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# The Influence of sociality on population dynamics in the Alpine Marmot

Pierre Dupont

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# **The Influence of sociality on population dynamics in the Alpine Marmot**

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# The Influence of sociality on population dynamics in the Alpine Marmot

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**Pierre DUPONT**

A thesis presented for the degree of  
**Doctor of Philosophy**





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## Abstract

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Population dynamics can be defined as the study of the forces responsible for the size and structure of a population. Several factors influencing population dynamics have already been identified. These factors can be categorized according to their level of influence. Some factors have a population-wide influence, such as climate change or population density, while others affect the individual level such as age or sex. Recently, many studies have emphasized the importance of this age structure for population dynamics.

In social species, an additional level of structuring of the population is the group. However, the consequences of this social group structuring are still poorly understood.

In this thesis, I try to answer this question in different ways. I first studied how the individual demographic parameters were influenced by the size and composition of the group. I was able to highlight in particular a negative effect of the number of juvenile females present during development on the probability of becoming dominant once in adulthood. In a second step, I studied the importance of interactions between groups by quantifying the impact of a change of dominant on the dispersion of subordinates. Finally, I also quantified the influence of different groups within the population showing that large groups contribute relatively less to the population growth rate. These various results are then discussed in a context of evolutionary demography and new avenues of research are proposed.

## Résumé

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La dynamique des populations peut être définie comme l'étude des forces responsables de la taille et de la structure d'une population. Plusieurs facteurs influençant la dynamique des populations ont déjà été identifiés. Ces facteurs peuvent être classés de par leur niveau d'influence, d'une influence à l'échelle de la population toute entière, comme par exemple les changements climatiques ou la densité de population, jusqu'à des facteurs individuels comme l'âge ou le sexe. Récemment, de nombreuses études ont insisté sur l'importance de la structure en âge pour cette dynamique.

Chez les espèces sociales, un niveau supplémentaire de structuration de la population est le groupe. Cependant, les conséquences de cette structuration en groupes sociaux est encore mal connue.

Au cours de ma thèse, j'ai tenté de répondre à cette question de différentes manières. J'ai tout d'abord étudié comment les paramètres démographiques individuels étaient influencés par la taille et la composition du groupe. J'ai pu notamment mettre en évidence un effet négatif du nombre de juvéniles femelles présents lors du développement sur la probabilité de devenir dominant une fois à l'âge adulte. Dans un deuxième temps, j'ai étudié l'importance des interactions entre groupes en quantifiant l'impact d'un changement de dominant sur la dispersion des subordonnés. Enfin, j'ai également quantifié l'influence des différents groupes au sein de la population démontrant que les grands groupes contribuent relativement moins au taux de croissance de la population. Ces différents résultats sont ensuite discutés dans un cadre de démographie évolutive et de nouvelles pistes de recherche sont proposées.



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Dianou, qui m'a pas mal supporté et psychanalysé aussi (presque autant que le contraire c'est dire...)

Flo, Jeanne et la p'tite Maïna qui prennent le vent là-bas en Bretagne très occidentale !

L'autre Flo, celui des baleines de l'univers, qui est tout autant à l'ouest !

Il y a aussi les parents qui ont bien du courage et que je n'ai pas ménagés...Merci !

Et puis il y a Marine...





**“All evolutionary biologists  
know that variation itself is  
nature's only irreducible essence...  
I had to place myself amidst the variation.”**

**S. J. Gould**



# Chapter I.

## Introduction

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**The influence of sociality on  
population dynamics**







## **Prologue**

When I started my PhD formation in October 2013, I joined the Evolution, Adaptation and Behaviour research team within the LBBE. However, I got the opportunity to start working for Prof. D. Allainé and Dr. A.Cohas a few years before, as a field work volunteer. I first came to the Grande Sassièrè nature reserve during the summer 2010 where I had my first close encounter with this fascinating mammal that is the Alpine marmot. At least fascinating enough to make me come back the following summer. Later on, and thanks to Dr. A. Cohas, I got to meet another fascinating mammal during my master internship: Dr. R. Pradel who introduced me to the world of Capture-Recapture methods and more generally to the universe of population ecology modelling.

Following this, the three of them were kind enough to support my application for a PhD thesis. As for all theses (or most of the theses at least), it did not go exactly according to the original plan, but in the end, I found myself going places I never thought I would go and working on topics I never thought I would be able to work on. Not to mention I enjoyed it! Starting from a main focus in ethology and behavioural ecology, with a particular interest in contemplating animals in their natural habitat, I ended up working hours and hours on programming obscure linear mixture models, whose existence I didn't suspect few months before. And I liked it! This manuscript compiles the work I did in the last three and a half years, almost in a chronological order, and I think it reflects quite well the evolution of my PhD subject but also my personal evolution (and understanding of the researchers' work).

In the first chapter, I give a general overview of the topic of my PhD journey: “The influence of sociality on the population dynamics, the case of the Alpine marmot”. One of the easiest and most efficient ways to circumscribe a subject is by giving its terms clear definitions. The structure of this introduction will thus be articulated around some definitions of the most important terms that are “population dynamics”, “sociality” and “influence”. I will start by introducing the concepts associated to population dynamics relevant to this study. The second part will introduce the different forms of sociality and especially the different features of social living susceptible to impact the population dynamics of species. In the third part of the introduction, I will briefly point out the importance of using appropriate methods to answer specific questions, with a focus on challenges related to population biology studies. Finally, a fourth part will be dedicated to the presentation of the different chapters of this thesis.



## 1. « Population Dynamics »

### 1.1. *What is population dynamics?*

“Population dynamics is the study of how and why population numbers change in time and space” (Turchin 2003). Even though humans surely noticed and cared about the fluctuations in animals’ numbers since the first ages (probably more so than we do now), population ecology became a scientific discipline on its own only in the 1920s (Kingsland 1995). At that time, ecology was largely dominated by both individual-level studies, with a particular focus on physiological responses to the environment, and community-level studies describing patterns of species associations, mostly among plants (Moore 1920). The “omission” of the population level is particularly obvious in a paper published in 1915 by V.E. Shelford, the first president of the Ecological Society of America. In this paper entitled “*Principles and problems of ecology as illustrated by animals*”, Shelford dedicated the first two parts to individuals, with topics such as the “characteristic physiological life history” while the four remaining parts of the publication were devoted to animal communities and how they compare to plant communities.

But both the individual and community levels are not sufficient to understand patterns at the population level, and population ecology began to receive much attention, partly because of the strong associated interests in agricultural and natural resources management (Kingsland 1995). It is therefore not surprising that among the first population dynamics articles published were studies on the populations of fur-bearing animals, of great economic interest at that time. These pioneering studies in the field of population dynamics are often traced back to the works of Elton (1924), Lotka (1925), Volterra (1926) or Nicholson (1954) (although Malthus' essay (1798) on the exponential growth rate and population regulation is often given credit as the first demographic study of importance). While Charles Elton was a naturalist above all who got interested in the periodic fluctuations in the abundance of Norwegian lemmings, Alfred Lotka was a mathematician and physical chemist by training and Vito Volterra was a physicist and mathematician. It is particularly interesting to note that population ecology, and especially population dynamics, brought together biology (and mainly zoology) and mathematics from the very beginning (although in practice both disciplines developed separately and their respective supporters were reluctant towards the other approach for quite a long time; Cooper 2007) .

Historically, as exemplified by the famous examples of Elton's work on lemmings' cycles or Canadian lynx (Elton & Nicholson 1942), population dynamicists were interested in quantifying the number of individuals present in a population and in describing the variation of these numbers in time. However, as noted by Lebreton (1981), the term "dynamics", comes from the branch of mechanics and supposes "the study of the forces or properties which stimulate growth, development, or change within a system or process." (Oxford dictionary). It appears very clearly from this definition that the discipline of population dynamics is not limited to the measure of population size and its temporal variation but contains in its own etymology the motivations to study the forces responsible for the changes observed in natural populations. Gaillard (1988) identified three different levels in the study of populations:

(i) *Population size*. Starting at the larger scale, this level is also the first historically. Counts data and time series of population size estimates may well inform about the general trend of a population and its potential susceptibility to extinction but it says nothing about the processes underlying the observed population changes. Nowadays, most studies on population size are either conservation studies trying to provide a general overview of a poorly known species (Botero-Delgado *et al.* 2015), of the efficiency of conservation measures (Ruegg *et al.* 2013) or population genetics studies with a focus on effective population size and genetic diversity (Palstra & Fraser 2012).

(ii) *Demographic rates*. Ultimately, as emphasized by Tuljapurkar & Caswell (1997), population dynamics result from the combination of individuals' capacity to survive, move and reproduce, and the rates at which these processes occur are the true determinants of population dynamics. Identifying variation in demographic rates between individuals is thus necessary to a thorough understanding of population dynamics (Benton *et al.* 2006). Notably, any variation in the population size or structure results from a variation in at least one of the demographic rates while the opposite is not true. Hence, the importance of population dynamics studies considering this level.

(iii) *Factors affecting demographic rates*. The relative influence of these different factors will be responsible for the variation in demographic rates and therefore population changes. Identifying and understanding the mechanisms through which these factors are responsible for the observed variation in demographic rates is thus the best way to characterize and understand population dynamics of animal species.

Accordingly, recent studies in population dynamics focused more and more on identifying these drivers of demographic rates (level three; León-Ortega *et al.* 2016), quantifying the relationships existing between these factors and the different demographic rates (levels two and three; Rézouki *et al.* 2016) and quantifying to what extent the overall population dynamic will be sensitive to these factors (levels one, two and three; Coulson *et al.* 2005).

### *1.2. Drivers of population dynamics*

Since the first population dynamics studies, great theoretical and methodological progress has been made (Tuljapurkar & Caswell 1997; Caswell 2001; Turchin 2003). Many of the factors affecting demographic rates, and ultimately population size and/or growth rate, were identified. These factors are often presented following a dichotomy: density-dependent *vs.* density-independent, biotic *vs.* abiotic, endogen *vs.* exogen and these different classifications sometimes overlap making it more difficult to understand. Hereafter, I present an overview of some of the factors affecting population dynamics based on their nature and on the scale of their influence, from internal factors affecting a single individual to large-scale factors affecting a whole population or even several species at the same time.

*Age/sex/stage structure.* Quite obviously, individuals in a population differ in many aspects (age, size, sex, developmental stage, physiology...). Even more obviously, these differences are translated into differences in demographic rates. Think for example about the reproductive rate of juvenile individuals or the survival probabilities of old-infected-stressed individuals. These differences in survival and/or reproduction between individuals are almost universal in animals. This leads to populations being structured and it has been shown that populations under the same environmental conditions but with different age structure will display different dynamics (Coulson 2001; Cameron & Benton 2004). Considering differences among individuals according to their age/sex/stage instead of demographic rates averaged over the whole population has proven very useful, and the study of structured populations considerably developed in the last 20 years (Tuljapurkar & Caswell 1997; Caswell 2001).

*Density dependence.* Another largely studied driver of population dynamics is population density. This was notably the subject of a famous debate that took place at the Cold Spring Harbor symposium in 1957. In this debate, Nicholson claimed that natural populations were self-regulated and that competition among conspecifics

increases with their number, thus leading to a decrease in the demographic rates at high densities. Since then, this population regulation mechanism was proven to be true under many circumstances (Clutton-Brock *et al.* 1987; Forchhammer *et al.* 1998). In addition, later research on this topic of density-dependence led to the proposition of a potential inverse density-dependence at low densities, known as the Allee effect (Allee *et al.* 1949). Several mechanisms have been proposed to explain this negative effect of low densities, such as genetic inbreeding and consecutive loss of genetic diversity, demographic stochasticity and social facilitation (Courchamp *et al.* 1999).

*Interspecific interactions.* Factors affecting population dynamics may also stem from interactions with other species. Predator/prey relationships were identified as a potential driver of population dynamics in the earliest studies on population dynamics. It was for example suggested as the main driver of the periodic fluctuations observed in lynx (*Lynx canadensis*) population size by Elton & Nicholson (1942) and it was studied from a mathematical point of view with the famous Lotka-Volterra equations (Lotka 1925; Volterra 1926). But interspecific interactions are not limited to predator/prey relationships. It also encompasses parasites/hosts interactions (Dobson 2004) or exclusive competition (Gurnell *et al.* 2004) amongst others and many examples of population dynamics driven by interspecific interactions were published in the last fifty years (Tilman & Kareiva 1997; Durrett & Levin 1998; Fenner 2000).

*Environmental variation.* Although the term “environment” is rather unclear and may apply to very different concepts, I refer here to abiotic factors such as temperature, precipitation, sun exposure... Although food resources availability is often classified as an environmental factor, I think it should rather be considered as belonging to the interspecific-interaction category. This is for example the case for vegetation-grazers dynamics (Pachzelt *et al.* 2013). This precision being made, variation in abiotic factors may affect demographic rates at very different scales, from local differences in chemical components in the soil (Dahlgren & Ehrlén 2009) to worldwide climate change (Grøtan *et al.* 2005; Wilmers & Getz 2005; Jenouvrier *et al.* 2005). The influence of these abiotic factors was also identified long ago. The opponents of the density-dependent population regulation during the 1957 Cold Spring Harbor symposium for instance, argued that survival and reproduction variations were mainly driven by abiotic conditions and notably the weather (Birch 1957). In addition, recent research on this topic highlighted

the importance of the variability of these abiotic factors for population dynamics (Frederiksen *et al.* 2008; Tuljapurkar 2013).

Nowadays, it is widely accepted that these different factors will not act separately and that observed population dynamics instead emerge from the interaction of numerous factors (Benton *et al.* 2006; Stopher *et al.* 2008a; Oro 2013). Additionally, a potential factor that is still largely overlooked in the context of population dynamics (but see Bateman 2013), and might have important effects on different demographic rates and population dynamics is sociality.

## **2. « Sociality »**

### *2.1. What is sociality?*

Sociality can be broadly defined as the tendency of individuals to live in groups. However, this very vague definition hides the multiplicity of social systems displayed by a multiplicity of animal species in nature. Comparable social systems may be found in very distinct taxa such as insects, birds, and mammals while closely related species may present very different social systems (Trivers 1985). For example, among primates, gorillas live in single-male harem systems, chimpanzees live in large multimale/multifemale groups and orangutans present a solitary lifestyle, even if the territory of a male may overlap several females territories (Kappeler & Schaik 2002), not to mention the variety of social systems in humans (Ségurel 2010).

The diversity of social systems ranges from eusociality in insects (and in naked mole rats *Heterocephalus glaber*, the mammal exception) or cooperative breeding in vertebrates to solitary life in many mammalian species. For a better definition, social systems are usually described using three different aspects: social organization, mating system, and social structure (Kappeler & Schaik 2002). Following the definitions given by Kappeler & Schaik, (i) social organization refers to the size, sexual composition and spatiotemporal cohesion of a group of individuals. (ii) mating system describes which males and females mate inside each group. Recent studies in birds and mammals showed that the social mating system may differ from the genetic mating system (Cohas *et al.* 2006). The social mating system describes pattern of association between males and females, namely mating couples, whereas the genetic mating system refers to the effective number of individuals of each sex who successfully reproduced. (iii) social structure is defined by the pattern of behavioural interactions and the resulting



relationships among the members of a society. The essentials of a social system can then be defined by combining these three components (Tab.I.1).

