

The evolution of delayed dispersal and helping behaviour in Alpine marmots has been so far mainly related to environmental harshness. Short growing seasons constrain young individuals to stay within the natal family group for one or more years to acquire a body condition high enough to cope with the high mortality risks of both natal dispersal and reaching a dominance status (Barash 1974; Arnold 1990a; Blumstein and Armitage 1999). Moreover, harsh winters select for hibernation and social thermoregulation. However, both Arnold (1993b) and Armitage (1999) proposed that ecological constraints influence marmot dispersal. The saturation of most favourable habitats in marmot populations could represent such a constraint. Subordinates can access dominance and reproduction by inheriting or dislodging a parent from the natal territory, by expelling a dominant individual from its territory,

or by occupying a vacant dominant position or territory (Arnold 1990a, 1993a). Habitat saturation thus directly limits the ability to access a territory and the possibility for independent reproduction, and should also select for remaining in the natal family. For these different reasons, the benefits of staying and help should exceed the benefits of dispersal in Alpine marmots, especially since helpers are generally related to the other members of the group, which promote cooperative breeding. Climate change may have impacted the strength of these selection pressures favouring cooperative breeding in Alpine marmots, both directly and indirectly. Harsh winters both increase the cost and decrease the benefits of subordinate males to stay in natal families and help juveniles during hibernation. By increasing their energetic cost of social thermoregulation, harsh winters should lead to increase mass loss of subordinate males in presence of siblings (Arnold 1990a). Similarly, harsh winters constrain the effectiveness of helping, leading helpers to benefit less in terms of increased inclusive fitness. In addition, climate change is likely to have indirect effect through decreased dispersal costs associated with habitat saturation, which increase the fitness cost of staying. Lower survival and reproductive rates we reported in the studied population of marmots (Tafani et al. 2013; Rézouki et al. 2016) should have led to smaller family group size (Fig. 4.6), and thereby to an increased probability of subordinates to settle in a new territory and/or to expel weak dominants. Climate change should then alter dispersal decision of subordinate Alpine marmots by improving the benefits of early dispersal through a faster access to reproduction. This situation generates the increased probability of becoming dominant we reported in the most recent years.

4.4.4. Conclusion

Climate change is impacting cooperative breeding in Alpine marmots. It could have indirectly changed the selection pressure that promotes delayed dispersal in this species by decreasing the benefits of juveniles to help. Accordingly, the population is currently decreasing and the selection for cooperative breeding is less, which could induce more conflict of interest between subordinates and the dominant male.

Our findings support the view that cooperative breeding behaviour is not a fixed trait in cooperative species (Hatchwell and Komdeur 2000). Finally, our results provide clear empirical evidence of a combined influence of ecological and life-history constraints in the evolution of cooperative breeding. Cooperative breeding behaviour in Alpine marmots has likely resulted from both environmental constraints and habitat saturation, which might be the consequence of a slowing down of the life cycle. Interestingly, while habitat saturation is generally associated with a slow pace of life involving a low population turn-over (Arnold and Owens 1998; Covas and Griesser 2007), the slow pace of life of the Alpine marmot population should rather be linked to the beneficial effect of hibernation, which allows for high survival of breeding individuals under harsh environmental conditions (Turbill et al. 2011). Hence, species' lifestyle should thus also be considered when studying the evolution of cooperative breeding. Lastly, it seems required to investigate the fitness benefits of cooperative breeding at different levels of the biological organization, from individuals (i.e. finess) to population (i.e. growth rate) to better understand both the evolution of social behaviour and the overall response of cooperative breeding species to climate change.

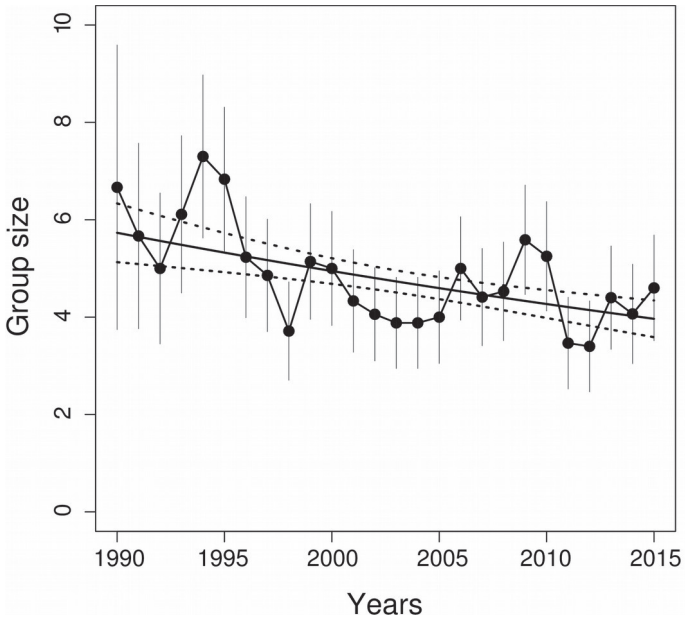

Figure 4.6. Annual estimates (± 95% CI, vertical grey segments) and the corresponding time trend (± 95% CI, dashed line) of mean group size in the Alpine marmot population of La Grande Sassière (France).

Appendix

Appendix 4.1. Details on statistical analyses of survival rate estimation

Appendix 4.2 Leslie matrix of the Alpine marmot

Appendix 4.3 Details on the Stochastic Life Table Response Experiment analysis

Appendix 4.1. Details on statistical analyses of survival rate estimation

Estimation of annual survival rates of the Alpine marmot was done using multi-state capture recapture models (MS-CR, Lebreton et al. 2009) in the same way as performed in Rézouki et al. (2016).

The influence of the presence of helpers on juvenile survival was tested by directly including a categorical individual variable "helpers" (i.e. presence or absence of helpers) in the models (same way as in Rézouki et al. 2016, see Table S4.1. for model selection).

The effect of different factors has been tested on the capture, survival, and state transition probabilities (see Table S4.1). Different age-classes were considered for each of these probabilities. Age-classes for capture probabilities included juveniles (from 0 to 1 year of age), yearlings (from 1 to 2 years of age), two years-old individuals, and adults (from 3 years of age). Age-classes for the probability of subordinates to become dominant included yearlings (from 1 to 2 years of age) and adults (from 2 to 5 years of age). At last, the age-classes were confounded with the individual social status for survival probabilities (i.e. *status*ageclass* in Table S4.1b), and then referred to juveniles (from 0 to 1 year of age), yearlings (from 1 to 2 years of age), subordinate adults (from 2 to 5 years of age), prime-aged dominants (from 2 to 8 years of age) and senescent dominants (from 8 to 16 years of age). The influence of the presence of helpers was then investigated by integrating an interactive effect of the presence of helpers on juvenile survival (i.e., *juv*helpers,* which can be rewritten as *juv_with+juv_without)*. As can be observed in Table S4.1b, this interactive effect was selected, so that juvenile survival differed according to the presence of helpers. The most parsimonious model included an effect of time on survival. We also investigated whether juveniles with vs. without helpers varied differently over years by testing for an interaction between time and the presence/absence of helpers on juvenile survival, which was selected (Table S4.1b). Survival rates of juvenile with and without helpers thus varied differently over years.

Table S4.1. Modeling capture (*p*), survival (*Φ)* and state transition probabilities (*Ψ)* for the Alpine marmots of La Grande Sassière, France using CMR methods. The four best explanatory models based on AICc are displayed for the (a) capture and (c) state transition probabilities, while a larger portion of the tested models are displayed for the survival probabilities (b). The subscripts *status, age-class, sex, time* and *helpers* stand for an effect of the social status (subordinate or dominant), the age-class (categorical variable), the sex, the year effect (categorical variable) and the presence of helpers, respectively. The subscript * indicates interactive effects. K= number of parameters; AICc= Akaike Information Criterion corrected for small sample size; wi= weight of the AICc.

Models	**K**	**Deviance**	**AIC_c**	**wi**
a) Capture model				
p ~ ageclass + sex + time	55	2718.24	4734.29	0.43
p ~ ageclass + time	54	2721.05	4735.00	0.30
p ~ status * ageclass + sex + time	56	2717.43	4735.58	0.13
p ~ status + ageclass + sex + time	56	2718.03	4736.19	0.10
...	...	...	...	...
b) Survival model				
Φ ~ status * ageclass + time + *juv * helpers * time*	96	2610.19	4714.03	0.94
Φ ~ status * ageclass + time + *juv * helpers*	56	2702.65	4720.80	0.03
Φ ~ status * ageclass + time + sex+ j*uv * helpers*	57	2701.66	4721.92	0.02
Φ ~ status * ageclass + *juv * helpers*	34	2753.54	4725.87	<0.01
...	...	...	...	...
Φ ~ status * ageclass + time	54	2717.68	4731.63	<0.01
Φ ~ status * ageclass + time + sex	55	2716.60	4732.65	<0.01
Φ ~ status * ageclass	32	2772.97	4741.19	<0.01
Φ ~ status * ageclass +sex	33	2771.91	4742.19	<0.01
...	...	...	...	...
c) State transition model				
Ψ ~ ageclass * sex	55	2718.70	4734.75	0.37
Ψ ~ ageclass + sex	54	2721.05	4735.00	0.33
Ψ ~ ageclass	53	2723.36	4735.22	0.29
Ψ ~ ageclass * sex + time	77	2684.24	4746.99	<0.01
...	...	...	...	...

Appendix 4.2. Leslie matrix of the Alpine marmot

Table S4.2. Leslie matrix used to compute the deterministic growth rate of the Alpine marmot population of La Grande Sassière.

t+1 / t	JUV_with	JUV_without	YEAR	SUB2	SUB3	SUB4	SUB5	DOM2	DOM3	DOM4	DOM5	DOM6	DOM7	DOM8	DOM9	DOM10	DOM11	DOM12	DOM13	DOM14	DOM15	DOM16
JUV_with	0	0	f1*H*s1*T1	f2*H*s2*T2	f2*H*s2*T2	f2*H*s2*T2	0	s3*f2*H	s3*f2*H	s3*f2*H	s3*f2*H	s3*f2*H	s3*f2*H	s4*f2*H	s4*f3*H	s4*f3*H	s4*f3*H	s4*f3*H	s4*f3*H	s4*f3*H	s4*f3*H	0
JUV_without	0	0	f1*(1-H)*s1*T1	f2*(1-H)*s2*T2*	f2*(1-H)*s2*T2	f2*(1-H)*s2*T2	0	s3*f2*(1-H)	s3*f2*(1-H)	s3*f2*(1-H)	s3*f2*(1-H)	s3*f2*(1-H)	s3*f2*(1-H)	s4*f2*(1-H)	s4*f3*(1-H)	s4*f3*(1-H)	s4*f3*(1-H)	s4*f3*(1-H)	s4*f3*(1-H)	s4*f3*(1-H)	s4*f3*(1-H)	0
YEAR	s0H	s0noH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB2	0	0	s1(1-T1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB3	0	0	0	s2(1-T2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB4	0	0	0	0	s2(1-T2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB5	0	0	0	0	0	s2(1-T2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM2	0	0	s1(T1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM3	0	0	0	s2(T2)	0	0	0	s3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM4	0	0	0	0	s2(T2)	0	0	0	s3	0	0	0	0	0	0	0	0	0	0	0	0	0
DOM5	0	0	0	0	0	s2(T2)	0	0	0	s3	0	0	0	0	0	0	0	0	0	0	0	0
DOM6	0	0	0	0	0	0	0	0	0	0	s3	0	0	0	0	0	0	0	0	0	0	0
DOM7	0	0	0	0	0	0	0	0	0	0	0	s3	0	0	0	0	0	0	0	0	0	0
DOM8	0	0	0	0	0	0	0	0	0	0	0	0	s3	0	0	0	0	0	0	0	0	0
DOM9	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0	0	0	0	0	0	0
DOM10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0	0	0	0	0	0
DOM11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0	0	0	0	0
DOM12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0	0	0	0
DOM13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0	0	0
DOM14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0	0
DOM15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0	0
DOM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	s4	0

Appendix 4.3. Details on the Stochastic Life Table Response Experiment analysis

We used a Stochastic Life Table Response Experiment (*sensu* Davison et al. 2010; Jacquemyn et al. 2012; Davison et al. 2013) to assess the influence of temporal change in vital rates that were induced by climate change on the population growth rate (see in Gaillard et al. 2013 for a previous application of a deterministic LTRE in a similar context). We expected that a regime shift of demography might have occurred in our population because of the negative impact climate change should had on juvenile survival and reproduction. We especially aimed at comparing the relative contribution to this shift of changes in the survival of juveniles hibernating with and without helpers.

Temporal changes in weather conditions

Overall, climate change mainly translated into trends in weather conditions at our study site of La Grande Sassière, with larger changes in the mean than in the year-to-year variability of the weather variables. This is well illustrated by changes that occurred in the winter conditions (e.g. Fig. S4.3.1), which have especially impacted the Alpine marmot population dynamics over years (Tafani et al. 2013; Rézouki et al. 2016).

Dividing the monitoring period in two time periods of similar length (P1=1990-2000 and P2=2001-2013) allowed us to capture temporal changes in environmental conditions and to measure their impact on vital rates. Winters are becoming harsher with time, as can be observed through the comparison of the two time periods (Fig. S4.3.1). For instance, mean monthly air temperatures in winter decreased by around 0.8°C between the two periods, while the winter snow cover was 15 cm thinner during the second period (i.e., a decrease by almost 15-20% for both winter variables, Fig. S4.3.1). Overall, a slight increase in the between-year variability of these winter variables occurred between the two periods (with an increased change in the CV from 2 to 8%, Fig. S4.3.1).

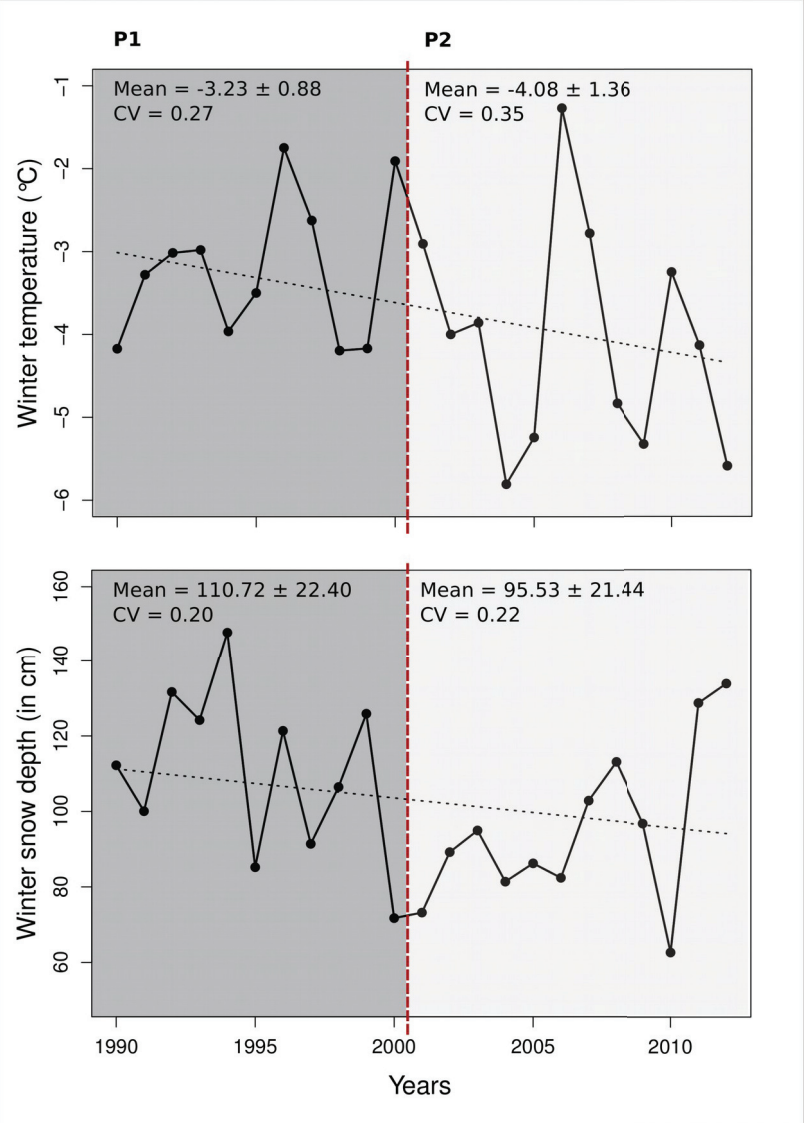

Figure S4.3.1. Yearly changes in the winter temperature (in °C, mean monthly values from December to March) and in the winter snow cover (in centimeters, mean monthly values from December to March) at the study site of La Grande Sassière Nature Reserve. The truncation in two time periods (i.e., P1=1990-2000 and P2=2001-2013) used to perform the Stochastic LTRE is shown with the red dashed vertical line. Mean and coefficient of variation are presented for each period and weather variables, illustrating the different environmental conditions the marmots faced during each time period.

Temporal changes in vital rates

Splitting the monitoring period into two periods then allows for the calculation of a stochastic population growth rate with respect to the different environmental conditions marmots faced during these periods, through the construction of two different population projection matrices. Vital rates and their associated variance were calculated again for the two periods following the same procedure as described in the main text.

In a same way as for the weather variables, we investigated changes in the mean and in the between-year variation of each vital rate across the two time periods (Fig. S4.3.2). Focusing on juvenile survival, a negative temporal trend in survival occurred in juveniles with, while the survival of juveniles without helpers changed only a little. In addition, the temporal variation increased between the two periods for juveniles with helpers (CV from 0.19 to 0.26), whereas it decreased for juveniles without helpers (CV from 0.45 to 0.32, Fig. S4.3.2). Increased temporal variance in the survival rate of juveniles with helpers could be regarded as being in line with the negative trends we reported in this vital rate. As discussed in the main text, the beneficial effect on juvenile survival of having helpers may have decreased over years, especially as a lesser number of helpers was observed within family groups during the last years. Furthermore, this temporal variance should also be partly induced by the negative trend observed in mean juvenile survival in itself. The apparent decrease in the variance of survival rates of juveniles without helpers was unexpected, but it could be mostly driven by extreme values in survival rates occurring within the first time period (in 1993 and 1996), which tended to increase temporal variation in survival of juveniles without helpers in this period. Overall, we can at last see that changes in elasticity values tended to follow these observed changes in both mean and variance of vital rates.

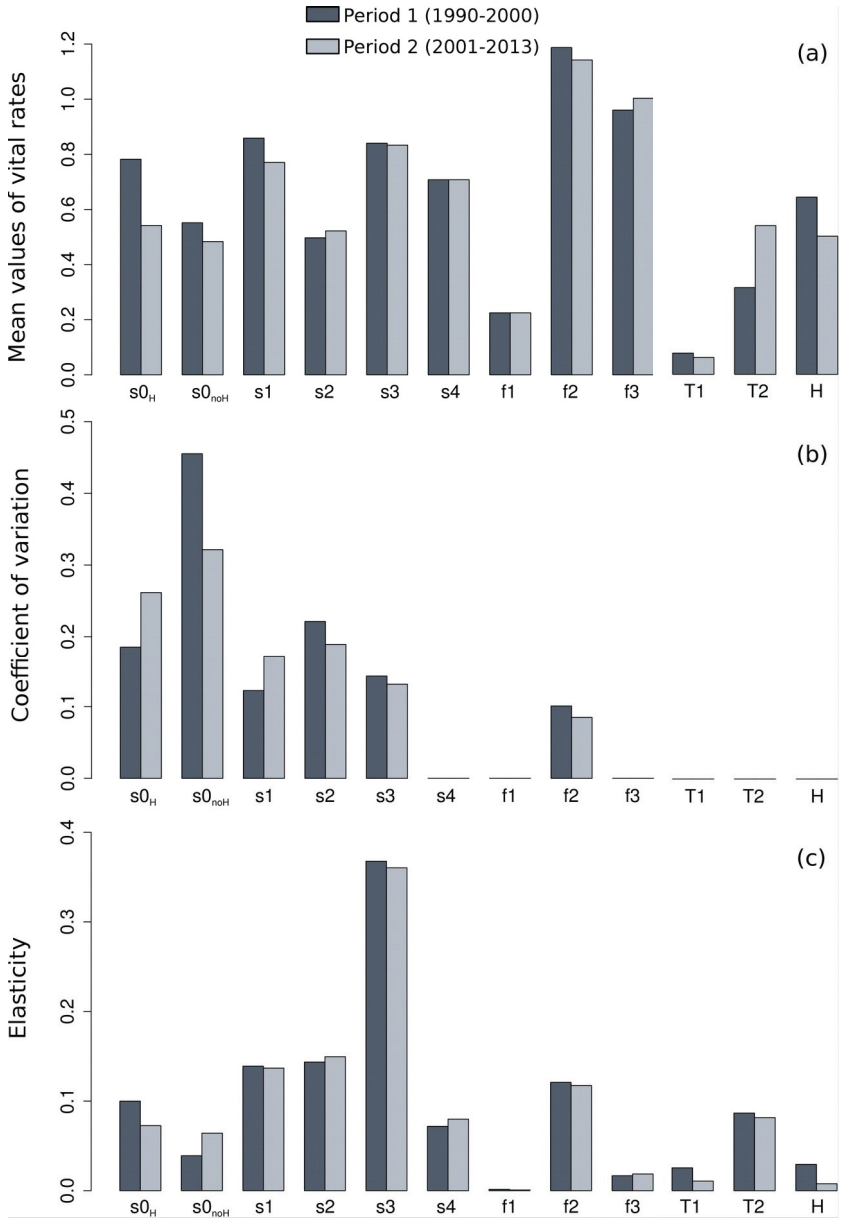

Figure S4.3.2. Differences in (a) mean value, (b) temporal variation (coefficient of variation), and (c) stochastic elasticity of each vital rate between the two periods P1 (1990-2000) and P2 (2001-2013).

SLTRE computation

The stochastic LTRE analysis aims to assess how changes in vital rates contributed to the observed difference in the stochastic population growth rate between the two periods. Following Davison et al. (2013)'s formula, the difference in the stochastic population growth rates (Δa) between the two periods *P1* (1990-200) and *P2* (2001-2013) could be approximated by the summation of four components:

$$\Delta a = a^{(P2)} - a^{(P1)}$$

$$\approx \left(\sum_k \left(\frac{\Delta \mu_k^{(P2)}}{\mu_k^{(P1)}}\right) e_k^{(P1)}\right) \quad \text{(a)}$$

$$-\frac{1}{2}\left(\sum_{k,l} \left(\overline{c_k c_l \rho_{kl}}\, \Delta\{e_k e_l\}\right)\right) \quad \text{(b)}$$

$$+\sum_{k,l} \overline{e_k e_l}\, \overline{\rho_{kl}}\, \Delta\{c_k c_l\} \quad \text{(c)}$$

$$+\sum_{k,l} \overline{e_k e_l}\, \overline{c_k c_l}\, \Delta\{\rho_{kl}\} \quad \text{(d)}$$

where the component (a) corresponds to the contribution of differences in the mean (Δmean); the component (b) is the contribution of differences in elasticity (Δelasiticity); the component (c) is the contribution of differences in coefficients of variation (ΔCV) and (d) the contributions of differences in correlations between vital rates (Δcorrelation).

Contributions of the differences in elasticity, in coefficient of variation and in correlation were computed for each vital rate and each pair of vital rates. Results on these detailed contributions are given below (in Tables S4.3.1, S4.3.2, S4.3.3, S4.3.4) for each component of the changes, for each vital rate and between each pair of vital rates. For more readability, these contributions have been synthesized for each vital rate in the main document on Figure 4.5, by separating the sum of positive vs. negative contributions to Δa.

Table S4.3.1. Contribution of the changes in mean vital rate values (*Δmean)* to the difference in the stochastic growth rate *(Δa)* between the two periods.

s0_H	-3.17E-02
s0_noH	-6.82E-03
s1	-1.49E-02
s2	7.21E-03
s3	-3.16E-03
s4	0.00E+00
f1	0.00E+00
f2	-4.62E-03
f3	7.72E-04
T1	-4.23E-03
T2	4.54E-02
H	-4.64E-03

Table S4.3.2. Contribution of the changes in mean elasticity values *(Δelasiticity)* to the difference in the stochastic growth rate *(Δa)* between the two periods. Contributions are shown for the elasticities ($e_k e_l$) of each vital rate (x_k) and each vital rate pair (x_k, x_l).

k / l	s0_H	s0_noH	s1	s2	s3	s4	f1	f2	f3	T1	T2	H
s0_H	-2.43E-04	-1.20E-05	-6.76E-05	-3.47E-05	-9.33E-05	0.00E+00	0.00E+00	-8.00E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s0_noH	-1.20E-05	4.04E-04	1.38E-06	-3.74E-05	9.41E-06	0.00E+00	0.00E+00	2.58E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s1	-6.76E-05	1.38E-06	-1.37E-05	5.94E-06	-1.34E-05	0.00E+00	0.00E+00	2.52E-08	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s2	-3.47E-05	-3.74E-05	5.94E-06	7.36E-05	-6.36E-06	0.00E+00	0.00E+00	5.04E-07	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s3	-9.33E-05	9.41E-06	-1.34E-05	-6.36E-06	-1.01E-04	0.00E+00	0.00E+00	2.65E-07	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s4	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f1	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f2	-8.00E-06	2.58E-06	2.52E-08	5.04E-07	2.65E-07	0.00E+00	0.00E+00	-7.23E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f3	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
T1	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
T2	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
H	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00

Table S4.3.3. Contribution of the changes in the coefficients of variation (*ΔCV)* to the difference in the stochastic growth rate *(Δa)* between the two periods. Contributions are shown for the coefficients of variation ($c_k c_l$) of each vital rate (x_k) and each vital rate pair (x_k,x_l).

k / l	s0_H	s0_noH	s1	s2	s3	s4	f1	f2	f3	T1	T2	H
s0_H	2.60E-04	2.66E-07	1.29E-04	2.49E-05	7.25E-05	0.00E+00	0.00E+00	4.02E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s0_noH	2.66E-07	-2.93E-04	-1.49E-08	4.30E-05	2.02E-06	0.00E+00	0.00E+00	9.33E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s1	1.29E-04	-1.49E-08	2.80E-04	4.59E-05	9.20E-05	0.00E+00	0.00E+00	-1.51E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s2	2.49E-05	4.30E-05	4.59E-05	-2.82E-04	7.79E-05	0.00E+00	0.00E+00	-1.93E-05	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s3	7.25E-05	2.02E-06	9.20E-05	7.79E-05	-4.13E-04	0.00E+00	0.00E+00	-1.60E-06	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s4	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f1	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f2	4.02E-06	9.33E-06	-1.51E-06	-1.93E-05	-1.60E-06	0.00E+00	0.00E+00	-4.25E-05	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f3	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
T1	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
T2	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
H	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00

Table S4.3.4. Contribution of the changes in correlation between vital rates (*Δcorrelation)* to the difference in the stochastic growth rate *(Δa)* between the two periods. Contributions are shown for the correlation coefficients (ρ_{kl}) between each vital rate pair (x_k,x_l).

k / l	s0_H	s0_noH	s1	s2	s3	s4	f1	f2	f3	T1	T2	H
s0_H	0.00E+00	1.12E-05	4.30E-05	-1.72E-04	-4.03E-05	0.00E+00	0.00E+00	-1.41E-05	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s0_noH	1.12E-05	0.00E+00	-9.61E-05	-1.30E-04	-2.34E-04	0.00E+00	0.00E+00	-1.87E-04	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s1	4.30E-05	-9.61E-05	0.00E+00	-6.73E-05	2.08E-04	0.00E+00	0.00E+00	1.99E-04	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s2	-1.72E-04	-1.30E-04	-6.73E-05	0.00E+00	-2.17E-04	0.00E+00	0.00E+00	1.70E-04	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s3	-4.03E-05	-2.34E-04	2.08E-04	-2.17E-04	0.00E+00	0.00E+00	0.00E+00	1.82E-04	0.00E+00	0.00E+00	0.00E+00	0.00E+00
s4	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f1	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f2	-1.41E-05	-1.87E-04	1.99E-04	1.70E-04	1.82E-04	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
f3	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
T1	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
T2	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
H	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00

Chapter 5

Contrasted demography and life history buffering of two long-lived Alpine mammals facing variable environments

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Preliminary results

Abstract

Identify factors which influence the sensitivity or resistance of species to environmental variation and/or perturbation has become an increasingly important challenge in recent years due to climate change. Species generation time represents one of the main factors shown to explain between-species differences in their response to environmental variation. However, whether other species-specific characteristics might also shape their demography in variable environment might be asked. Here, thanks to two long-term monitoring studies, we examined the influence of the lifestyles and reproductive tactics on the demography of two sympatric alpine species subjected to similar environmental variation, the Alpine marmot (*Marmota marmota)* and the Alpine chamois (*Rupicapra rupicapra*). We found that these differences in lifestyle and reproductive tactic impacted population's response to environmental variation at different levels. First, they impacted the buffering pattern of vital rates against environmental variation differently between these species, which was not theoretically expected given their close generation time. Specifically, sociality and underground hibernation allowed to strongly decrease the temporal variance in recruitment in Alpine marmots, contrary to Alpine chamois which present highly variable recruitment rates due to their conservative reproductive tactic. Second, lifestyle and reproductive tactic differences strongly influenced the underlying mechanisms of population demography in variable environments, by especially engendering different covariations between vital rates for these two species. And third, differences in lifestyle also appeared to explain differences in their demographic response to climate change. These findings overall demonstrate that considering the species lifestyle and reproductive tactic could be promising research perspectives to better understand and predict species response to environmental change.

Key-words: Buffering, reproductive tactic, lifestyle, sociality, population growth rate, Alpine marmot, Alpine chamois, climate change

5.1. Introduction

Environmental variations have now been recognized as an important factor shaping population dynamics and evolution of life history traits even over short time scales, from years to decades. In the same time, stochastic environmental variation is expected to increase in future years because of climate change (Giorgi et al. 2004; Rowell 2005). Consequently, increasing concerns about the impact of these fluctuations on population demography has raised in recent years. Specifically, there is now an urgent need to identify factors with the potential to influence the susceptibility of populations to future environmental variation and disturbance.

The position of a given species along the slow-fast continuum of life histories (Gaillard et al. 1989, 2005) appears as a potential predictor of responses to environmental variation and perturbation. This continuum is a major axis of variation in life history tactics of vertebrates (Gaillard et al. 2016), opposing species with low reproductive rates and long life expectancies to species with early onset of reproduction, high fecundity and short lifespan. Generation time was shown to be a reliable proxy of the position of a species on this slow-fast continuum (Gaillard et al. 2005). The generation time is known for driving sensitivity patterns of the population growth rate to demographic parameters (Hamilton 1966; Lebreton and Clobert 1991). Longer generation times are associated with higher sensitivities of population growth rates to a given relative changes in adult survival rates than to the same change in fecundity, while the reverse is true for species with short generation times (Lebreton and Clobert 1991). It was also evidenced that the demographic parameters with the greatest potential to affect population growth rate generally display the smallest temporal variations (Pfister 1998; Saether and Bakke 2000). Hence, generation time, and thus the species position on the slow-fast continuum, could help predicting how demographic parameters will be impacted by future environmental variations. In long-lived species, adult survival should be selected to be higher and less variable than other vital rates, while on the contrary, the fecundity should be generally lower and more variable. A reverse pattern in the variation of demographic parameters is expected for short-lived species. These differential responses of demographic parameters to environmental variation, according to the

life history strategy, have been reported from empirical analyses of both mammals (Gaillard et al. 2000b; Gaillard and Yoccoz 2003) and birds (Saether and Bakke 2000), reflecting a general pattern of environmental canalization of life histories along the slow-fast continuum.

Recently, the position of species along the slow-fast continuum has been also shown to influence overall resistance of populations to increasing environmental variability and disturbance (Morris et al. 2008; Sæther et al. 2013; Gamelon et al. 2014, 2016). Demographic properties of long- and slow-lived species make their populations dynamics more resistant to environmental stochasticity than populations of short- and fast-lived species. For instance, a long lifespan is generally related to low elasticities of the stochastic population growth rate to temporal variation in both reproduction and survival (Morris et al. 2008). Furthermore, in short-lived species, the effect of a disturbance in survival at young ages is amplified by further indirect effects of resulting changes in the age-structure, while such indirect effects are more dampened in long-lived species (Gamelon et al. 2016). This partially explains the larger fluctuations in population size reported in short-lived compared to long-lived species (see e.g. Sinclair 1996 in mammals), and illustrates another property of generation time. Lastly, populations with low growth rates generally exhibit smaller short-term variations in size after a disturbance compared to populations with high growth rates (Gamelon et al. 2014). Hence, since long-lived species typically display lower population growth rates than short-lived species, their resistance to disturbance should also arise from their demographic regimes (Gamelon et al. 2014). However, although a long generation time allows a higher resistance to environmental variation, the resilience after a disturbance is less for long-lived species compared to short-lived species (Lebreton 2006; Lebreton et al. 2012; Gamelon et al. 2014).

The structuring role of the generation time provides an interesting theoretical foundation to predict the future of current populations under environmental change, drawing a general pattern of population response to environmental variation at a large inter-specific scale. But it may not be sufficient. For instance, populations of different species sharing a similar position on the slow-fast continuum have been shown to display different demographic responses to

environmental change, both in magnitude and direction. Such differences in the demographic responses have been observed between the sympatric Emperor Penguin (*Aptenodytes forsteri*) and the Snow Petrel (*Pagodroma nivea*) (Jenouvrier et al. 2005), or between the Antarctic fur seal (*Arctocephalus gazella*) and the Weddell seal (*Leptonychotes weddellii*) (Forcada et al. 2008). This suggests other traits might structure between-species differences in demographic responses to environmental variation and calls the need for further investigations. In these two last examples, the differences in responses to environmental variation seem to originate from differences in the reproductive tactics between the species. Species with a flexible reproductive tactic, by skipping reproduction during unfavourable years, avoid a high cost of reproduction, thus appearing overall more resistant to the environmental changes they undergo (Jenouvrier et al. 2005; Forcada et al. 2008). Such reproductive tactic seems therefore to be one asset to deal with an increasingly variable environment.

Other species-specific characteristics might also be considered to understand between-species differences in their response to environmental variation, such as the species lifestyle (see Gaillard et al. 2016 for a definition). The lifestyle is known to influence life history traits and the species position on the slow-fast continuum (Gaillard et al. 2016). Some, as the flight capability or the fossoriality for instance, have been shown to reduce mortality from predation or bad weather conditions, thus allowing individuals to reach longer lifespan (Shattuck and Williams 2010; Healy et al. 2014). As a result, species with very different ecologies and demographic strategies can in fact occupy a similar position on the slow-fast continuum. Thus, mechanisms behind life history buffering fairly differ between species, as should also the mechanisms behind the demographic response of populations to environmental variation. However, the way these additional factors structure between-species differences in demography in variable environments has been poorly investigated so far.

Here, we try to fill this gap by investigating the demographic responses of two sympatric but ecologically different species, the Alpine marmot (*Marmota marmota*) and the Alpine chamois (*Rupicapra rupicapra*). We especially aimed at understanding how their differences in reproductive tactics and lifestyles influence

their respective demographic responses and resistance to environmental variability. The Alpine chamois is a long-lived ungulate that displays a fairly conservative reproductive tactic (Morin et al. 2016), and may seasonally migrate or change its space use to cope with the winter harshness (Lovari et al. 2006; Nesti et al. 2010). On the other hand, the Alpine marmot is a cooperative breeder living in family groups (Allainé et al. 2000; Allainé and Theuriau 2004), hibernating during half of the year within burrows (Arnold 1990a). As a result, even if these two different species display similar pace of life, we expect differences in their demographic responses to environmental variability, because of their demographic strategy and lifestyle. To test this hypothesis, we used long-term datasets obtained on the population of Alpine marmots of La Grande Sassière and on the population of Alpine chamois of Les Bauges, both located in French Alps.

Because of their lifestyle and reproductive tactic differences, we expected **(i)** vital rates of Alpine marmots, such as adult and juvenile survival or reproduction, to be less variable over time for the same elasticity, i.e. more buffered than the vital rates of the Alpine chamois. The Alpine marmot should indeed be less responsive to environmental variations because burrows provide efficient shelters against detrimental environmental conditions, and it should also benefit from buffering effects against environmental constraints brought by its social living. As a result we also expected **(ii)** the stochastic population growth rate to be less variable for the Alpine marmot population than for the Alpine chamois population.