**Table I.1.** Classification and description of social systems (from Berger 2015)

Social systems		description	
Solitary		<ul style="list-style-type: none"> <li>no interactions between adult individuals except for reproduction</li> </ul>	
Gregarious		<ul style="list-style-type: none"> <li>group formation</li> <li>no interactions between adults</li> <li>groups may last or exist only during mating season</li> <li>allo-parental care may occur</li> </ul>	
Colonial		<ul style="list-style-type: none"> <li>pair formation (sometimes for life)</li> <li>few interactions between pairs</li> </ul>	
Social groups	absence of allo-parental care	<ul style="list-style-type: none"> <li>group living</li> <li>cooperative interactions</li> <li>overlap of generations</li> </ul>	
	Plural breeders	<ul style="list-style-type: none"> <li>group living</li> <li>cooperative interactions</li> <li>overlap of generations</li> <li>allo-parental care</li> </ul>	
	communal breeders	<ul style="list-style-type: none"> <li>group living</li> <li>cooperative interactions</li> <li>overlap of generations</li> <li>synchronisation of reproduction</li> <li>equally shared parental care</li> </ul>	
	Singular breeders	cooperative breeders	<ul style="list-style-type: none"> <li>group living</li> <li>overlap of generations</li> <li>reproduction monopolized by dominant individuals</li> <li>delayed dispersal of subordinates</li> <li>allo-parental-care provided by subordinates</li> </ul>
		eusocial	<ul style="list-style-type: none"> <li>group living</li> <li>labour division</li> <li>reproduction monopolized by one or few individuals</li> <li>subordinates are sterile</li> <li>allo-parental-care</li> </ul>

Sociality in animals is most often considered from an evolutionary point of view. Group formation comes at a cost since individuals have to compete against each other for resources but it can also provide benefits. The balance between these costs and benefits in a given environment will determine the social system displayed by species. Female lions for example, are more efficient together to hunt and protect the young and the net fitness benefit they can expect is higher when living together even if they have to share the product of the hunt and compete for reproduction with other females of the group (Packer *et al.* 1990; Stander 1992). Similarly, colonial birds may suffer from the close proximity with conspecifics because of competition for nest locations but they will benefit from a better detection and defence against predators (Brown *et al.* 1990). Accordingly, Serrano *et al.* (2005) showed that lesser kestrels (*Falco naumanni*) living in larger colonies had higher survival rates than individuals of smaller colonies as a result of decreased predation pressure. They also found that larger colonies were more attractive with dispersal probabilities from small to large colonies being much higher than from large to small colonies. The emergence of group living is thus well explained in the context of natural selection by the balance between costs and benefits associated to group living.

While low levels of sociality are easily explained by the individual net benefits in terms of survival and/or reproduction provided by group living, the existence of costly behaviours (*i.e.* altruism) in species with high levels of sociality seemed paradoxical to biologists for a long time. Darwin himself considered the existence of altruistic behaviours as a direct threat to his theory: “It represents one special difficulty, which at first appeared to me as insuperable and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind” (Darwin 1859). Since then, many theories were proposed too explain the evolution of altruism in highly social species. One of the most well-known theories is the kin-selection theory by (Hamilton 1964a,b). In his papers, Hamilton demonstrates that altruistic behaviours can be selected for because of the indirect fitness benefits one can obtain by helping a kin-related individual to reproduce. Because kin-related individuals share parts of their genomes, by helping a kin to reproduce, one will also transmit some of its genes, hence indirectly increasing its representation in the population, *i.e.* its fitness value. This explanation is contained in the

surprisingly simple formula known as Hamilton's rule:  $B.r > C$ , where  $B$  is the fitness benefit of the recipient of the behaviour,  $r$  is the relatedness between considered individuals, and  $C$  is the cost incurred by the altruist individual (although in the original paper, Hamilton used a different formulation:  $k > 1/r$  where  $k$  is the ratio of gain to loss for the individual displaying a costly behaviour). Kin-selection theory proved very useful to explain apparently costly behaviours in social animals (e.g. Queller & Strassmann 1998; Covas *et al.* 2006; Hughes *et al.* 2008). However, other theories have been proposed to explain the existence of costly behaviours without involving the genetic relatedness between individuals. For example, individuals might help other members of their social group at their expense if they are likely to receive help from others in return (delayed reciprocity: Wiley & Rabenold 1984; Kokko *et al.* 2001). This is for example the case in vampire bats (*Desmodus rotundus*) that regurgitate blood to feed un-related individuals in need when they can expect to be fed in return when needed (Wilkinson 1990).

## 2.2. Sociality and population dynamics

As shown in the previous paragraph, for sociality to evolve, it must confer a net fitness benefit to the individuals living in groups compared to solitary individuals. It follows that, in social species, survival, reproduction or both are affected by the characteristics of the social groups, *i.e.* the social organization (group size, composition and stability). It is therefore expected that demographic rates will vary according to the social organization displayed by a species. A great deal of studies (mainly interested in the evolution of sociality) identified relationships between group size (McGuire *et al.* 2002), composition (Silk 2007), or stability (Baird & Whitehead 2000) and different demographic parameters (survival, reproduction, dispersal).

These different studies highlighted the link between social groups' characteristics and the performances of individuals within their group. These relationships will determine the number of individuals to survive and the number of young produced by each group, thus being responsible for the dynamic of the group. However, in a population, social groups are not isolated from each other and the overall population dynamics cannot be fully understood without considering the interactions between the different social groups of the population. In social species, the grouping of individuals will thus generate an additional level of structuration in the population, in between the

individual and the population level, and the potential for interactions between these social structures through dispersal events. In this aspect, population dynamics of social species may be compared to the dynamic of a meta-population with social groups playing the role of local populations (Bateman *et al.* 2013).

The population dynamics of social species is therefore expected to be much more complex than that of solitary species. Demographic rates will vary both within social groups because of the differences in age/sex and group composition but also between social groups. By contrast, these interactions between social groups were largely ignored despite their potential importance for the overall population dynamic. Understanding the population dynamics of social species thus requires to understand both interactions between individuals (responsible for group dynamics), and group-level interactions (linked to dispersal between groups).

### **3. « The Influence »**

Once the topic has been clearly defined, another issue arises. This issue concerns the “how to” part of the research. Namely, how can one *quantify* the influence of sociality on population dynamics? I already argued that the best scale at which to proceed is the individual level since it allows identifying the mechanisms responsible for the variation in demographic parameters and consequently for the overall population dynamics. Because these factors are susceptible to vary in their influence and intensity with the age of individuals (*e.g.* the age specific pattern of survival), data should be gathered over the lifetime of individuals. We therefore require data covering the entire life of individuals from the species we wish to study. Finally, and obviously, we need data on the social organization of the species under study.

#### *3.1. Long-term individual-based studies*

In a recent review, Clutton-Brock & Sheldon (2010) stressed out the importance of long-term individual-based studies in both ecology and evolutionary biology. They pointed out six characteristics of these studies that are of great importance in ecology and evolution; (i) it provides the necessary information to study age-related changes in demographic rates and potentially the differences between individuals in these patterns (Nussey *et al.* 2008); (ii) longitudinal studies allow to relate events at one stage during life to those at another such as early-life carry on effects (Lindström 1999); (iii) individual-based studies provide opportunities to assess the social interactions between

individuals and the kinship structure of populations and its effect on demographic parameters (Clutton-Brock 2016); (iv) it allows to quantify to what extent breeding success varies between individuals and sexes, *i.e.* to study the reproductive skew in animal populations (Allainé 2000a); (v) long-term studies over several cohorts enable different selection gradients to be calculated, thus providing unique opportunities to witness changes in selection strength and eventually direction; and (vi) when these studies extend over several generations, it makes it possible to study the quantitative genetics of phenotypic traits in wild populations (Kruuk *et al.* 2008).

However, and despite their tremendous potential and scientific importance, these long-term individual-based data sets are also faced with many challenges. The first (and probably most important) challenge is the difficulty to run and maintain these programs because of logistical problems. These limitations include providing accommodation for a large number of field workers, sometimes for a long time, sometimes in remote areas, dealing with changing governance policies during the course of the studies, changing protocols (implied by temporary experiments for examples), and funding inconsistency, just to name but a few. In addition, different methodological challenges are contingent to these long-term individual-based studies.

### 3.2. Capture-recapture methods

Indeed, in practice, it is (almost) always impossible to follow a large number of individuals over a long time period without missing some of them from time to time. Hence, some information is missing in the data and analyses ignoring this source of error will lead to flawed inference of the relationships between the factors under study and the demographic rates (Gimenez *et al.* 2008). In the last 30 years, Capture-Recapture methods were developed to account for this imperfection of the data. Present day Capture-Recapture models are very powerful and allow to model very complex life cycles (*e.g.* different survival, dispersal and reproductive rates according to age, sex, developmental stage, hierarchical state). This enables the estimation of unbiased demographic parameters in relation to covariates of interest, depending on the population dynamics question we wish to answer (*e.g.* the influence of sex and age on survival in Tavecchia *et al.* 2001; influence of previous breeding success on dispersal in Cam *et al.* 2004; influence of food availability on adult survival and emigration in Oro *et al.* 2004). The strength of Capture-Recapture methods is to simultaneously account for

the potential flaws in the data that can lead to mis-estimations of demographic parameters; whether it is unequal time intervals between capture occasions (White & Burnham 1999), heterogeneity in recapture probabilities (Bonner 2008a), uncertainty in observations (Pradel 2005). Capture-Recapture methods are thus the most appropriate tool to quantify how sociality will affect the different demographic parameters.

#### **4. Organization of the thesis**

In the following chapters, I will present the different studies I conducted to determine the influence of sociality on Alpine marmots population dynamics. The choice of the Alpine marmot as biological model to answer this question was motivated by several reasons:

- (i) Alpine marmots are highly social (Allainé 2000a; Armitage 2014). They are socially monogamous cooperative breeders organized in family groups. This social system implies strong differences among individuals inside each family group and a strong differentiation between social groups, thus a putatively strong influence on population dynamics.
- (ii) Social groups in this species are highly variable (ranging from 2 to 20 individuals, with variable sex-compositions) thus allowing us to relate the variation in demographic rates due to the variation in group composition.
- (iii) The availability of a long-term individual-based data for this species (26 years of study, see <https://thealpinemarmotproject.org/>) ensured the feasibility of this project by making it possible to study the influence of sociality with sufficient power and details in the analyses to draw reliable conclusions.
- (iv) The *Marmota* genus and the Alpine marmot especially have been extensively studied from very different angles (*e.g.* Cohas *et al.* 2006; Lardy *et al.* 2013; Ferrandiz-Rovira 2015; Berger 2015; Rézouki *et al.* 2016) thus providing a solid foundation for this study, and allowing enlightening comparisons with previous studies.

Over the course of my PhD formation, I was thus able to make the most of the long-term individual-based dataset on Alpine marmots from La Grande Sassièrre (chapter II) to conduct a first study on the influence of the early social context on the ability of individuals to access reproductive status later in life (chapter III). I then took advantage

of the latest developments in terms of Capture-Recapture methods to propose an Integrated Capture-Recapture model to rigorously study dispersal (chapter IV.A) and tested for the effect of an intrusion by a new dominant individual on the group dynamics of Alpine marmots (chapter IV.B). To understand the consequences of sociality at the level of the population, I used a measure of individuals' contribution to population growth rate. To do so, I had to develop a new formulation of linear mixture models and tested it by quantifying the influence of age on individuals' contributions to population growth rate (chapter V.A). Based on these results, I derived a measure of group contribution to population growth rate from the same metric to analyse how the size and composition of a social group impacted its contribution to the overall population dynamic (chapter V.B). Finally, I end this manuscript by a discussion of the relevance of these results to the understanding social species' population dynamics and propose further lines of inquiry (chapter VI).

# Chapter II

## Material & methods

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### *Marmota marmota* and the Grande Sassièrè population

**Abstract:** In this chapter, I present the biological model I used all along this study to answer questions about the influence of sociality on population dynamics: the Alpine marmot *Marmota marmota*. The Alpine marmot belongs to the *Sciuridae* family, the *Marmotini* tribe and the *Marmota* genus. Recent phylogenetical analyses considered this genus as composed of 15 species of marmots. These species differ mostly in their geographical distribution and variable social systems, from the solitary woodchuck to the highly social Alpine marmot.

The Alpine marmot is a socially monogamous and hibernating rodent living in family groups. Social status is clearly defined in each social group with dominant individuals monopolizing reproduction. The fact that subordinate males help the dominants' pups to survive qualifies this species as a cooperative breeder.

This species has been extensively studied in the French Alps thanks to an individual-based long-term monitoring program running for 26 years now. The study area is situated in the Grande Sassièrè nature reserve (Savoie, France) and increased from 11 to 34 family territories between 1990 and 2016. Each year, individuals are captured, measured, weighed and group compositions are determined by behavioural observations. In addition, genetic analyses based on biopsies and hair samples allow determining the reproductive success of all individuals each year.

**Keywords:** *Marmota marmota* · phylogeography · socio-spatial structure · CMR protocol · Sciurid rodent





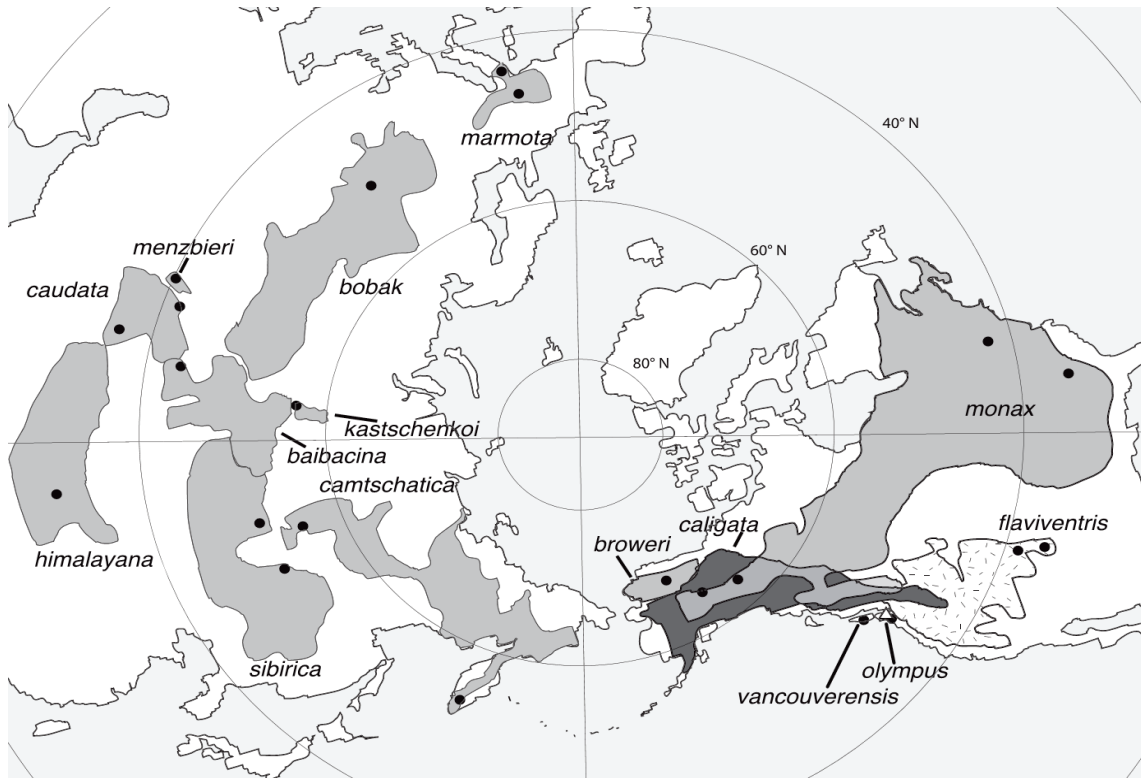
## 5. The Alpine marmot

### 5.1. The *Marmota* genus

Although the name “marmots” was applied to very different species until the XIX<sup>th</sup> and even early XX<sup>th</sup> centuries (Fig.II.1), it is now widely accepted that marmots are all species belonging to the same monophyletic clade subsequently called *Marmota*. This genus belongs to the *Mammalia* class, *Rodentia* order, *Sciuridae* family and *Marmotini* tribe. It originated in North America, spread into Eurasia during the Pliocene and further dispersed during the Pleistocene. 15 species are now recognised in this genus (Steppan *et al.* 2011) with six species located in North America and nine in Eurasia (Fig II.2).