However, the weather conditions are changing in the Alps, in a way that seems detrimental for the Alpine marmot: winters are becoming colder with less snow at the study site while snow depth in winter appears as a key parameter of marmot population dynamics. Snow layer acts as insulation layer that regulates the effectiveness of the shelter against harsh environmental conditions, and thus influence survival and reproductive success at emergence (Tafani et al. 2013; Rézouki et al. 2016). Based on these previous results, we also predicted that **(iii)** the Alpine marmot population should be more responsive to the directional change in weather conditions (i.e. climate change) than the Alpine chamois population. Vital rates of the Alpine marmot population should show higher fluctuations over time, with steeper negative trends compared to Alpine chamois. Consequently,

environmental variation should decrease/lower the Alpine marmot stochastic population growth rate to a greater extent than for chamois.

5.2. Material and methods

5.2.1. Study species

Alpine marmot

The Alpine marmot is a long-lived rodent (see Table 5.1) that is highly social and hibernates during almost half the year in burrows. This territorial species lives all year long in family groups from 2 to 20 individuals, composed of a dominant couple, subordinates of both sexes (i.e. sexually mature individuals from 2 years of age onward), immatures (yearlings) and pups of the year (Arnold 1990b; Perrin et al. 1993). This species is monogamous and the reproduction is monopolized by the dominant couple (Allainé 2000), with physiological suppression of reproduction of almost all mature subordinates through aggressive behaviours (Arnold and Dittami 1997; Hackländer et al. 2003). The mating occurs during the 15 days following the emergence from hibernation (from early to late April). Gestation lasts for 30 days, and marmots thus rely on the remaining fat body reserves of the mother and on the resource availability in spring. Litter size ranges from 1 to 7 juveniles, which are then nursed during 40 days in the natal burrow until weaning between mid-June and mi-July (i.e., emergence of the pups). Once the sexual maturity is reached at 2 years of age, individuals can delay dispersal and stay as a subordinate, or become dominant and start reproducing, either by inheriting the dominance status in its natal group or by dispersing and displacing the same-sex dominant from another territory (Magnolon 1999). Individuals then stay dominant and reproduce for several years until death or eviction by another individual (Lardy et al. 2011). To resist the winter harshness, group members hibernate together in the same burrow from mi-October to early, mid-April, a behaviour known as social thermoregulation (Arnold 1990a, 1993b). During this period, subordinate males have been shown to actively warm up the related juveniles of the group (Arnold 1988, 1993a), acting as helpers for them

as their presence increases juvenile probability to survive the first winter (Allainé et al. 2000; Allainé and Theuriau 2004).

Alpine chamois

The Alpine chamois is a long-lived ungulate (see Table 5.1) that typically display high adult survival rates (Loison et al. 1994; Corlatti et al. 2012). It is a medium-sized herbivorous bovid (Table 5.1), which exhibits a high level of polygyny (Loison et al. 1999a). The rut occurs at the beginning of the winter, mostly in November-December, during which males compete for access to reproduction and defend mating territories (von Hardenberg et al. 2000; Willisch and Ingold 2007). Females are monotocous and give birth to one kid a year, generally in late May and early June, after a gestation of 160 to 170 days (Loison 1995). Following this period females form nursery groups composed of juveniles, reproductive and non-reproductive females, while males are mostly solitary (Boschi and Nievergelt 2003). Females can start reproducing from the age of 2-3 years-old (Loison et al. 1999b; Pioz et al. 2008, in the study site of Les Bauges), and have a conservative reproductive tactic, restricting their reproductive effort to the most favourable years for reproduction, to avoid high energetic costs of gestation and lactation and ensure future winter survival or reproduction (Morin et al. 2016). Like other mountain dwelling ungulates, the Alpine chamois displays several morphological or behavioural adaptations to cope with the seasonal food shortage and harsh weather conditions of the winter, such as a thick fur or seasonal migration to lower altitudes for a part of the population (Loison 1995; Lovari et al. 2006) (see Table 5.1 for an overall summary of this species' life history strategy and lifestyle).

5.2.2. Study sites and data collection

Alpine marmot

The Alpine marmot population was located in the Grande Sassière Nature Reserve (2340 m a.s.l., French Alps, 45°29′N, 6°59′E). In this site, 24 different groups of marmots were monitored from 1990 to 2013, from mid-April to mid-July by a

combination of Capture-Mark-Recapture and visual observations. Individuals were trapped in two-door live traps, tranquillized with Zolétil 100 and marked with a transponder (Trovan^{TM,}, Germany) and a numbered ear tag. At each capture, marmots were aged, sexed and their social status determined according to the scrotal and teat development for males and females, respectively. The social status is equivalent to the reproductive status as virtually no subordinate individual reproduces in this species (Hackländer et al. 2003). We assessed age from individual size, allowing to define three age-classes; the juveniles (i.e., young of the year), the yearlings (i.e., one year-old individuals), and the adults (i.e., from two years of age onwards). The number of weaned pups produced in each family group was estimated from daily observations of the groups, from mid-June to mid-July, 40 days after birth, at emergence from the burrows (as neonates stay in the burrow until weaned, they were not accessible for a direct census). Emerged pups were trapped and marked within three days after the emergence and mother-pup relationships were confirmed by genetic analyses (Cohas et al. 2008). Overall, we included data collected on 1,172 individuals in our analyses of survival, including 225 litters from 74 females.

Alpine chamois

The studied population of Alpine chamois was located in the Game and Wildlife Reserve of the Bauges massif, in the northern French Alps (45°40′N, 6°13′E). It has been monitored by the Office National de la Chasse et de la Faune Sauvage (ONCFS) since the early 1980s. We studied data originated from the site of Armenaz (227.4ha, 1400 to 2200 m a.s.l.) where both capture and observation sessions took place. Hunting is restricted in this protected area and chamois have virtually no predators, except for the Golden eagle, *Aquila chrysaetos*, and the red fox, *Vulpes vulpes* that occasionally prey upon juveniles of less than 1 month. Chamois were captured each year from May to September since 1985. They were trapped below falling nests baited with salt and individually marked with a coloured collar. Individuals were aged by counting the horn annuli (Schröder and Elsner-Schack 1985). Between 1990 and 2015, 418 females were captured. Since the recapture rate

is low in this population, capture information was supplemented by sighting data collected each year from April to November to compute capture-resighting histories for each marked individual. Since 1995, counting sessions through visual observations are organised during the summer period. An observation itinerary has been repeatedly walked by the same observer from 1995 to 2003, and by multiple observers from 2006 to 2015. Counting data were recorded for each observed group of individuals, by distinguishing the number of adult females (i.e. $\geq$ 2 years old), adult males (i.e. $\geq$ 2 years old), kids and yearling for each group.

Table 5.1. Summary of the main life history traits and lifestyle of the Alpine marmot (*Marmota marmota*) and the Alpine chamois (*Rupicapra rupicapra*). Both species live in sympatry in most of the Alpine range, but show contrasting lifestyles.

Species characteristics		*Marmota marmota*	*Rupicapra rupicapra*	References
Generation time		*6.2*	*6.7*	*This study*
Life history strategy	Adult body mass	2 - 6.5 kg	30 - 40kg	1; 2
	Reproductive lifespan*	~2 to 16 years	~2 to 20 years	3; 4
	Litter size	1 to 7	1	5; 6
	reproductive tactic	Cooperative breeding	Conservative strategy	7; 8
Lifestyle	Altitude (range)	1,000-3,000	*900-3,000 m*	9; 10
	Habitat type	Alpine and sub-alpine grassland	Alpine grassland and woodland	9; 11
	Diet	Herbivorous	Herbivorous	12; 13
	Mating system	Monogamous	Polygynous	7; 14
	Social system	Territorial social groups	Gregarious	7; 6
	Energy saving strategy	Joint hibernation in burrows Ground-dwelling life	Large body size/mass ratio Thick fur in winter Seasonal migration	15; 6, 10

1. Körtner and Heldmaier 1995; **2.** Garel et al. 2009; **3.** Berger et al. 2016; **4.** Pioz et al. 2008; **5.** Tafani et al. 2013; **6.** Loison 1995; **7.** Allainé 2000; **8.** Mason et al. 2016; **9.** Allainé et al. 1994; **10.** Lovari et al. 2006 ; **11.** Nesti et al. 2010; **12.** Garin et al. 2008; **13.** Bertolino et al. 2009; **14.** Loison et al. 1999a; **15.** Arnold 1990a

5.2.3. Weather variables

Because of the geographical proximity of the two populations, we hypothesised they wouldbe subjected to similar environmental variation and change. We checked this assumption by comparing time-series of local scale weather variables between the two sites. Based on previous studies of the Alpine marmot (Tafani et al. 2013; Rézouki et al. 2016; Canale et al. 2016) and Alpine chamois (Loison et al. 1999c; Pioz et al. 2008; Rughetti et al. 2011; Willisch et al. 2013), we focused on the weather variables found to influence vital rates of both species. These environmental variables are representative of three critical seasons for the species: the early spring (April), the summer (July-August) and the winter (from December to March).

We used the Normalised Difference Vegetation Index (NDVI, Pettorelli et al. 2005b), a proxy of the vegetation production, measured in the second half of April, to compare the timing of snowmelt and thus the vegetation onset between the two sites. NDVI values were provided by the National Oceanic and Atmospheric Administration (NOAA) and were extracted from the AVHRR dataset from 1990 to 2000 (8x8 km resolution) and from the MODIS dataset from 2001 to 2013 (1x1km resolution) for the study site of La Grande Sassière. Similarly, NDVI values were extracted from the AVHRR dataset from 1990 to 1999 (8x8km resolution) and from the MODIS dataset from 2000 to 2013 (250x250m resolution) for the study site of Les Bauges.

We used an index of summer drought, the Bagnouls-Gaussen Index (BGI), to compare temporal variation in summer weather conditions between the sites. We calculated the BGI from July 1st to August 31^{st,} as the monthly cumulative precipitation minus twice the mean air temperature (see Gaillard et al. 1997). A low BGI means a dry summer, and hence a low vegetative productivity.

Finally, we calculated a winter harshness index (WIN), combining monthly mean air temperature and monthly mean snow depth from December 1st to March 31st (see Rézouki et al. 2016 for further information) to compare between-site variation in winter harshness.

Air temperature, precipitations and snow depth measurements were extracted from daily records from the Météo France weather stations of Val d'Isère

(1,840 m a.s.l., ID 73296400), Tignes Brevières (1,560m a.s.l., ID 73296002) and Tignes (2,080m a.s.l., ID 73296400), respectively, for La Grande Sassière. Air temperature and precipitations measurements computed for Les Bauges were obtained from the Météo France weather station of Lescheraines (591m a.s.l., ID 73146001), and snow depth from the weather station of Aillon-Le-Jeune (900m a.s.l., ID 73004001).

We tested for the correlation of weather variation between the two sites with Pearson correlation coefficients and tested for temporal trends in weather variables using linear models.

5.2.4. Estimation of the vital rates

Annual survival rates

Annual survival rates were estimated for both species from Capture-Mark-Recapture data collected between 1990 and 2013 for the Alpine marmot and from 1990 to 2015 for the Alpine chamois. We used the multi-state capture-recapture models developed by Rézouki et al. (2016) for the Alpine marmot and by Richard et al. (2017) for the Alpine chamois. Survival rates were estimated according to the age and the social status for the alpine marmot, which resulted in 5 classes: juveniles, yearlings, subordinates (from 2 to 5 years of age), dominant prime-aged adults (from 2 to 7 years of age) and dominant senescent adults (from 8 to 16 years of age) (see Table 5.2). Survival rates of the Alpine chamois population of Les Bauges were estimated according to age (Bleu et al. 2015). Survival estimates were divided into four age-classes: juveniles, prime-aged adults (from 1 to 7 years of age), old adults (from 8 to 12 years of age) and senescent adults (from 13 years old onwards) (see Table 5.2). However, since a very small number of juveniles have been trapped and marked over the years in the natural reserve of les Bauges, we were not able to obtain annual estimates of juvenile survival, but rather an overall estimate over the entire study period. In order to assess the potential influence of environmental variation on this vital rate and on the population demography, we generated annual survival rates of juveniles based on the mean approximated of our population (Sjuv = 0.75) and the

temporal variance found in the literature (CV = 0.29, Gaillard et al. 2000).

Finally, we tested for a temporal trend in each survival rate, calculated its temporal variance and computed the corresponding coefficient of variation (CV) for each age-class. However, as survival rates are bounded by 0 and 1, each age-specific vital rate may not have the same amount of possible variation, the later being lesser when the mean gets close to 1 or 0 (Morris and Doak 2004). We thus also computed scaled coefficients of variation corrected by the maximal amount of possible variation (CV/CVmax, Gaillard and Yoccoz 2003; Morris and Doak 2004) to enable reliable comparison of vital rates' variances.

Annual reproductive rates

Reproductive rates were estimated using generalised linear mixed-effects models (GLMER) and generalised linear models (GLM) for the Alpine marmot and the Alpine chamois, respectively. Mean and annual litter size of Alpine marmots were estimated from 1990 to 2013. Given that offspring are only captured when emerging from their burrows at weaning, this litter size measurement also takes into account the pre-weaning survival of the pups. We finally computed an overall fecundity index, *Fec*, as the product of the litter size with the mean proportion of dominant females that reproduce within the population (around 0.25 for the two years-old females and 0.68 for females older than 2 years-old) and the sex ratio (0.45, Allainé et al. 2000), in order to obtain the number of females offspring produced at birth per dominant female. Although the litter size has been shown to decrease at old ages in Alpine marmots (onset of senescence at 10 years of age, Berger et al. 2015b), we pooled prime-aged and senescent adults in our calculation of annual litter size to allow comparing reproduction with the Alpine chamois population, for which reproductive data was not as detailed.

Mean and annual reproductive rates of female alpine chamois were estimated based on observational data from 1995 to 2015 (with missing values for the years 2003, 2004 and 2005). We estimated the proportion of females that gave birth to one kid by calculating the ratio between the number of kids and the number of mature females (i.e. $\geq$ 2 years old) within nursery groups. We only considered

observational data from mid-June to the end of August, during which we were confident that calving occurred in our calculation(part of the pre-weaning survival was therefore included in the estimate). This proportion, multiplied by the sex ratio, then provides a proxy of the fecundity of the Alpine chamois population. Because visual observation of nursery groups did not allow accounting for age-variation in reproduction, we were not able to obtain age-specific fecundities as for the Alpine marmot. The annual fecundity estimates therefore applied to all mature females of the population (Fig. 5.1.a), whatever their age-class.

Finally, we tested for temporal trend in fecundity for each species, and estimated the temporal variance and the corresponding CVs of these reproductive rates. Because fecundities in chamois and marmots have different boundaries (the litter size being comprised between 0 and 7 for the Alpine marmot, and between 0 and 1 for the Alpine chamois), we also scaled the CV of the fecundity estimates by dividing its values by the maximum for each species to allow for comparison between species.

5.2.5. Demographic analysis

Demographic models and basic demographic analysis

For each species we constructed a female-based age-structured population projection matrix with a post-breeding census construction (Caswell 2001, see Appendix 5.1) based on their respective life cycle (Fig. 5.1). These population projection matrices were parametrised using survival (S_x) and reproductive rate (*Fec*) estimates adjusted for each different age-classes we considered for each species. The Alpine marmot life cycle and projection matrix also included the age-specific probability of transition from a subordinate to a dominant status (*Trans*).

Based on these population projection matrices, we were able to estimate the generation time, the deterministic population growth rate (λ) and the deterministic elasticities (E_v) of vital rates (Caswell 2001) for each population. These elasticities measure the effect of proportional changes in both mean and variance of the vital rates v_{ij} on the population growth rate. We then calculated the stochastic population

growth rate ($a = \log\lambda$) and its variance using Tuljapurkar's small variance approximation formula (Eq.1, see e.g. Tuljapurkar 1990), which integrates elasticities (i.e. e_{ij}, e_{kl}), the coefficient of variation of vital rates (i.e. c_{ij}, c_{kl}), and the correlation coefficients between the vital rates ($\rho_{ij,kl}$) of the matrix elements *ij* and *kl*, and we assumed here temporal autocorrelation does not occur (Tuljapurkar 1990, Horvitz et al. 1997).

$$a^{(m)} = \log \lambda_s^{(m)} \approx r^{(m)} - \frac{1}{2} \sum_{i,j} \sum_{k,l} \{e_{ij} e_{kl} c_{ij} c_{kl} \rho_{ij,kl}\}^{(m)} \qquad \text{Eq. 1}$$

Life history buffering hypothesis

The theory predicts a negative relationship between the coefficients of temporal variation (CVs) and the elasticities of the vital rates (Pfister 1998). Being two long-lived species, a general pattern of environmental canalization should be highlighted here with, for instance, high variation in reproduction associated with lower elasticities as opposed to low variation in adult survival with higher elasticity (Gaillard and Yoccoz 2003). Given the differences in the species lifestyle, we expected that reproductive and survival rates of the Alpine marmots should be less variable than those of the Alpine chamois for a similar elasticity. We tested this hypothesis by comparing graphically the relationship between the CVs and elasticities of the vital rates of the two populations. To make meaningful comparisons between these species with different life cycles, we pooled elasticities of the survival rates of yearling, subordinates, and dominant individuals of the Alpine marmot within a “prime-aged” survival parameter comparable to that of the Alpine chamois. The associated CV was then the average CV of these three vital rates. Finally, we also tested this hypothesis using the scaled CVs to see whether a similar pattern emerged when corrected by the amount of possible variation in each vital rate. This should allow disentangling a selection to reduce variability in vital rates from a selection to increase their means (Morris and Doak 2004).

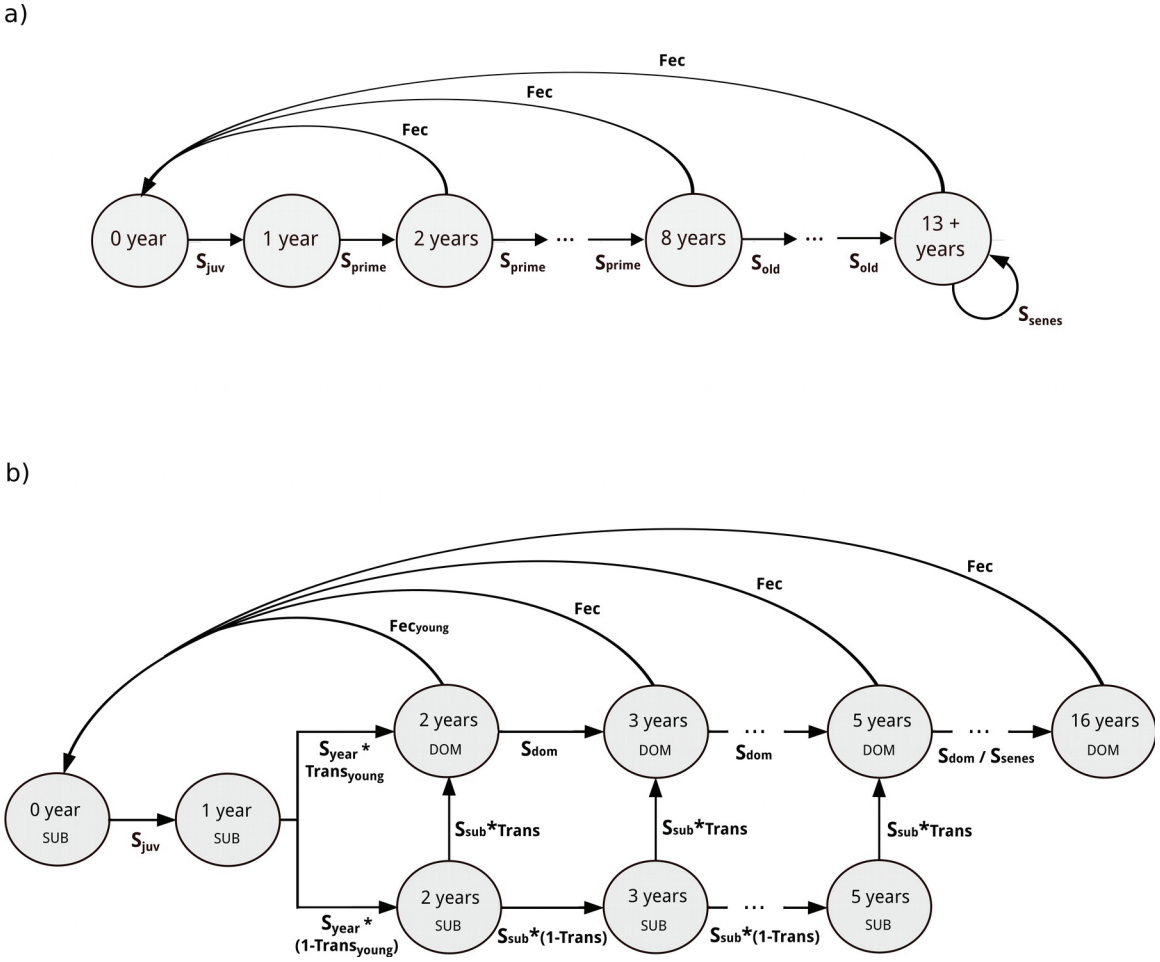

Figure 5.1. Life cycle graph of (a) the Alpine chamois and (b) the Alpine marmot population used for modelling the population demography of Les Bauges and La Grande Sassière, respectively (French Alps).

Table 5.2. Abbreviations used when defining the life cycle and the population projection model notations for the Alpine marmots of La Grande Sassière (France).

Vital rates		**Biological meaning**	
Abbreviations		*Marmota marmota*	*Rupicapra rupicapra*
Sjuv		Annual survival probability of juveniles, from 0 to 1 year	Annual survival probability of juveniles, from 0 to 1 year
Sprime	Syear	Annual survival probability of yearlings, from 1 to 2 years	Annual survival probability of prime-aged individuals between 1 and 7 years
	Ssub	Annual survival probability of subordinates between 2 to 5 years	
	Sdom	Annual survival probability of prime-aged dominants between 2 and 8 years	
Sold		-	Annual survival probability of old individuals between 8 and 12 years
Ssenes		Annual survival probability of senescent dominants (older than 8 years)	Annual survival probability of senescent individuals (older than 13 years)
Fec_young		Number of females produced at birth per year by 2 years-old females	-
Fec		Number of females produced at birth per year by dominant females between 3 and 10 years of age	Number of females produced at birth per year by females from 2 years of age onward
Trans_young		Mean annual probability of transition from the subordinate to dominant status for individuals between 1 and 2 years of age	-
Trans		Mean annual probability of transition from the subordinate to dominant status for individuals between 2 and 4 years of age	-

Contribution of the vital rate variation to the observed variance in λ

We used the approximation of variance of the population growth rate proposed by Tuljapurkar (1990) and Horvitz et al. (1997) to calculate the contribution of both the variation and the covariation of vital rates to the observed variance of the population growth rate. With this formula (Eq. 2), the absolute contribution C_{ij} of a given vital rate (*i,j*) could be measured as the product of its squared elasticity and its squared coefficient of variation (contribution of the variance) plus the product of the pairwise combinations of its elasticities, coefficients of variation and correlation coefficients with the other vital rates (*k,l*) (contribution of the covariance), when neglecting serial temporal autocorrelations (Fig. 2):

$$C_{ij} = e_{ij}^2 c_{ij}^2 + \sum_{k,l} \left\{ e_{ij} e_{kl} c_{ij} c_{kl} \rho_{ij,kl} \right\} \qquad \text{Eq. 2}$$

The sum of all contributions provides an approximation of the variance of the population growth rate. A positive contribution means that the variation or the co-variation in the vital rates increases the variance in λ, reflecting a fitness cost of these temporal variations. On the other hand, a negative contribution means that these variations tend to decrease the variance in λ, reflecting a positive effect of these variations on the population growth rate.

Population demographic responses to climate change

Because of current changes in the local weather conditions in the Alps, we hypothesised that the Alpine marmot stochastic population growth rate should be more negatively impacted than those of the Alpine chamois population. To test this hypothesis, we estimated the annual deterministic population growth rates over the study period for the two populations by constructing annual population matrices parametrised with the annual mean estimates of vital rates. This should allow approaching and comparing the influence of climate change on the population growth rate over years through its impact on the vital rates for the two species. Since estimating annual juvenile survival was not possible for the Alpine chamois population, we tested three scenarios for juvenile survival to grasp the change in the

population growth rate that may have occurred over time: (1) constant juvenile survival (S_{juv} = 0.75), (2) variable juvenile survival (mean = 0.75, CV = 0.29), and (3) variable and declining juvenile survival similar to the decrease in Alpine marmot (β = -0.06).

At last, to better understanding the mechanisms behind these annual changes in the population growth rates, we performed a Life Table Response Experiments (LTRE, Caswell 2001). Deterministic LTRE applied at the inter-annual scale may allow decomposing the between-year differences in the population growth rate ($\Delta\lambda$) into differences in the mean values of each vital rate from one year to another (ΔS_x, ΔFec or $\Delta Trans$). Because of climate change and its negative impact on the juvenile survival and litter size of the Alpine marmot population, we expected the annual $\Delta\lambda$ to be higher in the last years for this species as well as the contribution of $\Delta Sjuv$ and ΔFec to these changes, explaining the negative between-year changes in the population growth rate. On the other hand, no such change in the $\Delta\lambda$ was expected for the Alpine chamois over time, except for the scenario including decreasing juvenile survival in which a similar pattern was expected. Apart from this scenario, we expected between-year changes in the vital rates of the Alpine chamois to contribute uniformly to the decrease and increase in λ over the years.

5.3. Results

5.3.1. Weather environmental co-variation between the two study sites

The analysis of weather indices revealed statistically significant correlations between study sites in between-year variability of the weather conditions for all seasons. The BGI positively correlated between sites (r = 0.89, p > 0.001, Fig. 5.2) as well as the NDVI in April (r = 0.50, p = 0.01, Fig. 5.2), while the winter index WIN negatively correlated between the sites (r = -0.49, p = 0.01). However, when looking at the constitutive weather factors of this index, i.e. the mean monthly air temperature (Fig. 5.2) and the snow depth (Fig. 5.2) in winter, we found that only

the winter temperature correlated between the sites ($r = 0.83$, $p<0.01$), while the snow depth did not ($r = 0.36$, $p = 0.07$). The latter difference can be explained by the different altitudes at which snow depth measurement are taken, since the weather station of Les bauges sits at an altitude of around 1,000m below that of the weather station close to La Sassière. Similarly, while temporal variation in weather variables correlates between study sites, their mean values strongly differed (e.g. higher mean temperature over the seasons at Les Bauges) which could also be explained by the differences in altitude of the weather stations.

Finally, an opposite but statistically significant trend was found in the winter index for both sites, with a decrease in the site of La Grande Sassière ($\beta = -0.07$, $p = 0.02$), reflecting harsher winters in last years, and with lower mean temperatures and snow depth, and an increase in the site of Les Bauges ($\beta = 0.06$, $p = 0.05$), which here reflects a decrease in winter mean temperatures and an increase in recorded snow depth at the neighbouring weather stations. A positive trend in the NDVI was detected at les Bauges only ($\beta = 0.004$, $p = 0.03$ for les Bauges vs. $\beta < 0.001$, $p = 0.57$ for la Grande Sassière), indicating an earlier onset of vegetation in spring over the years. At last, no detectable change in the summer drought index was highlighted over years in the two sites ($\beta = 0.14$, $p = 0.95$ and $\beta = 0.79$, $p = 0.72$, for Les Bauges and La Grande Sassière, respectively).

Overall, the two populations of the Alps are submitted to similar environmental fluctuations, with a good synchrony in the local weather year-to-year variations reflecting the effect of a large-scale climatic variation. We might thus expect that differences in population dynamic between the two species should mainly originate from differences in their biology and ecology rather than from differences in the environmental variations they face.

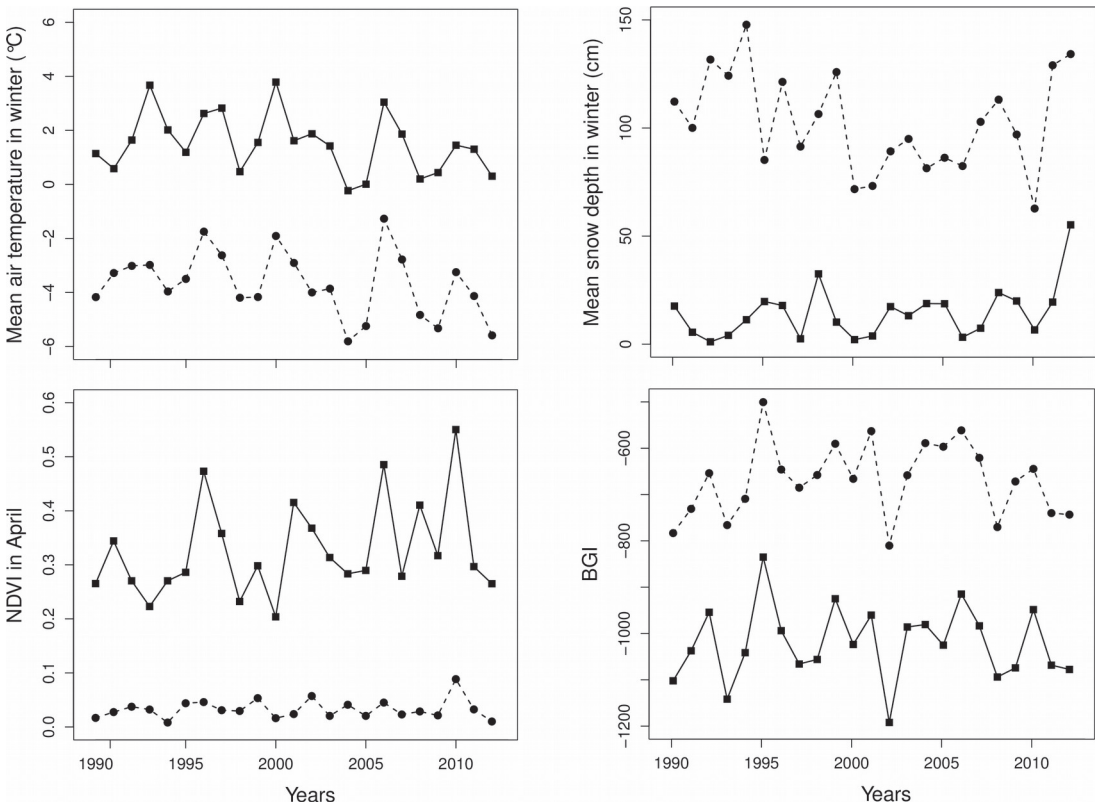

Figure 5.2. Annual variation in the observed weather variables and weather indices in the study site of Les Bauges (full line) and La Grande Sassière (dotted line). The two components of the winter index (WIN), i.e., the mean air temperature and the mean snow depth from December to March, are represented, as well as the spring vegetation index measured in April (NDVI), and the Bagnouls-Gaussen Index (BGI), an index of the summer drought, measured from June to July.

5.3.2. Demographic response of populations to environmental variation

Demographic analyses revealed that the generation time of these two populations of Alpine species was similar, being 6.2 and 6.7 years for the Alpine marmot and the Alpine chamois, respectively. The deterministic growth rate was, however, quite different between the two populations, being negative for the Alpine marmots (r = log(0.985) = -0.014), and positive for the Alpine chamois (r = log(1.108) = 0.102). The stochastic population growth rate displayed the same pattern (a = log(0.981) = -0.019 for the Alpine marmot *vs*. a = log(1.103) = 0.098 for the Alpine chamois). Finally, we found little difference in the long-term variance of the population growth

rate, with a slightly higher variance for the Alpine marmot compared to the Alpine chamois (0.009 and 0.008, respectively).

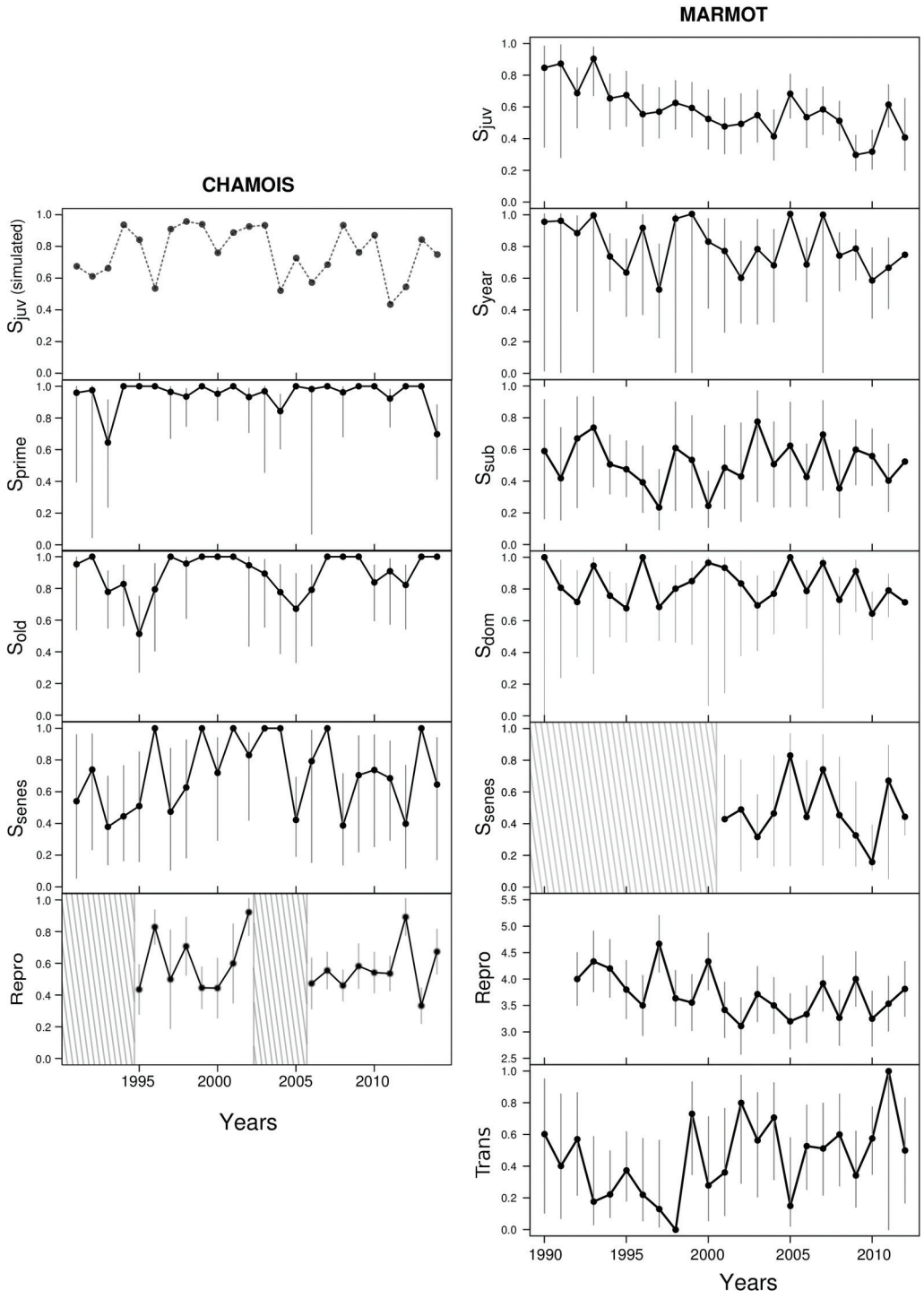

Figure 5.3.. Annual estimates from CMR data of each vital rate of the Alpine chamois population of les Bauges, between 1991 and 2015 and the Alpine marmot population of La Grande Sassière between 1990 and 2013. Shaded areas represent years for which no data were available.

Life history buffering against environmental variation

The between-species difference in population growth rate can be partially explained by important differences in the mean values of vital rates. Overall, mean survival rates of every age-classes was higher for the Alpine chamois than for the Alpine marmot (see Fig. 5.3, e.g. *Sjuv (simulated)* = 0.75 vs. *Sjuv* = 0.59 ± 0.08, *Sprime* = 0.97 ± 0.01 vs. *Sdom* = 0.81 ± 0.10, for the Alpine chamois and Alpine marmot, respectively).

As expected for long-lived species, similar elasticities were found for the vital rates. The general pattern of demographic buffering also followed the expected pattern with a negative relationship between the CV and E_v (see Fig. 5.4.a). For the two species, the vital rate with the lowest potential to impact population growth rate was the more variable (i.e. senescent survival, *Ssenes,* Fig. 5.4.a) while the vital rates with the greatest potential to affect the population growth rate was among the less variable (i.e. prime-aged survival, *Sprime,* Fig. 5.4.a). However, differences in the buffering of some vital rates emerged from this analysis, especially for reproductive parameters. For a same intermediate elasticity ($E \approx 0.15$), the annual reproductive rate (*Fec*) was less variable for the Alpine marmot than for Alpine chamois (CV = 0.10 vs. CV = 0.24 respectively, Fig. 5.4.a), which suggests a higher buffering of this trait against environmental variability in the Alpine marmot population.

However, when correcting the vital rate variability by the possible amount of variation (Fig. 5.4.b), the general pattern changed. Specifically, the pattern of demographic buffering for the Alpine chamois did not hold anymore. Survival of prime-aged individuals was no longer the least variable vital rate, as expected by its high elasticity ($CV/CV_{max} = 0.42$, as opposed to $CV/CV_{max} = 0.23$ for the Alpine marmot, Fig. 5.4.b). This result can be explained by the higher mean survival rates of the Alpine chamois, so that buffering occurs mainly by increasing mean survival rates in this species in addition to decreasing its variability. Similarly, the observed difference in the variation of the reproductive rate decreased after this correction ($CV/CV_{max}= 0.19$ for the Alpine marmot vs. $CV/CV_{max} = 0.29$ for the Alpine chamois, Fig. 5.4.b), while a stronger difference in the variation of juvenile survival

emerged (CV/CV_{max}= 0.31 for the Alpine marmot vs. CV/CV_{max} = 0.47 for the Alpine chamois, Fig. 5.4.b) with a smaller scaled variance for juvenile survival of the Alpine marmot.

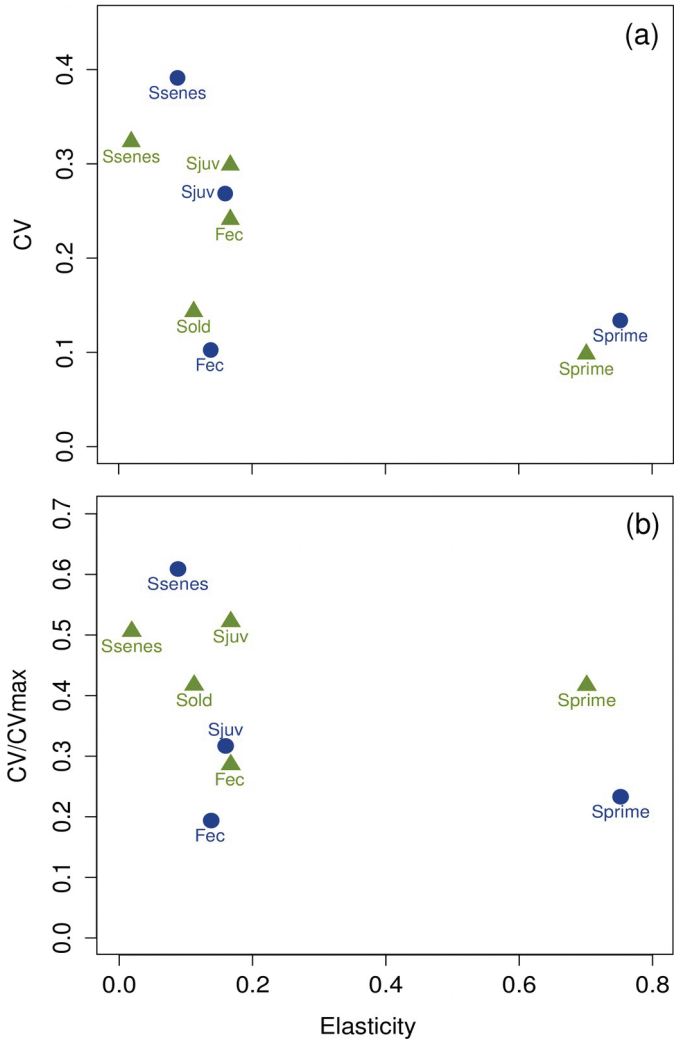

Figure 5.4. Relationships between (a) the coefficient of variation (CV) and (b) the scaled coefficient of variation (CV/CVmax) with the elasticity of each vital rate component of the Alpine chamois (green) and of the Alpine marmot (blue) life cycle, measured along a monitoring period from 1990 to 2013 for the Alpine marmot, and from 1990 to 2015 for the Alpine chamois.

Stochastic population demography and contribution of vital rate variation to the variance of the stochastic population growth rate

Retrospectively, the variability in survival of prime-aged individuals contributed the most to the variance in population growth rate for both species, with a total contribution C_{prime} = 0.0047 for the Alpine chamois and C_{prime} = 0.0049 for the Alpine marmot (see Fig. 5.5). The second largest total contribution was the variability in juvenile survival for both populations (C_{juv} = 0.0040 and CV_{juv} = 0.0025, for the chamois and the marmot, respectively, Fig. 5.5).

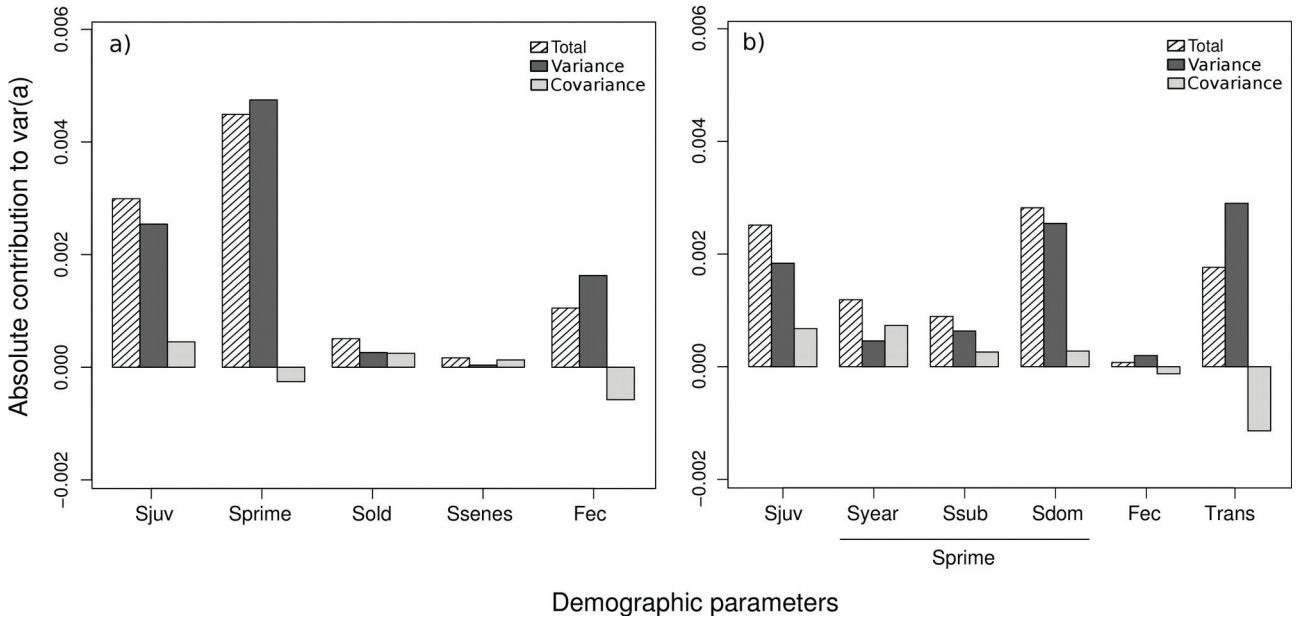

Figure 5.5. Total contribution and contribution of the variance and the covariance of the vital rates to the variance of the stochastic population growth rate, for (a) the Alpine chamois and (b) the Alpine marmot populations at Les Bauges and La Grande Sassière study site, respectively.

Despite these general similarities, we found a number of differences between species. First, the variation in fecundity of the Alpine marmot had a virtually null contribution to the temporal variance of λ in contrast with the Alpine chamois, where it contributed ten times more (C_{fec} < 0.0001 vs. C_{Fec} = 0.001 respectively, Fig. 5.5). Second, contributions of the covariation between vital rates strongly differed between species. A higher positive covariation between survival rates occurred in the

Alpine marmot (Table S5.2.1 in Appendix 5.2), which contributed more importantly in increasing the variance of λ compared to the Alpine chamois (contribution of the covariance $Ccova_{Survival}$ = 0.002 and $Ccova_{Survival}$ < 0.001, respectively, Fig. 5.5). Furthermore, a negative covariation between fecundity and survival rates occurred in the Alpine chamois, but could not be detected in the Alpine marmot (Table S5.2.1, Appendix 5.2). The covariation between fecundity and survival contributed negatively to the variance of λ in the Alpine chamois population, hence decreasing the variation in the population growth rate (Fig. 5.5, Fig. S5.2.2, Appendix 5.2). Finally, the variation in the probability to access dominance in the Alpine marmot had a non-negligible contribution to the variance of λ (total contribution C_{Trans}= 0.0018). Most importantly, this parameter buffered population growth rate against environmental variation. The probability of becoming dominant covaried negatively overall with the other vital rates (except with subordinate survival, Table S5.2.1, Appendix 5.2) and as a result it contributed negatively to the variance of λ (contribution of the covariance $Ccova_{Trans}$ = -0.001, Fig. 5.5).

5.3.3. The influence of climate change on population demography

Change in annual deterministic population growth rate

No temporal trend was detected in the vital rates of the Alpine chamois, (for which juvenile survival was unknown). On the other hand, we found a temporal trend in juvenile survival, fecundity and in the probability of accessing dominance in the Alpine marmot population (β = -0.06 ± 0.01, β =-0.008 ± 0.006, β = 0.065 ± 0.022, respectively, Fig. 5.3).

As expected, the deterministic population growth rate λ of the Alpine marmot decreased over time, but not continuously: it decreased rapidly below 1 between 1990 and 1998, from about 1.2 to 0.7, and then increased between 1998 and 1999 before remaining stable at around 0.95 (Fig. 5.6). On the other hand, the deterministic population growth rate λ of the Alpine chamois was almost always above 1, sign of an increasing population, whatever the scenario for juvenile survival considered (Fig. 5.6). We detected no temporal trend for this species, with

variation in λ remaining around 1.1. However, a steep decrease in λ, from 1.1 to 0.8-0.85, occurred in Alpine chamois between 1992 and 1993, with a fast recover in 1994. These results are in line with our expectation that Alpine marmots should suffer from climate change more than Alpine chamois.

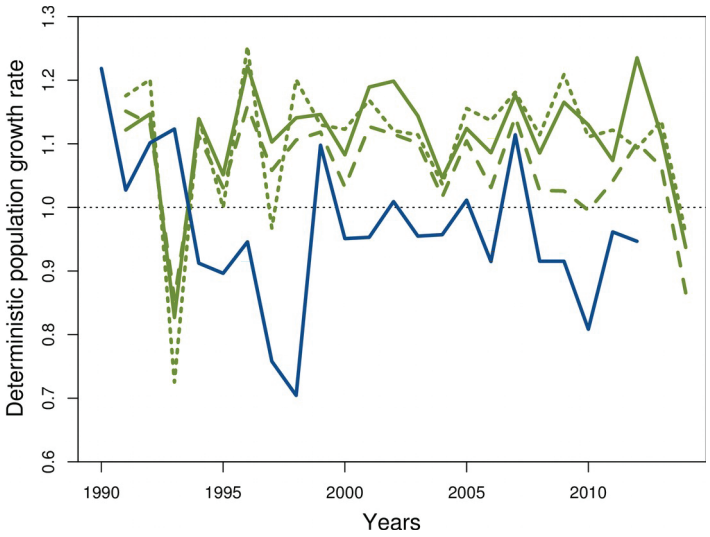

Figure 5.6. Comparison of the annual deterministic growth rate between the Alpine marmot (in blue) and the Alpine chamois (in green). Three scenarios were considered for juvenile survival in the Alpine chamois, including a constant (full line), a variable (dotted line) and a decreasing (dashed line) survival.

Vital rates driving inter-annual variation in population growth rate

Longitudinal patterns in between-year variation of the population growth rate ($\Delta\lambda$) differed between the two species (Figure 5.7.a.b). No apparent increase in the inter-annual variation in λ occurred in the Alpine marmot population, nor in the Alpine chamois population. For the Alpine marmot, important negative $\Delta\lambda$ of a same intensity occurred intermittently throughout the years (repetition of a decrease in λ of around -0.2, Figure 5.7.b) and were nonetheless more frequent before 2000. For the Alpine chamois, high inter-annual variation occurred early in the study (around 1993), but remained generally low thereafter (absolute $\Delta\lambda$ below 0.2). This variation was relatively uniform, alternating between increases and decreases in λ of similar intensities (Figure 5.7.a).

Besides the observed variation in the population growth rate, the year-to-year variation in vital rates was unexpectedly important (especially when virtually no change in λ was observed) (Fig. 5.7.c.d). Indeed between-year differences in the population growth rate were generally lower than expected given the high underlying total absolute contribution of vital rates. This result points out the occurrence of demographic compensation at an annual scale in both species; a negative contribution of one or more vital rates tends to be compensated by concurrent positive contribution of other(s). For the Alpine chamois, regardless of the juvenile survival whose variation could not be assessed from the data at hand, these demographic compensations were generally low, and mainly observed between adult survival and reproduction. Higher annual demographic compensations were observed in the Alpine marmot population. These compensatory changes seemed to involve each of the vital rates with each other, but demographic compensation was especially important between the probability of transition and other vital rates (see Fig. 5.7). This also supports previously reported negative covariation between vital rates.

Our results also revealed important between-year changes in the relative contribution of demographic rates to the change in the population growth rate (Fig. 5.7.b.c). Overall, the total contributions of changes in vital rates were skewed toward negative contributions, especially for the Alpine marmot (Fig. 5.7). For the Alpine chamois, three vital rates contributed the most and to a similar extent to total between-year variation in λ: juvenile survival *(ΔSjuv)*, prime-aged survival (*ΔSprime*) and reproduction (*Δfec*) (explaining around 30% of total *Δλ)*. A focus on increasing and decreasing population growth rate among years ($\Delta\lambda > 0$ and $\Delta\lambda < 0$, respectively) revealed that overall changes in these three vital rates contributed similarly to the observed change in λ, whether the latter increased or decreased (Fig. S5.3.1, Appendix 5.3). For the Alpine marmot, change in survival of dominant individuals the main factor explaining inter-annual variability in λ (explaining 30 % of total *Δλ,* Fig 5.7.d., Fig. S5.3, Appendix 5.3), followed by change in the probability of accessing dominance (*Δtrans,* explaining 24 % of total *Δλ*), and survival of other individuals. Annual change in juvenile survival only contributed to 12 % to the total *Δλ*. Similarly, annual change in fecundity (*ΔFec*) had virtually no

effect on $\Delta\lambda$ (explaining 5 % of total $\Delta\lambda$). However, some changes in the contribution of vital rates could be observed depending on whether λ was increasing or decreasing. This was highlighted for survival of dominants and juvenile survival, which both contributed more to change in the population growth rate when the latter decreased between two consecutive years than when it increased (Fig. S5.3, Appendix 5.3). In contrast, the contribution of subordinate survival was two times higher when λ increased than when it decreased (Fig. S5.3, Appendix 5.3). Overall contribution of the other vital rates did not change between these two types of demographic change.

Finally, by distinguishing vital rate contributions between increasing and decreasing population growth rate, it is clear that compensatory changes mostly occurred in the Alpine marmot population, with changes in the probability of transition and in subordinate survival contributing fairly in opposite direction to change in λ (Fig. S5.3, Appendix 5.3).

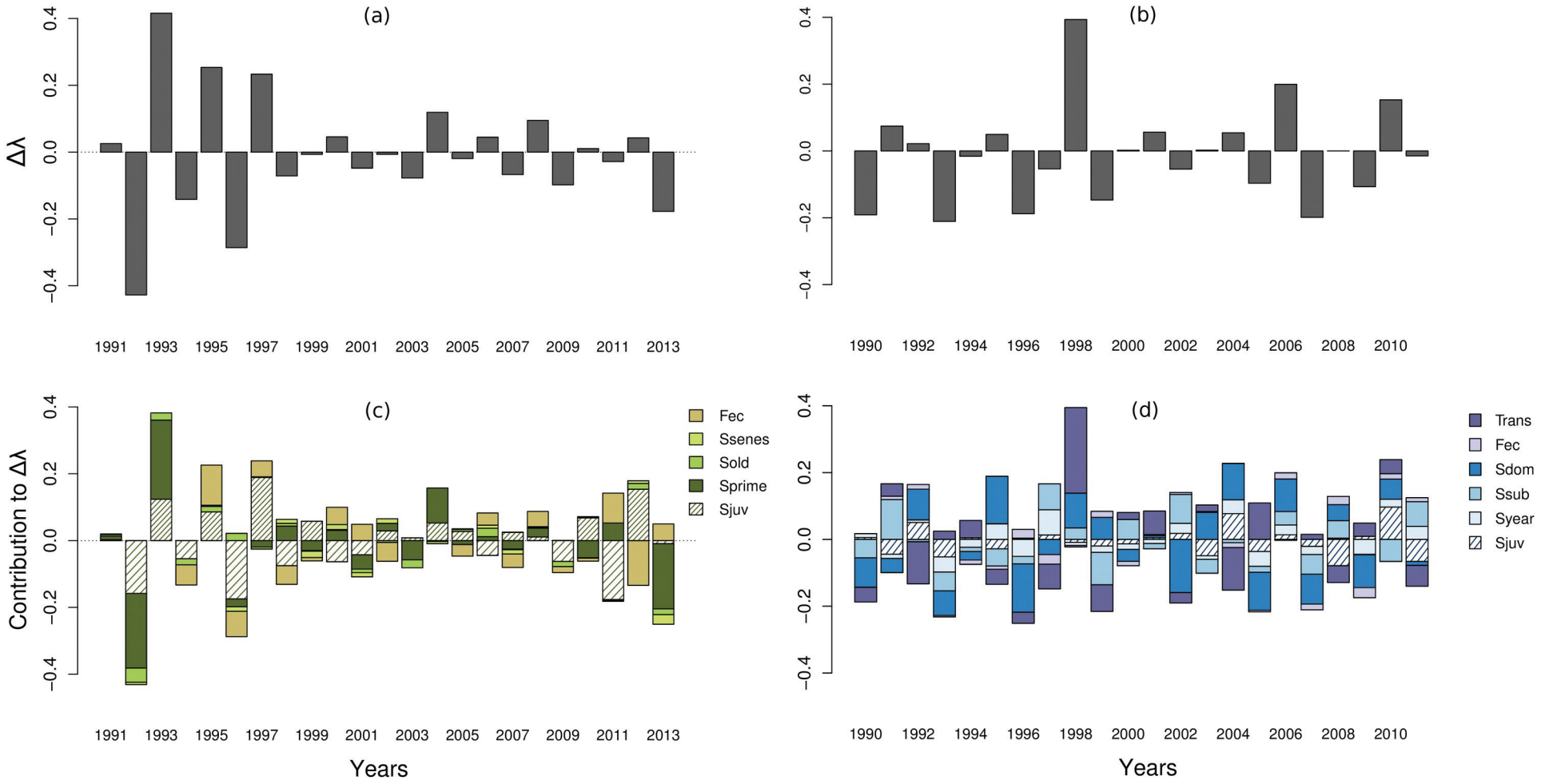

Figure 5.7. Annual between-year difference in the population growth rate (Δλ) for the Alpine chamois (a) and the Alpine marmot (b) population, and contribution of the between-year difference in the value of each vital rate to this Δλ, for the Alpine chamois (c) and the Alpine marmot (d) population.

5.4. Discussion

Our results highlight the differences in demographic responses between two sympatric species with a similar position on the slow-fast continuum due to their differences in lifestyle and reproductive tactics. This study provides some empirical evidence that the species lifestyle and reproductive tactic may explain between-species differences in response to environmental variation and disturbance, once generation time is accounted for.

5.4.1. Mechanisms behind species demography: the influence of the lifestyle and reproductive tactic

5.4.1.1. Demographic buffering

The two long-lived Alpine species we studied rank similarly on the slow-fast continuum and thereby (Hamilton 1966; Lebreton and Clobert 1991) display similar elasticities of their vital rates. The buffering of their vital rates, however, present theoretically unexpected dissimilarities; the recruitment (i.e. fecundity and juvenile survival) was less variable in the Alpine marmot population than in the Alpine chamois population (Fig. 5.4). This is in line with our hypothesis that a higher buffering of the vital rates should be observed for the Alpine marmot given its lifestyle and reproductive tactic compared with the Alpine chamois.

A result of a conservative reproductive tactic in the Alpine chamois

On one hand, the Alpine chamois presents the common environmental canalization of the vital rates, as generally highlighted in large ungulates (Gaillard et al. 2000; Gaillard and Yoccoz 2003), with a higher variance of the fecundity and juvenile survival compared to the prime-aged survival. The variance in recruitment appeared close to what is generally observed in large herbivores ($0.20 < CV_{fec/juv} < 0.30$, Gaillard et al. 2000). Large herbivores rely on a high longevity, which allows several

reproductive attempts, to increase individual fitness (Clutton-Brock 1988), as illustrated by the high elasticity of the prime-aged survival, indicative of selective pressures acting on this trait. Following this, their life history strategy is generally defined as a conservative reproductive tactic, including risk avoidance. Females reduce their reproductive investment when facing bad environmental conditions to maximize their own survival and future reproduction, at the expense of current reproduction (Festa-Bianchet and Jorgenson 1998; Gaillard and Yoccoz 2003; Martin and Festa-Bianchet 2010). The Alpine chamois displays such conservative reproductive tactic. Female chamois, and especially old females, seem to limit their reproduction and reproductive effort to favourable years that enable survival of juveniles to weaning (Morin et al. 2016). This explains the high adult survival generally found in Alpine chamois populations (Loison et al. 1994; Corlatti et al. 2012; Bleu et al. 2015) and in return the higher variability in fecundity. The recent findings of a high variability in the proportion of females giving birth in the Alpine chamois together with a high juvenile survival to weaning also corroborate the occurrence of this conservative reproductive tactic (Morin et al. 2016).

A result of sociality and of a fossorial hibernation in the Alpine marmot

Similarly, the Alpine marmot also relies on a high longevity, and especially on a long dominance's tenure (Lardy et al. 2015), to increase its individual fitness, but the high and constant adult survival does not emerge from the same mechanisms than in the Alpine chamois or other ungulates (i.e. through a large body mass and a conservative reproductive tactic, Table 5.1). Instead, its particular lifestyle, which combines hibernation and social living, ensures a long lifespan by decreasing environmentally driven mortality, as suggested in previous studies (Berger et al. 2015a, 2016). Thus, the low variation in survival of adult breeders in the Alpine marmot likely does not originate from a risk-avoidance strategy, but from fitness benefits brought by sociality for breeding females. In cooperative breeders, the presence of helpers allow for a load lightening of reproduction for mothers, decreasing their costs associated to reproduction (Crick 1992; Russell et al. 2003b). The Alpine marmot benefits from such released cost of reproduction (Berger et al.

2015a), as male subordinates support in part the cost of social thermoregulation (Arnold 1993a) during hibernation by warming related juveniles (Arnold 1990a, 1993b), thus ensuring a higher winter survival for the latter (Allainé et al. 2000; Allainé and Theuriau 2004, Chap. 3). In addition, during the active season breeding females may also benefit from the protection of the burrows against predation and/or detrimental weather events, so that the pre-weaning survival of juveniles is supposedly quite high and constant over the years for this species (Berger et al. 2015b). Through relaxing in part the costs of reproduction related to environmental conditions, these two points favour the allocation to reproduction regardless of the environmental conditions, and thus explain the higher and more stable reproductive success of dominant females in Alpine marmots compared to Alpine chamois. Finally, a relatively high and constant litter size should be especially advantageous for the Alpine marmot. Because of the benefits of sociality during hibernation, maintaining a suitable group size (around 6-7 individuals) should increase future survival and reproduction and thus the overall lifetime reproductive success (Lardy et al. 2015). Likewise, in addition to a long dominance tenure, juvenile survival was also shown to be an important determinant of reproductive success (Lardy et al. 2015).

5.4.1.2. Variance in the population growth rate and impact of environmental variation

Contrary to our expectations, and in spite of a much less variable recruitment rate, the Alpine marmot population did not display a lower variance in growth rate compared to the Alpine chamois population. Despite tremendous differences in their stochastic population growth rates, the demography of these two species was impacted to a same degree by stochastic environmental variability as expressed by the similar variance in population growth rates. Variances were overall low but corresponded to what may be expected for long-lived species, which should be more buffered against environmental stochasticity than short-lived species (Morris et al. 2008; Gamelon et al. 2016). This departure from our expectations might also reflect

the differences in the mechanisms through which the different species lifestyle and reproductive tactics modulate the influence of environmental variability on vital rates and their relationships.

Overall, the impact of environmental variation on vital rates can be observed on three features, which can, in turn, have an important influence on the stochastic population growth rate: (i) the variation in vital rates over time, (ii) the covariation between pairs of vital rates within a year, and (iii) the covariation of each vital rate or of vital rates pairs between successive years, better known as serial correlations, (which we did not consider in our analyses). The demographic consequences of variability in one trait will thus depend on these three aspects and on the corresponding elasticities, as described by the Tuljapurkar's formula (e.g. Tuljapurkar 1990). Also, while the variance in vital rates systematically decreases the stochastic population growth rate, covariations may act differently. While a positive covariation between vital rates will increase the variance in the population growth rate, by acting in synergy, negative covariations between vital rates can also occur and increase the stochastic population growth rate by decreasing its variance (Doak et al. 2005). The effects of environmental variability through such mechanisms can have important consequences on population demography, as increasingly reported in the last years (Coulson et al. 2005; Doak et al. 2005; Tuljapurkar et al. 2009). Most importantly, a same variance in population growth rates may hide very different driving mechanisms as we highlighted here.

Direct influence of vital rate variation on the population growth rate

First, the higher-than-expected variance in the population growth rate of the Alpine marmot was explained by the high variability in the probability of accessing dominance (*Trans*, Fig. 5.5). Comparatively, the low variability in juvenile survival and fecundity contributed to lower the variance in population growth rate, unlike what was observed for the Alpine chamois population. The probability of accessing dominance, and consequently reproduction for both males and females, does not exist in Alpine chamois and is directly the consequence of the Alpine marmot reproductive tactic, involving reproductive suppression of sexually mature

individuals (Arnold and Dittami 1997; Allainé 2000). The important impact of variation in this trait on the population growth rate was unexpected and could represent a cost of sociality, paid by subordinate individuals. While dominant individuals benefit from group living, with, to some extent, increasing reproductive success and survival with increasing group size (Allainé and Theuriau 2004; Lardy et al. 2015), subordinates are faced with the costs of sociality, among which suppression of reproduction and decreasing survival with increasing group size (Dupont 2017, Chap. V.B). As a result, subordinate individuals contribute negatively to the population growth rate, resulting in a relatively smaller contribution of large family groups with numerous subordinates compared to groups of smaller size (Dupont 2017, Chap. V.B). Between-year variation in the probability of accessing dominance (*Trans*) can be linked to group dynamics. Indeed, dominance change in a group generally results in a drastic decrease in group size (Dupont 2017, Chap.IV.B), with not only the replacement of the same-sex dominant, but also forced departures of mature and non-mature individuals, to avoid high intra-sexual competition (Lardy et al. 2012, 2013). Hence, at the population level, a high probability of accessing dominance might result in a higher proportion of small groups in the population, with a low number of subordinates. which should contribute in increasing population growth rate. Conversely, a low probability of accessing dominance a given year should coincide with large family groups in the population with numerous subordinates, which should then lower population growth rate. Our study thus reveals the importance of this parameter for the marmot population dynamics despite its low elasticity. In contrast to adult survival and recruitment whose variation was limited and under strong selection in this social species, variability in the probability of transition was less submitted to selection and varied widely over years in response to environmental variation.

Amplified influence of variability through positive covariation of vital rates

The observed positive covariation between survival rates in the Alpine marmot population also contributed, to a lesser degree, to increase the variance in population growth rate (Fig. 5.5). This synchrony amplifies the negative effect of their variation

on the population growth rate. This result was less highlighted in the Alpine chamois population, and can similarly be related to the Alpine marmot's lifestyle. Positive covariation between survival rates are generally supposed to arise when individuals are submitted to same environmental conditions within a year and when they respond similarly to it. The fact that such relationships were mainly found in the Alpine marmot could be explained by their high territoriality and proximity. Monitored individuals lived within family groups in spatially stable territories within a small and saturated habitat (Arnold 1993a; Armitage 1999). Individuals then face the exact same environmental constraints that occur locally at the study site, contrary to the Alpine chamois population, whose individuals present more mobility and flexibility in their habitat use (Nesti et al. 2010). Moreover, beyond the effect of environmental conditions, survival of marmots is also expected to be interrelated between individuals of a same family group because of their high level of sociality. For instance, the eviction and likely death of a dominant individual during the active season is often followed by the absence of reproduction or infanticide of the current offspring of the group (Hacklander and Arnold 1999; Lardy et al. 2011). Also, low survival of subordinate males before or during hibernation may also compromise the survival of juveniles within the same group (Allainé et al. 2000; Allainé and Theuriau 2004). Hence, both environmental and social factors interact in driving such synchrony in survival rates in Alpine marmots (Rézouki et al. 2016).

Buffering effect of negative covariations of vital rates

Negative covariations in vital rates have also been highlighted in both species contributing to limiting the effect of vital rates variation on the population growth rate (Fig. 5.5). Such opposite changes in vital rates in response to environmental variations may be the result of the life history strategy, and the reflect of microevolutionary trade-offs (Stearns 1992).

On one hand, a negative covariation between survival and reproduction occurred in the Alpine chamois population (Appendix 5.2.1, Table 5.2), which can be related to the well known survival-reproduction trade-off resulting from the cost of reproduction (Williams 1966; Stearns 1992). As posited by Williams (1966),

resources available for an individual are limited and have be allocated optimally among survival, reproduction, and growth to maximize individual fitness. Trade-off between survival and reproduction are then especially expected when individuals within a population are restricted in their acquisition of resources (van Noordwijk and de Jong 1986). Such cost of reproduction has been shown to increase with population density or severe environmental conditions in several species (e.g. Clutton-Brock et al. 1996 and Tavecchia et al. 2005 in the Soay sheep, *Ovis aries*, Robert et al. 2012 in the Monteiro's Storm-Petrel, *Oceanodroma monteiroi*). Therefore, in line with their conservative reproductive tactic, this result may highlight that, in bad years, female chamois decrease their reproductive effort or skip reproduction to limit the cost of current reproduction on survival, as generally expected for long-lived species (Hamel et al. 2010b).

In contrast, the Alpine marmot did not exhibit such trade-off, as no correlation was evidenced between the current reproduction and survival of adult individuals. This tends to confirm that the lifestyle and reproductive tactic of the Alpine marmot reduce the cost of reproduction for breeding individuals. However, important negative covariations were highlighted between the probability of accessing dominance and all other vital rates except subordinate survival (Appendix 5.2.1, Table 5.2). A change of dominance in a family group has important fitness implications for all members of a group, and may explain these covariations between vital rates. As previously mentioned, it first generally leads to the concurrent eviction of the same-sex dominant individual that can become floater and may probably die thereafter (*e.g.* Stephens et al. 2002; Grimm et al. 2003). Similarly, a change in dominance is often accompanied by a failure in reproduction within the group when dominance is taken by a new male, either through interruption of reproduction for the mothers or through infanticide (Hacklander and Arnold 1999; Lardy et al. 2011). At last, change in the dominance has been recently shown to decrease survival of sexually mature and non-mature subordinates of the same sex (Dupont 2017, Chap. IV.B), which may be forced to disperse by the new dominant, certainly to avoid high intra-sexual competition (Lardy et al. 2012, 2013). Overall, these strategies may explain the strong negative covariation observed between the access of dominance, reproduction and survival of dominant and yearling

individuals, but not the positive covariation with survival of subordinates. The latter can result from an increase in survival generated by more subordinates becoming dominant, instead of dispersing and failing to access a new territory within the study site. Accessing dominance can also occur by occupying a new territory, and does not necessarily involve the departure of other subordinates. From a demographic point of view, these results reveal that the positive effect on population growth rate of an increase in the probability of accessing dominance of subordinate individuals, will be in part counter-balanced by fitness costs paid by other individuals in terms of survival and reproduction, contributing to decrease population growth rate. Likewise, the negative effect on population growth rate of a decrease in the probability of accessing dominance will be in part counter-balanced by higher survival and reproductive rates for dominants individuals due to the benefits of sociality. Hence, this negative covariation between vital rates of the Alpine marmot is representative of the evolutionary conflict between costs and benefits of sociality between dominant and subordinate individuals. Overall, the observed total contribution of variation in the probability of accessing dominance on the variance of the population growth rate will be the result of this conflict.

5.4.2. Between-species resistance to current environmental change

Because of its lifestyle, we expected the Alpine marmot population to suffer more from the directional change in weather conditions than the Alpine chamois. Our results tend to support this expectation, as illustrated by the decrease in the deterministic population growth rate observed for the Alpine marmot, but not for the Alpine chamois. This between-species difference in demographic response is likely due to differences in how vital rates of these two species are impacted by the ongoing environmental change. Furthermore, the way the lifestyle influences the functional dependence of the population growth rate to vital rate may also explain these between-species differences in demographic response.

Impact of environmental change on vital rates

As highlighted in previous studies, juvenile survival and litter size decreased over years in the Alpine marmot population because of harsher winters (Tafani et al. 2013; Rézouki et al. 2016). It was shown to be related to decreasing mean snow depth and air temperature in winter, making winters colder and less snowy. These previous analyses also revealed that the impact of these environmental changes were complex and directly interacted with the marmot lifestyle to cause the observed decrease in juvenile survival and litter size.

It seems that the same lifestyle characteristics that we previously identified as buffering the recruitment parameters against environmental conditions may have been disrupted by recent environmental changes. First, the protective effect of hibernating in underground burrows has been negatively impacted by the decreasing snow layer in winter (Tafani et al. 2013). This singular dependence of the Alpine marmot to a high amount of snow in winter to succeed hibernation makes this species to differ from the Alpine chamois or other mountainous mammals that generally suffer from high snow cover in winter (e.g. Loison and Langvatn 1998 on *Cervus elaphus*, Crampe et al. 2002 on *Rupicapra pyreneica*, Rughetti et al. 2011 on *Rupicapra rupicapra*). Second, the buffering effect of cooperative breeding on juvenile survival during hibernation has been also decreased by environmental changes, leading to a decrease in the number of male subordinates within family groups during hibernation (Rézouki et al. 2016). Here again, this indirect impact of environmental variation on the marmot population dynamics may strongly differentiate this social species from mountainous ungulates, regarding their response to environmental change.

In contrast, no temporal trend was highlighted in vital rates of the Alpine chamois indicating a higher resistance of chamois to increasingly harsher winters. Adults may resist environmental constraints of the winter through important fat reserves and by seasonally selecting good quality habitats, generally moving to lower altitudes during the winter (Lovari et al. 2006; Nesti et al. 2010). Likewise, no strong influence of the winter conditions was found on prime-aged survival, but more on senescent individuals (Loison et al. 1999c and see Gonzalez and Crampe 2001 on *Rupicapra pyrenaica),* although exceptional weather events in winter, such as high snowfall, can represent a high mortality risk for individuals of all ages

(Bocci et al. 2010; Rughetti et al. 2011). On the other hand, the negative effect of colder and snowier winters might also have been efficiently counter-balanced by the positive effect of an earlier onset of vegetation in spring. Both survival and reproduction depend strongly on the body fat reserves during winter, and thus on the access to rich vegetation resources during warm months. This is in accordance with what was reported in Pioz et al. (2008), where high snowfalls in early spring tended to decrease the reproductive success of Alpine chamois. Finally, although we had no information about the temporal variation in juvenile survival for the Alpine chamois in the studied population, we can hypothesize that this vital rate also faces opposite influences of harsher winters and earlier springs. The negative influence of harsher winters, which might be particularly critical for this age class (see Willisch et al. 2013, Crampe et al. 2002, on *Rupicapra pyreneica*), might be counteracted by the positive effect of an earlier access to vegetation (see Garel et al. 2011 for a positive effect of early spring on juvenile body mass).