**Figure II.1.** “Marmots” plate from the *Johnson’s Household book of Nature: Containing Full and Interesting Descriptions of the Animal Kingdom*. (1880). Credit: <https://commons.wikimedia.org>



**Figure II.2.** Geographical distribution of the genus *Marmota*. Fifteen currently recognized species are labelled. Stippling (*M. flaviventris*) and darkest shading (*M. caligata*) are used to distinguish two species with overlapping ranges. Dots represent the locations of the samples sequenced in the original study by Stepan *et al.* (2011). See also fig II.4. for a more precise description of the Alpine marmot distribution.

All species of this genus share common morphological characteristics among which the two rodent-specific pairs of ever-growing incisors, a large and compact body with relatively short legs, a relatively short bushy tail (compared to other squirrels) and small round ears (Fig.II.3). Marmots are the largest of the ground squirrels. They are usually considered as monomorphic although some slight differences in size and weights exist between sexes and among species (Tab.II.1). Females tend to be smaller and lighter in all species and mean adult weight at the end of the active season varies from approximately 4 kg for *M. flaviventris* to up to 11 kg for *M. olympus* (Edelman 2003).

Another shared characteristic of marmot species is their use of burrows. These burrows have three functions, (i) provide shelter from heat, predators and/or antagonistic conspecifics; (ii) provide a place to rear young and (iii) serve as a place to hibernate, *i.e.* a hibernaculum (Armitage 2014). These three functions are most often distributed among different burrows. Marmots generally use the same burrow system over several years, sometimes for many generations thus defining territories with highly stable boundaries. For instance, Armitage (2014) reported that in a 41-year study on Yellow-

bellied marmots the same major burrows were used year after year. Similarly, in the rare cases of new territory creations, Alpine marmots of the population we studied generally converted existent peripheral burrows rather than excavating new ones (personal observation). A territory is usually composed of several burrows, with the hibernaculum usually located in a place where the snow cover is the thickest to provide a good insulation during winter, the main burrow (used during the active period) where young are raised situated at the centre of the territory and numerous auxiliary flight burrows disseminated near the edges of the territory (Armitage 2014).



**Figure II.3.** Examples of marmot species showing the characteristic morphology of the *Marmota* genus. Clockwise from the top left: adult *M. monax* in up-alert posture, adult *M. flaviventris*, adult *M. olympus* sun-bathing, adult *M. himalayana* on the look-out while feeding, two adult *M. caudata* in nose to nose greeting and adult *M. caligata* resting on a rock. Photo credits: <http://thealpinemarmotproject.org>

Marmots occupy a wide range of open habitats, from flat and well-drained steppes in central Eurasia to cultivated croplands and high altitude alpine meadows. The only exception is *M. kastschenkoi*, which is the only forest-dwelling marmot. Even though they occupy very different habitats, all marmot species inhabit regions with marked seasonality and very cold winters. Marmots typically cope with these harsh winters through hibernation. The length of the hibernation phase varies among species but also according to a latitudinal and/or altitudinal gradient with higher elevation and/or higher latitude populations emerging later. Barash (1989) reported examples of Hoary marmot (*M. caligata*) populations only active four months (from mid-May to mid-September) while some woodchuck (*M. monax*) populations in southern Illinois may

**Table II.1.** Body mass of adult females and hibernation length of *Marmota* species. From Armitage (2014)

Species	Body mass (g)		Length of hibernation (months)
	Immergence	Emergence	
Subgenus <i>Petromarmota</i>			
<i>M. caligata</i>	6187	3283	7.5
<i>M. flaviventris</i>	3431	2422	7.5
<i>M. olympus</i>	5550	4110	7.5
<i>M. vancouverensis</i>	5328	3899	7.0
Subgenus <i>Marmota</i>			
<i>M. broweri</i>	3094	2055	7.5
<i>M. baibacina</i>	5583	3978	7.0
<i>M. bobak</i>	4120	2910	7.7
<i>M. camtschatica</i>	4748	2900	8.2
<i>M. caudata</i>	3923	2631	7.6
<i>M. himalayana</i>	6420	3445	7.5
<i>M. kastschenkoi</i>	4600	3450	7.5
<i>M. marmota</i>	3987	2825	6.5
<i>M. menzbieri</i>	3760	2321	8.0
<i>M. monax</i>	4804	3084	4.5
<i>M. sibirica</i>	3960	2550	6.6

**Table II.2.** Sociality in the *Marmota* genus. 1: Allainé (2000); 2: Blumstein & Armitage (1999); 3: Schwartz *et al.* (1998); 4: Armitage (2014); 5: Berger *et al.* (2015)

Species	Social structure	Sociality	References
<i>M. monax</i>	Solitary	Solitary	1,4
<i>M. flaviventris</i>	Matriline	Social groups without allo-parental care	2,3,4
<i>M. caligata</i>			4
<i>M. olympus</i>			4
<i>M. vancouverensis</i>		Social groups without allo-parental care	4
<i>M. broweri</i>	Restricted families	Dispersal at the age of sexual maturity	4
<i>M. baibacina</i>		4	
<i>M. bobak</i>		4	
<i>M. camtschatica</i>		4	
<i>M. caudata</i>			1,4
<i>M. himalayana</i>			1
<i>M. kastschenkoi</i>	Extended families	Cooperative breeders	NA
<i>M. marmota</i>		Delayed dispersal	1,4,5
<i>M. menzbieri</i>			1,4
<i>M. sibirica</i>			1,4

stay active for more than ten months a year. Because of this hibernation phase, all marmot species also display a characteristic pattern of annual weight gain and loss, with a continuous gain of weight during the active season and an important weight lost during hibernation (Tab.II.1).

Winter mortality is generally considered as the main mortality cause in marmot species, the two others main causes being antagonistic interactions and predation (Armitage 2014). Predators of marmots consist in terrestrial mammals, mostly canids (*e.g.* coyotes (*Canis latrans*) in North America or red foxes (*Vulpes vulpes*) in Europe), and aerial predators such as the golden eagle (*Aquila chrysaetos*). Most of the time, only disappearances of individuals are recorded on the fields thus making it very difficult to assess the relative contribution of these different mortality causes to the overall population dynamics. However, some studies were able to quantify the importance of predation for marmots by showing that summer mortality was mainly driven by predation in yellow-bellied marmots (Van vuren 2001), Vancouver Island marmots (Bryant & Page 2005) and Olympic marmots (Griffin 2007), leading to drastic population declines in the last two cases.

Social structure is highly variable among marmot species and often presented in four different categories: solitary species (*M. monax*), matriline (*M. flaviventris*), restricted families and extended families (Tab.II.2). These differences in social structure and mating system likely evolved in response to the harsh wintering conditions encountered by the different species (Arnold 1990; Allainé 2000 and see below).

## 5.2. *Marmota marmota*

### 5.2.1. Generalities

Alpine marmots can be found in most of European mountain chains between 1000 and 3000 meters a.s.l. Its natural geographical distribution encompasses both the Alps (from France, Italy, Swiss and Germany to Austria) and the Carpathian Mountains where a sub-species has been described (*M. marmota latirostris*, Kratochvil 1961) It was successfully introduced in the Pyrenees between 1948 and 1988 from different Alpine populations (see Appendix I) and the Pyrenean population now constitutes the second in size after the Alpine one (López *et al.* 2010). Other introductions occurred in the Massif Central (France), in the Black Forest (Germany) and in the Apennines (Italy) (Fig.II.4).



**Figure II.4.** Contemporaneous distribution of the Alpine marmot. Yellow areas: natural populations; purple areas: introduced populations. Image credit: <http://iucnredlist.org>

Alpine marmots are characterized by their brown coat with orange marking on the back, beige to orange belly, brown muzzle with a grey-white band between the muzzle and the eyes (Fig.II.5). As all marmots, they possess small ears and short legs and a bushy brown tail with a black tip. Adult Alpine marmots measure between 45 and 68 cm without the tail (between 13 and 16 cm). Their body mass is highly variable throughout the year with a minimum weight at the emergence from hibernation in April (around 2.2 kg for adults) and a maximum weight around 6.5 kg at the entry into hibernation (Körtner & Heldmaier 1995).

The average lifespan of a marmot is around seven years but strongly depends on the hierarchical status of the individual. In the population under study, no subordinate individual was captured older than seven years whereas dominant individual of up to 15 years for males and 16 years old for females were identified. The small number of individuals attaining such old ages is explained by the survival senescence that was evidenced for dominant individuals after approximately seven years of age (see Appendix II). Alpine marmots are herbivorous and sometimes insectivorous although rare cases of carnivory and/or cannibalism have been reported in this species (Ferrari *et al.* 2012 and S. Pardonnet, personal communication).



**Figure II.5.** Male adult Alpine marmot sun-bathing. Photo credit: Marie-Léa Travert

### *5.2.2. Life cycle*

The Alpine marmot annual life cycle revolves around hibernation. From approximately mid-October to early April, all members of a family group hibernate in the same burrow chamber. Hibernation is characterized by alternate periods of torpor (characterised by a very low physiological activity and body temperature) and euthermia (characterised by wakefulness and an increase of body temperature; Fig.II.6). Reproduction takes place just after the awakening from hibernation. Females are only receptive during a short 24-hour period within 15 days after the end of hibernation (Müller-Using 1957). After approximately 30 days of gestation, dominant females give birth to a litter of one to seven pups. The altricial young are born hairless, blind, weigh about 30 g and are entirely dependent on their mother. The female nurses them (approximately 40 days) until their emergence from the burrows around the end of June. At that time, they weigh around 350 g and start to feed on plants. The rest of the active season is dedicated to foraging in order to accumulate enough fat reserves for hibernation. Because of the shortness of the active season, all late litters are doomed to fail and one litter at most is produced each year. This demonstrates how the life cycle, and especially reproduction, is highly constrained in Alpine marmots. As the active season passes, daily activity rhythm decreases and becomes clearly divided: marmots are active at the beginning and



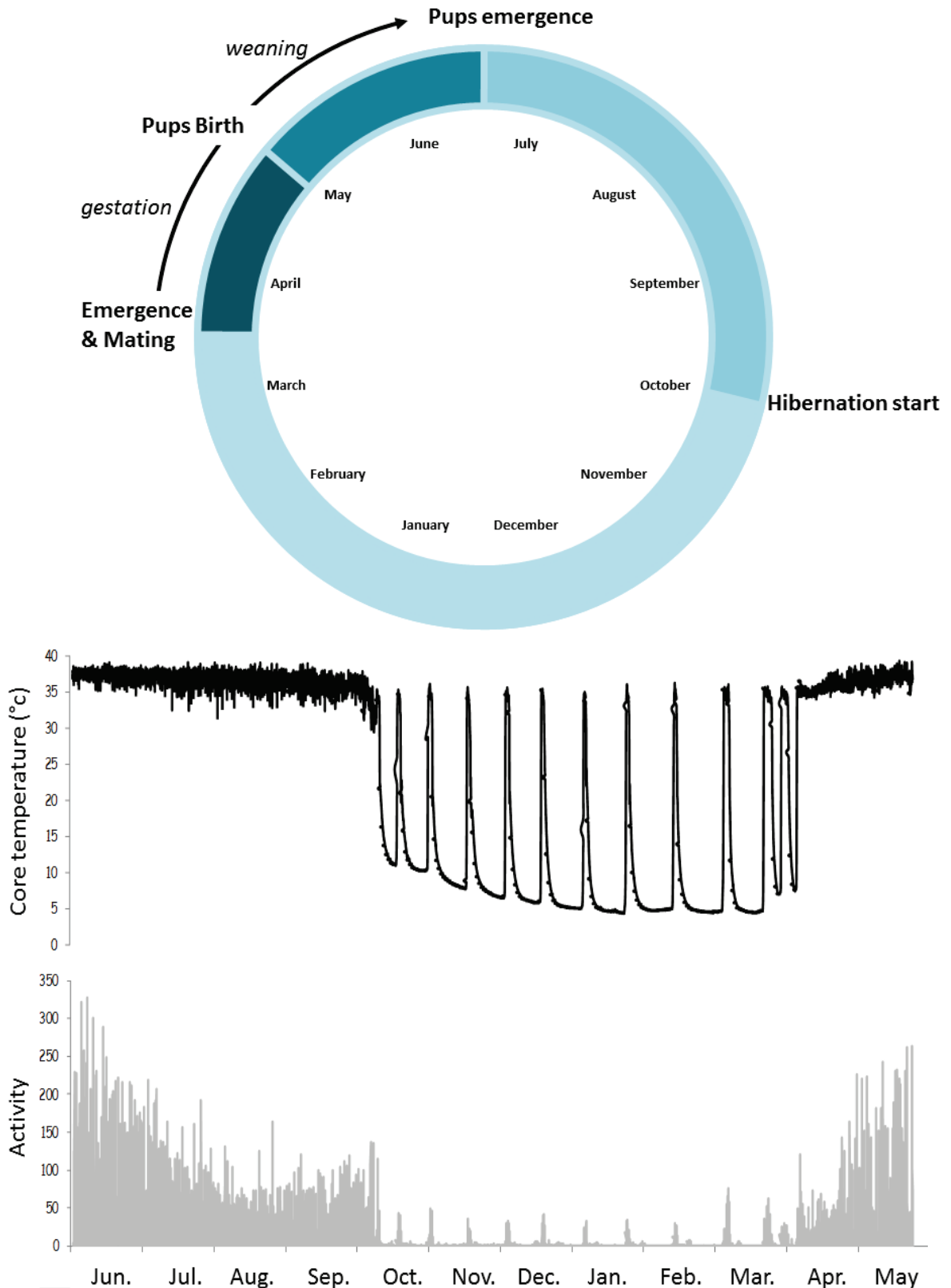
end of the day while they rest for long periods near the entrance or inside the burrow in the middle of the day (Perrin & Berre 1993). Finally, individuals immerse around mid-October, hibernation starts again, and another cycle begins.

### 5.2.3. *Social organization and mating system*

Most marmot species display high levels of sociality compared to the other members of the *Sciuridae* family (composed of squirrels, chipmunks and prairie dogs). The social systems displayed by the different species of this genus are thought to be mainly related to the harshness of winter conditions and therefore to hibernation. Because of the short active season, hibernators have relatively slow life-histories; they grow and reproduce at lower rates compared to non-hibernators of similar size (Turbill *et al.* 2011). As a consequence, in Alpine marmots, age at sexual maturity is delayed until two years old and full adult size is only achieved at three years of age. Because of this delay, the young remain with their parents at least until two years of age thus creating the conditions for a more complex social system to evolve.

By comparison, the only solitary species of the *Marmota* genus, *M. monax*, lives in a milder environment and hibernates for a shorter period of time (Tab.II.1). The growing period is thus long enough for juveniles to become independent and disperse in their first summer. In addition, dispersal in Alpine marmots is delayed, in the sense that it generally occurs at least one year beyond the age of sexual maturity. Some individuals may even never leave their natal territory. The resulting social organization of the Alpine marmot is often called an extended family group (Armitage 2014). A typical Alpine marmot social group thus consists of a dominant couple with variable numbers of subordinates, *i.e.* adults that delayed dispersal (two years and older), yearlings (one-year-old) and juveniles of both sexes (pups of the year).

Previous studies on sociality in Alpine marmots showed that in each family group, the dominant couple monopolizes reproduction but some subordinate males might escape reproductive suppression through extra-pair copulations (Cohas *et al.* 2006). When extra-pair copulations occur, the dominant male may lose all or only some of the paternities. Most extra-pair paternities were the fact of transient individuals. Approximately 14% of the litters contain at least one extra-pair young. Altogether, these extra-pair young account for 7% of all pups produced in the population (Ferrandiz-Rovira *et al.* 2016).



**Figure II.6.** Alpine marmot annual life cycle and annual core temperature and activity profiles of an adult male Alpine marmot from La Garde Sassièrè population (profiles courtesy of Benjamin Rey).

The mating system of the Alpine marmot can thus be described as socially monogamous but genetically facultative polyandrous. Both the probability to successfully monopolize reproduction and the dominance tenure of dominant males decrease with the number of subordinate males present in the family group (Allainé & Theuriau 2004; Lardy *et al.* 2012). Dominant females are also influenced by the presence of same-sex subordinates in the family group. Although dominant females always manage to monopolize reproduction (with the exception of one sister and one daughter of two different dominant females that reproduced once in 26 years of study), their probability to lose dominance increases with the number of female subordinates (Lardy *et al.* 2013). These results indicate high levels of intra-sexual competition in the Alpine marmot.

But the presence of male subordinates is also associated to an increased survival of juveniles. During hibernation, Alpine marmots periodically arise for euthermia bouts during which their body temperature increases sharply (Fig.II.6). These bouts, although physiologically necessary for the survival of individuals, are very costly and most of the fat reserves are consumed during these body-temperature increase. By producing heat when they arise, subordinate males will allow pups to save energy and thus increase their survival. Subordinate males may thus be considered as helpers because of their role in social thermoregulation increasing juvenile survival (Arnold 1993). Because pup survival is highly correlated to the number of subordinate males present in the family group during their first hibernation (Allainé & Theuriau 2004) a trade-off exists between the juvenile survival benefits and lost reproduction costs for dominant males.

## **6. Data collection**

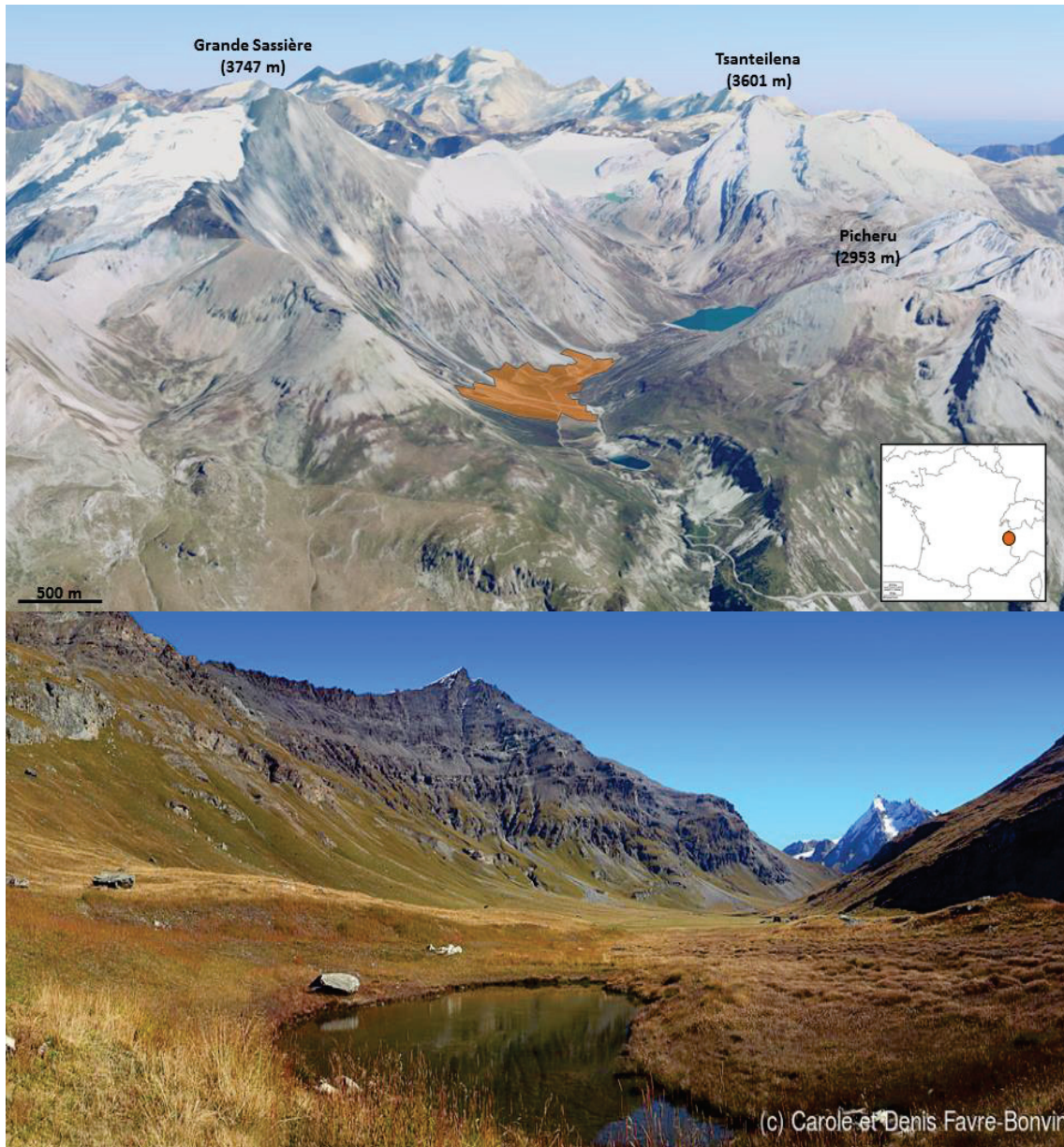
### *6.1. La Grande Sassièrè*

The Alpine marmot population monitoring in the Grande Sassièrè Nature reserve (French Alps, 45°29'N, 6°59'E) started in 1990. The nature reserve is situated in a small glacial valley oriented along the East-West axis of the National Park “La Vanoise” close to the Italian border (Fig.II.7). The study area only concerns a subpart of the reserve. The size of the study area increased with the number of family territories monitored between 1990 and 2016. Nowadays, it covers approximately 60 ha between 2300 and 2450 m a.s.l. and contains up to 34 marmot families monitored every year.

The climate presents typical Alpine characteristics, with low temperatures, strong daily and annual temperature amplitude and marked precipitations. The flora is composed of Alpine and sub-Alpine grass types and hosts a profusion of flowers during late spring (early June). The fauna includes many emblematic Alpine species, among which the chamois (*Rupicapra rupicapra*), the Alpine ibex (*ibex ibex*), the bearded vulture (*Gypaetus barbatus*), the ermine (*Mustela ermine*) or the snow vole (*Chyonomys nivalis*). It also includes marmot predators such as the golden eagle and the red fox. 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 Sassièrè population dynamics (personal observation).

### 6.2. Capture –Recapture protocol

Each year between mid-May and mid-July, individuals living in the study area are captured using two-door live traps baited with dandelions (*Taraxacum densleonis*). Traps are placed near the entrance of the main burrows of each territory to easily assign captured individual to their family group (Fig.II.8). Once captured, marmots are put in a Hessian bag and tranquilized with Zolétil 100 (0.1 mL.kg<sup>-1</sup>). Individuals are then sexed based on their ano-genital distance, aged from their size (up to three years) and weighed. Dominance status is determined based on morphological characteristics visible testis for dominant males and developed teats for dominant females (Hackländer *et al.* 2003). All marmots captured for the first time are marked with a transponder chip (Trovan Ltd, Germany) injected under the neck skin and a metal tags on the ear. The metal ring is placed on the right ear for females and left ear for males for easier sex determination in further observations. In addition, dominant individuals are marked with a family-specific coloured plastic tag on the opposite ear. Around the end of June, burrows are scrutinized to determine the exact date of the first emergence of pups. Since pups are very naive at that time, they can be captured by hand within few days of their emergence. They are subsequently marked with both transponders and ear-tags.



**Figure II.7.** Three dimensional view and photograph taken from the entrance of the Grande Sassièrè nature reserve. Orange area on the 3D view represents the study area. Photo credit: Carole & Denis Favre-Bonvin.

Additional handlings at capture include morphological measurements, skin biopsies, hair and blood samples and anal, jugal and buccal glands secretion samples. Microsatellite genotyping of all captured individuals based on hair samples or skin biopsies allowed parentage analyses to be run, allowing us to precisely determine kinship among individuals from a family group (details on the genetic and parentage analyses can be found in Cohas *et al.* (2006) or Ferrandiz-Rovira (2015)). 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.

During the entirety of the field season, behavioural observations are conducted on a daily basis to determine group compositions and sizes (Fig.II.8). To avoid disturbing the animals, behavioural observations are performed from the distance using binoculars. This setting does not allow reading the unique numbered ear-tag and therefore the exact identification of the animals but the size of the individuals and the side of their ear-tag allows us to determine the number of individuals in each age class (juveniles, yearlings, two-years or adults) and of each sex. In addition, any immigration event is detected by the arrival of an un-marked individual in the family group. Scent-marking and antagonistic behaviours are also reported, allowing us to confirm the hierarchical status of the different individuals (Bel *et al.* 1995). See also <http://thealpinemarmotproject.org> for more information about the study area.



**Figure II.8.** Two Alpine marmots near a trap situated on the earth and rock mound formed during the burrow excavation. Photo credit: <http://thealpinemarmotproject.org>.



# Chapter III

## Sociality & early life consequences

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### Litter sex composition influences dominance status in the Alpine marmot

**Abstract:** In social species, the hierarchical status of an individual has important consequences for its fitness. While many studies have focused on individual condition to explain access to dominance, very few have investigated the influence of the social environment, especially during early life. Yet it is known that environmental conditions early in life may influence several traits at adulthood. Here, we examine the influence of early social environment on accession to dominance by investigating the influence of litter size and sex composition on survival and the probability of ascending to dominance later in life using a 20-year dataset from a wild population of Alpine marmots (*Marmota marmota*). Although litter size had no effect on the fate of individuals, litter sex composition affected male juvenile survival and both male and female probabilities of reaching dominant status when adult. Male juveniles incur lower survival when the number of male juveniles in the litter increases, and individuals of both sexes from male-biased litters are more likely to become dominant than individuals from female-biased litters. However, the absolute number of sisters in the litter, rather than the sex ratio, seems to be an important predictor of the probability of acquiring dominant status: pups having more sisters are less likely to become dominant. Several potential mechanisms to explain these results are discussed.

**Keywords:** Delayed effects· Group composition· Multi-event models· Reproduction access· Rodent· Social context

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## 7.1. Introduction

In animal societies, the hierarchical status an individual can reach has important implications. It may affect many aspects of its life, such as access to food (Baker *et al.* 1981), health and physiology (Sapolsky 2005) or reproductive success (Ellis 1995; Creel *et al.* 1997), therefore entailing serious fitness consequences. Many factors have been proposed to favour access to dominance, *e.g.* body condition (Poisbleau *et al.* 2006), genetic factors (Dewsbury 1990) or experience (Hansen & Slagsvold 2004). In long-lived mammals, another potential factor affecting the ability to reach dominant status is the environmental conditions encountered early in life. However, few studies have evaluated the influence of early conditions on access to dominance. Most have investigated the effect of early conditions on other traits later in life (*e.g.* growth, survival, habitat selection, sexual attractiveness; reviewed in Lindström 1999), and focus has been mainly on early environmental conditions (Cam *et al.* 2003; Lee *et al.* 2013; Douhard *et al.* 2013), whereas social factors have been largely overlooked. Nevertheless, some laboratory studies have highlighted the impact of early social conditions on individual performances (Zielinski *et al.* 1992; Correa *et al.* 2013). Particularly, a negative link between litter size and body size/mass has been evidenced in mammals (Charnov *et al.* 2006). In litter-bearing mammals, Mendi (1988) has shown that offspring from small litters usually weigh more, have a higher growth rate and faster physical development, and that these differences may last beyond the end of the lactation period. Other studies have shown that larger and/or bigger animals have a higher survival probability and are more likely to become dominant (Clutton-Brock *et al.* 1986; Jonart *et al.* 2007). Litter size can thus impact future body size and/or mass and therefore future hierarchical status.

In addition, litter composition can potentially influence the future hierarchical status of an individual through different pre- or post-natal mechanisms. Before parturition, the composition of the litter may directly affect the development of individuals because androgens, secreted by male foetuses, and oestrogens, secreted by female foetuses, diffuse across the foetal membranes in utero (Vom Saal *et al.* 1999). These hormones, particularly testosterone, affect the differentiation of morphological, physiological and behavioural traits such as ano-genital distance, oestrous cycle length or aggressiveness (Clemens *et al.* 1978; Even *et al.* 1992). Thus, the sex ratio of the litter, which is often used as a proxy of prenatal exposure to testosterone (Uller *et al.*

2004; Monclús & Blumstein 2012; Hackländer & Arnold 2012), may have long-term consequences on access to dominance by impacting juvenile survival and/or competitive abilities (Monclús *et al.* 2014). After birth, the sex of surrounding siblings can also influence the fate of juveniles since the levels of competition and/or cooperation among same-sex siblings can differ between males and females. In spotted hyenas (*Crocuta crocuta*), for instance, intra-sexual competition is higher among young females than among young males. This higher level of competition among young females results in a higher rate of siblicide in all- female litters, and leads in turn to lower survival of young females (Golla *et al.* 1999). Conversely, in African lions (*Panthera leo*), kin-related males cooperate and coalitions between male siblings are frequently observed. This particular form of cooperation allows them to secure access to a group of females, therefore ensuring a dominant position and high reproductive success (Packer *et al.* 1991). Such sex-specific interactions can thus influence the probability to survive to adulthood and/or to hold a dominant position.

The aim of this study is to investigate whether early social conditions, *i.e.* litter size and composition, can influence individual probability of acquiring a dominant position later in life. For this purpose, data from a 20-year study on the Alpine marmot (*Marmota marmota*) in the French Alps was used. The Alpine marmot is well suited for such a study because reproduction is strongly constrained by social status as the dominant pair monopolizes reproduction in the social group (Goossens *et al.* 1998a; Cohan *et al.* 2006), and litters exhibit high variability in size (from 1 to 7 pups) and sex composition (from exclusively male to exclusively female litters; Allainé *et al.* 2000). We investigated whether individuals from small litters, assumed to be in better condition than those from large litters, were more likely to survive and to become dominant. As for the effect of litter composition, we considered the following three possibilities. First, we investigated whether the sex ratio of the litter influenced the fate of individuals of both sexes, *i.e.* whether individuals born to male-biased litters were more prone to become dominant. Second, we examined the possibility that intra-sexual competition between siblings decreases the probability of further access to dominance either by decreasing juvenile survival or the probability of reaching a dominant position. Thus, females with many sisters and males with many brothers should display lower overall probabilities to become dominant. Third, we considered the possibility that cooperation between siblings of the same sex (formation of coalitions, for instance) outweigh the

effect of intra- sexual competition within litters. In this case, individuals with numerous same-sex siblings should be more likely to become dominant.