Finally, our results also highlighted an increase in the probability of accessing the dominance over years for the Alpine marmot (Fig. 5.3). Long-term changes in this parameter have received little attention so far, yet its potential importance in understanding the way climate change impacts the marmot population demography was highlighted in our previous study (Chap. 4). The positive trend we found here agrees with our hypothesis that this transition probability continuously changes over time as a response to climate change. More precisely, we propose that an increase in this probability results from the observed decrease in mean group size that occurred in the population over years which may have originated from a decreasing juvenile survival and litter size. The smaller the group, the higher the possibility for subordinates to create or occupy a new territory, in turn increasing the probability to access to dominance (Chap. 4). This hypothesis seems to be supported by complementary analyses that revealed a negative relationship between group size and the probability of transition (Fig. S5.4). We also proposed that climate change may have disrupted the dispersal decision pattern of subordinates by decreasing their fitness benefits associated to sociality, hence also increasing the number of attempts to access dominance (Chapter 4). The more the group size decreases, the more the probability of transition may increase, especially with decreasing benefits of

sociality for subordinates, and in return the more family groups suffer from drastic decrease in their size. Thus, a self-sustaining chain reaction between variation in group size and dominance access, initially driven by environmental change, could have led to the observed increase in the probability of transition.

Different long-term population demographic responses, which underlying mechanisms?

As predicted, in contrast with the Alpine chamois, the Alpine marmot population suffered from a decrease in its population growth rate. We expected the continuous decrease in juvenile survival and reproduction to negatively impact the marmot demography over years. However, the observed decrease in the population growth rate was not continuous over time and resulted mostly from important decreasing events occurring early in the study (Fig. 5.6). Mechanisms behind the long-term changes in the population growth rate of this species appeared also more complex than expected. As revealed by the annual LTRE, variation in reproduction virtually did not impact population growth rate, whereas dominant survival unexpectedly played an important role in this decrease (Fig. 5.7, Fig. S5.3). Likewise, the long-term change in λ can be depicted in two steps.

First, the overall decrease in population growth rate mostly resulted from a strong decrease that occurred during the first period of the study (from 1990 to 2000, Fig. 5.6). Three major between-year decreases occurred in this period, and were not counter-balanced by similar subsequent between-year increase in λ. These exceptionally high decreases in population growth rate coincided with low demographic compensations between changes in vital rates, as most vital rates tended to decrease in these years (Fig. 5.7). Hence the long-term decrease in population growth rate was not only caused by juvenile survival, but also by a synchronous decrease with other vital rates in the early study period (see early decrease in *Syear*, *Ssub, Sdom* and *Trans* in Fig. 5.3). This pattern was unexpected given the negative covariations we previously highlighted between survival and transition vital rates. We may then ask whether this synchrony could be the result of particularly detrimental environmental conditions that impacted globally marmot

individuals of all ages and social status. A concurrent decrease in mean group size was also observed over this period, supporting the hypothesis that environmental variation rather than social factors drove the general decrease in λ (Chap. 4). In a second step, the decrease in the marmot population growth rate was importantly dampened since the year 1999 (Fig. 5.6), when a strong increase in the probability of accessing dominance occurred. The population was more resistant to detrimental environmental change from there, as a result of many compensatory changes among vital rates, especially brought by opposite variation in the probability of transition and subordinate survival with other vital rates (Fig. 5.5). Likewise, higher probability of accessing dominance then met lower mean group size during this period (Fig. S5.4). Hence, the Alpine marmot population may have shifted toward a quite different group and population dynamics in this second period, as discussed above.

Overall, our findings illustrate the interest of investigating inter-annual changes in population growth rate. Our approach allowed highlighting unexpected and important contributions of vital rates, which did not show any temporal trend (such as the dominant survival), to the temporal long-term decrease of the growth rate. It also allowed grasping that a continuous trend in environmental variables impacting vital rates will not necessarily impact the population growth rate in the same way, as the effect of environmental change in the marmot population was altered by temporal changes in vital rates relationships, strongly shaped by sociality.

Finally, we expected no temporal trend to arise from annual projection of the population growth rate in the Alpine chamois given the absence of a trend in its vital rates. However, the lack of a pronounced trend for models including a decrease in juvenile survival was more surprising, especially as survival rate importantly explained between-year difference in λ in this population (Fig. 5.6). This contrasting result confirms the importance of the interaction between juvenile survival and other vital rates in driving the observed decrease in the Alpine marmot population growth rate, thus highlighting that a same change in a vital rate can lead to very different demographic responses according to the lifestyle of the species.

5.4.3. Conclusion

The species' reproductive tactic and lifestyle strongly structure the influence of environmental variation on the population demography of our two alpine species, therefore explaining the observed between-species differences in their demographic responses to environmental changes. For species sharing similar paces of life, differences in reproductive tactics and/or lifestyle can thus result in different mechanisms underlying their demographic buffering. Furthermore, the effects of such species characteristics are not only to be investigated on vital rate variance, but also on vital rate covariance, especially for social species (see also Morris et al. 2011), to better understand mechanisms underlying their demography in variable environments. As highlighted here, the lifestyle impacts population responses at two levels, (i) by directly influencing the relationship between vital rates and environmental factors, and (ii) by structuring differently the demographic properties of populations, so that a same change in a vital rate will not necessarily have the same impact on the population growth rate according to the species, as it may depend on its relationship with other vital rates, and on further specific behavioural changes. Furthermore, this study also revealed an important and unexpected cost of sociality on the population demography and asks for further investigations on the influence of sociality and notably of the influence of group dynamics on population growth rate. Overall, it offers promising prospects, stressing the importance to consider the structuring role of the reproductive tactic and lifestyle, in addition to the role of the generation time to better understand inter-specific population responses to environmental change.

Appendix

Appendix 5.1 Projection matrix used in the demographic analyses for the two species

Appendix 5.2 Detailed temporal covariation between vital rates of each population and on the contribution to the variance in population growth rate

Appendix 5.3 Additional results concerning the annual Life Table Response Experiment (LTRE) analysis

Appendix 5.4 Complementary results regarding the probability of accessing dominance (*Trans*)

Appendix 5.1. Projection matrix used in the demographic analyses for the two species

$$\mathbf{A_m} = \begin{pmatrix}
0 & Syear*Trans_young*Fert_young & Ssub*Trans*Fert & Ssub*Trans*Fert & Ssub*Trans*Fert & 0 & Sdom*Fert & Sdom*Fert & Sdom*Fert & Sdom*Fert & Sdom*Fert & Sdom*Fert & Ssenes*Fert & Ssenes*Fert & Ssenes*Fert & Ssenes*Fert & Ssenes*Fert & Ssenes*Fert & Ssenes*Fert & Ssenes*Fert & 0 \\
Sjuv & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & Syear*(1-Trans_young) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & Ssub*(1-Trans) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & Ssub*(1-Trans) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & Ssub*(1-Trans) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & Syear*Trans_young & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & Ssub*Trans & 0 & 0 & 0 & Sdom & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & Ssub*Trans & 0 & 0 & 0 & Sdom & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & Ssub*Trans & 0 & 0 & 0 & Sdom & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Sdom & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Sdom & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Ssenes & 0 & 0
\end{pmatrix}$$

Figure S5.1.1. Population projection matrix $\mathbf{A_m}$ used in the demographic analyses for the Alpine marmot population of La Grande Sassière.

$$\mathbf{A_c} = \begin{pmatrix}
0 & \text{Sprime*Fert} & \text{Sprime*Fert} & \text{Sprime*Fert} & \text{Sprime*Fert} & \text{Sprime*Fert} & \text{Sprime*Fert} & \text{Sprime*Fert} & \text{Sold*Fert} & \text{Sold*Fert} & \text{Sold*Fert} & \text{Sold*Fert} & \text{Sold*Fert} & \text{Ssenes*Fert} & \text{Ssenes*Fert} & \text{Ssenes*Fert} & \text{Ssenes*Fert} & \text{Ssenes*Fert} & \text{Ssenes*Fert} & \text{Ssenes*Fert} & 0 \\
\text{Sjuv} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Sprime} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Sold} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Sold} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Sold} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Sold} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Sold} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \text{Ssenes} & 0
\end{pmatrix}$$

Figure S5.1.2. Population projection matrix $\mathbf{A_C}$ used in the demographic analyses for the Alpine chamois population of Les Bauges.

Appendix 5.2. Detailed temporal covariation between vital rates of each population and on the contribution to the variance in population growth rate

Table S5.2.1. Variance and covariation between vital rate for A) the Alpine marmot and B) the Alpine chamois population

A)	Sjuv	Syear	Ssub	Sdom	Fec	Trans
Sjuv	2,44E-02	1,16E-02	2,37E-03	3,17E-03	4,12E-03	-7,94E-03
Syear	1,16E-02	1,81E-02	6,10E-03	5,16E-03	2,91E-04	-9,38E-03
Ssub	2,37E-03	6,10E-03	1,55E-02	-2,83E-03	5,82E-04	3,72E-03
Sdom	3,17E-03	5,16E-03	-2,83E-03	1,35E-02	-4,22E-05	-2,12E-03
Fec	4,12E-03	2,91E-04	5,82E-04	-4,22E-05	1,21E-02	-1,01E-02
Trans	-7,94E-03	-9,38E-03	3,72E-03	-2,12E-03	-1,01E-02	5,92E-02

B)	*Sjuv_simul*	Sprime	Sold	Ssenes	Fec
Sjuv_simul	*4,24E-02*	*-3,08E-03*	*3,48E-03*	*5,59E-03*	*-4,77E-03*
Sprime	*-3,08E-03*	8,66E-03	1,48E-04	4,63E-03	-2,37E-03
Sold	*3,48E-03*	1,48E-04	1,64E-02	8,56E-03	-1,39E-03
Ssenes	*5,59E-03*	4,63E-03	8,56E-03	5,27E-02	-2,36E-03
Fec	*-4,77E-03*	-2,37E-03	-1,39E-03	-2,36E-03	2,86E-02

Table S5.2.2. Detailed contribution of the variation and covariation of the vital rates to the variance of the population growth rate λ for A) the Alpine marmot population and B) the Alpine chamois population.

A)	Sjuv	Syear	Ssub	Sdom	Fec	Trans
Sjuv	1,84E-03	5,06E-04	1,31E-04	3,78E-04	1,45E-04	-4,82E-04
Syear	5,06E-04	4,56E-04	1,96E-04	3,55E-04	5,94E-06	-3,30E-04
Ssub	1,31E-04	1,96E-04	6,33E-04	-2,48E-04	1,51E-05	1,67E-04
Sdom	3,78E-04	3,55E-04	-2,48E-04	2,54E-03	-2,36E-06	-2,04E-04
Fec	1,45E-04	5,94E-06	1,51E-05	-2,36E-06	2,00E-04	-2,89E-04
Trans	-4,82E-04	-3,30E-04	1,67E-04	-2,04E-04	-2,89E-04	2,90E-03
C_var	1,84E-03	4,56E-04	6,33E-04	2,54E-03	2,00E-04	2,90E-03
C_covar	6,78E-04	7,33E-04	2,61E-04	2,78E-04	-1,25E-04	-1,14E-03
Tot	2,52E-03	1,19E-03	8,94E-04	2,82E-03	7,49E-05	1,76E-03

B)	*Sjuv_simul*	Sprime	Sold	Ssenes	Fec
Sjuv_simul	*2,36E-03*	*2,11E-03*	*-1,02E-04*	*6,86E-05*	*-1,98E-04*
Sprime	*2,11E-03*	4,75E-03	1,38E-05	9,09E-05	-5,30E-04
Sold	*-1,02E-04*	1,38E-05	2,60E-04	2,85E-05	-4,08E-05
Ssenes	*6,86E-05*	9,09E-05	2,85E-05	3,71E-05	-1,60E-05
Fec	*-1,98E-04*	-5,30E-04	-4,08E-05	-1,60E-05	1,63E-03
Tot	*1,78E-03*	3,82E-03	8,34E-05	6,79E-05	1,02E-03
C_var	*2,55E-03*	4,75E-03	2,60E-04	3,71E-05	1,63E-03
C_covar	*-7,65E-04*	-9,21E-04	-1,76E-04	3,07E-05	-6,05E-04

Appendix 5.3. Additional results regarding the annual Life Table Response Experiment (LTRE) analysis

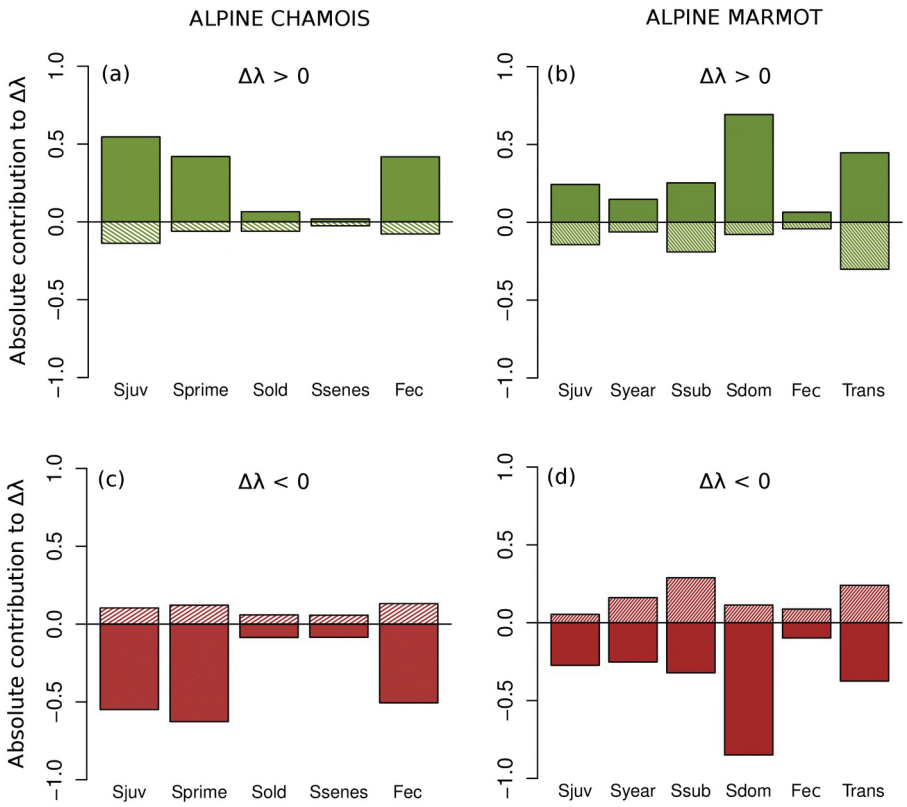

Figure S5.3. Absolute contribution of each vital rates to the annual difference in the population growth rate, for the cases where the population growth rate increases between two years ($\Delta\lambda>0$, in green) and when the population growth rate deceases between two years ($\Delta\lambda<0$, in red), for the Alpine chamois (a,c) and the Alpine marmot (b,d) population.

Appendix 5.4. Complementary results regarding the probability of accessing dominance (*Trans*)

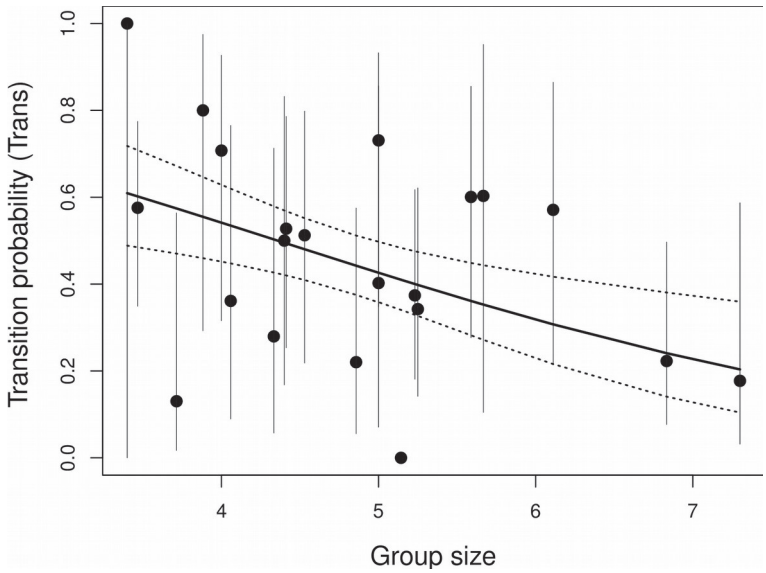

Figure S5.4. Annual probability of transition from the subordinate to the dominant status (± 95% CI, vertical grey segments) as a function of the mean group size in the Alpine marmot population of La Grande Sassière (French Alps). Solid black line represents the model prediction and dashed lines its associated confidence intervals (± 95% CI).

Chapter 6

Discussion

6.1. Overview of main results

The aim of this thesis was to better understand the role of the species' lifestyle in influencing population dynamics and their responses to environmental variation. We addressed this question by focusing on the Alpine marmot as a study model because of its particular lifestyle (i.e., hibernation and social-living) combined with its reproductive tactic (i.e., cooperative breeding). We highlighted that the lifestyle strongly allowed for increasing demographic rates in this species by providing them advantages to face environmental variation. Importantly, these benefits were disrupted by climate change, which negatively impacted marmot demography over the years.

In *chapter 3*, we expected social hibernation to buffer individual survival against weather variation in winter, and therefore survival rates of the Alpine marmot to be mostly enhanced by earlier springs over time. In contrast, our results showed that juvenile survival continuously decreased over the years because of the overwhelming detrimental winter conditions; colder winters associated to a thinner snow layer might have resulted in a poorer thermal insulation of burrows. Moreover, we saw that the observed decrease in juvenile survival was also promoted by a parallel decrease over-time in the presence of helpers in family groups. This disruption in the social composition of groups appeared also to be a consequence of winter weather conditions, which have caused the overall recruitment of this population to decrease in previous years, leading to decrease both litter size and juvenile survival. These results thus highlight both direct and indirect (lifestyle-mediated) effects of climate change on Alpine marmot population dynamics.

We found in *chapter 4*, that cooperative breeding may not be especially affiliated to a bet-hedging strategy in our population, contrary to what was recently proposed from studies carried out on cooperative breeding birds. The beneficial effect of helpers' presence on juveniles of the family group was mostly brought by increasing mean survival than by decreasing temporal variance of the survival of this age-class. As a general rule, helpers contribute to a large extent to increase the population growth rate. However, we suggest that the adaptive value of cooperative breeding decreased with climate change; in the last decade, it appears no more

beneficial for young to hibernate with helpers because of higher costs of thermoregulation. Demographic analyses also revealed that a parallel change in the probability of accessing to dominance occurred in last years and have partly compensated for this loss of benefits from cooperative breeding, hence limiting its resultant negative impact on the population growth rate. This study clearly illustrates the dynamic relationship between environmental variation and cooperative breeding in our population, and how this interplay impacted the Alpine marmot population over the years.

In the last part, *chapter 5*, we hypothesized the species lifestyle and reproductive tactic can be important determinants of population demography in variable environment, and should then account for differences in demographic response between the sympatric Alpine marmot and chamois to current environmental change. Accordingly we found that these factors influenced the way environmental variation impacted vital rates and differed between these two species. They resulted in different variance of the vital rates; the recruitment rate of the Alpine marmot population appeared especially buffered against environmental variation compared to the chamois. They also resulted in different covariation and trade-offs between vital rates for these two species. However, while we expected the Alpine marmot population to be more buffered against environment variation thanks to hibernation, our results suggest an unexpected cost of sociality on population demography, so that population growth rate of these two species seemed impacted to the same degree by environmental variation despite very different underlying mechanisms. Finally, as expected, the Alpine marmot appeared more negatively impacted by climate change than the chamois, definitely because of differences in their lifestyle. This study overall evidences how lifestyle can influence the effect of environmental variation population demography, and its potential to explain between-species differences in response to climate change.

6.2. The influence of the Alpine marmot lifestyle on its demographic response to climate change, current and future challenges

Overall, this thesis led to better understand the way Alpine marmot population responded to environmental variation and climate change, highlighting a major role of the species' lifestyle in mechanisms underlying its response (see Fig. 6.1 for a synthesis). I propose in this part to assess our current knowledge as well as the remaining questions regarding mechanisms of response of the Alpine marmot to climate change. This response, which was depicted separately throughout the chapters, can be described in three different stages (Fig. 6.1) that will be detailed below.

6.2.1. Litter size, juvenile survival and winter weather conditions, the first main perceptible changes

The main vital rates impacted by climate change in the Alpine marmot population appeared to be juvenile survival (Chap. 3) and litter size (Tafani et al. 2013) which both continuously decreased over years. These demographic parameters are known to be especially sensitive to environmental variation in population of long-lived species (Gaillard et al. 2000; Gaillard and Yoccoz 2003). Likewise, several studies revealed young age-classes contributed the most to the demographic responses to climate change. Whether the impact was positive (e.g. Hegel et al. 2010; Hamel et al. 2010a) or negative (e.g. Pettorelli et al. 2007; Gaillard et al. 2013), recruitment parameters appeared the most affected. Our results highlighted that change in the winter conditions played a crucial role in decreasing marmot recruitment (Chap. 3), a season known to be very constraining for individuals inhabiting high Alpine environments.

However, that the Alpine marmot fits the general pattern of response observed in other non-hibernating species was in theory unexpected. Its lifestyle, and especially hibernation, which directly evolved as a response to the harsh winters experienced at high altitude, was supposed to limit the impact of detrimental

changes in winter conditions, as previously discussed (Tafani et al. 2013, Chap. 3). Conversely, vital rates supposed to be buffered against environmental variation by the species lifestyle were the very ones that were most impacted by climate change, which first questions the role of the lifestyle in these changes. Our first explanation was that the success of hibernation should strongly depend on snow-depth, which influences the insulation of the burrow from variation in winter air temperatures. Both snow-depth and external temperature determine the amount of energy required to survive winter for the hibernating marmot. A detrimental combination between these factors, as observed in our study site, with a thinner snow layer and colder temperatures, should hamper the probability of a successful hibernation. Hence our results stress that this energy saving strategy might have reached a limit. Individuals in torpor within the burrows can only undergo these detrimental local weather conditions encountered in winter, which are all the more harmful for the youngest individuals, and which should increase body mass loss during hibernation, hampering successful reproduction at emergence (Tafani et al. 2013). The limits of the hibernation strategy may also constitute a tipping point for the keeping up with cooperative breeding (Chap. 3). This second aspect of the response, closely linked to sociality, has to be understood in order to have a complete understanding of the Alpine marmot population response.

6.2.2. From less effective hibernation to disruption of the social structure and change in individual behaviour ?

Relationship between hibernation and sociality appeared important in the response of the Alpine marmot population to climate change (Chap. 3, 4). This relationship has been previously discussed within the gender *Marmota,* for which hibernation is generally seen as a prerequisite for the evolution of sociality *(*see Chap. 2, Arnold 1990a, 1993b; Blumstein and Armitage 1999; Armitage 2007).

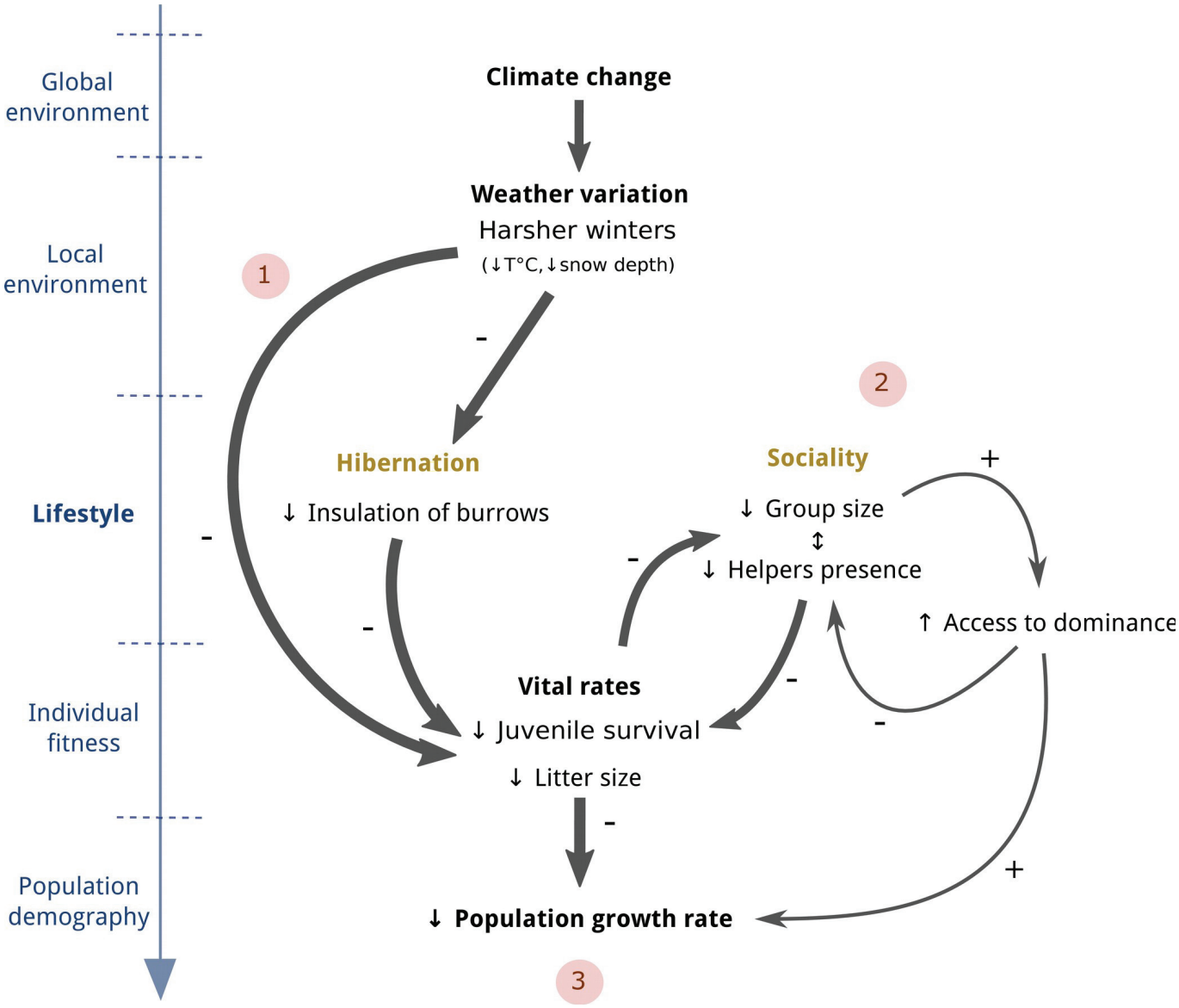

Figure 6.1. Main pathways by which climate change impacts on the Alpine marmot population dynamics of La Grande Sassière. The species' lifestyle appears as a central component of the response, lying at the interface between environmental conditions and population demography. Overall the impact of climate change can be decomposed in three steps. Harsher winters (1) decreased the effectiveness of hibernation within burrows impacting individual fitness, (2) disrupted indirectly group dynamics and (3) impacted the population growth rate because of both changes in the demographic and social structure of the population. These three response mechanisms are detailed in the main text.

We may then ask whether a disturbance in the effectiveness of hibernation can overcome the advantage of sociality in Alpine marmots, which could be a second mechanism of the Alpine marmot population response to current climate change (Fig. 6.1). As a consequence of the increasing winter harshness, benefits of helpers presence for young to sustain hibernation has been impaired over the years (Chap. 4). Furthermore, the overall decrease in recruitment within family groups may have caused an overall decrease in mean group size and thus in the proportion of groups with helpers (Chap. 3, 4). Both the effectiveness of helping behaviours and the composition of social groups are determinants of the adaptive value of cooperative breeding, being important factors of individual fitness of Alpine marmot (Allainé et al. 2000; Lardy et al. 2015; Berger et al. 2015a). Consequently, changes in these factors have contributed in turn in decreasing juvenile survival. This consequence of climate change on survival rate of juveniles in groups with and without helpers illustrates the importance of the relationship between hibernation and sociality in influencing population dynamics. Benefits of joint hibernation is expressed only when the hibernaculum is well buffered against external air temperatures.

Disruption in the adaptive value of hibernation and sociality may have also changed individual behaviours, as suggested by the large unexpected increase in the access to dominance for subordinates (Chap. 4, 5). As discussed over the chapters, this increase in the access to dominance should follow from a higher dispersal of subordinates given that the benefits of dispersing should, in last years, exceed the benefits for subordinates of remaining in the natal burrow. The negative relationship we found between group size and the probability of accessing dominance tends to support this theory and can be envisioned in two ways. First, the decrease in group size may have limited the habitat saturation in the marmot population, which should increase the benefit of dispersing by providing new opportunities for subordinates to settle down (see Fig. 6..4). This possibility of settling in nearby areas can be assessed by subordinates through exploration displacement during the active season. Second, group dynamic is known to be closely related to dispersal in social species (e.g. Bateman et al. 2012, 2013 in meerkats, *Suricata suricatta*). A decrease in group size can in part result from intense dispersal of subordinates of the family, or from

immigration of a new subordinate, involving the removal of the previous dominant and potential eviction of immature and mature subordinates (see Discussion in Chapter 5). A decrease in mean group size in the population may thus be positively linked to dispersal events. These relationships between group size and access to dominance can be synthesized within a general hypothetical scheme (Fig. 6.2), which establishes the link between the environment, the individual behaviour and the group dynamics in this social species. We witness that climate change can be currently impacting these two components of sociality as well.

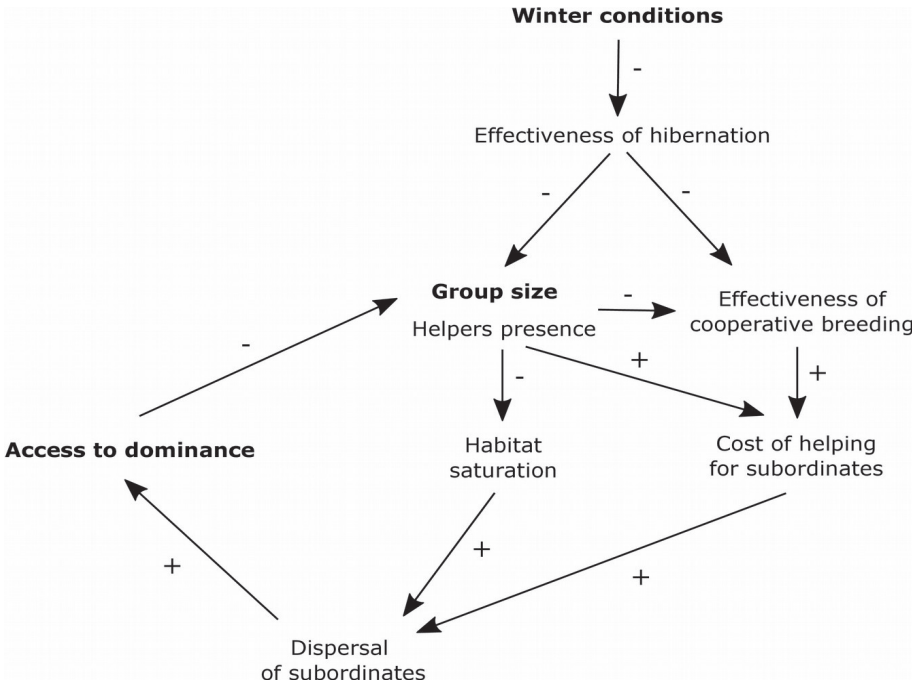

Figure 6.2. Details of main hypotheses proposed regarding mechanisms underlying the observed increase in the access to dominance and decrease in group size in our Alpine marmot population.

The influence of environmental variation on group dynamics is complex, as reported by Bateman et al. (2013) in the cooperatively breeding meerkat. In this species, variation in group size has been related to yearly variation in rainfall (Bateman et al. 2012, 2013). Overall, in meerkats dispersal was the main driver of group dynamics, and was directly influenced by weather conditions but also, indirectly by change in the age-structure of the groups (Bateman et al. 2012, 2013). In the same way, it would be interesting to better understand which factors (e.g., social, demographic, or environmental factors) mainly influenced group dynamics in our population, which especially means to understand causes and consequences of dispersal in our population.

6.2.3. Mechanisms underlying the overall population demographic response

In the Alpine marmot, changes in juvenile survival and in the probability of accessing dominance had opposite effects on the population growth rate (Chap. 4, 5). As expected, the decrease in juvenile survival contributed substantially to decreasing the population growth rate. On the other hand, the marked increase in the probability of accessing dominance contributed to increasing the population growth rate, compensating in part the negative impact of lower individual fitness (Chap. 4). Mechanisms underlying this positive impact of a higher access to dominance at the population level are less obvious at first glance. Overall the probability to access dominance can be seen as a proxy of the social structure of the population (Chap. 5). A very high probability to access dominance in a year should match a population subdivided in groups of small size on average, composed of few subordinates, while a very low probability to access dominance in a year should be associated with a population subdivided in less numerous but larger groups with more subordinates. Variation in the overall composition of groups should have an important influence on the population demography, as shown by the strong influence of variation in the probability of accessing dominance on the population growth rate (Chap. 5). Recently, Dupont (2017) found that family groups of more than five individuals contribute negatively to population growth rate, which should be linked to higher

costs associated to sociality for subordinates. Thus, the positive influence of a higher access to dominance on the population growth rate may overall reflect a released cost of sociality for subordinates which now live within smaller groups. The costs and benefits of sociality that individuals face can be reflected at the population level, where the loss of benefits of sociality for juveniles negatively impact the population while a released cost of sociality for subordinates positively influence the population. All of this being indirect results of the disruption of benefits to hibernate with others.

Finally, some mechanisms underlying the long-term change in the population growth rate remain unclear, as highlighted in Chapter 5. Switching from a two-periods LTRE to annual LTREs allowed us to better grasp the influence of change in each vital rates throughout the years, showing that the decrease in the population growth rate over time was not linear. Mechanisms behind the decrease in population growth rate appeared complex, and the strong negative influence of other vital rates, as of dominant survival was for instance revealed. Overall from our results, we can roughly observe three time periods in the dynamics of the marmot, which are related to particular combinations of group size and vital rates (see Fig. 6.3 for a schematic view of these three-steps changes).

- In a *first period* (from 1990 to 1998), a decrease in main vital rates, including in the access to dominance, may have strongly decrease mean group size and the population growth rate as well. This short-period could result from changes in the demographic structure of the population.
- In a *second period* (from 1998 to 2006), the situation stabilized following an increase in the access to dominance. This stable situation can also be detected in group size, with low yearly variation around a small mean size, and partially in the other vital rates, with the probability of accessing dominance varying around 0.5. This may represent a period of transition with balanced alternance between years of high dispersion and years of low dispersion, allowing the presence of both average and very small groups within the population.
- Finally in the *third period* (from 2006 to 2013), growth rate decreased again. This period is characterized by opposing changes in vital rates and group size (Fig. 6.3), which might combine negative and positive influence of change in the demographic

and social structure of the population. High dispersal rates of helpers might result in new groups and limit the accumulation of large groups. This hypothetical scenario founds some supports with the observed change in the total number of group (Fig. 6.4), and in the changes in the distributions of group size within the population over time (Fig. 6.5).

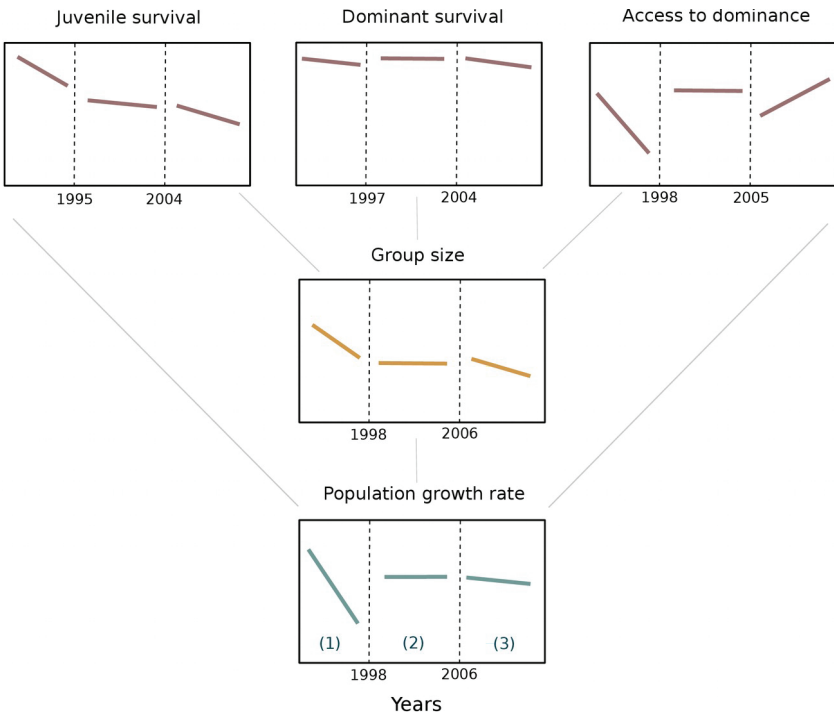

Figure 6.3. Simplified situations of the three different time periods we identified at La Grande Sassière based on annual variation in main vital rates, group size and population growth rate from 1990 to 2013 in the Alpine marmot population. The demography of the Alpine marmot differs markedly among the three time period we identified.