## **7.2. Materials and methods**

### *7.2.1. Study species*

The Alpine marmot is a hibernating ground-dwelling squirrel. This territorial and social mammal lives in family groups composed of a dominant couple, sexually mature and immature subordinates of both sexes, and pups born that year (Allainé 2000a). Pups stay together as subordinates in their natal group at least until they reach sexual maturity at 2 years old. From this age, both males and females can reach dominance either by replacing the dominant of their natal territory when he/she dies or by dispersing and displacing a dominant of a neighbouring territory. Dispersal is often limited in space since more than 80 % of the dominant individuals captured were born in the study area and dominant individuals coming from outside the study area settled in its periphery. Dispersal patterns differ between sexes. Females inherit their dominant position more often than males do with, respectively, 35 % of the dominant females and 15 % of the dominant males which occupy their natal territory (Lardy *et al.* 2012a). In addition, males seem to disperse further away than females. Since dispersing individuals never become subordinates in a new family group, they are at a high risk of death and very rarely survive overwinter if they do not reach dominance during the active season (winter mortality of 0.9; Grimm *et al.* 2003). Male subordinates that delay dispersal are considered as helpers since their presence greatly increases the survival probability of pups during their first hibernation (Arnold 1988; Allainé & Theuriau 2004).

Within family groups, reproduction is monopolized by the dominant couple. After 35 days of gestation, the dominant female gives birth to a litter of 1–7 pups in the second half of May. Given the gestation and weaning length, only one litter can be produced each year. A few sexually mature males manage to partially escape the reproductive control of the dominant male. Hence, while dominant females generally monopolize all reproduction, dominant males may lose some paternities (Cohas *et al.* 2006). Individuals of both sexes may stay dominant for several years (up to 11 for males and 14 for females in the study population), until natural death or eviction by a challenger (Lardy *et al.* 2011). Eviction of one of the dominants further leads to the loss

of the litter produced, either by infanticide or by abandonment of the pups, and to the death of the evicted individual in most cases (Hackländer *et al.* 2003; Lardy *et al.* 2011).

### 7.2.2. *Study site and data collection*

Individuals were captured in a wild population of Alpine marmots located in the Grande Sassièrè nature reserve (2340 m a.s.l., French Alps, 45°29'N, 6°59'E) from 1990 to 2010. Marmots from up to 24 territories (five territories were created while one disappeared during the study) were monitored, from mid-April to mid-July each year, using both capture–mark–recapture and observations. Marmots were captured using two-door live-capture traps baited with dandelion *Taraxacum densleonis*. Traps were placed near the entrances of the main burrows to easily assign each captured individual to its family group. Juveniles were counted and caught by hand within the 3 days following their first emergence from the burrows, (*i.e.* approximately 40 days after their birth). Captured animals were tranquillized with Zolétil 100 and marked with a transponder (Trovan™, Germany) and a numbered ear tag. At each capture, marmots were aged from their size in three age classes (pups, yearlings and adults), sexed and their social status was determined according to scrotal development for males and teats development for females (Hackländer & Arnold 1999; Hackländer *et al.* 2003). Thanks to daily observations, the number of individuals of each sex and age class was further assessed for each family and scent-marking behaviour was used to confirm the identity of the dominant pair (Bel *et al.* 1995).

### 7.2.3. *Litter characteristics*

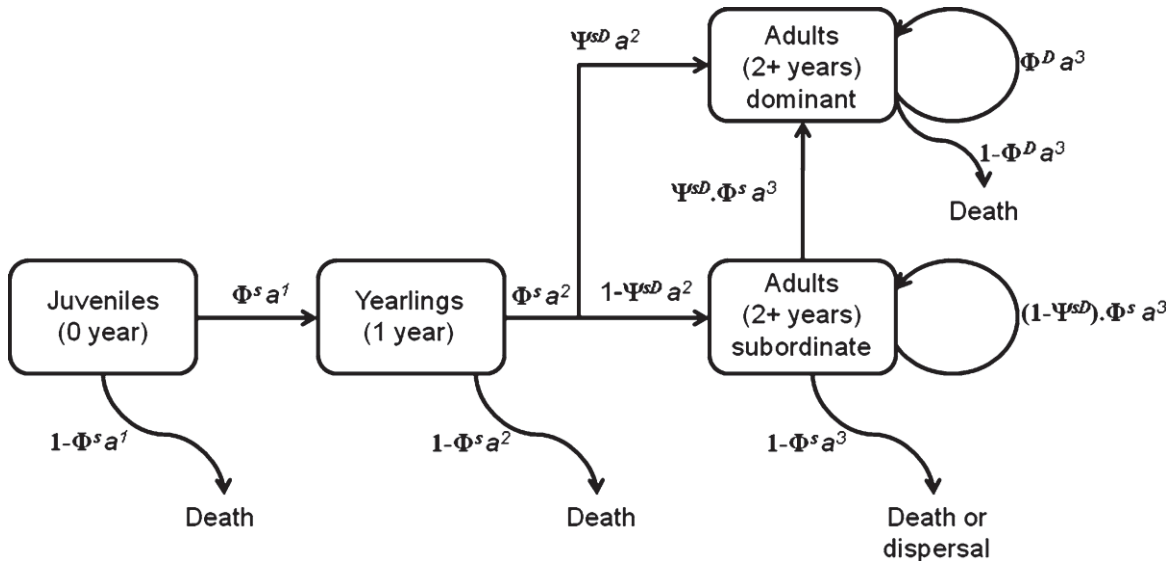
The exact composition of every litter and the identity of individuals that reproduced each year were determined using microsatellite markers and kinship analyses (Supplementary Material III.1). Litter size was calculated as the total number of pups from the same mother emerging a given year. The litter sex ratio was calculated as the number of males in a litter divided by the litter size. The number of brothers was calculated as the number of male pups in a litter minus one when the focal individual was a male. The same procedure was used to determine the number of sisters for each individual.

#### 7.2.4. Capture–recapture analysis

We considered 806 individuals first captured as pups between 1990 and 2010 for which the litter size, litter sex ratio, number of brothers and number of sisters were known.

*Model structure.* Multi-Event Capture–Recapture models (ME-CR; Pradel 2005) were used to investigate the influence of the litter size and composition on marmot survival ( $\phi$ ) and access to dominance ( $\psi$ ) because recapture probability ( $p$ ) of individuals was lower than 1 (recapture probability varying from 0.380 to 0.886; Cochas *et al.* 2007). We defined 3 states: subordinate (s), dominant (D), and dead or permanent emigrant from the study site ( $\dagger$ ). We further incorporated information about the reproductive status (E) of each individual to refine the estimation of the probability to access dominance. Since the probability to reproduce is strongly linked to the dominant status (only 20 of the 806 pups studied were produced by subordinates), there is a high probability that an individual that successfully reproduced a given year was dominant even when its dominance status could not be determined. Thus, the different observable events retained were: no information (event 0), individual with uncertain dominance status that successfully reproduced, i.e. with its pups captured (event 1), individual captured as dominant but no reproduction observed, i.e. no pups captured (event 2), individual captured as dominant that successfully reproduced (event 3), individual captured as subordinate without pups of its own observed (event 4), individual captured as subordinate that successfully reproduced (event 5). Based on these events, recapture histories were then constructed for each individual (Supplementary Material III.2). The constructed multi-events model can be summarised by a transition matrix and associated vectors of survival, capture and successful reproduction probabilities (see Fig.III.1 and Supplementary Material III.3 for further details on the model construction). For pups, the model reduces to a single survival parameter because they cannot stay as pups more than 1 year and they are not able to reproduce or to become dominant. For yearlings, the model reduces to the estimation of probabilities of capture, survival, and access to dominance the following year. They are never captured as dominant and are not yet sexually mature. For older individuals, since dominant individuals never revert to the subordinate status (Farand *et al.* 2002; Stephens *et al.* 2002a; Grimm *et al.* 2003a), the model reduces for older individuals to two capture parameters, two survival parameters

(one for subordinate and one for dominant individuals) and to the probability to access dominance when they are still subordinate.



**Figure III.1.** Life cycle of Alpine marmots with three age classes ( $a^1$  pup,  $a^2$  yearling,  $a^3$  adult) and two social status ( $s$  subordinate and  $D$  dominant); arrows represent the transition from one age class to the next with its associated probability:  $\Phi$  represents survival probabilities and  $\Psi$  represents transition from the subordinate to the dominant status.  $\Psi$  is conditional on  $\Phi$ .

*Preliminary analysis.* Data analyses were performed following three steps (Lebreton *et al.* 1992a). We first tested whether a general model, namely the Cormack–Jolly–Seber model (Pollock *et al.* 1985), fitted our data. To this purpose, goodness-of-fit (GOF) tests were performed using the program U-CARE (Choquet *et al.* 2009a). Following Burnham & Anderson (2002), the second step was to select the most parsimonious model, hereafter called the root model, among a set of models built by considering only a priori biological hypotheses based on our field experience and the literature (Arnold 1993; Allainé 2000a; Farand *et al.* 2002; Stephens *et al.* 2002a; Grimm *et al.* 2003a). We thus considered age, year, sex effects and their interactions on all capture, survival, state transition and reproduction probabilities (Tab.III.1). In addition, we considered an effect of the number of male helpers on juvenile survival during their first hibernation since it has been demonstrated to be an important factor (Arnold 1993; Allainé & Theuriau 2004). To do this, the logarithm of the number of male helpers [ $\log(\text{helpm})$ ] was used as an individual covariate because the effect of male helpers was found to be non-linear (Allainé & Theuriau 2004). Following a step-down approach, models were sequentially fitted with constrained parameterizations for

recapture, survival, transitions and reproduction probabilities, in that order. We then checked that the root model could not be improved by exploring all neighbouring models. Model selection relied on the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). Model selection and parameters' estimation were performed using the program E-SURGE 1.8.5 (Choquet *et al.* 2009b).

**Table III.1.** Abbreviations used in model notations

Abbreviations	Meanings
$p$	recapture probability
$\Phi$	survival probability
$1-\Phi$	mortality probability (encompass both mortality and dispersal probabilities for individuals older than 2 years of age)
$\Psi$	state transition probability (conditional on survival)
$E$	event probability (probability of successful reproduction)
<b>Subscript</b>	
$a$	all age classes (1 to 3)
$a^1$	age from 0 to 1 year
$a^2$	age from 1 to 2 years
$a^3$	age more than 2 years
$a^{x,y}$	age classes x and y
$sex^{f,m}$	sex (f: female; m: male)
$t$	Time as the number of years from the beginning of the study
*	interactive effect
+	additive effect
<i>sex ratio</i>	litter sex ratio at emergence
<i>litter size</i>	litter size at emergence
<i>brothers</i>	number of male pups from the same mother in a litter
<i>sisters</i>	number of female pups from the same mother in a litter
<i>helpm</i>	number of male helpers present during the first hibernation
<b>Superscript</b>	
$s$	subordinate status
$D$	dominant status
†	dead

*Effect of litter characteristics.* Once the root model was obtained, we investigated in the final step whether the early social conditions affected both the survival rate and the probability to access dominance. To test our hypotheses on juvenile survival, we built a model including every retained effect on probabilities to access dominance (model R1, Tab.III.2) while the parameterization of all other parameters was set as in the root model. We then added an effect of the tested litter characteristic (*i.e.* litter size, litter sex ratio, number of brothers or number of sisters) as a logit linear relationship with the juvenile survival in a separate model. In addition, whenever a litter characteristic was



found to influence juvenile survival, models with an effect of this covariate on yearling and adult subordinate survival were built to account for possible long-lasting effects. They were compared to a model with the effect of the litter characteristic considered on the juvenile survival only (model R2, Tab.III.3). Because the main effects of the litter characteristics are likely to be on juvenile survival, we did not investigate the effect of the early conditions on yearling and adult survivals whenever no effect on juvenile survival was found. Similarly, to test the same hypotheses on the probability to access dominance, we built model R3 (Tab.III.4) that included all retained effects on survival, and compared it to models with a logit linear effect of the litter characteristic to test on the probability to access dominance for both yearlings and adults. Finally, models with a sex-specific effect of the different covariates were constructed and compared to models without sex effects to test for a sex-specific competition or cooperation.

The importance of the tested litter characteristic was then assessed by comparing model using AICc weights ( $W_i$ , Burnham *et al.* 2011) Estimates and standard errors for the different regression slopes given in the results are on the logit scale. All other parameters are given on the natural scale.

### 7.3. Results

Mean litter size was  $4.15 \pm 0.05$  pups in the population, ranging from 1 to 7. Mean sex-ratio was  $0.53 \pm 0.01$  among all litters. Mean number of brothers was  $1.66 \pm 0.04$  (from 0 to 5) while the mean number of sisters was  $1.44 \pm 0.04$  (from 0 to 4). Correlation coefficients between the different litter characteristics are given in Tab.III.5.

#### 7.3.1. Preliminary analysis

After checking for the goodness of fit of the model and AICc-based model selection (see Online Resource 4 for more details on the GOF tests and root model selection), the root model was  $p^{s}_{a,y+sex} \Phi^{s}_{a1.sex.log(helpm); a2,3} E^{s}_{a3}, p^{D}_{a3.y+sex} \Phi^{D}_{a3} E^{D}_{a3} \Psi^{sD}_{a2,a3}$ .

Recapture probabilities varied with year, sex, age and hierarchical status. The average recapture rate decreased with age, from yearlings ( $0.87 \pm 0.06$  for females;  $0.83 \pm 0.09$  for males) to adults (subordinates  $0.68 \pm 0.11$  for females;  $0.60 \pm 0.15$  for males; dominants  $0.64 \pm 0.09$  for females;  $0.57 \pm 0.10$  for males).

Survival probabilities varied with age and status and male helpers had a strong sex-specific effect on juvenile survival. Juvenile survival varied from  $0.38 \pm 0.04$  in the absence of helpers to over  $0.80 \pm 0.04$  when five helpers or more were present for females and from  $0.24 \pm 0.05$  to  $0.93 \pm 0.03$  for males. Yearling survival rate was  $0.77 \pm 0.04$ , dominant adults survival rate was  $0.81 \pm 0.02$ . The apparent subordinate survival rate was much lower ( $0.53 \pm 0.03$ ) due to dispersal outside the study area that could not be distinguished from mortality. Access to dominance ( $0.04 \pm 0.01$  for yearlings and  $0.49 \pm 0.04$  for adults) and annual reproduction probabilities ( $0.02 \pm 0.01$  for subordinates and  $0.64 \pm 0.03$  for dominants) were found to be constant over time and sex.

**Table III.2.** Model selection for the effects of litter size, litter sex ratio, number of brothers and number of sisters in the litter on the juvenile survival probability of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model:  $p^s a^t + sex \Phi^s a^{2,3} E^s a^3, p^D a^3 + t + sex \Phi^D a^3 E^D a^3 \Psi^D a^2, a^3 * sisters$  (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters;  $\Delta AICc$ : difference in AICc with the best model of the set;  $W_i$ : AICc weight ; bold characters indicate the best model of the set and the root model for comparison).

	Juvenile survival models	Deviance	k	AICc	$\Delta AICc$	$W_i$
<b>B1.3</b>	<b><math>\Phi a^l * sex^m * (\log(helpm) + brothers) + sex^f * \log(helpm)</math></b>	<b>3617.04</b>	<b>72</b>	<b>3767.56</b>	<b>0.00</b>	<b>0.31</b>
B1.1	$\Phi a^l + brothers + sex * \log(helpm)$	3618.74	72	3769.08	1.52	0.14
B1.2	$\Phi a^l * sex * (\log(helpm) + brothers)$	3616.93	73	3769.63	2.07	0.11
<b>R1</b>	<b><math>\Phi a^l * sex * \log(helpm)</math></b>	<b>3621.41</b>	<b>71</b>	<b>3769.75</b>	<b>2.19</b>	<b>0.10</b>
L1.1	$\Phi a^l + litter\ size + sex * \log(helpm)$	3619.06	72	3769.85	2.29	0.10
SR1.1	$\Phi a^l + sex\ ratio + sex * \log(helpm)$	3620.60	72	3770.93	3.37	0.06
L1.2	$\Phi a^l * sex * (\log(helpm) + litter\ size)$	3618.48	73	3771.18	3.62	0.05
B1.4	$\Phi a^l * sex^m * \log(helpm) + sex^f * (\log(helpm) + brothers)$	3621.30	72	3771.63	4.07	0.04
S1.1	$\Phi a^l + sisters + sex * \log(helpm)$	3621.39	72	3771.73	4.17	0.04
SR1.2	$\Phi a^l * sex * (\log(helpm) + sex\ ratio)$	3619.85	73	3772.55	4.99	0.03
S1.2	$\Phi a^l * sex * (\log(helpm) + sisters)$	3620.32	73	3773.02	5.46	0.02

### 7.3.2. Effect of litter size

No effect of the litter size was evidenced, neither on survival nor on the probability to become dominant. All models including an effect of litter size performed poorly compared to the root model (R1 vs. L1.1 and L1.2, Tab.III.2; R3 vs. L3.1 and 3.2, Tab.III.4).

### 7.3.3. Effect of litter composition

*Sex ratio effect.* The litter sex ratio did not affect the juvenile survival (models SR1.1 and SR1.2 vs. R1, Table 2). It was found to influence the probability to access dominance for adults but not for yearlings (models SR3.2 vs. SR3.1, Tab.III.4). The probability for an adult to access dominance increased with the sex ratio from  $0.35 \pm 0.08$  when no males were present to  $0.63 \pm 0.09$  for an all-male litter (Model SR3.2, Tab.III.4;  $\beta_{adults} = 1.15 \pm 0.64$ ; Fig.III.3a).

**Table III.3.** Model selection for the effect of number of brothers in the litter on the yearling and subordinate adult survival probability of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model:  $p^s a^t + sex \Phi^s a^l * sex^m * (\log(helpm) + brothers) + sex^f * \log(helpm) E^s a^3, p^D a^3 * t + sex \Phi^D a^3 E^D a^3 \Psi^D a^2, a^3 * sisters$  (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters;  $\Delta AICc$ : difference in AICc with the best model of the set;  $W_i$ : AICc weight; bold characters indicate the best model of the set).

Yearling and adult survival models	Deviance	k	AICc	$\Delta AICc$	$W_i$
<b>R2</b> $\Phi^s a^{2,3}$	<b>3617.04</b>	<b>72</b>	<b>3767.56</b>	<b>0.00</b>	<b>0.47</b>
B2.2 $\Phi^s a^2, a^3 * sex^m * brothers + sex^f$	3615.64	73	3768.15	0.59	0.35
B2.1 $\Phi^s a^2 * sex^m * brothers + sex^f, a^3$	3616.99	73	3769.5	1.94	0.18

*Sex specific effects.* The number of brothers negatively affected male juvenile survival (model B1.3 vs. R1, Tab.III.2). It decreased from  $0.64 \pm 0.07$  to  $0.28 \pm 0.13$  when the number of brothers in the litter increased from 0 to 5 ( $\beta_{males} = -0.26 \pm 0.12$ ; Fig.III.2) for an average number of helpers (3.6 in our population). This effect was no longer detected on the yearling or adult subordinate survival (R2 vs. B2.1 and B2.2, Tab.III.3). The number of brothers did not influence male dominance access probability (models B3.3, B3.2 and B3.1 vs. R3, Tab.III.4). The number of sisters had no effect on juvenile survival (models S1.1 and S1.2 vs; R1, Tab.III.3) but negatively affected the probability that adult females (but not yearlings) accessed to dominance (model S3.1. vs.

S3.2, Tab.III.4). Interestingly, this effect was not sex-specific (S3.3 vs. S3.2, Tab.III.4), and male dominance access probability was also found to be negatively related to the number of sisters in the litter. The dominance access probability decreased from  $0.61 \pm 0.08$  to  $0.30 \pm 0.09$  as the number of sisters increased from 0 to 4 (Model S3.2, Tab.III.4;  $\beta_{adults} = -0.32 \pm 0.17$ ; Fig.III.3b).

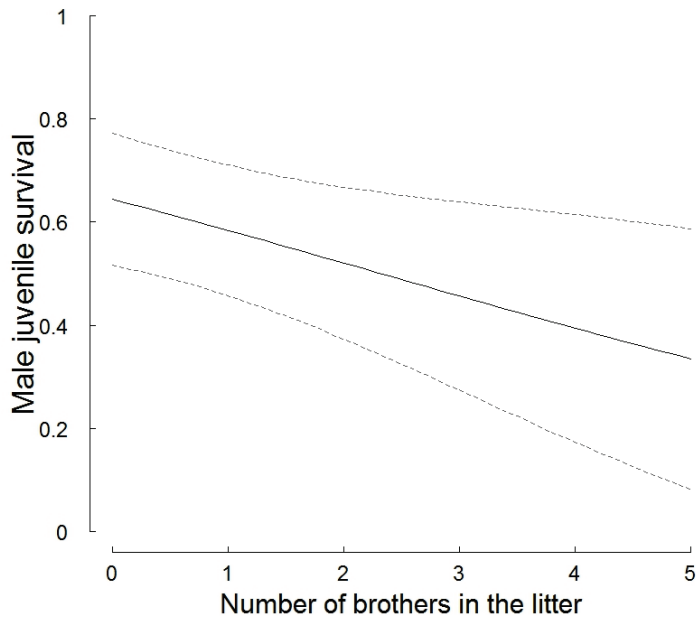
**Table III.4.** Model selection for the effects of litter size, litter sex ratio, number of brothers and number of sisters in the litter on the probability to become dominant of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model:  $p^s a^t + sex \Phi^s a^l * sex^m * (\log(helpm) + brothers) + a^l * sex^f * \log(helpm)$ ;  $a^{2,3} E^s a^3, p^D a^3 * t + sex \Phi^D a^3 E^D a^3$ . (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters;  $\Delta AICc$ : difference in AICc with the best model of the set;  $W_i$ : AICc weight; bold characters indicate the best model of the set and the root model for comparison).

Transition models	Deviance	k	AICc	$\Delta AICc$	$W_i$
<b>S3.2</b> $\Psi^{SD} a^2, a^3 * sisters$	<b>3617.04</b>	<b>72</b>	<b>3767.56</b>	<b>0.00</b>	<b>0.23</b>
SR3.2 $\Psi^{SD} a^2, a^3 * sex\ ratio$	3617.41	72	3767.93	0.37	0.19
S3.1 $\Psi^{SD} a^{2,3} * sisters$	3616.23	73	3768.93	1.37	0.12
<b>R3</b> $\Psi^{SD} a^{2,3}$	<b>3620.90</b>	<b>71</b>	<b>3769.24</b>	<b>1.68</b>	<b>0.10</b>
SR3.1 $\Psi^{SD} a^{2,3} * sex\ ratio$	3617.34	73	3770.04	2.48	0.07
B3.2 $\Psi^{SD} a^2, a^3 * brothers$	3619.80	72	3770.32	2.76	0.06
L3.2 $\Psi^{SD} a^2, a^3 * litter\ size$	3620.66	72	3771.18	3.62	0.04
B3.1 $\Psi^{SD} a^{2,3} * brothers$	3618.58	73	3771.28	3.72	0.04
S3.3 $\Psi^{SD} a^2, a^3 * sex * sisters$	3616.64	74	3771.53	3.97	0.03
SR3.3 $\Psi^{SD} a^2, a^3 * sex * sex\ ratio$	3616.58	74	3771.47	3.91	0.03
L3.1 $\Psi^{SD} a^{2,3} * litter\ size$	3620.50	73	3773.20	5.64	0.01
B3.3 $\Psi^{SD} a^2, a^3 * sex * brothers$	3619.03	74	3773.92	6.36	0.01

#### 7.4. Discussion

Our results confirm that the dominance status in Alpine marmots was influenced by the early social conditions encountered and more specifically by the composition of the litter in which an individual is born. The probability of becoming dominant was found not to be related to the litter size. Instead, our results indicate that the sex composition of the litter, in interaction with the sex of the focal individual, did impact future social status via an impact on both juvenile survival and dominance access probability.

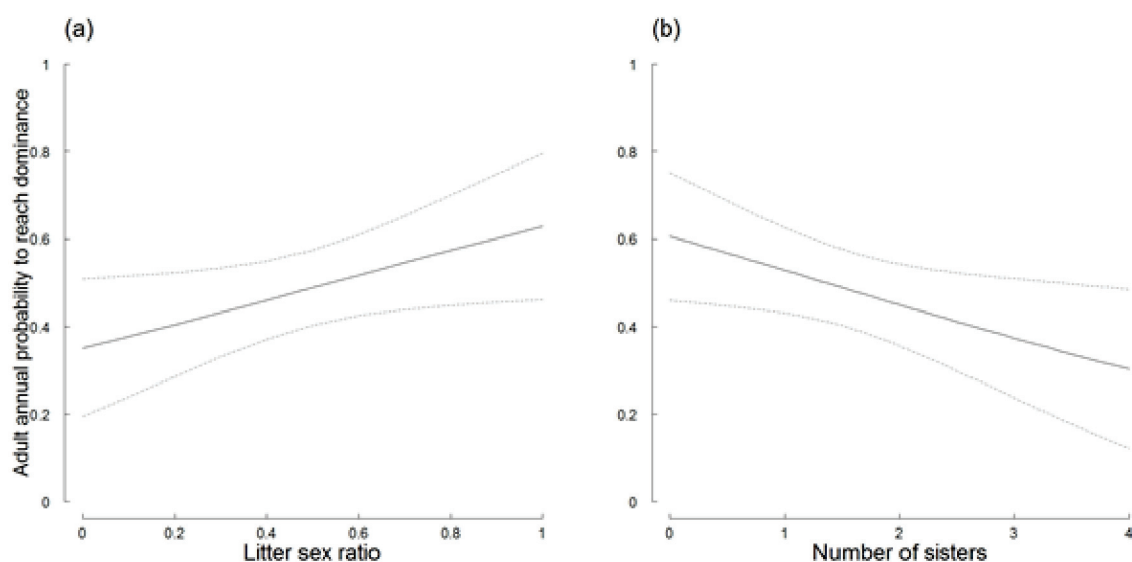
In most litter-bearing mammals, single pups are usually heavier with a faster growth rate and development than pups born with littermates (Mendi 1988). These litter size effects on body mass can persist until adulthood and may largely determine the hierarchical status (Poisbleau *et al.* 2006; Hodge *et al.* 2008). In accordance in Alpine marmots, both mass at emergence and post-weaning growth rate decrease as the litter size



**Figure III.2.** Effect of the number of brothers in the litter at weaning on juvenile survival probability of males. Solid line indicates the estimated survival probabilities from model B1.2; dashed lines represent the 95% confidence interval.

increases (Allainé *et al.* 1998), but we did not find any effect of the litter size, either on the juvenile survival or on the probability to become dominant once sexually mature. Pups from large litters instead had as many chances as singletons to survive and to later become dominant. Several mechanisms may explain this result. First, the expected effect of litter size on juvenile survival may exist but may not be detected if it takes place before weaning (i.e. before emergence from the natal burrow), for example via a competition for teats access and/or maternal care. In this scenario, the pups captured at weaning are only those that survived to this early competition between siblings. Thus, the effect of litter size on survival may not be visible in our data. An alternative explanation is that juveniles growing with several littermates may profit from their presence, like in rabbits (*Oryctolagus cuniculus*), where pups have a higher body temperature and consequently a higher survival when experimentally raised with

littermates compared to their siblings raised alone (Bautista *et al.* 2003). This thermoregulation effect can be of great importance, especially for a hibernating species like the Alpine marmot in which social thermoregulation has already been evidenced (Arnold 1988), and may explain why a single pup, even though heavier, does not survive better than pups raised with littermates. Although many studies have highlighted the negative consequences of a poor start on reproduction-related traits later in life (Metcalf & Monaghan 2001; Yearsley *et al.* 2004), no effect of the litter size was found on the probability to reach dominance. Further studies are thus needed to investigate whether these early differences in mass and growth rate impact other traits related to fitness such as reproduction onset, number of offspring produced per litter or lifetime reproductive success.



**Figure III.3.** Effect of (a) the litter sex ratio (model SR3.2) and (b) number of sisters in the litter (model S3.2) at weaning on annual transition probability from the subordinate to the dominant status for individuals of more than 2 years. Solid line indicates the estimated transition probabilities; dashed lines represent the 95% confidence interval.

Conversely, the litter composition had important effects on male juvenile survival and male and female probabilities to reach a dominant status. Neither the juvenile survival nor the probability to access dominance were positively affected by the number of same-sex littermates. Thus, our third hypothesis suggesting that cooperation between same-sex littermates may outweigh the possible cost of intra-sexual competition can be discarded. Our second hypothesis was partly supported. Indeed, only male pups had reduced chance to survive when raised with numerous brothers. However, this effect did not last after the first year of life. A higher level of competition

among male than among female littermates may explain the negative effect of same-sex littermates on male juvenile survival. Alternatively, a higher requirement of male compared to female pups may also explain this pattern. In such a case, the mother of numerous males may not always fulfil their needs and male pups might reach hibernation in a poorer body condition, thus reducing their chances to survive overwinter. However, the reason for such a differential requirement in a monomorphic species remains unclear.

Once they reach adulthood, females had lower probabilities to reach dominance when raised with numerous sisters. A high proportion of females becomes dominant by inheriting their mother position (35 % of the dominant females). Consequently, the more sisters a female pup has, the higher the competition for a single dominant position. A high number of sisters is therefore a disadvantage for female pups. No such an acute intra-sexual competition is expected for males with numerous brothers since most of them reach dominance by dispersing and displacing another dominant in a neighbouring territory (88 % of the dominant males). Accordingly, no effect of the number of brothers was detected on the probability to reach a dominant position.

However, males also had lower probabilities to reach dominance when raised with numerous sisters. Males as well as females can suffer from the presence of numerous sisters because of long-lasting effects of the exposition to in utero hormones. The fact that models including sex ratio were well ranked is in accordance with this hypothesis. Recently, Hackländer & Arnold (2012) reported that female Alpine marmots from male-biased litters were more likely to become dominant. In our study, this relationship was not limited to females, and males were also more likely to become dominant when born in a male-biased litter, thus supporting our first hypothesis. Such an effect of sex ratio is generally interpreted as a potential masculinisation due to pre-natal androgens exposure (Monclús *et al.* 2014). Being born in a male-biased litter results in a higher probability to develop adjacent to males in utero and thus coincides with higher levels of circulating testosterone and higher testosterone sensitivity, which in turn have several morphological, physiological and behavioural consequences (Ryan & Vandenberg 2002). For instance, female Alpine marmots born in male-biased litters are more aggressive (Hackländer & Arnold 2012), while female yellow-bellied marmots

(*Marmota flaviventris*) disperse more (Monclús & Blumstein 2012), two features favouring the access to dominance in Alpine marmots.