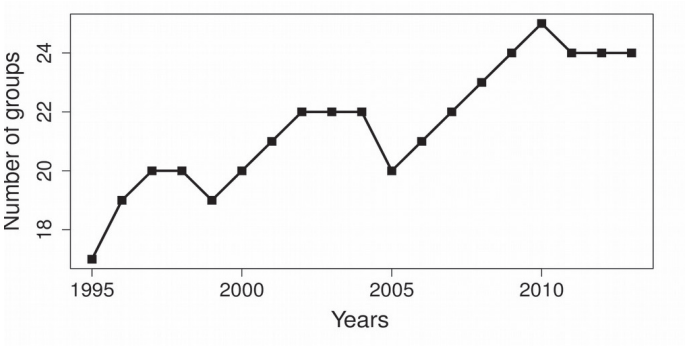

Figure 6.4. Number of groups observed each year within the Alpine marmot population of La Grande Sassière from 1995 to 2013. Before 1995, the sampling effort strongly increased in the field, while from 1995 to 2013, family groups have been monitored over a same delimited area in the study site allowing to reliably approach the creation of new groups within the population.

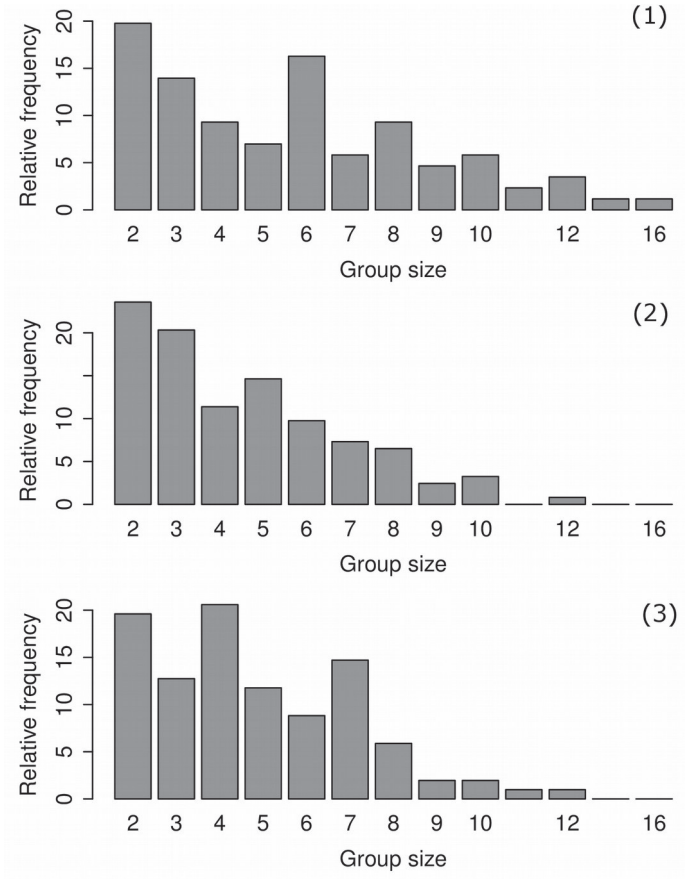

Figure 6.5. Distribution of group size in the Alpine marmot population of La Grande Sassière between the three periods with different short-term population trends, (1) from 1990 to 1998, (2) from 1999 to 2006 and (3) from 2007 to 2013.

6.2.4. Further analysis perspectives

Annual LTREs is a clear illustration of the very short time-scale at which the population dynamics may respond to changes in environment and to social perturbations. These preliminary analyses give an overview of the main demographic drivers of the population dynamics, but are based on rather strong assumptions, such as the assumption of a stable population structure over time. Like most populations facing climate change, our population seems subjected to a non-stationary environment (Chap. 1, Wolkovitch et al. 2014). It should be interesting to account for this non-stability of the environment and in the population to have a complete overview of its demographic drivers. Transient dynamics (Koons et al. 2005) are particularly appropriate in this environmental context, allowing to estimate short-term (transient) population growth rate, which may possibly quite differ from the asymptotic growth rate (Koons et al. 2005). Transient dynamics quantify also the interplay between change in vital rates and in the population age-structure on growth rate (e.g. Gamelon et al. 2014). Likewise, newly developed transient LTREs (Koons et al. 2016) appear as a very promising tool that should be implemented to fine tune our results on marmots.

Finally, just as it should be interesting to understand group dynamics over time (as discussed previously, see Bateman et al. 2013), it should also be interesting to investigate how change in the composition of groups and in group size distribution impacted the population growth rate over the years. Overall, benefits of cooperative breeding should have decreased over years, while at the same time, cost of sociality, and especially costs for individuals of being in large groups, should have increase. We propose this effect of climate change to be the key to understanding subsequent change observed in group dynamics. Following this hypothesis, we predict the contribution of large groups to the population growth rate to decrease throughout the years. Just as we observed a shift in distribution of group size over time (Fig. 6.5), a shift in the contribution of groups to growth rate according to their size should have occurred, with large groups contributing more to decreasing population in last years than at the beginning of the study.

6.2.5. What future for the Alpine marmot population ?

Climate change mostly impacted the Alpine marmot population by disrupting the success of hibernation and as a consequence, by decreasing the benefits from cooperative breeding in this population. The lower presence of helpers is no beneficial anymore for juveniles whether facing good or bad environmental conditions. What does it imply for the marmot population on the long term ?

The Alpine marmot is not an obligate cooperative breeder, that is, successful reproduction and survival of juveniles without helpers is possible and frequent within the population. It rather is an obligate social living species, as the youngest individuals and adult floaters can not survive solitary hibernation (Stephens et al. 2002). We may consider that the decrease in group size was promoted/triggered by an inverse density-dependent effects (Allee effects, Allee et al. 1949) over the years because of less effective social thermoregulation of smaller groups (Stephens et al. 2002). In future years juvenile survival is doomed to be lower and more variable as it might be the case for survival of adults marmots for which reproduction should become more costly without cooperative breeding (see the beneficial effect of helpers presence on fitness of dominants in Lardy et al. 2015; Berger et al. 2015a, 2016). Moreover, increasing variability are all the more expected in the following years that increasing social conflicts between subordinates and dominants should lead towards even more unstable groups over time, which might induce additional variability in demographic parameters through dominance take-overs and infanticides.

Overall, we suggest future changes in the marmot population should move in the same direction as lately observed, with more unstable and smaller family groups on average in the following years. The population growth rate might be more variable because of the increased vital rates variability and could remain negative. It should not necessarily decreased furthermore because of possible rapid spatial restructuring of the social groups. An overall population decline is thus expected in the long term. The speed of decline and the long-term population persistence will then depend on future local changes in weather conditions as the population should be more sensitive to environmental variation overall.

If future changes consist in a series of detrimental weather conditions in winter over several years, then a drastic decrease in population size may occur and stochastic extinctions of small groups might be difficult to compensate through dispersal. The population should be increasingly sensitive to demographic stochasticity, and as suggested by Stephens et al. (2002), may suffer from demographic Allee effects because of difficulties in finding a mate, which may prevent the recovery from such population crash.

On the other hand, positive effects of earlier springs have been highlighted for marmots, notably on litter size (Tafani et al. 2013) and body condition (Canale et al. 2016). These effects did not compensate for the negative influence of harsher winters though, but are interesting to consider, especially if future changes involve an even greater access to a good quality vegetation at emergence from hibernation and less important changes in winter conditions. Under these circumstances, spring phenology would be able to limit the population decline. As recently highlighted by Canale et al. (2016), Alpine marmots are in better condition in recent years through an early growing season; individuals body size and body growth decreased over time while body mass remained constant, hence individuals become fatter relatively to their size. These changes can be beneficial for the marmots, as it may decrease their food requirements while increasing their fasting resistance to face winters, and should also allow individuals to increase their foraging time in summer, as it allows for greater body heat loss to resist higher temperatures (Canale et al. 2016). However, such increased heat dissipation might also be detrimental during hibernation. The implications of these phenotypic changes on individual fitness remains to be understood, and are not to be excluded from further investigations regarding the Alpine marmot response to climate change.

6.3. Sociality and population demography in variable environment

Overall, new insights emerged from this thesis regarding the relationship between environmental variation and sociality, and the way sociality drives population dynamics. Our results contradict what has been reported on other cooperative breeding species in some points but provide perspectives regarding the response of social species to continuous environmental change.

6.3.1. Cooperative breeding and its relationship with environmental variation.

Whether cooperative breeding stems from a bet-hedging strategy has been asked recently, while helpers presence was shown to decrease temporal variance in reproductive success of cooperative breeding birds (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Cockburn and Russell 2011). This hypothesis also originated from the observation that cooperative breeding was especially favoured in fluctuating environments (Jetz and Rubenstein 2011 in birds, Lukas and Clutton-Brock 2017 in mammals). Our results did not support this hypothesis for the Alpine marmot despite the harsh and variable winters in high altitudes (Chap. 4). Helpers presence mainly allowed to increase marmot juvenile fitness through increasing their mean survival, much more than by keeping temporal variance in survival low (Chap. 4). The key factor to this discrepancy between the influence of cooperative breeding in Alpine marmot and in birds might be hibernation. The influence of climate change revealed the strong buffering effect that the burrow and snow-cover provided so far against external winter weather conditions for the Alpine marmot. Hibernaculum constitutes the immediate environment of marmots during hibernation, consequently, the evolution of cooperative breeding should be apprehended conjointly with a stable environment in this species, rather than with the fluctuating external environment. Environmental stability that the burrow offers is quite obvious when comparing time-series of temperature measurements within and outside the burrow from October to June (e.g. Fig. 6.6). For a very variable external air temperature,

inside air temperature remains stable over the winter period thanks to a high snow cover. Nonetheless, inside burrow environment appears sensitive to extremely low external air temperatures (Fig. 6.6), so that with decreasing snow cover, hibernating marmots might be increasingly subjected to variation in external temperatures and especially to low extreme temperatures.

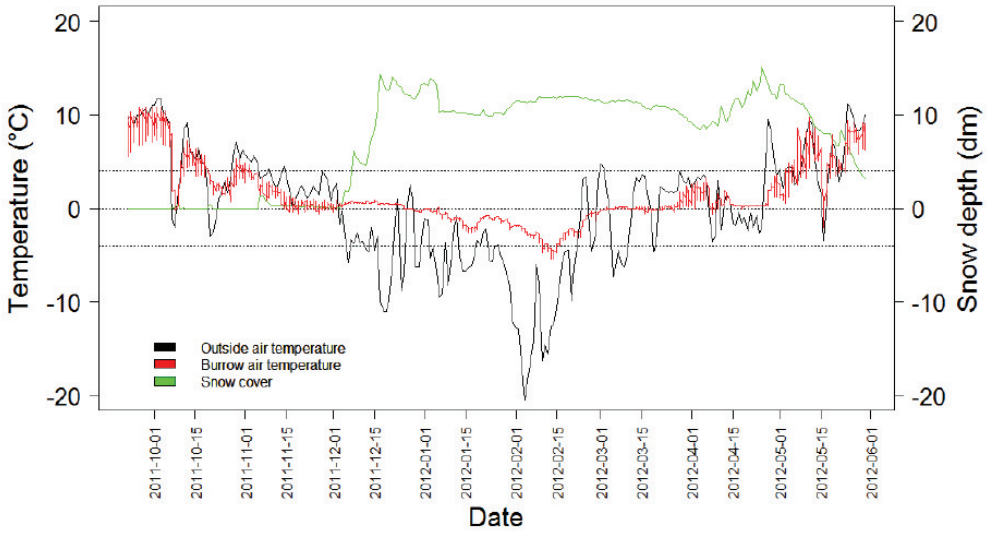

Figure 6.6. Daily air temperature (in black), inside burrow air temperature (around one meter deep in the ground, in red) and snow cover (in green) during the 2011-2012 winter at La Grand Sassière study site (from appendix of Tafani et al. 2013).

The relationship between environmental stability and benefits of social hibernation has been put forward in bats also, for which the thermal benefits of clustering is supposed to mainly occur when individuals hibernate in relatively stable environment, as in caves (Boyles et al. 2008). Likewise, bat species hibernating in less stable environment (i.e. under leaf litter or tree cavities) are mostly solitary or hibernate in smaller groups (Boyles et al. 2008). Huddling in stable environment in these species allows to resist the metabolic cost of active rewarming while solitary species relies on less costly passive rewarming based on changes in external conditions (Geiser et al. 2004). Clustering then might not directly allow to buffer thermal fluctuations in these species (Boyles et al. 2008). A parallel might be made

with the Alpine marmot, for which social thermoregulation, provided by subordinate males at the end of hibernation, allows to limit the energetic cost of rewarming for juveniles with lower fat reserve and body size (Arnold 1988; 1993b). Helpers actively rewarm from hibernation earlier than others, providing heat for juveniles which benefit from this passive warming to end hibernation with little energetic costs. Hence, thanks to the helpers' presence and the thermal stability of the hibernaculum, juveniles have almost not to thermoregulate against cold, as proposed by Arnold (1988). With climate change, individuals have now to hibernate in less stable environment within burrows which may limit the efficiency of social warming at the end of hibernation, during which occurrence of cold temperatures is still observed, while increasing the cost of active rewarming for subordinates (Arnold 1988, 1993). Hence, cooperative breeding shall not be promoted by environmental variability in the Alpine marmot, the increase of juvenile survival is mostly effective in stable environments in the burrow as observed in the early years of the study. The decrease in temporal variance observed in survival of juveniles hibernating with helpers should mostly be a concomitant effect of social thermoregulation, but must not represent the main way through which helpers increase individual fitness.

The relationship between cooperative breeding and environmental variation is still debated, with disagreement about the role of the environment in the evolution of this breeding strategy (Cockburn and Russell 2011; Lukas and Clutton-Brock 2017; Cornwallis et al. 2017; Griesser et al. 2017; Koenig 2017). We see from our study the importance of considering mechanisms through which the fitness gain originate from, as to identify environmental factors limiting or promoting this behaviour. Even if cooperative breeding may conjointly occur in fluctuating environments among species, it might not directly represent a response to environmental variability in itself. Likewise, Marshall et al. (2016) emphasized the plural mechanisms from which helping behaviours may evolve in response environmental variation. They concluded that cooperative breeding was promoted by environmental variation in the banded mongoose (*Mungos mungo*), but did not correspond to a bet-hedging strategy. In this species, the helping behaviour is mainly promoted by changes in the social group composition induced by high rainfall variability, which led to strong male-biased group composition and thus a decrease

in the number of females available for mating (Marshall et al. 2016). In this species, population is subdivided into very large groups which can host several breeding pairs, and several breeding attempts occur within a year. As a result, males does not necessarily trade their reproduction for helping, and this behaviour is mainly constraint by female availability (Marshall et al. 2016).

Helping behaviour thus differs from a risk-averse strategy, as described in the superb starling (*Lamprotornis superbus),* for which subordinates increase their helping effort when facing variable environmental conditions, rather than attempting to breed, as a way to reduce their fecundity variance (Rubenstein 2011). The Alpine marmot differs also from these species in the sense that reproduction is annual, because of a short active season and the following hibernation, so that subordinates do not have the possibility to breed a given year and to rather help their relatives on another year. Once dominance is acquired, individuals never revert to the subordinate status. The access to reproduction is much more constrained in this species, as it requires to take over a territory (but see Cohas et al. 2006 for males) by force or inheritance, and to keep it thereafter. The saturation of marmots' habitat (Armitage 1999, Chap. 4) influences helping behaviour in this species, while being itself constrained by the marmot lifestyle rather than by environmental variation. The hibernation slowing down the pace of life and increasing longevity (Turbill et al. 2011), natural turn-over of groups within the population quickly becomes limiting.

Thus, our results show the extent to which the species lifestyle can mediate the effect of environmental variation. It provides individuals with a different immediate environment and constraints, which may then promote for cooperative breeding. Likewise, such influence of the whole lifestyle should be taken into account when it comes to understand the adaptive value of cooperative breeding. This underlines how misleading it could be in some case to associate the evolution and the adaptive value of cooperative breeding with the environmental conditions largely encountered by cooperative breeding species, as discussed lately (Cornwallis et al 2017; Griesser et al. 2017; Lukas and Clutton-Brock 2017).

6.3.2. From individual benefits and costs of sociality, to variation in population demography

Group living and cooperative breeding strongly shape population growth rate of the Alpine marmot. While we showed that, as expected, benefits gained from the presence of helpers strongly increased the population growth rate (Chap. 4), we also evidence a cost of sociality on the variance of the population growth rate (Chap. 5). We suggest our results describe demographic properties shared by to numerous populations of cooperatively breeding species living in variable environment.

Benefits of sociality on the population growth rate…

The beneficial effect of sociality has been extensively studied on individual fitness (e.g. Silk 2007), especially to understand its adaptive value and get insight in factors driving its evolution. Its effects on the population demography has been less investigated, but was increasingly asked lately (e.g. Vucetich et al. 1997; Grimm et al. 2003; Mortensen and Reed 2016). As well highlighted by Grimm et al. (2003), the main process through which social behaviour might increase the population growth rate should be by increasing adult and juvenile survival. Our results support this general observation for social species, as we could document that helpers' presence would increase by up to 0.02 the population growth rate through its effect on juvenile survival (Chap. 4). Another important positive effect of sociality should be expected on the growth rate through increased dominant survival, especially given the strong benefits of helpers presence early in life and during adulthood evidenced on adult longevity (Berger et al. 2015a). As a result, populations of social species should be less influenced by environmental stochasticity than populations of similar-size solitary species, then sharing the general demographic properties of long-lived species (Morris et al. 2008; Gamelon et al. 2014, 2016). These positive influence of sociality on the population growth rate should be combined with a decrease in variation in adult survival, which might limit the temporal variation in the population growth rate in variable environment (see Morris et al. 2011 on primates). Such decrease in adult survival variation has been highlighted in the

Alpine marmot by Grimm et al. (2003) which compared adult survival of dominant in the presence or not of subordinates, and should also explain in part the low variability observed for dominant individuals in our population (Chap. 5). Our results on the Alpine marmot population thus provide additional quantitative supports for the beneficial effects that sociality can induce on the population growth rate.

...opposed to a cost of sociality on variance of the population growth rate

Costs and benefits of group living are not the same between members of a family group in social species, especially when a high reproductive skew is displayed, as in cooperatively breeding species (Solomon and French 1997). Dominant individuals generally benefit from group living, at the expense of subordinates, which incur reproductive suppression, but are limited in their possibilities to do better outside of the group (Vehrencamp 1983). This discrepancy in the benefits and costs of sociality between individuals creates a conflict over group size between subordinates and dominants (Vehrencamp 1983). On the one hand, subordinates incur higher fitness costs than dominants with group size. On the other hand, dominants gain higher fitness benefits than subordinates from increased group size, until a too large group size increases the risk of dominance takeover (e.g. Lardy et al. 2012, 2013 for the Alpine marmot). The optimal group size (Giraldeau 1988), at which individual fitness is maximized, can then generally differ between subordinates and dominants. This social conflict over group size may affect the stability or instability of the group, and generates what has been described as a boom-and-bust dynamic (Avilés 1999) in cooperatively breeding species. Group grows and are stable until conflicts become too important, or the cost-benefit balance of grouping change for individuals, leading to dominance takeover or dispersion of subordinates, resulting in a strong decrease in group size.

We suggest that this group instability induced variation in the population growth rate, and in the case of the Alpine marmot, resulted in marked temporal variation in the probability of accessing dominance, but also generated variation in survival and reproduction as a consequence. The variation in the two demographic

rates partly compensate one for for the other because of the temporal negative covariation between the access to dominance and the other vital rates (Chap. 5). Group instability and its influence on the population growth rate should be all the more important when additionally promoted by environmental fluctuations. Change in environmental conditions can disrupt the cost-benefit balance of sociality from one year to another. It may favour synchronous instability in most of the groups within the population in a year (e.g. years of high mortality within groups may promote higher dominance takeovers or the possibility of occupying a new territory), which may then be followed by a year of overall increased stability of the groups (e.g. recovery and growth of the majority of groups after important take-over events). Hence, environmental fluctuation may interplay with social conflicts in generating group instability (e.g. Spinks et al. 2000 on the common mole-rat, *Cryptomys hottentotus hottentotus*, Bateman et al. 2012, 2013 on *Suricata suricatta*), and thus in changing the probability of accessing dominance at the population level, amplifying vital rates variability, as found for the Alpine marmot.

Hence, just as sociality generates costs and benefits for individuals, its influence on population dynamics is also mixed, but overall allows an increase in the population growth rate in variable environment, since costs of sociality on the population growth rate are overall much lower than its benefits, as highlighted for the Alpine marmot (Chap. 4, 5).

6.3.3. Population persistence of social species facing environmental change

As discussed above, environmental variations can strongly influence the cost-benefit balance of group living for individuals. The question then arises as to what extent a long-term environmental change can impact benefits and costs of sociality and overall population dynamics of cooperatively breeding species. This also asks whether sociality can buffer populations against environmental change. Our results on the Alpine marmot population provide one of the first detailed illustration of such response. Our findings can be put in perspective with other results and general discussions regarding populations persistence of cooperatively breeding species.

Clutton-Brock et al. (1999) early highlighted the relationship that exists between environmental conditions and the influence of group size on individual fitness in the cooperative meerkats. More precisely, they showed that large groups are beneficial for juvenile survival in populations submitted to high predation rates, while on the contrary large groups negatively impact juvenile survival when population density is high and predation rate is low, because of increased competition between juveniles and helpers (Clutton-Brock et al. 1999). Overall, there are two non-exclusive ways from which environmental change can be detrimental for populations of social species: (i) by decreasing survival or reproductive rates of individuals, or (ii) by increasing costs and/or by decreasing benefits of sociality. Both these effects of environmental change can lead to variation and context-dependent optimal group size for individuals, and should result in an overall decrease in mean group size over years while increasing group instability. This may increase group extinction probability and impact population persistence. Such decrease in group size has been observed in our Alpine marmot population accordingly (Chap. 4), and has been similarly evidenced in a population of the red-fronted brown lemur (*Eulemur fulvus rufus*, Erhart and Overdorff 2008). In this lemur population, the availability of food resources continuously decreased from 1988 to 2003. As a consequence, female reproductive rate decreased while dispersal rates of males increased because of higher competition for resources within groups. Overall, group size decreased by almost half in this population over the years, and groups are more unstable at the end of the study period than is was at an earlier stage (Erhart and Overdorff 2008).

In the face of such continuous detrimental change in environmental conditions, strong impacts can be expected both on mean and variance of the population growth rate. In this context, the influence of sociality on population dynamics and its response to environmental variation is seen as ambivalent (Grimm et al. 2003). Sociality was first suggested to buffer the population against environmentally-driven mortality and against decreasing group size on one hand, but also to increase overall population extinction risk on the other hand (Courchamp et al. 1999a).

Buffering effect of sociality against population extinction

As described in recent years for the Alpine marmot population, sociality can limit the negative influence of environmental change on the population growth rate in first place (Chap. 4, 5). In social species strong environmentally-driven decrease in individual survival and/or reproduction can be counteracted by changes in the social structure of the population, limiting the negative impact of environmental change on the population growth rate. Typically, the loss of breeding individuals can be rapidly compensated by a higher access to reproduction of subordinates in the population. Such a buffering effect of sociality is possible because of the continuous presence of a pool of sexually-mature non-breeders in the population, and is thus especially expected in species displaying reproductive skew. This effect was advanced for the grey wolf (*Canis lupus*) where the consequence of breeder loss on the population growth rate was almost compensated by a rapid replacement of the breeders by younger individuals of the pack (Vucetich et al. 1997; Borg et al. 2015). The same buffering mechanism was also at work in cooperatively breeding birds such as the Galápagos Mockingbird (*Mimus parvulus*, Curry and Grant 1989) or the red-cockaded woodpecker (*Picoides borealis*, Walters et al. 2002). Here the presence of non-breeding helpers has a stabilizing effect on on the number of breeders within the population over years. Furthermore, a restructuring of the social groups in the population can also buffer the populations from environmental change. For instance, a study on the long-tailed bat (*Chalinolobus tuberculatus*) showed that the impact on the population of a crash in a colony was in part limited by the expansion of the neighbouring colonies rapidly after, hosting the remaining individuals from the extinct colony, which were not able to survive anymore the cost of thermoregulation (Monks and O'Donnell 2017)

In our Alpine marmot population, the observed restructuring of the population into more numerous smaller groups in last years also allowed to compensate the impact of declining individual fitness at the population level by increasing the number of reproductive units. That is, even if recruitment was lower at the group-level, it was relatively maintained stable at the population level in last years. Overall these results support the idea that sociality may allow populations to

be resilient to periods of environmental change and to group crashes, allowing for a response over short-time scales such as few years.

Allee effects and increased probability of extinction

On the long run, a decrease in mean group size combined with low population density can increase the extinction probability of populations. The bell-shaped relationship between individual fitness and group size found in social species leads to Allee effects (i.e. inverse density-dependence, Allee et al. 1949) in small groups. These negative effects of a low density on population growth rate can originate from several factors, such as a decrease in genetic diversity and inbreeding, demographic stochasticity, or a decrease in cooperative interactions, as particularly expected in social species (Courchamp et al. 1999a). In social species, small groups can enter into an extinction vortex when the low presence of individuals within the groups becomes insufficient to guarantee successful reproduction (e.g. insufficient allo-parental care) or good survival (e.g. insufficient defence from predators). This may lower the overall recruitment and group size in the next generation which in turn lowers the probability to reproduce and to survive for individuals in the following year and which ultimately leads to rapid group extinction (Courchamp et al. 1999a). The intensity of the Allee effect should increase with the degree of sociality (Courchamp et al. 1999a). Hence, this inverse density-dependence at the group level has been especially highlighted in obligate cooperative breeders, such as in meerkats (e.g. Courchamp et al. 1999b; Clutton-Brock et al. 1999) or in wild dogs (*Lycaon pictus,* e.g. (Courchamp and Macdonald 2001), and has been recently reported in eusocial species, as in ants (Luque et al. 2013). In these species, reproduction and the survival of pups rely heavily on the presence of helpers (*i.e*. reproduction in groups without helpers is likely to fail), to such an extent that below critical group size the group is increasingly likely to become extinct, and may not recover or maintain its size because of Allee effect (Courchamp et al. 1999a). A critical group size was for instance found around six individuals in meerkats (Clutton-Brock et al. 1999), and five individuals in wild dogs (Courchamp et al. 2002; Angulo et al. 2013). Likewise, intrinsic constraints associated with obligate cooperative breeding

was notably proposed to explain the continuous decline and increasing extinction risk that faces the endangered wild dog, threatened by habitat fragmentation and anthropogenic activities (see the modelling study, Courchamp et al. 2000).

However, while the Allee effect has been repeatedly shown at the group level, empirical evidences at the population level are very scarce in social species (but see Keynan and Ridley 2016 for a first example on the Arabian babbler, *Turdoides squamiceps*). An explanation for that is that group size might not map directly on population size in some cases, contrary to what is generally expected. Such discrepancy between group and population dynamics has been recently highlighted in wild dogs (see Woodroffe 2011; Angulo et al. 2013), explaining the failures encountered as to relate the decrease in wild dog populations to Allee effects. Our results on the Alpine marmot population support in part this hypothesis, with an apparently changing relationship between the group size and the population size over time (see previous discussion). Likewise, in a recent review, Angulo et al. (2018) identified several factors which can buffer populations of social species against Allee effects. More specifically, they showed that additionally to the group size, its heterogeneity and number in the population, as well as the type of interaction between groups are also strong determinants of populations persistence. A high group size heterogeneity combined with cooperative interactions among the groups buffer the most the Allee effects (by favouring inter-groups interactions through dispersal rates), and should prevent populations from extinction due to this process (Angulo et al. 2018).

Hence, populations persistence of social species facing detrimental environmental changes may be predicted at first by its level of sociality. The more social the species is, the more the helpers' presence may become a constraint for individual fitness and likely to generate group Allee effect. On this basis, the relative resistance of a population to long-term changes in the environment should then be species-specific, as between-species differences in behaviours and in population structure will determine when sociality is no longer a buffer and instead become a cost for the population (e.g. Keynan and Ridley 2016). In this broad context, the Alpine marmot, which displays an intermediate level of sociality, should be less submitted to Allee effects than obligate cooperatively breeding species. Its group

size structure still appears heterogeneous in last years, however, among group interactions are mostly negative in this species. It will be interesting to investigate how group characteristics are going to be impacted by future environmental changes and to understand the implications for the population dynamic in return. We can especially ask whether climate change will in part generates synchrony in group dynamics and increase group instability, and then homogenise group sizes over time.

6.4. The influence of the lifestyle on demographic responses to climate change

In conclusion, from this thesis work emerged another possible way by which climate change can impact individuals and populations: by lowering the adaptive value of the lifestyle in the new environmental conditions imposed by climate change. Likewise, these results support the fact that the lifestyle strongly shapes individuals response to environmental variation. On that basis, several questions can be asked. Once the advantage of the adaptive value of the lifestyle is impacted, how can the populations cope with these changes ? Similarly, does the lifestyle may help predict populations response to climate change ?

The species lifestyle lies at the interface between environmental conditions and individuals (Dobson et al. 2007, see Fig. 6.1). This close interaction between the lifestyle and environmental conditions provides individuals with a specific local environmental context, which may strongly influence individual's fitness and more generally species life history traits (Stearns 1992, e.g. Healy et al. 2014 or Wasser and Sherman 2010). We suggest different types of lifestyle's traits can be differentiated according to the way they generate a specific environmental context to individuals and constrain life history traits as a consequence. One can first distinguish lifestyle traits which refer to the species environment or the direct relationship of individuals with the latter, such as the habitat type (Wiersma et al. 2007), or the diet (Saether and Gordon 1994). Second, some lifestyle traits provide individuals with a different immediate environment by mediating the effect of environmental conditions encountered in the habitat. For instance, fossorial or arboreal lifestyles can offer protection against predators or bad external weather conditions (Shattuck and Williams 2010). Finally, another kind of lifestyle can be envisioned: those which act directly on the way individuals interact with their immediate environment, such as the flight capacity (Healy et al. 2014), hibernation (Turbill et al. 2011) and sociality (Williams and Shattuck 2015), and which may involve behavioral or physiological traits.

Climate change has been increasingly shown to induce mismatches between energy requirements or physiological tolerance of individuals, and the new environmental conditions they are facing (see Chap. 1). These mismatches generally find their roots from changes in habitat , that directly impact individuals (e.g. increase in temperatures, decrease in sea ice extent), or may correspond to trophic-mismatches when weather changes indirectly impact individuals by decreasing food resource availability (e.g. phenological mismatches through altered seasonal patterns, Stenseth and Mysterud 2002). We suggest that a “lifestyle mismatch” can also be defined as a additional consequence of climate change, when long-term changes in weather conditions indirectly impact individual fitness because the adaptive value of the lifestyle is no longer beneficial. This mismatch mainly apply to lifestyle's traits which strongly mediate the influence of the environment on individuals. We know the lifestyle generally evolved as allowing a better acquisition of food resources, protection against predators or to protect against environmental conditions (Dobson 2007). Hence, unlike the other mismatches, deviation from the environmental conditions to which lifestyle evolved should involve important fitness costs for individuals due to the loss of benefits that the lifestyle brought, besides the fact that individuals will be submitted to new environmental constraints and variability. The impact of such mismatch should be expected to be all the more detrimental that the lifestyle's trait provides strong fitness benefits (e.g. see the extraordinary longevity of some social subterranean species, Williams and Shattuck 2015, Healy 2015).

My work on the Alpine marmot provides an example of the extent to which such indirect influence of climate change can impact population dynamics. This work may help orienting further investigations regarding the response of other Alpine marmot populations or of populations of species sharing similar lifestyle. More generally, we suggest such response mechanism would be to consider more frequently when it comes to understand and predict the impact of climate change on populations and species. Likewise, in their recent study on hibernating rodents, Turbill and Prior (2016) highlighted another way through which climate change might disrupt the fitness benefits of hibernation. They suggested warmer temperatures might shorten the duration of hibernation in the long term, and

consequently reduce annual survival rates of individuals, which might be more exposed to predation or other detrimental environmental conditions, benefiting less from prolonged inactivity (Turbill and Prior 2016). As a result, the pace of life of hibernating species is expected to become faster, and population dynamics should be impacted as well, as decreasing adult survival may lead to strong population decline if not compensated by an increase in reproductive rates (Turbill and Prior 2016).

Overall, species' responses to climate change might be envisioned according to the local weather changes the populations may face, but also according to the species lifestyle and whether it is still effective in the new environmental conditions. The intensity of the climate change impact should differ depending on whether it disrupts the effectiveness of the lifestyle: it should determine whether a particular lifestyle allows individuals resisting the change (as it has been proposed, e.g. Liow et al. 2009), or on the contrary should interact with environmental changes in impacting individuals (this study). The different responses to climate change we highlighted between the Alpine marmot and the Alpine chamois relied heavily on their lifestyle characteristics (Chap. 5). The Alpine marmot currently suffers from less effective hibernation and social thermoregulation, while the Alpine chamois is not constrained by such lifestyle traits which stand at the interface between the environment and individuals. It would be interesting to expand such comparative analysis at a larger geographic scale and on more species, living in similar environment but displaying a variety of lifestyle. Better understanding the relationship between the environment and the lifestyle can be challenging but should allow envisioning from which environmental change a mismatch between the lifestyle and the environment may occur. Such large-scale approach would also allow to test and to quantify the effect of lifestyle's adaptive costs with climate change. Finally, certain lifestyle traits could also be identified as more beneficial than others for population persistence when facing detrimental environmental changes. We pointed out how sociality and resilience of the social structure induced a strong decrease in individual fitness, while others can become traps, as highlighted with hibernation if thermoregulation becomes less efficient. However this avenue of research deserves more empirical investigations to evaluate if lifestyle traits can be used as a basis for predict species’ responses to climate change.

References

Adamík P, Král M (2008) Climate- and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. Journal of Zoology 275:209–215.

Adams RA (2010) Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91:2437–2445.

Adolph SC, Porter WP (1996) Growth, Seasonality, and Lizard Life Histories: Age and Size at Maturity. Oikos 77:267.

Alerstam T, Hedenstrom A, Akesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260.

Alexander RD (1974) The evolution of social behavior. Annual review of ecology and systematics 325–383.

Allainé D (2000) Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. Behavioural Processes 51:21–34.

Allainé D (2004) Sex ratio variation in the cooperatively breeding alpine marmot Marmota marmota. Behavioral Ecology 15:997–1002.

Allainé D, Brondex F, Graziani L, et al (2000) Male-biased sex ratio in litters of Alpine marmots supports the helper repayment hypothesis. Behavioral Ecology 11:507–514.

Allainé D, Rodrigue I, Berre ML, Ramousse R (1994) Habitat preferences of alpine marmots, Marmota marmota. Canadian Journal of Zoology 72:2193–2198.

Allainé D, Theuriau F (2004) Is there an optimal number of helpers in Alpine marmot family groups? Behavioral Ecology 15:916–924.

Allee, W.C. et al. (1949) Principles of Animal Ecology, Saunders

Angulo E, Luque GM, Gregory SD, et al (2018) Review: Allee effects in social species. Journal of Animal Ecology 87:47–58.

Angulo E, Rasmussen GSA, Macdonald DW, Courchamp F (2013) Do social groups prevent Allee effect related extinctions?: The case of wild dogs. Frontiers in Zoology 10:11.

Armitage KB (2000) The evolution, ecology, and systematics of marmots. Oecologia Montana 9:1–18.

Armitage KB (1999) Evolution of Sociality in Marmots. Journal of Mammalogy 80:1–10.

Armitage KB (2007) Evolution of sociality in marmots: it begins with hibernation. In: Rodent societies: an ecological and evolutionary perspective, Wolff JO, and Sherman PW. Chicago, IL: University of Chicago Press.

Armitage, KB (2014). Marmot biology: sociality, individual fitness, and population dynamics. Cambridge University Press, Cambridge

Armitage KB (1981) Sociality as a life-history tactic of ground squirrels. Oecologia 48:36–49.