The number of brothers in the litter can also be considered as a proxy of the intrauterine exposition to androgens. Sex-ratio and the number of brothers within the litter are correlated but they do not match perfectly (see Tab.III.5), and hence do not contain the exact same information. According to (Even *et al.* 1992), the testosterone produced by a male foetus diffuses to the surrounding foetuses through the foetal membrane and the quantity of hormone approximately decreases by half when the distance to the secreting foetus increases by one foetus. Thus, an individual with a large number of brothers is thought to be generally exposed to a high amount of additional testosterone, whatever its position in utero. Interestingly, the absence of any effect of the number of brothers in the litter on access to dominance contradicts this general interpretation, and suggests that dominance status of Alpine marmots might not only be determined by the in utero exposure to testosterone and that other effects are likely to play a role.

**Table III.5.** Correlation coefficients between the different covariates tested

	Sex ratio	Brothers	Sisters
Litter size	0.01	0.64	0.53
Sex ratio		0.62	-0.63
Brothers			-0.28

Instead, our results highlighted the effect of the number of sisters on the probability of becoming dominant. Following the same reasoning as for the number of brothers and the quantity of androgens, we can suppose that the number of sisters increases the probability to develop between two female foetuses, and thus the quantity of oestrogens received in utero. Although poorly studied, examples of oestrogen-mediated long-lasting effects can be found in the literature. For example, Vom Saal *et al.* (1990) showed that female mice (*Mus musculus*) that developed between two other females had higher levels of circulating oestradiol and consequently affected reproductive traits, such as shorter oestrous cycle length, and Fadem & Tesoriero (1986) demonstrated that exposition to oestrogens during an early period of development could block testicular development in male gray opossum (*Monodelphis*



*domestica*), while exposition to testosterone had no impact on both males and females. Thus, Alpine marmots born with many sisters may become dominant less often because they present more feminised characteristics due to higher levels of circulating oestrogens. However, our results do not allow us to disentangle the different mechanisms proposed here and further studies assessing the levels of circulating oestrogens and testosterone would be of great interest to understand the underlying mechanisms of such long-lasting effects of the early social environment.

Finally, even though our results do not take into account dispersal outside and into the study area, it seems rather unlikely that the impact of the litter composition (particularly the number of sisters and litter sex ratio) on the probability to access dominance would be different when doing so. We believe that, for several reasons, litter composition does not impact differently on the individuals permanently emigrating outside the study area. First, when dispersing, Alpine marmots settle in a vast majority in a neighbouring territory and only one individual dispersed further than four territories from its natal territory in 20 years. Thus, within the study area, all the range of dispersal distances usually encountered in this species is covered and successful longer distance dispersal seems at best to occur very rarely in the Alpine marmot. Second, if litter composition influenced the propensity of individuals to disperse outside the study area, a positive effect would have been detected on the apparent subordinate mortality since it includes both the actual mortality of subordinate individuals and the survival of individuals that left the study area and were never encountered again. Thus, if individuals with a certain litter composition dispersed more, they should have a lower apparent survival. No such effect was found in our data.

In summary, the survival and later hierarchical status of Alpine marmots are influenced by social conditions encountered during the early stages of life. More specifically, these results suggest that they are influenced by the sex composition of the litter. The number of female juveniles present during the development seems to have long-lasting effects on Alpine marmots' ability to reach a dominant position for both males and females despite potential differences in the underlying mechanisms. In addition, males seem to suffer from the presence of other males in the litter inducing a reduced survival when juveniles. It therefore appears that males' fitness expectancies are probably higher when raised alone while females seem to benefit from the presence of

male siblings. These results provide new insights on the costs and benefits of a litter composition and should be taken into account when studying the pay offs parents can expect from their offspring.

## 7.5. Supplementary material

### 7.5.1. Genetic analyses and kinship analysis

For genetic analyses, hairs and skin biopsies were collected from all captured individuals since 1992. From these samples, all individuals were typed at 16 microsatellite loci: SS-Bib11, SS-Bib14, SS-Bib18, SS-Bib20, SS-Bib31 (Klinkicht, 1993), MS41, MS45, MS47, MS53, MS56, MS6, ST10 (Hanslik & Kruckenhauser, 2000), Ma002, Ma018, Ma066, Ma091 (Da Silva *et al.*, 2003). Details on microsatellite characteristics and methods can be found in Cohas *et al.* (2008).

Genetic exclusion was used to confirm kinship relationships. The genotypes of each pup were compared with those of the dominant pair to check maternity. From 16x806 mother-pup comparisons, no mismatch between the putative mother and its pups were found. The dominant male was considered as the father whenever no mismatch was observed with the dominant male genotype (753 of 806 pups). The 53 pups having at least one mismatch with the dominant male genotype (one to nine mismatches) were not considered as fathered by the dominant male. Several reasons allowed us to exclude the dominant male even when only one mismatch was found. First, genotyping error rate was low (probability of finding an error for one allele should not exceed 0.0003, for details see Cohas *et al.*, 2008). Second, all these pups and their parents were retyped and their genotypes confirmed. Third, the average mutation rate for microsatellites is low ( $1.67 \times 10^{-4}$  per generation in *Marmota marmota*) according to Rassmann *et al.* (1994) and finally, no mismatch with the putative mother has been found (see above). We thus compared the genotypes of these pups to the genotypes of all known sexually mature males in the family group. Among the 53 pups not fathered by the dominant male, 21 had genotypes compatible with that of a subordinate male in their family and 32 had a genotype incompatible with all subordinate males of their family.

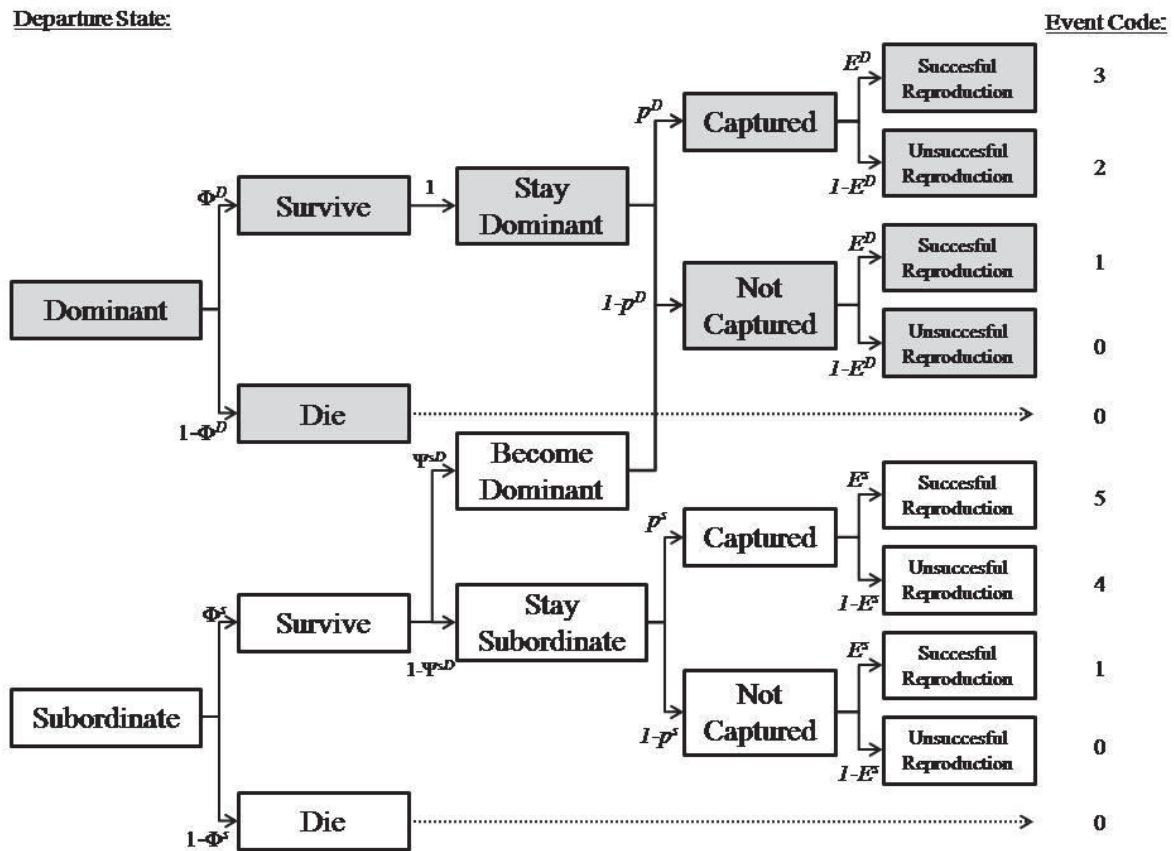
A second parentage analysis was conducted on all 806 pups using the software CERVUS 3.0.3 (Kalinowski *et al.*, 2007) with 20 candidate fathers per pup, 95% of candidate parents sampled, an error rate of 1% to allow for mistyping and for mutations or null alleles, and assignment at a 95% confidence level. The parentage analysis was run with the mother identity known and all sexually mature males present a given year in the population as putative fathers. The previous results were confirmed except for 14 pups where paternity could be assigned to both the dominant and a subordinate male.

However, MHC markers (Ferrandiz *et al.*, 2015) confirmed the dominant male to be the father of six pups. In the last eight cases the pup could still be assigned to both the dominant and a subordinate male. However, the sexual organs of the putative subordinate father showed no sign of development at capture, and all the other pups of the litter were assigned with no ambiguity to the dominant male. Thus, we parsimoniously considered these eight pups as fathered by the dominant male. Among the 32 pups that were neither fathered by the dominant male nor by a subordinate of the groups, 13 were found to be fathered by an individual born in our study population in dispersal while the other 19 were fathered by unknown males.

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7.5.2 Fate diagram and recapture histories construction.



**Figure III.4.** Fate diagram illustrating the different observable events for a subordinate (*s*) or dominant (*D*) marmot and associated probabilities and codes as used in the recapture histories.

H:	H:	H:	H:	H:	H:	H:	H:	H:	H:	S:	\$COV:sex	COV:sisters	COV:logHm
0	0	4	4	0	5	0	0	0	0	1	f	2	0.477
0	0	0	4	0	4	0	0	0	0	1	f	2	0.124
4	4	4	4	0	1	3	0	0	0	1	f	2	0.477
4	4	0	2	3	2	0	0	0	0	1	f	2	0.477
0	0	4	0	0	0	0	0	0	0	1	f	2	0.602

**Figure III.5.** Subset of the "headed" format recapture histories file built from the fate diagram above. For more details, see E-SURGE 1.8.5 user's manual (Choquet *et al.*, 2009). Column names are: "H:" for each occasion of capture, "S:" for the number of individual with a given capture history, "\$COV:" for categorical variables, "COV:" for quantitative variables

### 7.5.3. Multi-Event model construction using E-SURGE

The constructed multi-events model can be summarized by a transition matrix and associated vectors of survival, capture and successful reproduction probabilities (only the two live states are shown since the dead state parameters are trivially fixed to:  $p^\dagger = 0$ ;  $\Psi^{\dagger\dagger} = 1$ ;  $E^\dagger = 0$ ).

$$\begin{bmatrix} 1 - \Psi^{sD} & \Psi^{sD} \\ 1 - \Psi^{Ds} & \Psi^{Ds} \end{bmatrix}_y \begin{bmatrix} \Phi^s \\ \Phi^D \end{bmatrix}_y \begin{bmatrix} p^s \\ p^D \end{bmatrix}_y \begin{bmatrix} E^s \\ E^D \end{bmatrix}_y$$

where capture ( $p$ ), survival ( $\Phi$ ), reproduction ( $E$ ) and state transition conditional on survival ( $\Psi$ ) probabilities are defined as:  $p^x_y$ , the probability that an individual in state  $x$  was captured during the year  $y$ ;  $\Phi^x_y$ , the probability that an individual in state  $x$  in year  $y$  survived and did not permanently emigrate from the study area between  $y$  and  $y+1$ ;  $\Psi^{xz}_y$ , the probability that an individual in state  $x$  in year  $y$  is in state  $z$  in year  $y+1$  given that it survived and did not permanently emigrate from the study area between  $y$  and  $y+1$  and  $E^x_y$ , the probability that an individual in state  $x$  at time  $y$  had successfully reproduced this same year.

Given that pups are not able to reproduce or to become dominant, transition probability and reproduction parameter are null for pups. Moreover, since individuals in the pup class cannot stay as pups more than one year, no recapture parameter is estimable for pups. The model thus reduces for pups to a single survival parameter:

$$[\Phi^s]_y$$

For older individuals, since dominant individuals never revert to subordinate state (Farand *et al.* 2002; Stephens *et al.* 2002; Grimm *et al.* 2003), the transition probability from the dominant to the subordinate state was fixed to 0 ( $\Psi^{Ds} = 0$ ), thus constraining the state transition probability from dominant to dominant to 1. Hence, only one state transition probability was to be estimated (*i.e.* the probability of becoming dominant =  $\Psi^{sD} = 1 - \Psi^{ss}$ ). Moreover, given that yearlings are never captured as dominant and are not yet sexually mature, the dominant state was removed and the

annual reproduction probability was fixed to 0 for yearlings ( $E^S = E^D = 0$  for yearlings). It is to be noticed that, since transition probability is conditional on survival, yearlings can become dominant only if they survived. They are then aged two years, and thus sexually mature, while adults becoming dominant are at least three years old. Thus the model for yearlings simplifies to:

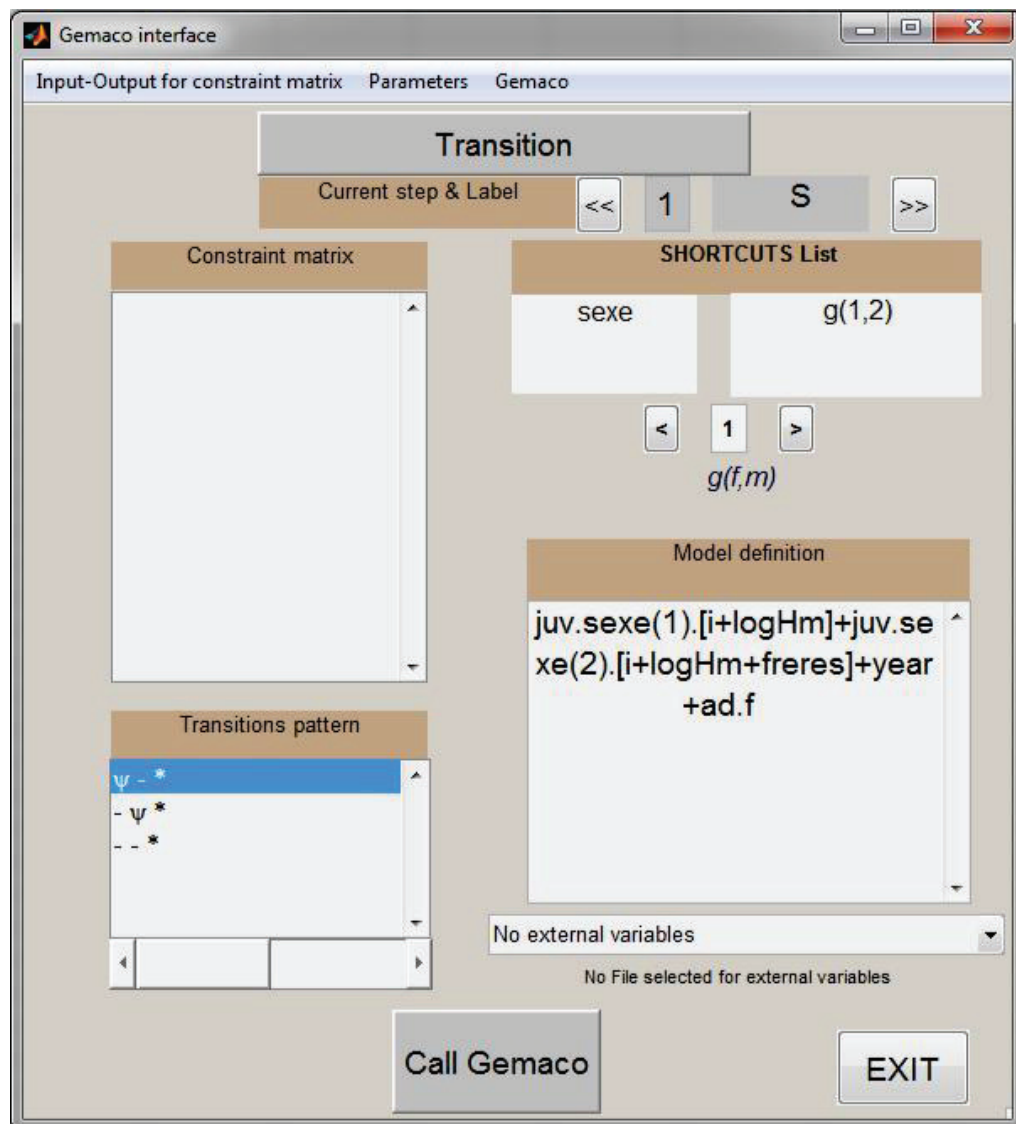
$$[1 - \Psi^{SD} \quad \Psi^{SD}]_y [\Phi^S]_y [p^S]_y$$