Armitage KB, Blumstein D. (2002) Body-mass diversity in marmots. In: Holarctic marmots as a factor of biodiversity: proceedings of the 3d International Conference on Marmots. K.B. Armitage, V. Yu Rumiantsev, Cheboksary, Chuvash Republic, Russia.

Armitage KB, Blumstein DT, Woods BC (2003) Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 134:101–114.

Arnold KE, Owens IP (1998) Cooperative breeding in birds: a comparative test of the life history hypothesis. Proceedings of the Royal Society of London B: Biological Sciences 265:739–745.

Arnold W (1993a) Energetics of social hibernation. ResearchGate 65–80.

Arnold W (1990a) The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behavioral Ecology and Sociobiology 27:239–246.

Arnold W (1993b) Social evolution in marmots and the adaptive value of joint hibernation. Verhandlungen der Deutschen Zoologischen Gesellschaft 79–93.

Arnold W (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). Journal of Comparative Physiology B 158:151–156.

Arnold W (1990b) The evolution of marmot sociality: I. Why disperse late? Behavioral Ecology and Sociobiology 27:

Arnold W (1993c) Energetics of social hibernation. In: Life in the Cold: Ecological, Physiological, and Molecular Mechanism, eds Carey, C., Florant, G.L., Wunder, B.A., Horwitz, B. Boulder: Westview Press, pp 65–80.

Arnold W, Dittami J (1997) Reproductive suppression in male alpine marmots. Animal Behaviour 53:53–66.

Arnold W, Heldmaier G, Ortmann S, et al (1991) Ambient temperatures in hibernacula and their energetic consequences for alpine marmots Marmota marmota. Journal of Thermal Biology 16:223–226.

Ashton KG (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography 11:505–523.

Austad SN, Fischer KE (1991) Mammalian Aging, Metabolism, and Ecology: Evidence From the Bats and Marsupials. Journal of Gerontology 46:B47–B53.

Avilés L (1999) Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. Evolutionary Ecology Research 1:459–477.

Barash DP (1974) The Evolution of Marmot Societies: A General Theory. Science 185:415–420.

Bårdsen B-J, Henden J-A, Fauchald P, et al (2011) Plastic reproductive allocation as a buffer against environmental stochasticity - linking life history and population dynamics to climate. Oikos 120:245–257.

Barnosky AD (2001) Distinguishing the effects of the Red queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. Journal of Vertebrate Paleontology 21:172–185.

Bateman AW, Ozgul A, Coulson T, Clutton-Brock TH (2012) Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*: Group dynamics in a highly social species. Journal of Animal Ecology 81:628–639.

Bateman AW, Ozgul A, Nielsen JF, et al (2013) Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*. Ecology 94:587–597.

Beebee TJC (2002) Amphibian Phenology and Climate Change. Conservation Biology 16:1454–1454.

Beniston M (2006) Mountain Weather and Climate: A General Overview and a Focus on Climatic Change in the Alps. Hydrobiologia 562:3–16.

Benson KR (2000) The emergence of ecology from natural history. Endeavour 24:59–62.

Benton MJ (2009) The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time. Science 323:728–732.

Benton TG, Grant A (1999) Optimal Reproductive Effort in Stochastic, Density-Dependent Environments. Evolution 53:677

Benton TG, Grant A (1996) How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. The American Naturalist 147:115–139

Berger V (2015) Senescence and sociality: the example of the Alpine marmot (*Marmota marmota*). PhD thesis, Université Claude Bernard Lyon1, Lyon.

Berger V, Lemaître J-F, Allainé D, et al (2015a) Early and adult social environments have independent effects on individual fitness in a social vertebrate. Proceedings of the Royal Society B: Biological Sciences 282:20151167.

Berger V, Lemaître J-F, Dupont P, et al (2016) Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence. Journal of Mammalogy 97:992–1000.

Berger V, Lemaître J-F, Gaillard J-M, Cohas A (2015b) How do animals optimize the size–number trade-off when aging? Insights from reproductive senescence patterns in marmots. Ecology 96:46–53.

Bergmann C (1847) Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. Gottinger Studien 3:595–708.

Berteaux D, Réale D, McAdam AG, Boutin S (2004) Keeping pace with fast climate change: can arctic life count on evolution? Integrative and Comparative Biology 44:140–151.

Bertolino S, di Montezemolo NC, Bassano B (2009) Food-niche relationships within a guild of alpine ungulates including an introduced species. Journal of Zoology 277:63–69.

Bickford D, Howard SD, Ng DJJ, Sheridan JA (2010) Impacts of climate change on the amphibians and reptiles of Southeast Asia. Biodiversity and Conservation 19:1043–1062.

Bieber C, Ruf T (2009) Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. Naturwissenschaften 96:165–171.

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and distributions 5:165–174.

Bleu J, Herfindal I, Loison A, et al (2015) Age-specific survival and annual variation in

survival of female chamois differ between populations. Oecologia 179:1091–1098.

Blumstein DT, Armitage KB (1999) Cooperative Breeding in Marmots. Oikos 84:369

Bocci A, Canavese G, Lovari S (2010) Even mortality patterns of the two sexes in a polygynous, near-monomorphic species: is there a flaw? Journal of Zoology 280:379–386.

Boer GJ, Flato G, Ramsden D (2000) A transient climate change simulation with greenhouse gas and aerosol forcing: projected climate to the twenty-first century. Climate Dynamics 16:427–450.

Borg BL, Brainerd SM, Meier TJ, Prugh LR (2015) Impacts of breeder loss on social structure, reproduction and population growth in a social canid. Journal of Animal Ecology 84:177–187.

Boschi C, Nievergelt B (2003) The spatial patterns of Alpine chamois (*Rupicapra rupicapra rupicapra*) and their influence on population dynamics in the Swiss National Park. Mammalian Biology - Zeitschrift für Säugetierkunde 68:16–30.

Both C, Artemyev AV, Blaauw B, et al (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society B: Biological Sciences 271:1657–1662.

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Boyce MS (1979) Seasonality and Patterns of Natural Selection for Life Histories. The American Naturalist 114:569–583.

Boyles JG, Storm JJ, Brack Jr V (2008) Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. Functional Ecology 22:632–636.

Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. Science(Washington) 312:1477–1478

Brandler OV, Lyapunova EA (2009) Molecular phylogenies of the genus *Marmota* (Rodentia Sciuridae): comparative analysis. Ethology Ecology & Evolution 21:289–298.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach., 2nd edition Springer-Verlag. New York, USA.

Burnham KP, Anderson DR, White GC, et al (1987) Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture. American Fisheries Society monograph, Bethesda, Maryland, USA

Canale CI, Ozgul A, Allainé D, Cohas A (2016) Differential plasticity of size and mass to environmental change in a hibernating mammal. Global Change Biology 22:3286–3303.

Canário F, Matos S, Soler M (2004) Environmental constraints and cooperative breeding in the azure-winged magpie. The Condor 106:608–617.

Cardillo M (2005) Multiple Causes of High Extinction Risk in Large Mammal Species. Science 309:1239–1241.

Cardillo M (2003) Biological determinants of extinction risk: why are smaller species less vulnerable? Animal Conservation 6:63–69.

Caswell H (2001) Matrix Population Models: Construction, Analysis, and Interpretation, 2nd edn. Sinauer Associates Inc. Sunderland, MA, USA.

Caswell H (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619–627.

Charnov EL, Schaffer WM (1973) Life-History Consequences of Natural Selection: Cole's Result Revisited. The American Naturalist 107:791–793.

Choquet R, Reboulet AM, Lebreton J-D, et al (2005) U-CARE 2.2 user's manual. CEFE, Montpellier, France.

Clutton-Brock TH (2001) Effects of Helpers on Juvenile Development and Survival in Meerkats. Science 293:2446–2449.

Clutton-Brock TH (1988) Reproductive success. Studies of individual variation in contrasting breeding systems, University of Chicago Press.

Clutton-Brock TH, Gaynor D, McIlrath GM, et al (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology 68:672–683.

Clutton-Brock TH, Stevenson IR, Marrow P, et al (1996) Population Fluctuations, Reproductive Costs and Life-History Tactics in Female Soay Sheep. The Journal of Animal Ecology 65:675.

Cockburn A, Russell AF (2011) Cooperative Breeding: A Question of Climate? Current Biology 21:R195–R197.

Cody ML (1966) A General Theory of Clutch Size. Evolution 20:174.

Cohas A, Bonenfant C, Gaillard J-M, Allainé D (2007a) Are extra-pair young better than within-pair young? A comparison of survival and dominance in alpine marmot. Journal of Animal Ecology 76:771–781.

Cohas A, Yoccoz NG, Allainé D (2007b) Extra-pair paternity in alpine marmots, Marmota marmota: genetic quality and genetic diversity effects. Behavioral Ecology and Sociobiology 61:1081–1092.

Cohas A, Yoccoz NG, Bonenfant C, et al (2008) The genetic similarity between pair members influences the frequency of extrapair paternity in alpine marmots. Animal Behaviour 76:87–95.

Cohas A, Yoccoz NG, Da Silva A, et al (2006) Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. Behavioral Ecology and Sociobiology 59:597–605.

Cole LC (1954) The Population Consequences of Life History Phenomena. The Quarterly Review of Biology 29:103–137.

Colwell RK (1974) Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148–1153.

Conover DO (1992) Seasonality and the scheduling of life history at different latitudes.

Journal of Fish Biology 41:161–178.

Corlatti L, Lebl K, Filli F, Ruf T (2012) Unbiased sex-specific survival in Alpine chamois. Mammalian Biology - Zeitschrift für Säugetierkunde 77:135–139.

Cornwallis CK, Botero CA, Rubenstein DR, et al (2017) Cooperation facilitates the colonization of harsh environments. Nature Ecology & Evolution 1:0057.

Coulson T (2001) Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. Science 292:1528–1531.

Coulson T, Gaillard J-M, Festa-Bianchet M (2005) Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74:789–801.

Coulson T, Kruuk LEB, Tavecchia G, et al (2003) Estimating selection on neonatal traits in red deer using elasticity path analysis. Evolution 57:2879–2892.

Courchamp F, Clutton-Brock T, Grenfell B (1999a) Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405–410.

Courchamp F, Clutton-Brock T, Grenfell B (2000) Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. Animal Conservation 3:277–285.

Courchamp F, Grenfell B, Clutton-Brock T (1999b) Population dynamics of obligate cooperators. Proceedings of the Royal Society B: Biological Sciences 266:557–563.

Courchamp F, Macdonald DW (2001) Crucial importance of pack size in the African wild dog *Lycaon pictus*. In: Animal Conservation forum. Cambridge University Press, pp 169–174.

Courchamp F, Rasmussen GS, Macdonald DW (2002) Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. Behavioral Ecology 13:20–27.

Covas R, du Plessis MA, Doutrelant C (2008) Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. Behavioral Ecology and Sociobiology 63:103–112.

Covas R, Griesser M (2007) Life history and the evolution of family living in birds. Proceedings of the Royal Society B: Biological Sciences 274:1349–1357.

Crampe J-P, Gaillard J-M, Loison A (2002) L'enneigement hivernal : un facteur de variation du recrutement chez l'isard (*Rupicapra pyrenaica pyrenaica*). Canadian Journal of Zoology 80:1306–1312.

Crick HQ (1992) Load-lightening in cooperatively breeding birds and the cost of reproduction. Ibis 134:56–61.

Crick HQ, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature 388:526.

Curry, RL, and Grant PR(1989). Demography of the cooperatively breeding Galapagos Mockingbird, *Nesomimus parvulus*, in a climatically variable environment. Journal of Animal Ecology 58:441–463.

Darwin C (1859) The Origin Of Species, John Murray.

Davison R, Jacquemyn H, Adriaens D, et al (2010) Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments. Journal of Ecology 98:255–267.

Davison R, Nicolè F, Jacquemyn H, Tuljapurkar S (2013) Contributions of Covariance: Decomposing the Components of Stochastic Population Growth in *Cypripedium calceolus*. The American Naturalist 181:410–420.

Doak DF, Morris WF, Pfister C, et al (2005) Correctly Estimating How Environmental Stochasticity Influences Fitness and Population Growth. The American Naturalist 166:E14–E21.

Dobson FS (2007) A lifestyle view of life-history evolution. Proceedings of the National Academy of Sciences 104:17565–17566.

Dobzhansky T (1950) Evolution in the tropics. American Scientist 38:209–2011.

Dobzhansky T (1973) Nothing in Biology Makes Sense except in the Light of Evolution. The American Biology Teacher 35:125–129.

Drent RH, Daan S (1980) The Prudent Parent: Energetic Adjustments in Avian Breeding. Ardea 38–90:225–252.

Dupont P (2017) The influence of sociality on population dynamics in the Alpine Marmot. PhD thesis, Université Claude Bernard Lyon1, Lyon.

Easterling DR, Meehl GA, Parmesan C, et al (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Emlen ST (1982a) The Evolution of Helping. I. An ecological constraints model. The American Naturalist 119:29–39

Emlen ST (1982b) The Evolution of Helping. II. The role of behavioral conflict. The American Naturalist 119:40–53

Emlen ST, Wrege PH (1991) Breeding biology of white-fronted bee-eaters at nakuru: the influence of helpers on breeder fitness. The Journal of Animal Ecology 60:309.

Erhart EM, Overdorff DJ (2008) Population demography and social structure changes inEulemur fulvus rufus from 1988 to 2003. American Journal of Physical Anthropology 136:183–193.

Farand é., Allainé D, Coulon J (2002) Variation in survival rates for the alpine marmot (*Marmota marmota*): effects of sex, age, year, and climatic factors. Canadian Journal of Zoology 80:342–349.

Ferguson SH, McLoughlin PD (2000) Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography 23:193–200.

Ferrari C, Pasquaretta C, von Hardenberg A, Bassano B (2012) Intraspecific killing and cannibalism in adult Alpine marmots *Marmota marmota*. Ethology Ecology & Evolution 24:388–394.

Festa-Bianchet M, Jorgenson JT (1998) Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144–150.

Fisher RA (1930) The genetical theory of natural selection, Oxford University Press. Oxford.

Forcada J, Trathan PN, Murphy EJ (2008) Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. Global Change Biology 14 : 2473–2488.

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020–1029.

French AR (1990) Age-class differences in the pattern of hibernation in yellow-bellied marmots, Marmota flaviventris. Oecologia 82:93–96.

Fretwell JR (1972) Populations in a Seasonal Environment, Princeton University Press, Princeton, NJ.

Frick WF, Reynolds DS, Kunz TH (2010) Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. Journal of Animal Ecology 79:128–136.

Gadgil M, Bossert WH (1970) Life Historical Consequences of Natural Selection. The American Naturalist 104:1–24.

Gaillard J -M., Yoccoz NG, Lebreton J -D., et al (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. The American Naturalist 166:119–123.

Gaillard J-M, Boutin J-M, Delorme D, et al (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502–513.

Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, et al (2000a) Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of ecology and Systematics 31:367–393.

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, et al (2000b) Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of ecology and Systematics 31:367–393

Gaillard J-M, Lemaître J-F, Berger V, et al (2016) Axes of Variation in Life Histories. In: Encyclopedia of Evolutionary Biology.

Gaillard J-M, Mark Hewison AJ, Klein F, et al (2013) How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. Ecology Letters 16:48–57.

Gaillard J-M, Pontier D, Allainé D, et al (1989) An Analysis of Demographic Tactics in Birds and Mammals. Oikos 56:59.

Gaillard J-M, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306.

Gamelon M, Gaillard J-M, Gimenez O, et al (2016) Linking demographic responses and life history tactics from longitudinal data in mammals. Oikos 125:395–404.

Gamelon M, Gimenez O, Baubet E, et al (2014) Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. The American Naturalist 184:673–683.

Gardner JL, Peters A, Kearney MR, et al (2011) Declining body size: a third universal response to warming? Trends in Ecology & Evolution 26:285–291.

Garel M, Forsyth DM, Loison A, et al (2011) Age-related male reproductive effort in two mountain ungulates of contrasting sexual size dimorphism. Canadian Journal of Zoology 89:929–937.

Garel M, Loison A, Gaillard J-M, et al (2004) The effects of a severe drought on mouflon lamb survival. Proceedings of the Royal Society of London B: Biological Sciences 271:S471–S473.

Garel M, Loison A, Jullien J-M, et al (2009) Sex-specific growth in alpine chamois. Journal of Mammalogy 90:954–960.

Garin I, Aldezabal A, Herrero J, et al (2008) Diet selection of the alpine marmot (*Marmota m. marmota L.*) in the Pyrenees.

Geiser F (1998) Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clinical and Experimental Pharmacology and Physiology 25:736–740.

Geiser F, Drury RL, Körtner G, et al (2004) Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Life in the Cold: Evolution, Mechanisms, Adaptation, and Application. 12th International Hibernation Symposium, Barnes BM, Carey HV (eds). University of Alaska, Fairbanks, pp 51–62.

Geiser F, Körtner G (2010) Hibernation and daily torpor in Australian mammals. Australian Zoologist 35:204–215.

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiological Zoology 68:935–966.

Geiser F, Turbill C (2009) Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften 96:1235–1240.

Gienapp P, Teplitsky C, Alho JS, et al (2008) Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17:167–178.

Gillespie JH (1974) Natural selection for within-generation variance in offspring number. Genetics 76:601–606.

Giorgi F, Bi X, Pal J (2004) Mean, interannual variability and trends in a regional climate change experiment over Europe. II: climate change scenarios (2071-2100). Climate Dynamics 23:839–858.

Giraldeau L-A (1988) The stable group and the determinants of foraging group size. In: The Ecology of Social Behavior, C.N. Slobodchikoff, . CA: Academic Press., San Diego, pp 33–53.

Gonzalez G, Crampe J-P (2001) Mortality patterns in a protected population of isards (*Rupicapra pyrenaica*). Canadian Journal of Zoology 79:2072–2079.

Gonzalez J-CT, Sheldon BC, Tobias JA (2013) Environmental stability and the evolution of

cooperative breeding in hornbills. Proceedings of the Royal Society B: Biological Sciences 280:20131297–20131297.

Goossens B, Graziani L, Waits LP, et al (1998) Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. Behavioral Ecology and Sociobiology 43:281–288.

Griesser M, Drobniak SM, Nakagawa S, Botero CA (2017) Family living sets the stage for cooperative breeding and ecological resilience in birds. PLOS Biology 15:e2000483.

Grimm V, Dorndorf N, Frey-Roos F, et al (2003) Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. Oikos 102:124–136.

Grosbois V, Gimenez O, Gaillard J-M, et al (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83:357–399.

Hacklander K, Arnold W (1999) Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). Behavioral Ecology 10:592–597.

Hackländer K, Möstl E, Arnold W (2003) Reproductive suppression in female Alpine marmots*, Marmota marmota.* Animal Behaviour 65:1133–1140.

Haeckel E (1876) History of Creation, D. Appleton

Hallett TB, Coulson T, Pilkington JG, et al (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75.

Hamel S, Côté SD, Festa-Bianchet M (2010a) Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology 91:2034–2043.

Hamel S, Gaillard J-M, Yoccoz NG, et al (2010b) Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations: Fitness costs of reproduction in mammals. Ecology Letters 13:915–935.

Hamel S, Garel M, Festa-Bianchet M, et al (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582–589.

Hamilton WD (1964a) The genetical evolution of social behaviour. I. Journal of Theoretical Biology 7:1–16.

Hamilton WD (1964b) The genetical evolution of social behaviour. II. Journal of Theoretical Biology 7:17–52.

Hamilton WD (1966) The moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Haridas CV, Tuljapurkar S (2005) Elasticities in variable environments: properties and implications. The American Naturalist 166:481–495.

Harvey PH, Purvis A (1991) Comparative methods for explaining adaptations. Nature 351:619–624.

Harvey PH, Zammuto RM (1985) Patterns of mortality and age at first reproduction in natural populations of mammals. Nature 315:319–320.

Hatchwell BJ (1991) An Experimental study of the effects of timing of breeding on the reproductive success of Common guillemots (*Uria aalge*). The Journal of Animal

Ecology 60:721.

Hatchwell BJ, Komdeur J (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. Animal Behaviour 59:1079–1086.

Healy K (2015) Eusociality but not fossoriality drives longevity in small mammals. Proceedings of the Royal Society B: Biological Sciences 282:20142917–20142917.

Healy K, Guillerme T, Finlay S, et al (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. Proceedings of the Royal Society B: Biological Sciences 281:20140298–20140298.

Hegel TM, Mysterud A, Ergon T, et al (2010) Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. Journal of Animal Ecology 79:471–482.

Hodge SJ, Manica A, Flower TP, Clutton-Brock TH (2008) Determinants of reproductive success in dominant female meerkats. Journal of Animal Ecology 77:92–102.

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. Nature 470:479–485.

Holmes DJ, Austad SN (1994) Fly now, die later: life-history correlates of gliding and flying in mammals. Journal of Mammalogy 75:224–226.

Horvitz C, Schemske DW, Caswell H (1997) The relative "importance" of life-history stages to population growth: prospective and retrospective analyses. In: Tuljapurkar S, Caswell H (eds) Structured-Population Models in Marine, Terrestrial, and Freshwater Systems. Springer US, Boston, MA, pp 247–271.

Hufnagl S, Franceschini-Zink C, Millesi E (2011) Seasonal constraints and reproductive performance in female Common hamsters (Cricetus cricetus). Mammalian Biology - Zeitschrift für Säugetierkunde 76:124–128.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15:56–61.

Humphries MM, Thomas DW, Kramer DL (2003) The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiological and Biochemical Zoology 76:165–179.

Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature 418:313–316.

Humphries MM, Umbanhowar J, McCann KS (2004) Bioenergetic prediction of climate change impacts on northern mammals. Integrative and Comparative Biology 44:152–162.

Hüppop O, Hüppop KH (2003) North Atlantic Oscillation and timing of spring migration in birds. Proceedings of the Royal Society B: Biological Sciences 270:233–240.

Hurrell JW (1995) Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. Science 269:676–679.

Husby A, Hille SM, Visser ME (2011) Testing mechanisms of bergmann's rule: phenotypic decline but no genetic change in body size in three passerine bird populations. The American Naturalist 178:202–213.

Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences 97:1630–1633.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M.), pp. 1535. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jacquemyn H, Brys R, Davison R, et al (2012) Stochastic LTRE analysis of the effects of herbivory on the population dynamics of a perennial grassland herb. Oikos 121:211–218.

Jenouvrier S, Barbraud C, Weimerskirch H (2005) Long-term contrasted responses to climate of two antarctic seabird species. Ecology 86:2889–2903.

Jetz W, Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Jiguet F, Julliard R, Thomas CD, et al (2006) Thermal range predicts bird population resilience to extreme high temperatures. Ecology Letters 9:1321–1330.

Johnson DD, Kays R, Blackwell PG, Macdonald DW (2002) Does the resource dispersion hypothesis explain group living? Trends in Ecology & Evolution 17:563–570.

Jorgenson JT, Festa-Bianchet M, Gaillard J-M, Wishart WD (1997) Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology 78:1019–1032

Kager T, Fietz J (2009) Food availability in spring influences reproductive output in the seed-preying edible dormouse (*Glis glis*). Canadian Journal of Zoology 87:555–565.

Keller L, Genoud M (1997) Extraordinary lifespans in ants: a test of evolutionary theories of ageing. Nature 389:958.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences 105:11823–11826.

Keynan O, Ridley AR (2016) Component, group and demographic Allee effects in a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*). Oecologia 182:153–161.

King LAL, Russell ES (1909) A method for the study of the animal ecology of the shore. Proceedings of the Royal Physical Society of Edinburgh 17:566–593.

Kneip É, Van Vuren DH, Hostetler JA, Oli MK (2011) Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. Journal of Mammalogy 92:367–377.

Knight MH, Jaarsveld ASV, Mills MGL (1992) Allo-suckling in spotted hyaenas (*Crocuta crocuta*): an example of behavioural flexibility in carnivores. African Journal of Ecology 30:245–251.

Koenig WD (2017) What drives cooperative breeding? PLOS Biology 15:e2002965.

Koenig WD, Pitelka FA, Carmen WJ, et al (1992) The evolution of delayed dispersal in cooperative breeders. The Quarterly Review of Biology 67:111–150.

Koenig WD, Walters EL (2015) Temporal variability and cooperative breeding: testing the bet-hedging hypothesis in the acorn woodpecker. Proceedings of the Royal Society B: Biological Sciences 282:20151742.

Koons DN, Grand JB, Zinner B, Rockwell RF (2005) Transient population dynamics: Relations to life history and initial population state. Ecological Modelling 185:283–297.

Koons DN, Iles DT, Schaub M, Caswell H (2016) A life-history perspective on the demographic drivers of structured population dynamics in changing environments. Ecology Letters 19:1023–1031.

Koons DN, Metcalf CJE, Tuljapurkar S (2008) Evolution of delayed reproduction in uncertain environments: a life-history perspective. The American Naturalist 172:797–805.

Körtner G, Heldmaier G (1995) Body Weight Cycles and Energy Balance in the Alpine marmot (*Marmota marmota*). Physiological Zoology 68:149–163.

Laake J, Rexstad E (2008) RMark - an alternative approach to building linear models in MARK

Lande R, Shannon S (1996) The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50:434–437.

Lane JE, Kruuk LEB, Charmantier A, et al (2012) Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature 489:554–557.

Lardy S, Allainé D, Bonenfant C, Cohas A (2015) Sex-specific determinants of fitness in a social mammal. Ecology 96:2947–2959.

Lardy S, Allainé D, Cohas A (2013) Intrasexual competition and female dominance in a singular breeding mammal, the Alpine marmot. Animal Behaviour 86:1155–1163.

Lardy S, Cohas A, Desouhant E, et al (2012) Paternity and dominance loss in male breeders: the cost of helpers in a cooperatively breeding mammal. PLoS ONE 7:e29508.

Lardy S, Cohas A, Figueroa I, Allainé D (2011) Mate change in a socially monogamous mammal: evidences support the “forced divorce” hypothesis. Behavioral Ecology 22:120–125.

Law R (1979) Optimal life histories under age-specific predation. The American Naturalist 114:399–417.

Lebreton J, Nichols JD, Barker RJ, et al (2009) Chapter 3 Modeling individual animal histories with Multistate Capture–Recapture Models. In: Advances in Ecological Research. Elsevier, pp 87–173.

Lebreton J-D (2006) Dynamical and statistical models of vertebrate population dynamics. Comptes Rendus Biologies 329:804–812.

Lebreton J-D (2011) The impact of global change on terrestrial Vertebrates. Comptes Rendus Biologies 334:360–369.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case Studies. Ecological Monographs 62:67–118.

Lebreton JD, Clobert J (1991) Bird population dy- namics, management, and conservation: the role of math- ematical modeling. In: Bird population studies, Oxford University Press, New York. New York, USA, pp 102–125.

Lebreton J-D, Devillard S, Popy S, et al (2012) Towards a vertebrate demographic data bank. Journal of Ornithology 152:617–624.

Lenoir J, Gegout JC, Marquet PA, et al (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771.

Lindstedt SL, Boyce MS (1985) Seasonality, Fasting Endurance, and Body Size in Mammals. The American Naturalist 125:873–878.

Lindstedt SL, Calder, WA (1981) Body Size, physiological time, and longevity of homeothermic animals. The Quarterly Review of Biology 56:1–16.

Link WA, Nichols JD (1994) On the importance of sampling variance to investigations of temporal variation in animal population size. Oikos 69:539.

Liow LH, Fortelius M, Lintulaakso K, et al (2009) Lower extinction risk in sleep-or-hide mammals. The American Naturalist 173:264–272.

Loison A (1995) Approches intra- et inter-spécifiques de la dynamique des populations : l'exemple du chamois. PhD thesis, Université Claude Bernard Lyon1, Lyon.

Loison A, Festa-Bianchet M, Gaillard J-M, et al (1999a) Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539–2554.

Loison A, Gaillard JM, Houssin H (1994) New insight on survivorship of female chamois (*Rupicapra rupicapra*) from observation of marked animals. Canadian Journal of Zoology 72:591–597.

Loison A, Jullien J-M, Menaut P (1999b) Subpopulation structure and dispersal in two populations of chamois. Journal of Mammalogy 80:620–632.

Loison A, Jullien J-M, Menaut P (1999c) Relationship between chamois and isard survival and variation in global and local climate regimes: contrasting examples from the Alps and Pyrenees. Ecological Bulletins 126–136.

Loison A, Langvatn R (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116:489–500.

Loison A, Sæther B-E, Jerstad K, Røstad OW (2002) Disentangling the sources of variation in the survival of the European dipper. Journal of Applied Statistics 29:289–304.

López BC, Pino J, López A (2010) Explaining the successful introduction of the alpine marmot in the Pyrenees. Biological Invasions 12:3205–3217.

Lovari S, Sacconi F, Trivellini G (2006) Do alternative strategies of space use occur in male Alpine chamois? Ethology Ecology & Evolution 18:221–231.

Lukas D, Clutton-Brock T (2017) Climate and the distribution of cooperative breeding in mammals. Royal Society Open Science 4:160897.

Lyman CP, Willis JS, Malan A, Wang LCH (1982) Hibernation and torpor in mammals and birds. Academic Press, New York.

Macdonald DW, Newman C (2002) Population dynamics of badgers (*Meles meles*) in

Oxfordshire, U.K.: numbers, density and cohort life histories, and a possible role of climate change in population growth. Journal of Zoology 256:121–138.

Magnolon S (1999) The natal dispersal of Alpine marmot (*Marmota marmota*). Pattern and the influence of some proximal factors. PhD thesis, Université de Tours, Tours.

Magrath RD (2001) Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds? Journal of Animal Ecology 70:370–385.

Maldonado-Chaparro AA, Martin JGA, Armitage KB, et al (2015) Environmentally induced phenotypic variation in wild yellow-bellied marmots. Journal of Mammalogy 96:269–278.

Marshall HH, Sanderson JL, Mwanghuya F, et al (2016) Variable ecological conditions promote male helping by changing banded mongoose group composition. Behavioral Ecology 27:978–987.

Martin JGA, Festa-Bianchet M (2010) Bighorn ewes transfer the costs of reproduction to their lambs. The American Naturalist 176:414–423.

Martin K (2001) Wildlife in alpine and sub-alpine habitats. Johnson DH.

McNutt JW, Silk JB (2008) Pup production, sex ratios, and survivorship in African wild dogs, *Lycaon pictus*. Behavioral Ecology and Sociobiology 62:1061–1067.

Melis C, Herfindal I, Kauhala K, et al (2010) Predicting animal performance through climatic and plant phenology variables: The case of an omnivore hibernating species in Finland. Mammalian Biology - Zeitschrift für Säugetierkunde 75:151–159.

Menzel A, Fabian P (1999) Growing season extended in Europe. Nature 397:659–659.

Menzel A, Sparks TH, Estrella N, et al (2006) European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969–1976.

Merilä J (2012) Evolution in response to climate change: In pursuit of the missing evidence. BioEssays 34:811–818.

Michod RE (1979) Evolution of Life Histories in Response to Age-Specific Mortality Factors. The American Naturalist 113:531–550.

Millar JS, Hickling GJ (1990) Fasting Endurance and the Evolution of Mammalian Body Size. Functional Ecology 4:5.

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200

Monks JM, O'Donnell CFJ (2017) Social implications of a colony collapse in a highly structured vertebrate species (long-tailed bat, *Chalinolobus tuberculatus*). Animal Conservation 20:360–369.

Moreno J, Møller AP (2011) Extreme climatic events in relation to global change and their impact on life histories. Current Zoology 57:375–389.

Morin A, Rughetti M, Rioux-Paquette S, Festa-Bianchet M (2016) Older conservatives: reproduction in female Alpine chamois (*Rupicapra rupicapra*) is increasingly risk-

averse with age. Canadian Journal of Zoology 94:311–321.

Moritz C, Patton JL, Conroy CJ, et al (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–264.

Morris WF, Altmann J, Brockman DK, et al (2011) Low demographic variability in wild primate populations: fitness impacts of variation, covariation, and serial correlation in vital rates. The American Naturalist 177:E14–E28.

Morris WF, Doak DF (2004) Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. The American Naturalist 163:579–590.

Morris WF, Pfister CA, Tuljapurkar S, et al (2008) Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89:19–25.

Mortensen JL, Reed JM (2016) Population Viability and vital rate sensitivity of an endangered avian cooperative breeder, the White-Breasted Thrasher (*Ramphocinclus brachyurus*). PLOS ONE 11:e0148928.

Moyes K, Nussey DH, Clements MN, et al (2011) Advancing breeding phenology in response to environmental change in a wild red deer population: Advancing breeding phenology in wild red deer. Global Change Biology 2455–2469.

Mumme RL (1992) Do helpers increase reproductive success? an experimental analysis in the Florida Scrub Jay. Behavioral Ecology and Sociobiology 31:319–328.

Murphy GI (1968) Pattern in life history and the environment. The American Naturalist 102:391–403.

Mysterud A, Yoccoz NG, Langvatn R, et al (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2357–2366.

Nesti I, Posillico M, Lovari S (2010) Ranging behaviour and habitat selection of Alpine chamois. Ethology Ecology & Evolution 22:215–231.

Niel C, Lebreton J-D (2005) Using demographic invariants to detect overharvested bird populations from incomplete data. Conservation Biology 19:826–835.

Nussey DH, Clutton-Brock TH, Albon SD, et al (2005) Constraints on plastic responses to climate variation in red deer. Biology Letters 1:457–460.

Okie JG, Boyer AG, Brown JH, et al (2013) Effects of allometry, productivity and lifestyle on rates and limits of body size evolution. Proceedings of the Royal Society B: Biological Sciences 280:20131007–20131007.

Oro D, Torres R, Rodríguez C, Drummond H (2010) Climatic influence on demographic parameters of a tropical seabird varies with age and sex. Ecology 91:1205–1214.

Orzack SH, Tuljapurkar S (1989) Population dynamics in variable environments. VII. The demography and evolution of iteroparity. The American Naturalist 133:901–923.

Ozgul A, Childs DZ, Oli MK, et al (2010) Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Ozgul A, Tuljapurkar S, Benton TG, et al (2009) The Dynamics of Phenotypic Change and

the Shrinking Sheep of St. Kilda. Science 325:464–467.

Paquet M, Doutrelant C, Hatchwell BJ, et al (2015) Antagonistic effect of helpers on breeding male and female survival in a cooperatively breeding bird. Journal of Animal Ecology 84:1354–1362.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81:443–450

Parmesan C, Ryrholm N, Stefanescu C, et al (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37.

Patil VP, Karels TJ, Hik DS (2015) Ecological, evolutionary and social constraints on reproductive effort: are hoary marmots really biennial breeders? PLOS ONE 10:e0119081.

Patil VP, Morrison SF, Karels TJ, Hik DS (2013) Winter weather versus group thermoregulation: what determines survival in hibernating mammals? Oecologia 173:139–149.

Pelletier F, Clutton-Brock T, Pemberton J, et al (2007) The evolutionary demography of ecological change: linking trait variation and population growth. Science 315:1571–1574.

Perrin C, Allainé D, Le Berre M (1993) Socio-spatial organization and activity distribution of the Alpine marmot *Marmota marmota*: preliminary Results. Ethology 93:21–30.

Perrins CM (1970) The timing of birds‘ breeding seasons. Ibis 112:242–255.

Perrins CM (1965) Population Fluctuations and clutch-size in the Great Tit, *Parus major L*. The Journal of Animal Ecology 34:601.

Pettorelli N, Mysterud A, Yoccoz NG, et al (2005a) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society B: Biological Sciences 272:2357–2364.

Pettorelli N, Pelletier F, Hardenberg A von, et al (2007) Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pettorelli N, Vik JO, Mysterud A, et al (2005b) Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Pettorelli N, Weladji RB, Holand Ø, et al (2005c) The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. Biology Letters 1:24–26.

Pfister CA (1998) Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213–218.

Philippi T, Seger J (1989) Hedging one's evolutionary bets, revisited. Trends in Ecology & Evolution 4:41–44.

Pioz M, Loison A, Gauthier D, et al (2008) Diseases and reproductive success in a wild mammal: example in the alpine chamois. Oecologia 155:691–704.

Plard F, Gaillard J-M, Coulson T, et al (2014a) Mismatch between birth date and vegetation phenology slows the demography of roe deer. PLoS Biology 12:e1001828.

Plard F, Gaillard J-M, Coulson T, et al (2014b) Long-lived and heavier females give birth earlier in roe deer. Ecography 37:241–249.

Pomeroy D (1990) Why fly? The possible benefits for lower mortality. Biological Journal of the Linnean Society 40:53–65.

Post E, Forchhammer MC (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2367–2373

Pradel R, Wintrebert C, Gimenez O (2003) A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. Biometrics 59:43–53.

Prestrud P, Nilssen K (1992) Fat deposition and seasonal variation in body composition of Arctic Foxes in Svalbard. The Journal of Wildlife Management 56:221.

Pretzlaff I, Dausmann KH (2012) Impact of climatic variation on the hibernation physiology of *Muscardinus avellanarius*. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a Seasonal World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 85–97.

Promislow DEL, Harvey PH (1990) Living fast and dying young: A comparative analysis of life-history variation among mammals. Journal of Zoology 220:417–437.

R Development Core Team. (2011) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria.

Räisänen J (2002) CO2-induced changes in interannual temperature and precipitation variability in 19 CMIP2 experiments. Journal of Climate 15:2395–2411

Reale D, McAdam AG, Boutin S, Berteaux D (2003) Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society B: Biological Sciences 270:591–596.

Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16:561–576.

Reed JM, Walters JR (1996) Helper effects on variance components of fitness in the cooperatively breeding Red-Cockaded Woodpecker. The Auk 113:608–616.

Reznick D, Bryant MJ, Bashey F (2002) r- and K-selection revisited: the role of population regulation in life-history evolution. Ecology 83:1509.

Rézouki C, Tafani M, Cohas A, et al (2016) Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. Journal of Animal Ecology 85:761–773.

Richard Q, Toïgo C, Appolinaire J, et al (2017) From gestation to weaning: Combining robust design and multi-event models unveils cost of lactation in a large herbivore. Journal

of Animal Ecology 86:1497–1509.

Ricklefs RE (2010) Life-history connections to rates of aging in terrestrial vertebrates. Proceedings of the National Academy of Sciences 107:10314–10319.

Robert A, Paiva VH, Bolton M, et al (2012) The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. Ecology 93:1944–1952.

Rödel HG, Bora A, Kaetzke P, et al (2005) Timing of breeding and reproductive performance of female European rabbits in response to winter temperature and body mass. Canadian Journal of Zoology 83:935–942.

Rödel HG, Dekker JJA (2012) Influence of weather factors on population dynamics of two lagomorph species based on hunting bag records. European Journal of Wildlife Research 58:923–932.

Rowe L, Ludwig D, Schluter D (1994) Time, condition, and the seasonal decline of avian clutch size. The American Naturalist 143:698–722.

Rowell DP (2005) A scenario of European climate change for the late twenty-first century: seasonal means and interannual variability. Climate Dynamics 25:837–849.

Rubenstein DR (2011) Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proceedings of the National Academy of Sciences 108:10816–10822.

Rubenstein DR, Lovette IJ (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. Current Biology 17:1414–1419.

Ruf T, Bieber C, Turbill C (2012) Survival, aging, and life-history tactics in mammalian hibernators. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a Seasonal World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 123–132.

Rughetti M, Toïgo C, Von Hardenberg A, et al (2011) Effects of an exceptionally snowy winter on chamois survival. Acta Theriologica 56.

Russell AF, Brotherton PNM, McIlrath GM, et al (2003a) Breeding success in cooperative meerkats: effects of helper number and maternal state. Behavioral Ecology 14:486–492.

Russell AF, Clutton-Brock TH, Brotherton PN, et al (2002) Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. Journal of Animal Ecology 71:700–709.

Russell AF, Hatchwell BJ (2001) Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. Proceedings of the Royal Society B: Biological Sciences 268:2169–2174.

Russell AF, Sharpe LL, Brotherton PNM, Clutton-Brock TH (2003b) Cost minimization by helpers in cooperative vertebrates. Proceedings of the National Academy of Sciences 100:3333–3338.

Rutberg AT (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. The American Naturalist 130:692–710.

Saether B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic

traits to the population growth rate. Ecology 81:642–653.

Sæther B-E, Coulson T, Grøtan V, et al (2013) How life history influences population dynamics in fluctuating environments. The American Naturalist 182:743–759.

Saether B-E, Gordon IJ (1994) The adaptive significance of reproductive strategies in ungulates. Proceedings of the Royal Society B: Biological Sciences 256:263–268.

Salinger MJ (2005) Climate variability and change: past, present and future–an overview. Climatic Change 70:9–30.

Salomon M, Lubin Y (2007) Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (*Araneae, Eresidae*). Behavioral Ecology and Sociobiology 61:1743–1750.

Schaffer WM (1974a) Selection for optimal life histories: the effects of age structure. Ecology 55:291–303.

Schaffer WM (1974b) Optimal reproductive effort in fluctuating environments. The American Naturalist 108:783–790.

Schröder W, von Elsner-Schack I (1985) Correct age determination in chamois. In: Lovari S (ed) The Biology and managementmountain ungulates. Croom Helm, London, pp 65–70.

Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. Global Change Biology 12:343–351.

Schwartz OA, Armitage KB (2005) Weather influences on demography of the yellow-bellied marmot (*Marmota flaviventris*). Journal of Zoology 265:73–79.

Schwartz OA, Armitage KB, Van Vuren D (1998) A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). Journal of Zoology 246:337–346.

Shattuck MR, Williams SA (2010) Arboreality has allowed for the evolution of increased longevity in mammals. Proceedings of the National Academy of Sciences 107:4635–4639.

Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. Nature Climate Change 1:401–406.

Sheriff MJ, Kenagy GJ, Richter M, et al (2011) Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. Proceedings of the Royal Society B: Biological Sciences 278:2369–2375.

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Sibly RM, Brown JH (2007) Effects of body size and lifestyle on evolution of mammal life histories. Proceedings of the National Academy of Sciences 104:17707–17712.

Silk JB (2007) The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B: Biological Sciences 362:539–559.

Sinclair A (1996) Frontiers of population ecology. In: Mammal populations: fluctuation, regulation, life history theory and their implications for conservation, CSIRO. Melbourne, pp 127–154.

Skalski JR, Hoffman A, Smith SG (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. In: Marked individuals in the study of bird population, eds J.D. Lebreton & P. M. North. Birkaüser, Basel, Switzerland, pp 9–28.

Slatkin M (1974) Hedging one's evolutionary bets. Nature 250:704–705.

Sokolov LV, Markovets MY, Shapoval AP, Morozov YG (1998) Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. Avian Ecol Behav 1:1–21.

Solomon NG, French JA (1997) The study of mammalian cooperative breeding. Cooperative breeding in mammals, Eds Solomon, N.G., French, J.A. Cambridge: Cambridge University Press.

Spinks AC, Jarvis JU, Bennett NC (2000) Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. Journal of Animal Ecology 69:224–234.

Stacey PB, Ligon JD (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. The American Naturalist 137:831–846.

Stearns SC (1989) Trade-offs in life-history evolution. Functional Ecology 3:259.

Stearns SC (1976) Life-history tactics: a review of the ideas. The Quarterly Review of Biology 51:3–47.

Stearns SC (1992) The evolution of life histories. Oxford: Oxford University Press.

Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. Proceedings of the National Academy of Sciences 99:13379–13381.

Stephens PA, Frey-roos F, Arnold W, Sutherland WJ (2002) Model complexity and population predictions. The alpine marmot as a case study. Journal of Animal Ecology 71:343–361.

Steppan SJ, Kenagy GJ, Zawadzki C, et al (2011) Molecular data resolve placement of the Olympic marmot and estimate dates of trans-Beringian interchange. Journal of Mammalogy 92:1028–1037.

Tafani M, Cohas A, Bonenfant C, et al (2013) Decreasing litter size of marmots over time: a life history response to climate change? Ecology 94:580–586.

Tavecchia G, Coulson T, Morgan BJ, et al (2005) Predictors of reproductive cost in female Soay sheep. Journal of Animal Ecology 74:201–213.

Teplitsky C, Millien V (2014) Climate warming and Bergmann's rule through time: is there any evidence? Evolutionary Applications 7:156–168.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. Nature 399:213–213.

Thomas DW, Blondel J, Perret P, et al (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598–2600.

Thomas WK, Martin SL (1993) A recent origin of marmots. Molecular Phylogenetics and Evolution 2:330–336.

Toïgo C, Gaillard J-M, Van Laere G, et al (2006) How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography 29:301–308.

Tuljapurkar S (1990) Population dynamics in variable environments. Springer Berlin Heidelberg, Berlin, Heidelberg.

Tuljapurkar S, Gaillard J-M, Coulson T (2009) From stochastic environments to life histories and back. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1499–1509.

Tuljapurkar S, Haridas CV (2006) Temporal autocorrelation and stochastic population growth: Autocorrelation and stochastic growth rate. Ecology Letters 9:327–337.

Tuljapurkar S, Wiener P (2000) Escape in time: stay young or age gracefully? Ecological Modelling 133:143–159.

Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proceedings of the Royal Society B: Biological Sciences 278:3355–3363.

Turbill C, Prior S (2016) Thermal climate-linked variation in annual survival rate of hibernating rodents: shorter winter dormancy and lower survival in warmer climates. Functional Ecology 30:1366–1372.

Turbill C, Smith S, Deimel C, Ruf T (2012) Daily torpor is associated with telomere length change over winter in Djungarian hamsters. Biology Letters 8:304–307.

Türk A, Arnold W (1988) Thermoregulation as a limit to habitat use in alpine marmots (*Marmota marmota*). Oecologia 76:544–548.

Van Horne B, Olson GS, Schooley RL, et al (1997) Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. Ecological Monographs 67:295–315.

van Noordwijk AJ, de Jong G (1986) Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. The American Naturalist 128:137–142.

Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø (2007) Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. Oikos 116:1331–1342.

Vehrencamp SL (1983) Optimal Degree of Skew in Cooperative Societies. American Zoologist 23:327–335.

Verboven N, Tinbergen JM, Verhulst S (2001) Food, reproductieve success and multiple breeding in the Great Tit *Parus major*. Ardea 89:2.

Verhulst S, Nilsson J-A (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B: Biological Sciences 363:399–410.

Via S, Lande R (1985) Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505–522.

Viechtbauer W (2010) Conducting meta-analyses in *R* with the metafor Package. Journal of Statistical Software 36.

Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649–659.

von Hardenberg A, Bassano B, Peracino A, Lovari S (2000) Male alpine chamois occupy territories at hotspots before the mating season. Ethology 106:617–630.

Vucetich JA, Peterson RO, Waite TA (1997) Effects of Social Structure and Prey Dynamics on Extinction Risk in Gray Wolves. Efectos de la Estructura Social y Dinamica de las Presas Sobre el Riesgo de Extincion de Lobos Grises. Conservation Biology 11:957–965.

Vuren DV, Armitage KB (1991) Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Canadian Journal of Zoology 69:1755–1758.

Walters JR, Crowder LB, Priddy JA (2002) Population viability analysis for Red-Cockaded Woodpeckers using an individual-based model. Ecological Applications 12:249–260.

Walther G-R, Berger S, Sykes MT (2005) An ecological "footprint" of climate change. Proceedings of the Royal Society B: Biological Sciences 272:1427–1432.

Wasser DE, Sherman PW (2010) Avian longevities and their interpretation under evolutionary theories of senescence. Journal of Zoology 280:103–155.

Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. Proceedings of the Royal Society B: Biological Sciences 275:419–425.

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Wiersma P, Muñoz-Garcia A, Walker A, Williams JB (2007) Tropical birds have a slow pace of life. Proceedings of the National Academy of Sciences 104:9340–9345.

Wilbur HM, Rudolf VHW (2006) Life-history evolution in uncertain environments: bet hedging in time. The American Naturalist 168:398–411.

Wilbur HM, Tinkle DW, Collins JP (1974) Environmental certainty, trophic level, and resource availability in life history evolution. The American Naturalist 108:805–817.

Wilkinson GS, South JM (2002) Life history, ecology and longevity in bats: Longevity in bats, G. S. Wilkinson and J. M. South. Aging Cell 1:124–131.

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist 100:687–690.

Williams SA, Shattuck MR (2015) Ecology, longevity and naked mole-rats: confounding effects of sociality? Proceedings of the Royal Society B: Biological Sciences 282:20141664–20141664.

Willisch CS, Bieri K, Struch M, et al (2013) Climate effects on demographic parameters in an unhunted population of Alpine chamois (*Rupicapra rupicapra*). Journal of Mammalogy 94:173–182.

Willisch CS, Ingold P (2007) Feeding or resting? the strategy of rutting male Alpine Chamois. Ethology 113.

Wolkovich EM, Cook BI, McLauchlan KK, Davies TJ (2014) Temporal ecology in the Anthropocene. Ecology Letters 17:1365–1379.

Woodroffe R (2011) Demography of a recovering African wild dog (*Lycaon pictus*) population. Journal of Mammalogy 92:305–315.

Yoccoz NG, Ims RA (1999) Demography of small mammals in cold regions: the importance of environmental variability. Ecological Bulletins 47:137–144.

Yom-Tov Y, Roos A, Mortensen P, et al (2010) Recent changes in body size of the Eurasian otter *Lutra lutra* in Sweden. AMBIO 39:496–503.

Appendix I

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RESEARCH ARTICLE

Multiple geographic origins and high genetic differentiation of the Alpine marmots reintroduced in the Pyrenees

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Abstract Reintroductions inherently involve a small number of founders leading reintroduced populations to be prone to genetic drift and, consequently, to inbreeding depression. Assessing the origins as the genetic diversity and structure of reintroduced populations compared to native populations are thus crucial to foresee their future. Here, we aim to clarify the origins of the Alpine marmots reintroduced in the Pyrenees and to evaluate the genetic consequences of this reintroduction after almost 30 years without monitoring. We search for the origins and compare the genetic structure and the genetic variability of three reintroduced Pyrenean and eight native Alpine populations using pairwise genetic distances, Bayesian clustering method and multivariate analyses. Our results reveal that the Alpine marmots reintroduced in the Pyrenees originated both from the Northern and the Southern Alps, and that, despite these multiple origins, none of the current Pyrenean marmots are admixed. The reintroduction led to a strong genetic differentiation and to a decrease in genetic diversity. This pattern likely results from the small number of founders and the low dispersal capacities of Alpine marmots and thus, highlight the necessity to consider both genetic characteristics and natural history when reintroducing a species.

Keywords Alpine marmots · *Marmota marmota* · Reintroduction · Variability · Structuration

Introduction

Reintroductions involve the release of a species into its native range from which it disappeared within historical times (IUCN, Anonymous 1998). Although reintroductions appear as powerful conservation tools, at least a third of the projects fail (Germano and Bishop 2009), in part due to a failure to identify a priori targets concerned with assessing success and to inadequate post-release monitoring (Armstrong and Seddon 2008). Although the need for genetic monitoring of reintroduced populations has long been recognized (Haig et al. 1990), most studies focus on the demographic aspects to evaluate the success of reintroduction, and genetic states have only recently received attention (Seddon et al. 2007). However, Armstrong and Seddon (2008) argue that the progression of reintroduced populations from the establishment phase to the persistence phase strongly depends not only on the ability of the habitat to sustain a population, but also on the genetic makeup of the reintroduced population.

The restoration of genetic diversity can be especially challenging because reintroductions inherently involve a

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small number of founders which may retain only a subset of the genetic variation of the source population (i.e. founder effect; e.g. Cardoso et al. 2009), as it has been shown in empirical studies (Williams et al. 2000; Mock et al. 2004). This effect may further be intensified by genetic drift, especially when the number of founders is small (Nei et al. 1975; Leberg 1993; Sjoberg 1996). Reduced genetic diversity can impact individual fitness and decreases the viability and the evolutionary potential of the populations (Franklin and Frankham 1998). Understanding the genetic consequences of reintroductions is therefore necessary to evaluate the success of a reintroduction and to inform wildlife managers on best practices.

Alpine species are among the species the most threatened by climate change (Sala et al. 2000; Galbreath et al. 2009). Among these species, Alpine marmot (*Marmota marmota*) has been found to be highly sensitive to global warming with body mass, litter size and pup survival being negatively impacted (Tafani et al. 2013; Canale et al. 2016; Rézouki et al. 2016). And, according to the IUCN red list (IUCN 2015), one of the 14 marmot species is critically endangered (*Marmota vancouverensis*), one is endangered (*Marmota sibirica*) and one is vulnerable (*Marmota menzbieri*). Thus, research on a sister species such as the Alpine marmots are critical for developing proactive conservation strategies on other species with similar life histories. In this context, the Alpine marmot reintroduction in the Pyrenees represents an interesting case study Pyrenean populations presumably disappeared after the last glaciation (Herrero et al. 2002). Efforts to establish populations of Alpine marmots in the Pyrenees began in France in 1948 (Couturier 1955), were intensified in the 1960s and 1970s (Ramousse et al. 1993) and continued until 1988 (Ramousse et al. 1992). Although there is no detailed data about these reintroduction events, estimates suggest that around 400 marmots from La Vanoise and Mercantour National Parks in the French Alps were released in the French Pyrenees (Ramousse et al. 1992, 1993). Quickly, stable populations were established and probably reach now more than 10,000 individuals (Lopez et al. 2010) distributed across the Pyrenees (Lopez et al. 2009).

Although the success of the reintroduction of the Alpine marmot in the Pyrenees, based on population size is indisputable, it is still unknown whether this successful establishment has resulted in a population structure and a level of genetic diversity similar to that of the source population. Thus, we compared the genetic structure and variability of eight native Alpine populations and three reintroduced Pyrenean populations. Our goals were (1) to decipher the origin of the reintroduced populations, and (2) to investigate the consequences of reintroductions on the genetic structure and diversity. Given historical records, we expected that the reintroduced Pyrenean mainly originated from the Vanoise National Park. Due to the rapid demographic expansion of the reintroduced populations, we expected that reintroduced populations formed admixed populations, fused from the source populations and thus, not genetically differentiated. Moreover, due to the founder effect, we expected a lower genetic variability in the reintroduced populations compared to the native populations.

Materials and methods

Study species

Alpine marmots are territorial, socially monogamous and cooperative breeding ground-dwelling squirrels inhabiting alpine meadows (Allainé 2000). They live in family groups of two to 16 individuals composed of a dominant couple, sexually mature and immature subordinates of both sexes, and offspring of the year (Allainé 2000). A family group occupies and actively defends a territory including a main burrow and side burrows (2.5 ± 0.53 ha, Perrin et al. 1993). The status of dominance is established for several years until the dominant marmot will be evicted by another individual or will die (Lardy et al. 2011). Within family groups, reproduction is monopolized by the dominant pair (Cohas et al. 2006) which inhibits reproduction of same-sex subordinates (Arnold and Dittami 1997; Hacklander et al. 2003). At sexual maturity (i.e. 2 years of age), individuals can stay as subordinates in their natal groups, or attempt to become dominants by inheriting the dominance status in their natal groups or dispersing to gain dominance in another territories. Dispersal distances between the natal and the dominance territory are usually short (1.4 km for males and 0.95 km for females, Ferrandiz-Rovira et al. in prep), even if long distance dispersal (more than 25 km) can occur (Frey-Roos 1998).

Field methods and sample collection

We captured 338 free-ranging unrelated individuals between mid-April and mid-July in 2011, 2013 or 2014 from eleven continuous populations (Fig. 1) with a size large enough (around thirty families) to catch a sufficient number of individuals from different families and reach a sufficient statistical power to conduct the genetic analyses (Table 1). Eight native populations cover the Alpine arc from North to South: one from the Gran Paradiso, three from the Vanoise (Aussois, Sassière, Tignes), three from the Ecrins (Chambran, Lautaret, Prapic) and one (Maljasset) further south, close to the Mercantour National Park. Three reintroduced populations were located in the Pyrenees (Andorra, Cerdanya, Ripollès).

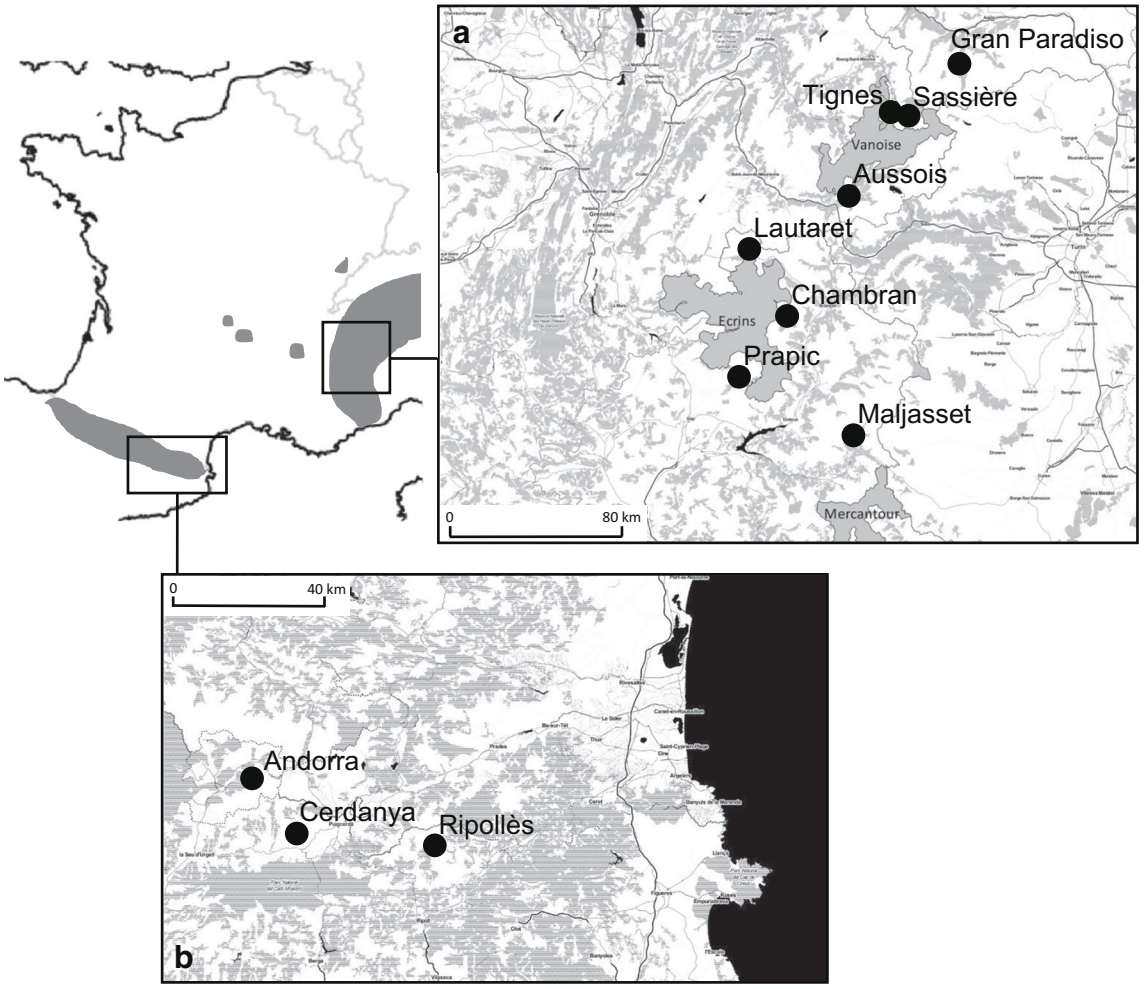


Fig. 1 Geographical locations of the eight native populations of Alpine marmots of the Alps (**a**) and of the three reintroduced populations of the Pyrenees studied (**b**). The areas in *dark grey* in the France map represent the current geographical distribution of the Alpine marmots

Following the observation and capture-mark-recapture protocols used for long-term monitoring of Alpine marmots' populations (details in Cohas et al. 2008 and Ferrari et al. 2013), marmots were captured using two-door live traps baited with dandelions (*Taraxacum densleonis*) and placed near the entrances of the main burrows (formed important mounts of bared soil and stones with several holes and situated in the middle of the territory) in order to assign each captured individual to its family group. Traps were checked every half hour. Once captured, individuals were anesthetized with Zolétil 100 (0.1 ml kg^{-1}), sexed, aged from their size (up to 3 years), and their social status was confirmed through examination of sexual characteristics (scrotum for males and teats for females). All individuals were marked using a numbered metal ear-tag for permanent individual recognition. In addition, skin biopsies (<1 mm^3) were collected with a biopsy punch (Alcyon, Lyon, France) on all trapped individuals for genetic analysis. To avoid bias in the genetic structure estimation caused by marmots of a same family group being highly related, we avoided sampling several individuals of the same family. We sampled the two dominant individuals, since they are a priori unrelated (Cohas et al. 2008), or only one subordinate per family.

Microsatellite genotyping

The 338 individuals were genotyped at sixteen microsatellites following previously validated protocols (Cohas et al. 2008; Supplementary material 1).

Hardy–Weinberg and linkage equilibrium

Departures from Hardy–Weinberg equilibrium for each locus and population were tested using Fisher's exact tests and linkage disequilibrium was examined for all loci with exact tests. These tests were carried out with GenePop 4.3 (Rousset 2008). p values were adjusted for multiple

Table 1 Sample size (N) and within-population genetic variability of the eight populations of Alpine marmots of the Alps and the three populations of the Pyrenees

Population	Mountain range	Status	Longitude	Latitude	N (number of families)	Expected heterozygosity	Observed heterozygosity ± SE	Allelic richness ± SE
Aussois	Alps	Native	45°16′2.98″N	6°43′13.22″E	30 (28)	0.58	0.57 ± 0.03	3.54 ± 0.19
Chambran	Alps	Native	44°54′14.64″N	6°29′37.22″E	23 (20)	0.59	0.60 ± 0.04	3.68 ± 0.21
Gran Paradiso	Alps	Native	45°34′44.94″N	7°11′27.74″E	28 (27)	0.56	0.51 ± 0.04	3.79 ± 0.25
Lautaret	Alps	Native	45°2′14.54″N	6°26′2.87″E	29 (28)	0.65	0.59 ± 0.03	4.29 ± 0.22
Maljasset	Alps	Native	44°35′39.55″N	6°50′5371″E	29 (29)	0.55	0.53 ± 0.05	4.09 ± 0.35
Prapic	Alps	Native	44°41′5.51″N	6°22′43.41″E	33 (28)	0.54	0.53 ± 0.04	3.70 ± 0.22
Sassière	Alps	Native	45°29′28.86″N	6°59′21.27″E	56 (32)	0.57	0.54 ± 0.02	3.78 ± 0.18
Tignes	Alps	Native	45°27′44.13″N	6°53′59.88″E	29 (21)	0.63	0.59 ± 0.03	4.18 ± 0.27
Andorra	Pyrenees	Reintroduced	42°32′22.15″N	1°38′14.92″E	15 (15)	0.44	0.42 ± 0.07	2.71 ± 0.31
Cerdanya	Pyrenees	Reintroduced	42°25′25.87″N	1°44′16.24″E	54 (30)	0.46	0.46 ± 0.03	2.91 ± 0.12
Ripollès	Pyrenees	Reintroduced	42°21′51.58″N	2°14′48.03″E	12 (12)	0.53	0.55 ± 0.08	3.44 ± 0.33

SE: standard error

comparisons using the false discovery rate (Benjamini and Hochberg 1995).

Assessment of the genetic structure

To identify the origin and to understand the genetic structure of the reintroduced Pyrenean populations, we first determined the level of genetic differentiation between the populations using pairwise genetic distances (F_{ST} and D_{EST} values) and then we assigned individuals to the eleven populations studied, using the STRUCTURE Bayesian clustering method (Pritchard et al. 2000; Falush et al. 2007). Bayesian clustering approaches are based on the assumptions that loci are at the Hardy–Weinberg equilibrium and in linkage equilibrium (Falush et al. 2003). These prerequisites are often violated in natural populations, as here (*cf.* Results). Thus, to corroborate the genetic structure inferred from the Bayesian analysis, we complemented this approach by two multivariate analyses, implemented in the adegenet R package (Jombart 2008), that make no assumptions regarding the underlying data structure and population genetic model: (1) a Discriminant Analysis of Principal Components (DAPC, Jombart et al. 2010) and (2) a spatial Analysis of Principal Components (sPCA, Jombart et al. 2008).

Assessment of the genetic structure using pairwise F_{ST}

Genetic distances between populations were quantified using pairwise F_{ST} values (Weir and Cockerham 1984) tested for significance using the exact test implemented in GenePop 4.3 (Rousset 2008). To test for an isolation by distance pattern of genetic differentiation between pairs of populations, we tested for a correlation between the matrix of genetic distances (linearized Fst = $F_{ST}/(1-F_{ST})$) and the matrix of log-transformed geographical distances using Mantel tests (9999 permutations, Mantel 1967) implemented in the ade4 package (Dray and Dufour 2007). We considered either all populations or the native Alpine populations only. Since the geographic distances between the reintroduced Pyrenean and the native Alpine populations are up to ten times larger than within Alpine or Pyrenean mountain ranges, we conducted partial Mantel tests to ensure that the isolation by distance was not due only to these huge geographic distances. The partial Mantel test was performed using the package vegan (Oksanen et al. 2015).

Assessment of the genetic structure using the STRUCTURE Bayesian clustering method

We used the Bayesian model-based clustering algorithm implemented in the software STRUCTURE 2.3.4 (Pritchard et al. 2000; Falush et al. 2007) to depict the population structure and to determine the origin of the sampled individuals. We assumed K, the number of clusters, to vary from one to eleven (i.e. the numbers of sampled populations). We ran 20 independent runs for each K value with 1,000,000 Markov chain-Monte Carlo steps and 100,000 burn-in iterations, using the admixture model, and correlated allele frequencies (Pritchard and Wen 2003). We used the *ad hoc* statistic ΔK, based on the rate of change in the likelihood of the data between successive K values (Evanno et al. 2005), to determine the most likely number

of clusters (Supplementary material 2). Evanno et al. (2005) stated that ΔK identifies only the uppermost level of structure and did not detect the potential substructures. Thus, we also conducted assignment analyses from the most likely number of clusters (K at ΔK) to the number of clusters corresponding to the number of sampled populations (K = 11; Supplementary material 3).

Assessment of the genetic structure using multivariate analyses

Assessment of the genetic structure using a DAPC DAPC provides an efficient description of genetic clusters, using few discriminant functions. This method seeks linear combinations of the original genotypes maximizing between-cluster differences while minimizing within-cluster variation (Jombart et al. 2010). After optimization steps, the analysis derives the probabilities for each individual to be a member of each cluster. This coefficient can be interpreted as the "genetic proximity" of individuals to the different clusters (Jombart et al. 2010). The optimization procedure followed three steps. First, we determined the optimal number of genetic clusters needed to adequately describe our data using Bayesian Information Criterion (BIC, Supplementary material 2). As recommended by Jombart (2014), we set the minimal number of clusters to one and the maximum to eleven because we did not expect more than one cluster in each population studied. Second, we used a cross-validation method to determine the optimal number of principal components (PCs) to retain. Cross-validation allows to choose the number of PCs that maximizes assignment success while minimizing the root mean squared error. Third, we determined the minimal number of discriminant functions to retain in order to maximize the total explained genetic variance. We further performed a constrained DAPC analysis by setting K = *3* (i.e. the optimal number of clusters determined using STRUCTURE) to compare the assignments obtained with STRUCTURE and the DAPC.

Assessment of the genetic structure using a sPCA We finally used a sPCA to investigate the spatial patterns of genetic variability using georeferenced genotypes (Jombart et al. 2008). This method aims to investigate cryptic spatial patterns of genetic variability using georeferenced genotypes. It corresponds to a modification of the PCA where spatial autocorrelation between the studied entities is taken into account. The analysis reveals two types of patterns: *global* (inter-population) and *local* (intra-population) structures. Global structures display positive spatial autocorrelation whereas local structures display negative spatial autocorrelation. The detection of spatial structures uses the Moran's index (*I*; Moran 1948, 1950), which relies on the comparison of the value of quantitative variables (allelic frequencies) observed at one site (populations) to the values observed at neighbouring sites. The sPCA procedure implies to select the minimal number of positive axes (representing global structure) and negative axes (representing local structure) that maximize the variance and the spatial autocorrelation explained. Relevance to consider global and/or local structures was assessed using global and local tests (Jombart et al. 2008).

All analyses involving R packages were conducted with R 3.1.2 (R Core Team 2014). Unless otherwise stated all parameters are given with ±standard errors.

Assessment of the within-population genetic variability

We characterized the within-population genetic diversity by computing, for each population and all microsatellite loci, the observed and expected heterozygosity and the rarefied value of allelic richness on randomized subsamples of twelve individuals (i.e. minimal number of individuals sampled from Ripollès) to avoid bias due to the variable number of individuals sampled among the different populations (see Table 1). These two indexes were calculated with the R package hierfstat (Goudet 2014).

To assess whether genetic diversity differed between the native and the reintroduced populations, we compared the observed heterozygosity and the allelic richness of the native Alpine and the reintroduced Pyrenean populations using a linear model in which the populations was nested in the mountain range (Alps or Pyrenees) with the package stats (R Core Team 2014).

Results

Hardy–Weinberg and linkage equilibrium

Among the eleven studied populations, Andorra, Gran Paradiso, Lautaret, Sassière and Tignes, showed a significant deficit of heterozygotes, as indicated by Hardy–Weinberg equilibrium global tests. Seven out of the 160 population-locus tests, involving different loci and different populations, showed a significant deviation from Hardy–Weinberg equilibrium after the adjustment of p-values for multiple comparisons. Thirty three of the 1154 linkage disequilibrium tests showed significant linkage disequilibrium, after correction for multiple comparisons.

Assessment of the genetic structure using pairwise F_{ST}

All populations showed significant genetic differentiation (global $F_{ST} = 0.2 \pm 0.01$) with Chambran and Lautaret being the most genetically similar ($F_{ST} = 0.04$), while Aussois and Cerdanya were the most genetically differentiated ($F_{ST} = 0.32$) (Table 2). The F_{ST} among the native Alpine populations is 0.18 ± 0.01 and 0.22 ± 0.09 between the reintroduced Pyrenean ones.

Geographic distances between the studied populations strongly explained the observed genetic differentiation (linearized F_{ST}: $r = 0.60$, $p = 0.001$; Fig. 2). However, while the isolation by distance explained the genetic differentiation between the native Alpine populations, the more genetically differentiated populations were the more geographically distant ($r = 0.81$, $p < 0.01$), it did not explain the differentiation between the native Alpine and the reintroduced Pyrenean populations ($r = -0.21$, $p = 0.92$; Fig. 2). The differentiation levels between Alpine–Pyrenean populations were similar to the differentiation among native Alpine or reintroduced Pyrenean populations, despite the huge geographic distance between the Alps and the Pyrenees (Fig. 2).

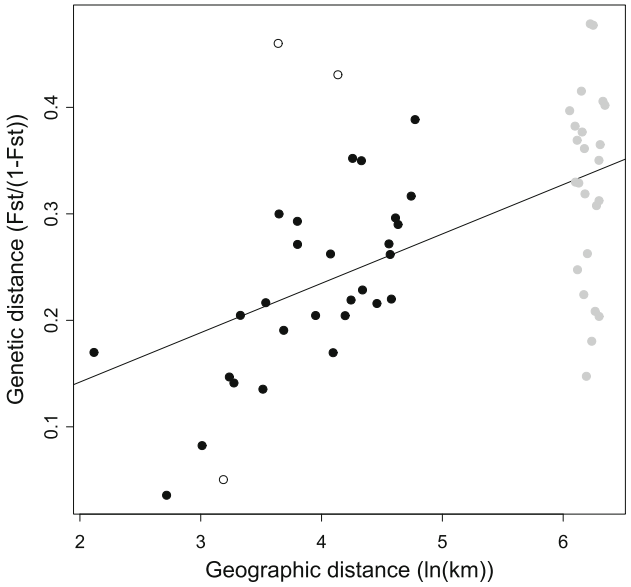


Fig. 2 Correlation between the genetic and the spatial structure of the eight native populations of Alpine marmots of the Alps and the three reintroduced populations of the Pyrenees studied. *Black dots* symbolized Alpine pairs, *white dots* symbolized Pyrenean pairs, and *grey dots* Alpine–Pyrenean pairs

Assessment of the genetic structure using the STRUCTURE Bayesian clustering method

The Bayesian model suggested that the eleven studied populations were structured in three clusters, as indicated by the strong mode of the ΔK criterion at $K = 3$ (Supplementary material 2). The first cluster was composed by four native populations including the three Vanoise populations (Aussois, Sassière and Tignes), and the Gran Paradiso population, as well as one reintroduced Pyrenean population (Ripollès) (Fig. 3a). The second cluster was composed by the three native Ecrins populations (Chambran, Lautaret and Prapic) (Fig. 3a). The last cluster was composed by the southern native Alpine population (Maljasset) and by two reintroduced Pyrenean populations (Andorra and Cerdanya) (Fig. 3a). The genetic structure did not exhibit a strong admixture, although the native populations of Lautaret and Maljasset could be considered the most admixed populations (Fig. 3a). The majority (98.8 %) of our 338 individuals were assigned to a single cluster with a probability superior to 0.8. Solely individuals

Table 2 Pairwise genetic distances (F_{ST} values) between the eight native Alpine populations of Alpine marmots and the three reintroduced populations of the Pyrenees (Andorran, Cerdanya, Ripollès)

Populations	Aussois	Chambran	GranParadiso	Lautaret	Maljasset	Prapic	Sassière	Tignes	Andorra	Cerdanya	Ripollès
Aussois	–										
Chambran	0.213	–									
GranParadiso	0.170	0.214	–								
Lautaret	0.178	0.035	0.178	–							
Maljasset	0.259	0.227	0.241	0.208	–						
Prapic	0.260	0.124	0.280	0.160	0.231	–					
Sassière	0.119	0.186	0.076	0.170	0.229	0.225	–				
Tignes	0.128	0.180	0.170	0.145	0.180	0.208	0.145	–			
Andorra	0.323	0.265	0.287	0.242	0.208	0.248	0.267	0.238	–		
Cerdanya	0.324	0.293	0.289	0.274	0.183	0.277	0.259	0.235	0.05	–	
Ripollès	0.129	0.248	0.169	0.198	0.270	0.284	0.173	0.153	0.301	0.315	–

All population pairs show significant genetic differentiation

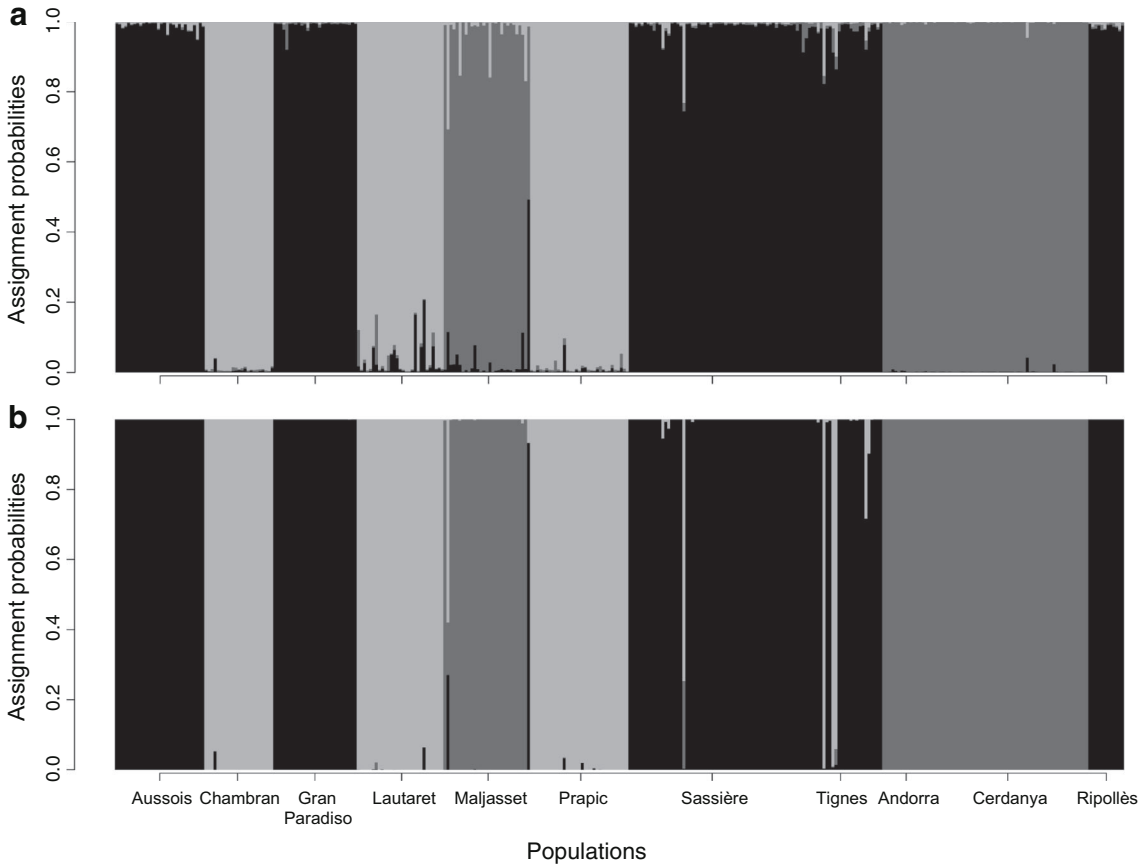


Fig. 3 Assignment probabilities of the 338 sampled individuals into the three clusters inferred with **a** the STRUCTURE Bayesian clustering method and **b** discriminant analysis of principal component (DAPC). Individuals are represented by a *vertical line* partitioned into three colored segments that represented the individuals' assignment probability to each of the three clusters. Cluster 1 (*black*) groups the populations of Aussois, Gran Paradiso, Sassière, Tignes and Ripollès, cluster 2 (*light grey*) groups the populations of Chambran, Lautaret and Prapic, cluster 3 (*dark grey*) groups the populations of Maljasset, Andorra and Cerdanya

from native populations were considered admixed: one individual from Lautaret, two individuals from Maljasset and one individual from Sassière were assigned to a given cluster with a probability inferior to 0.8. The analyses of the potential substructures (Supplementary material 3) revealed that Ripollès is closer to Aussois than to the other Vanoise populations (Sassière and Tignes) and the Italian population (Gran Paradiso). Andorra and Cerdanya appeared to be the closest to the native population of Maljasset. These three populations stayed grouped in the same cluster until $K = 6$, while Andorra and Cerdanya stayed grouped until $K = 11$.

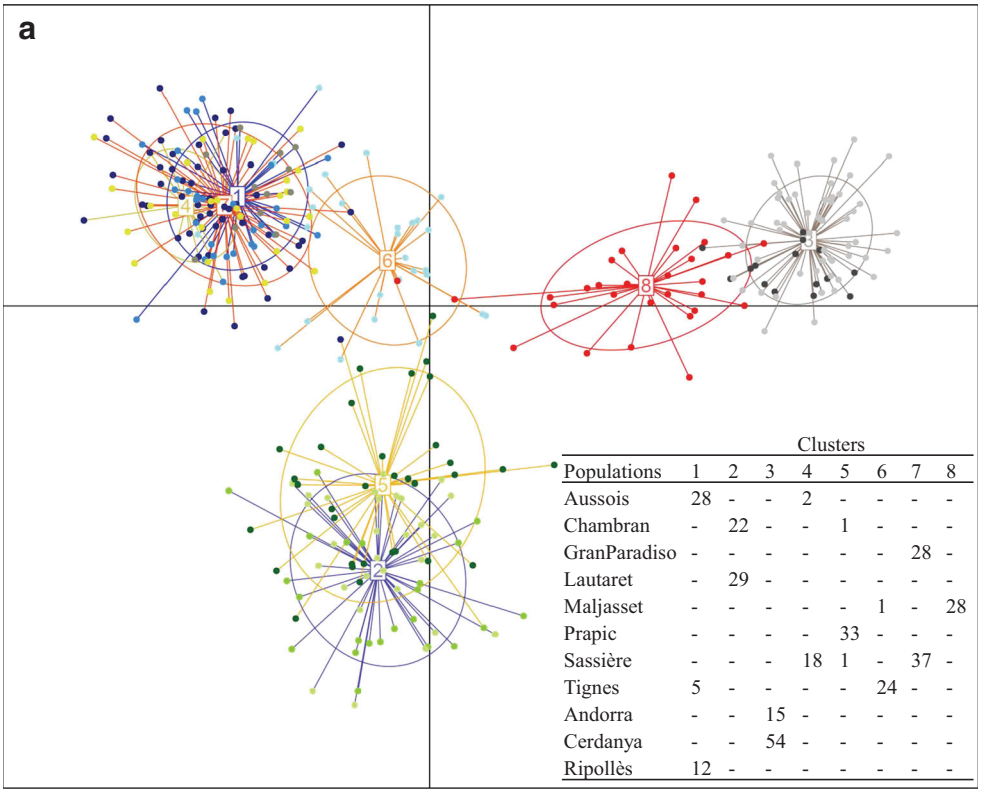
Assessment of the genetic structure using multivariate analyses

Assessment of the genetic structure using a DAPC

We identified eight genetic clusters (Supplementary material 2). After the cross-validation procedure (Supplementary material 2), the DAPC (Fig. 4) revealed that the native Gran Paradiso and Vanoise (Aussois, Sassière, Tignes) populations were genetically close as were the native Ecrins (Chambran, Lautaret, Prapic) populations. Secondly, it highlighted that the native Vanoise populations were genetically close to the reintroduced Ripollès population, while the native Maljasset population was the closest to the reintroduced Andorra and Cerdanya populations. These results perfectly matched those of STRUCTURE (Fig. 3a; Supplementary material 3) and were further confirmed by the DAPC constrained to three clusters (Figs. 3b, 4b).

Assessment of the genetic structure using a sPCA

The sPCA results were also in agreement with those given by STRUCTURE and the DAPC. They revealed a global structure in three clusters ($p = 0.001$ with 999 permutations) and the absence of local structure ($p = 0.129$ with 999 permutations). A first cluster was composed of the native Gran Paradiso and Vanoise populations and the



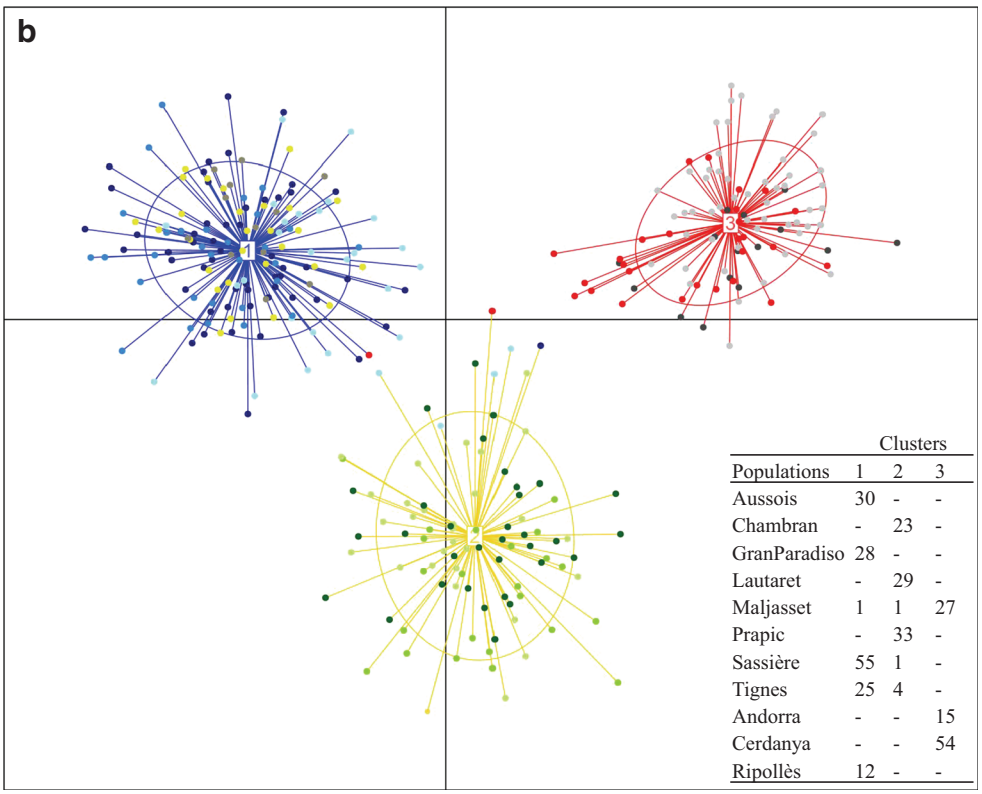


Fig. 4 Genetic proximity among the 338 individuals sampled from the eight native populations of Alpine marmots of the Alps and the three reintroduced populations of the Pyrenees (Andorra, Cerdanya, Ripollès) studied obtained by discriminant analysis of principal component (DAPC) defining **a** eight and **b** three clusters. The first principal components PC I (abscissa) explain respectively **a** 51.40 % and **b** 69.53 % of the total genetic variance, while the second principal components PC II (ordinate) explain respectively **a** 19.45 % and **b** 30.47 %. Genetic clusters and their 95 % inertia ellipses obtained from the DAPC are shown by different colors. *Dots* represent individuals. The colors of the *dots* represent the populations. The *grey dots* represent the reintroduced Pyrenean populations (Andorra: *dark grey*, Cerdanya: *light grey* and Ripollès: *grey*), the *green dots* represent the native Ecrins populations (Chambran: *green*, Lautaret: *light green* and Prapic: *dark green*), the *blue dots* represent the native Vanoise populations (Aussois: *blue*, Sassière: *dark blue* and Tignes: *light blue*), the *yellow dots* represent Gran Paradiso, and the *red dots* represent Maljasset. The tables on the *bottom right* give the assignment of the individuals from the different populations into respectively the eight and the three clusters obtained by the DAPCs. (Color figure online)

reintroduced Ripollès population, a second of the native Ecrins populations and a last one grouped the native Maljasset population and the two reintroduced Andorra and Cerdanya populations. The first cluster was genetically close to the second cluster, which was close to the third cluster (Fig. 5).

Assessment of the within-population genetic variability

Despite a low level of allelic richness, ranging from 2.71 ± 0.31 in Andorra to 4.18 ± 0.37 in Tignes, the eleven populations presented a rather high level of heterozygosity: from 0.42 ± 0.10 in Andorra to 0.60 ± 0.15 in Chambran (Table 1). While the eleven populations presented different levels of observed heterozygosity ($F = 2.13$, $df = 9$, $p = 0.03$), their allelic richness did not differ significantly ($F = 0.84$, $df = 9$, $p = 0.58$). The native Alpine populations showed a higher heterozygosity and allelic richness than the reintroduced Pyrenean populations (observed heterozygosity: 0.56 ± 0.01 vs. 0.47 ± 0.01, $F = 27.22$, $df = 1$, $p < 0.001$; allelic richness: 3.81 ± 0.12 vs. 3.00 ± 0.16, $F = 13.99$, $df = 1$, $p < 0.001$).

Discussion

Our results reveal two distinct origins for the reintroduced Alpine marmots of the Pyrenees. The Ripollès marmots descend from ancestors living in the Vanoise while the Andorra and Cerdanya marmots descend from ancestors living in the Mercantour. None of the reintroduced marmots originate from the Ecrins. Admixed individuals were absent in the Pyrenees and the reintroduction has led to different differentiation patterns (i.e. absence of isolation by distance in Pyrenees contrary to Alps) and to a decrease in genetic diversity in reintroduced Pyrenean populations compared to native populations.

Origins of the reintroduced Pyrenean marmots

The three studied reintroduced Pyrenean populations clearly have two distinct origins. Ripollès is genetically close to the native Vanoise populations, and more precisely to Aussois; while the westernmost two reintroduced Pyrenean populations, Cerdanya and Andorra, are more closely related to the southernmost native population, Maljasset (the geographically closest population to Mercantour), than to any other native Alpine populations. If Maljasset is the closest native population to Andorra and Cerdanya, these two reintroduced populations would probably found their exact source in populations even more in the South of the Alps. These results confirm the documented origins of individuals translocated to the French Pyrenees (Ramousse et al. 1993). They further refine findings from Kruckenhauser and Pinsker (2004), who showed that the individuals from two populations in the west of the Pyrenees were closer to populations from Vanoise than from Ecrins.

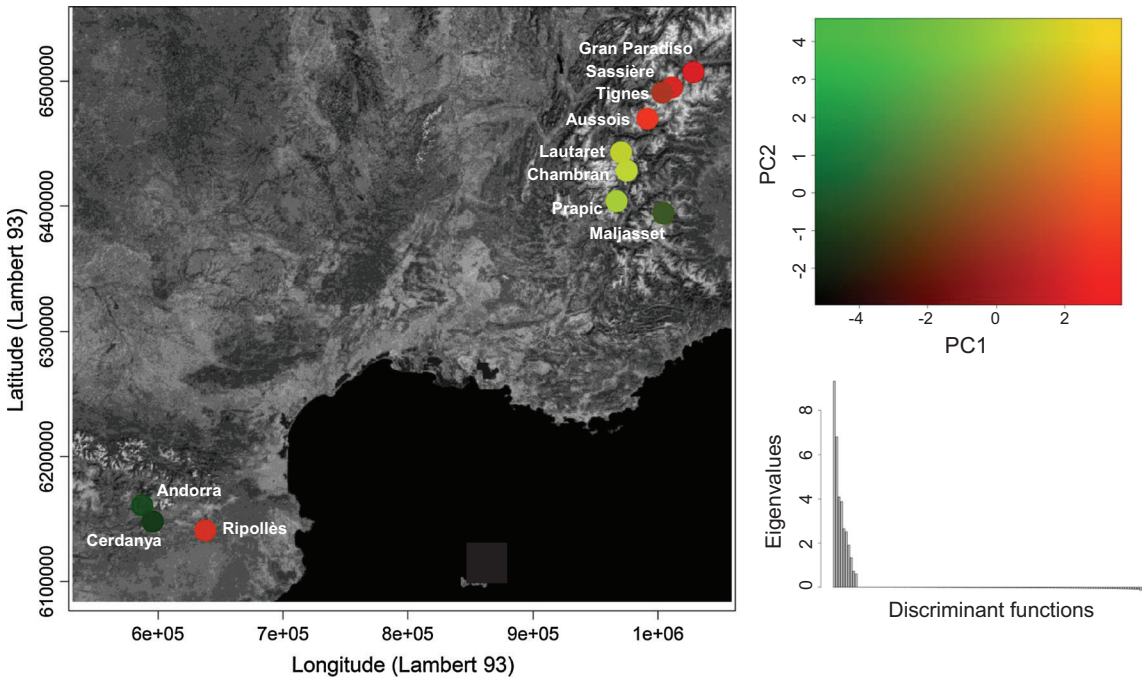


Fig. 5 Spatial genetic proximity of the eleven Alpine marmot populations studied obtained by spatial principal component analysis (sPCA). The first principal component explains 90 % of the total genetic variance, while the second principal component explains 80 %. The *dots* represent the eleven populations. The *box* on the *top right* represents the color code for the different axis values and reflects the genetic proximity between populations. The *box* on the *bottom right* gives the eigenvalues of the discriminant functions of the sPCA

Given the different localizations of the five populations sampled (three from this study and two from the study by Kruckenhauser and Pinsker 2004), and the lack of information about the release localization of the individuals from Vanoise and Mercantour, we cannot conclude that most actual Pyrenean marmots descend from ancestors captured in the Vanoise National Park, as previously suggested by (Ramousse and Le Berre 1993).

Genetic structure of the reintroduced Pyrenean populations

The Pyrenean populations are significantly differentiated from one another. Ripollès is the most differentiated and show virtually no admixture with Andorra and Cerdanya. This counteracts the colonization scheme previously accepted: a rapid expansion of the species to the southern Pyrenees, from an initial reintroduction in the northern Pyrenees (Gonzalez-Prat et al. 2001). Despite the fact that marmots are strongly associated with open Alpine meadows, it was suggested that the land use in the Pyrenees and, more specifically, the creation of new open habitats at low elevations for human activities, would have facilitated the success of the marmots' colonization (Herrero et al. 1994; Lopez et al. 2010). Under this scenario, we should observe strongly admixed individuals and low differentiation between the Pyrenean populations. On the contrary, our results indicate that individuals from different Alpine populations were reintroduced in several localizations and that the reintroduced populations are still isolated from one another. Even if significantly differentiated, Andorra and Cerdanya could have a common origin. Thus, with the three Pyrenean sampled populations, we can identified at least two different reintroduction events: one for Ripollès and another for Andorra and Cerdanya.

Genetic structure and variability between reintroduced and native populations

In the Alps, the farther away populations are located, the more genetically differentiated they are, with the three mountain ranges (Vanoise/Gran Paradiso, Ecrins and Mercantour) appearing as independent genetic units. In the Pyrenees, the number of sampled populations was too small to definitely rule out an isolation by distance. But, population pairs always appear more differentiated than Alpine pairs separated by similar distances. In addition, Pyrenean populations located at the eastern (this study) and at the western (Kruckenhauser and Pinsker 2004) parts of the Pyrenees are likely less differentiated, due to their common Vanoise origin, than populations located in the central Pyrenees (this study) despite being farther away. Given the rapid and wide colonization of marmots in the Pyrenees, the significant genetic differentiation in the reintroduced Pyrenean populations probably reflect more the distinct geographical origins of the founders rather than the dispersal capacities of the Alpine marmots or the existence of dispersal barriers in the Pyrenees. The reintroductions of the Alpine marmot in the Pyrenees also has observable consequences on the genetic diversity: a decrease in heterozygosity and allelic richness is observed in the Pyrenean compared to the Alpine populations. This is a rather common pattern reported in several native/reintroduced population comparisons in a wide range of taxa (e.g. Williams et al. 2000; Zachos et al. 2009).

Management recommendations

Added to the quick demographic growth (Gonzalez-Prat et al. 2001) and the rapid geographic expansion (Lopez et al. 2010), the level of genetic diversity attests to the success of the reintroduction of Alpine marmots in the Pyrenees. This success clearly contrasts with the failure of reintroductions in the Eastern Alps (Borgo 2003). Native Alpine marmots from the Eastern Alps went extinct, probably due to over-hunting, in the middle of the 19th century (Kruckenhauser and Pinsker 2004) and, since then, several reintroduction attempts were conducted (Preleuthner et al. 1995). Although the differentiation pattern is similar to the one observed in the populations reintroduced in the Pyrenees, a huge decrease in genetic variability was observed in the Austrian reintroduced populations (Preleuthner and Pinsker 1993; Kruckenhauser et al. 1997; Bruns et al. 1999) compared to the Pyrenean populations (this study; Kruckenhauser and Pinsker 2004). For instance, the Grison reintroduced population (Switzerland) has an observed heterozygosity of 0.42 and it is below 0.29 in the Eisenerzer Alpen population (east Austrian Alps; Kruckenhauser and Pinsker 2004).

Such contrast may find its roots in the reintroductions schemes themselves. First, despite the very few details about the reintroduction in the Pyrenees (Ramousse et al. 1992; Lopez et al. 2010) and in the Eastern Alps (Kruckenhauser and Pinsker 2004), which make both the exact number of introduction events and the sample size of founders impossible to know, it has been reported that, in the Pyrenees, around 400 individuals were translocated between 1948 and 1988 to different places (Ramousse et al. 1992, 1993) and that the recommendations were to use around ten mature adults, with an equilibrate sex-ratio, for each reintroduction event (Ramousse and Le Berre 1995). In the eastern Alps, the reintroduction events covered a longer time period and the number of founders was lower. Although the total number of reintroduced individuals of reached 600, they were reintroduced over 140 years and with an average of five individuals per reintroduction event

(Preleuthner 1993; Kruckenhauser and Pinsker 2004). Pyrenean individuals were translocated from the most genetically variable populations located in French Alps, (observed heterozygosity from 0.57 to 0.72; (Goossens et al. 2001; Kruckenhauser and Pinsker 2004); the present study), while individuals reintroduced in the Eastern Alps were often translocated from non-autochthonous source populations originating from previous introductions (Kruckenhauser and Pinsker 2004). The differences in this initial genetic state were probably magnified by the rapid demographic expansion of the Pyrenean population allowed by favorable ecological factors (habitats and climate patterns in the Pyrenees and in the Alps clearly coincide; Lopez et al. 2010). This rapid expansion has with no doubt limited genetic drift while the Eastern Alps reintroduced populations were exposed to repeated bottlenecks (Borgo 2003).

Our recommendations could also be helpful for the other species of the *Marmota* gender. Among the 14 marmots species, three are endangered or vulnerable (*Marmota vancouverensis*, *Marmota sibirica* and *Marmota menzbieri*). The Vancouver Island marmot is critically endangered and a study found that the genetic variability is extremely low (observed heterozygosity between 0.07 and 0.29, allelic richness between 1.27 and 1.64 for eleven microsatellite loci; Kruckenhauser et al. 2009). A captive breeding program is currently conducted to restore this species. It aims to maintain the remaining genetic variation of the species and manages all captive animals as a single population even if they come from different regions of the Vancouver Island and could be locally adapted (Kruckenhauser et al. 2009). In light of our findings, we encourage this program to continue along this line because genetic variability seems to be primordial for the viability of reintroduced marmot populations. In the Alpine marmot, disregard of local adaptation did not hinder genetically diverse founders to successfully colonize the Pyrenees, while low genetic diversity seems to have contributed to the failure of more locally adapted marmots to colonize the Eastern Alps.

Conclusion

In contradiction with the previously admitted reintroduction scenario, the use of powerful molecular techniques even many years after unmonitored releases allows to identify two distinct origins for the reintroduced Pyrenean populations. The low dispersal capacities of Alpine marmots and/or the presence of natural and anthropogenic barriers could explain why reintroduced Pyrenean populations are still so genetically differentiated. Despite that Eastern Alps and Pyrenees offered comparable environments, the contrasted success rates of reintroductions between the two regions stress the importance of choosing a sufficient number of founders as well as founders originating from genetically diverse native populations to ensure successful reintroductions. Finally, our study highlights the necessity to consider both genetic characteristics and natural history in the management of reintroductions.

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References

Allainé D (2000) Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. Behav Process 51:21–34. doi:10.1016/S0376-6357(00)00116-9

Anonymous. 1998. IUCN Guidelines for Re-Introductions. IUCN/SSC Re-Introduction Specialist Group, Gland, Switzerland

Armstrong DP, Seddon PJ (2008) Directions in reintroduction biology. Trends Ecol Evol 23:20–25. doi:10.1016/j.tree.2007.10.003

Arnold W, Dittami J (1997) Reproductive suppression in male alpine marmots. Anim Behav 53:53–66. doi:10.1006/anbe.1996.0277

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate—a practical and powerful approach. J R Stat Soc Ser B 57:289–300

Borgo A (2003) Habitat requirements of the Alpine marmot *Marmota marmota* in re-introduction areas of the Eastern Italian Alps. Formulation and validation of habitat suitability models. Acta Theriol (Warsz) 48:557–569. doi:10.1007/BF03192501

Bruns U, Haiden A, Suchentrunk F (1999) Allozyme variability in autochthonous colonies of Swiss Alpine marmots (*Marmota m. marmota*): a confirmation of the "species-wide bottleneck hypothesis"? Folia Zool 48:11–22

Canale CI, Ozgul A, Allainé D, Cohas A (2016) Differential plasticity of size and mass to environmental change in a hibernating mammal. Glob Change Biol. doi:10.1111/gcb.13286

Cardoso MJ, Eldridge MDB, Oakwood M et al (2009) Effects of founder events on the genetic variation of translocated island populations: implications for conservation management of the northern quoll. Conserv Genet 10:1719–1733. doi:10.1007/s10592-008-9774-z

Cohas A, Yoccoz NG, Da Silva A et al (2006) Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. Behav Ecol Sociobiol 59:597–605. doi:10.1007/s00265-005-0086-8

Cohas A, Yoccoz NG, Bonenfant C et al (2008) The genetic similarity between pair members influences the frequency of extrapair paternity in alpine marmots. Anim Behav 76:87–95. doi:10.1016/j.anbehav.2008.01.012

Couturier AJ (1955) Acclimatation et acclimatement de la Marmotte des Alpes, *Marmota marmota marmota* (Linne, 1758) dans les Pyrenées françaises. Saugetierkundliche Mitteilungen 3:105–108

Dray S, Dufour A-B (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14:2611–2620. doi:10.1111/j.1365-294X.2005.02553.x

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567–1587

Falush D, Stephens M, Pritchard JK (2007) Inference of population structure using multilocus genotype data: dominant markers and null alleles. Mol Ecol Notes 7:574–578. doi:10.1111/j.1471-8286.2007.01758.x

Ferrari C, Pasquaretta C, Carere C et al (2013) Testing for the presence of coping styles in a wild mammal. Anim Behav 85:1385–1396. doi:10.1016/j.anbehav.2013.03.030

Franklin IR, Frankham R (1998) How large must populations be to retain evolutionary potential? Anim Conserv 1:69–70. doi:10.1111/j.1469-1795.1998.tb00228.x

Frey-Roos F (1998) Geschlechtsspezifisches abwanderungsmuster beim alpenmurmeltier (*Marmota marmota*). PhD thesis, Philipps-University Marburg,Marburg

Galbreath KE, Hafner DJ, Zamudio KR (2009) When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an Alpine specialist (American Pika, *Ochotona Princeps*). Evolution 63:2848–2863. doi:10.1111/j.1558-5646.2009.00803.x

Germano JM, Bishop PJ (2009) Suitability of amphibians and reptiles for translocation. Conserv Biol 23:7–15. doi:10.1111/j.1523-1739.2008.01123.x

Gonzalez-Prat F, Puig D, Folch A (2001) Distribution of the Alpine marmot *Marmota marmota* (Linnaeus, 1758) in the outermost southeastern Pyren. Galemys 13:139–148

Goossens B, Chikhi L, Taberlet P et al (2001) Microsatellite analysis of genetic variation among and within Alpine marmot populations in the French Alps. Mol Ecol 10:41–52. doi:10.1046/j.1365-294X.2001.01192.x

Goudet J (2014) hierfstat: Estimation and tests of hierarchical F-statistics. R package version 0.04-14. http://CRAN.R-project.org/package=hierfstat

Hacklander K, Mostl E, Arnold W (2003) Reproductive suppression in female Alpine marmots, *Marmota marmota*. Anim Behav 65:1133–1140. doi:10.1006/anbe.2003.2159

Haig S, Ballou J, Derrickson S (1990) Management options for preserving genetic diversity reintroduction of guam rails to the wild. Conserv Biol 4:290–300. doi:10.1111/j.1523-1739.1990.tb00291.x

Herrero J, Garciagonzalez R, Garciaserrano A (1994) Altitudinal distribution of Alpine Marmot (*Marmota marmota*) in the Pyrenees, Spain/France. Arct Alp Res 26:328–331. doi:10.2307/1551793

Herrero J, Garcia-Gonzalez R, Garcia-Serrano A (2002) Research on alpine marmot (*Marmota marmota*) in the Spanish Pyrenees. In: Armitage KB, Rumiantsev VU (eds) Holarctic marmots as a factor of biodiversity. International Marmot Network, Cheboksary, pp 190–197

IUCN (2015) The IUCN red list of threatened species. Version 2015-4. www.iucnredlist.org. Accessed on 19 April 2016

Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405. doi:10.1093/bioinformatics/btn129

Jombart T (2014) A tutorial for discriminant analysis of principal components (DAPC) using adegenet 1.4–1

Jombart T, Devillard S, Dufour A-B, Pontier D (2008) Revealing cryptic spatial patterns in genetic variability by a new multivariate method. Heredity 101:92–103. doi:10.1038/hdy.2008.34

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet 11:94. doi:10.1186/1471-2156-11-94

Kruckenhauser L, Pinsker W (2004) Microsatellite variation in autochthonous and introduced populations of the Alpine marmot (*Marmota marmota*) along a European west-east transect. J Zool Syst Evol Res 42:19–26

Kruckenhauser L, Miller WJ, Preleuthner M, Pinsker W (1997) Differentiation of Alpine marmot populations traced by DNA fingerprinting. J Zool Syst Evol Res 35:143–149

Kruckenhauser L, Bryant AA, Griffin SC et al (2009) Patterns of within and between-colony microsatellite variation in the endangered Vancouver Island marmot (Marmota vancouverensis): implications for conservation. Conserv Genet 10:1759–1772. doi:10.1007/s10592-008-9779-7

Lardy S, Cohas A, Figueroa I, Allaine D (2011) Mate change in a socially monogamous mammal: evidences support the "forced divorce" hypothesis. Behav Ecol 22:120–125. doi:10.1093/beheco/arq168

Leberg P (1993) Strategies for population reintroduction-effects of genetic-variability on population-growth and size. Conserv Biol 7:194–199. doi:10.1046/j.1523-1739.1993.07010194.x

Lopez BC, Figueroa I, Pino J et al (2009) Potential distribution of the alpine marmot in Southern Pyrenees. Ethol Ecol Evol 21:225–235

Lopez BC, Pino J, Lopez A (2010) Explaining the successful introduction of the alpine marmot in the Pyrenees. Biol Invasions 12:3205–3217. doi:10.1007/s10530-010-9712-0

Mock KE, Latch EK, Rhodes OE (2004) Assessing losses of genetic diversity due to translocation: long-term case histories in Merriam's turkey (*Meleagris gallopavo merriami*). Conserv Genet 5:631–645. doi:10.1007/s10592-004-1849-x

Moran P (1948) The interpretation of statistical maps. J R Stat Soc Ser B 10:243–251

Moran P (1950) Notes on continuous stochastic phenomena. Biometrika 37:17–23. doi:10.2307/2332142

Nei M, Maruyama T, Chakraborty R (1975) Bottleneck effect and genetic-variability in populations. Evolution 29:1–10. doi:10.2307/2407137

Oksanen J, Blanchet GF, Kindt R, et al (2015) vegan: Community Ecology Package

Perrin C, Allaine D, Leberre M (1993) Sociospatial organization and activity distribution of the Alpine Marmot marmota-marmota-preliminary-results. Ethology 93:21–30

Preleuthner M (1993) Das Alpenmurmeltier *Marmota m. marmota*, Linné 1758): Verbreitungsgeschichte und genetische Variation in Ö sterreich. Ph.D. thesis, University of Vienna

Preleuthner M, Pinsker W (1993) Depauperated gene pools in *Marmota M-Marmota* are caused by an ancient bottle neck-electrophoretic analysis of wild populations from Austria and Switzerland. Acta Theriol (Warsz) 38:121–139

Preleuthner M, Pinsker W, Kruckenhauser L et al (1995) Alpine marmots in Austria. The present population structure as a result of the postglacial distribution history. Acta Theriol (Warsz) 40:87–100

Pritchard JK, Wen W (2003) Documentation for Structure software: Version2

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramousse R, Le Berre M (1993) Management of alpine marmot populations. Oecol Mont 2:23–29

Ramousse R, Le Berre M (1995) Pour un projet de charte de réintroduction de la Marmotte Alpine en France. In: Ramousse R, Le Berre M (eds) Laboratoire de Socioécologie et Conservation. International Marmot Network, Villeurbanne

Ramousse R, Martinot JP, Le Berre M (1992) Twenty years of reintroduction policy of alpine marmots from the national park of La Vanoise (French Alps). In: Bassano B, Durio P; Gallo Orsi, U, Macchi E (eds.). Saint Vincent, Aosta

Ramousse R, Leberre M, Massemin S (1993) The paradox of reintroductions of Alpine Marmots in France. Bull Soc Zool Fr 118:287–294

Rézouki C, Tafani M, Cohas A, Loison A, Gaillard JM, Allainé D, Bonenfant C (2016) Socially-mediated effects of climate change decrease survival of the hibernating Alpine marmots. J Anim Ecol 5:36–43

Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. Mol Ecol Resour 8:103–106. doi:10.1111/j.1471-8286.2007.01931.x

Sala OE, Chapin FS, Armesto JJ et al (2000) Biodiversity-global biodiversity scenarios for the year 2100. Science 287:1770–1774. doi:10.1126/science.287.5459.1770

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conserv Biol 21:303–312. doi:10.1111/j.1523-1739.2006.00627.x

Sjoberg G (1996) Genetic characteristics of introduced birds and mammals. Wildl Biol 2:159–164

Tafani M, Cohas A, Bonenfant C et al (2013) Decreasing litter size of marmots over time: a life history response to climate change? Ecology 94:580–586

Weir B, Cockerham C (1984) Estimating F-statistics for the analysis of population-structure. Evolution 38:1358–1370. doi:10.2307/2408641

Williams RN, Rhodes OE, Serfass TL (2000) Assessment of genetic variance among source and reintroduced fisher populations. J Mammal 81:895–907. doi:10.1644/1545-1542(2000)081

Zachos FE, Cirovic D, Kirschning J et al (2009) Genetic variability, differentiation, and founder effect in golden jackals (*Canis aureus*) from serbia as revealed by mitochondrial DNA and nuclear microsatellite loci. Biochem Genet 47:241–250. doi:10.1007/s10528-009-9221-y

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