Finally, for individuals older than 2 years of age, the model can be written:

$$\begin{bmatrix} 1 - \Psi^{SD} & \Psi^{SD} \\ 0 & 1 \end{bmatrix}_y \begin{bmatrix} \Phi^S \\ \Phi^D \end{bmatrix}_y \begin{bmatrix} p^S \\ p^D \end{bmatrix}_y \begin{bmatrix} E^S \\ E^D \end{bmatrix}_y$$

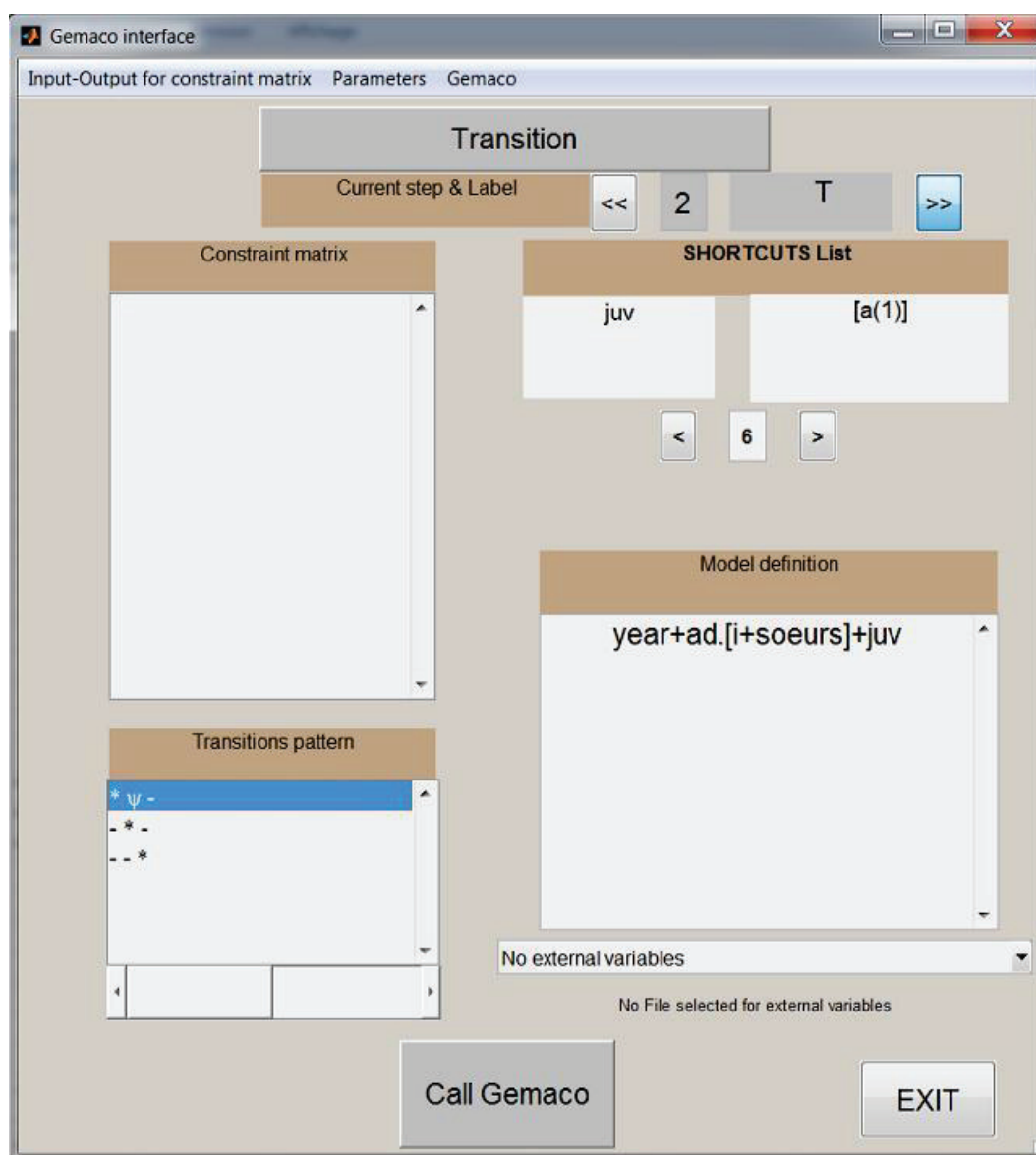
Below are the different matrices ("Transition pattern" box) and how they are constrained using the GEMACO language ("Model definition" box) as implemented in E-SURGE (Choquet *et al.* 2009) to define the best model of the study (model S3.2, Table 4). All matrices are row stochastic (the sum of each row equals one) and the complementary parameter is indicated by \*.

The first elementary matrix (S) draws the survival probabilities between time  $y$  and  $y+1$  for each state. The survival parameter is constrained to be linearly related to the logarithm of the number of helpers for female juvenile individuals and to the logarithm of the number of helpers and the number of brothers for male juveniles ("juv" class) while it is constrained to be separately estimated for adults in each state.

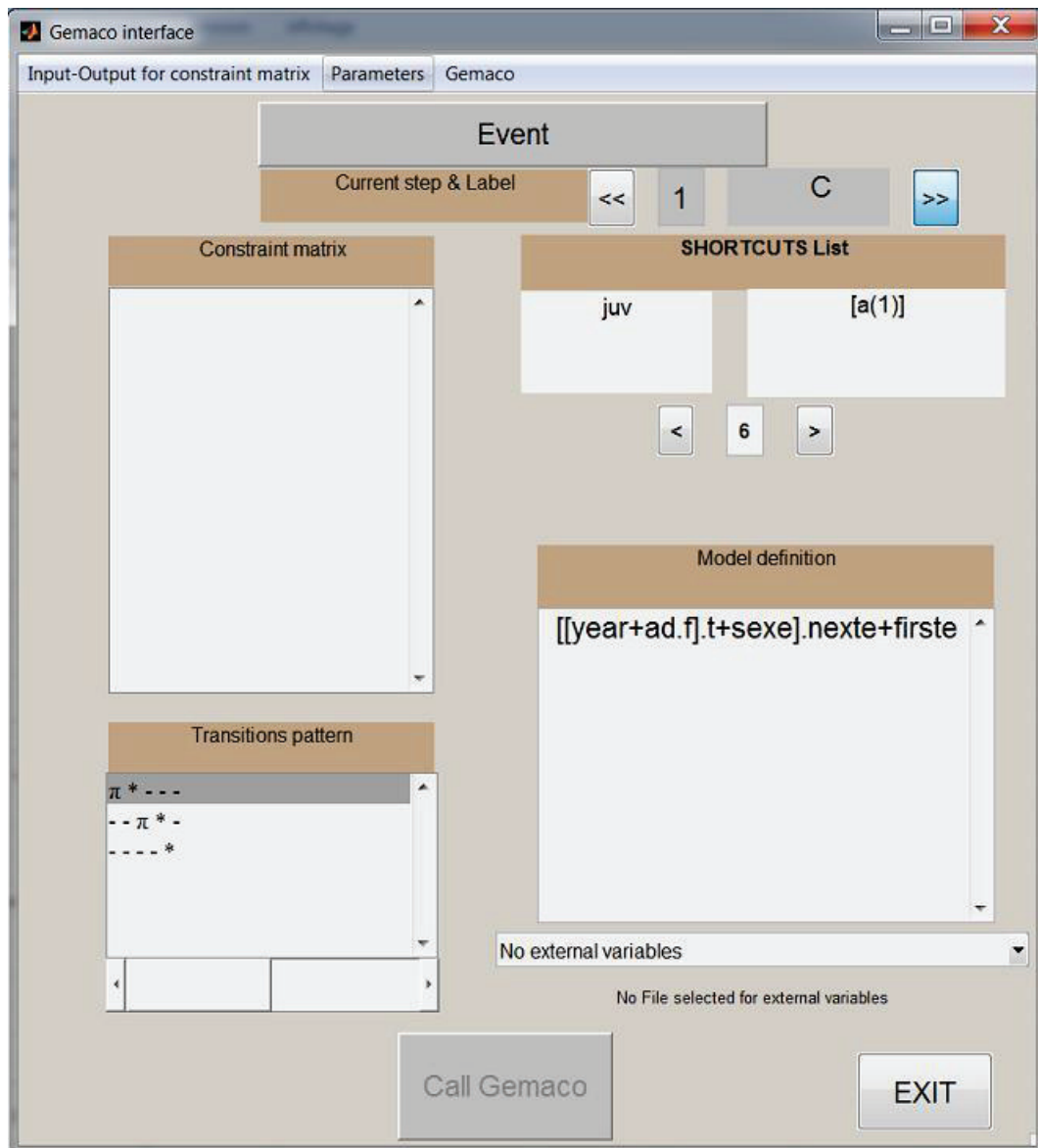




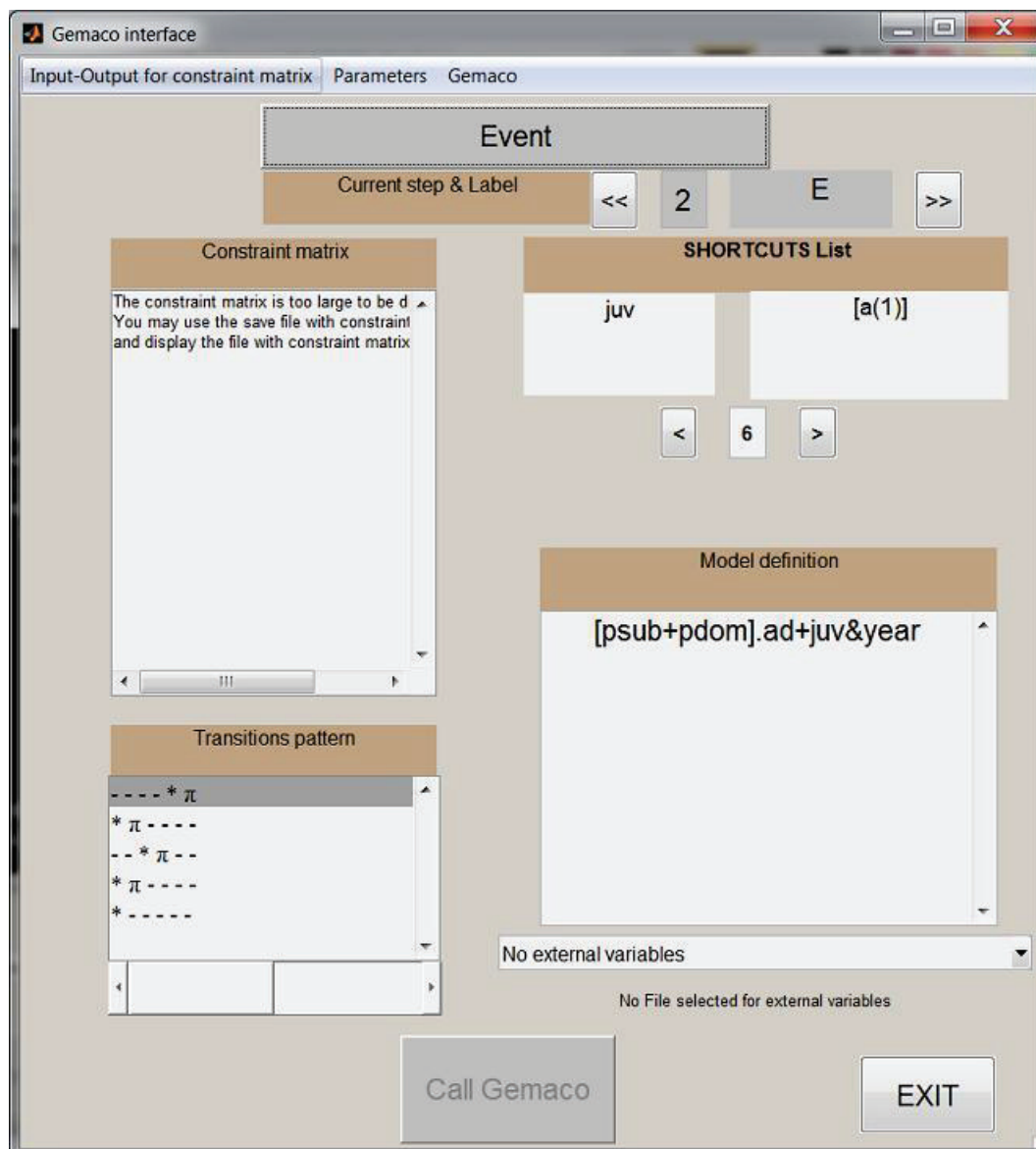
The second elementary matrix (T) draws the transition probabilities from the subordinate to the dominant state conditional on survival between time  $y$  and  $y+1$ , which is the only transition possible. The transition parameter is constrained to be linearly related to the number of sisters for adults and independently estimated for yearlings and juveniles. Since juveniles cannot become dominant, the juvenile transition parameter is then fixed to 0 when initiating the model (IVFV step, Choquet *et al.*, 2009).



The third elementary matrix (C) draws the first capture and recapture probabilities at each occasion  $y$ . The first capture probability (firste) is fixed to 1. Recapture probabilities are set to differ between age classes (yearlings and adults only since all juveniles captures are first captures given the model structure), between states for adults, between sexes and from year to year.



The last elementary matrix (E) draws the probability of having a successful reproduction at each time  $y$  for every individual, whether it is captured or not. "psub" and "pdom" represent the probability for a subordinate and for a dominant to have a successful reproduction a given year. These probabilities only apply to the adult age class since juveniles and yearlings are not sexually mature. The juvenile and yearling probability to reproduce is thus set to 0 at the following IVFV step.



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#### 7.5.4. Goodness-of-fit tests and root model selection

The overall GOF test of the Cormack-Jolly-Seber model was significant ( $\chi^2 = 149.9$ ; d.f. = 74;  $P < 0.01$ ) particularly in its transience (test 3SR;  $\chi^2 = 32.67$ ; d.f. = 19;  $P = 0.03$ ) and trap-dependence (test 2CT;  $\chi^2 = 31.73$ ; d.f. = 18;  $P = 0.02$ ) components. This can be due to the known lower survival of pups as compared to more aged individuals and, if so, can easily be treated by fitting a model with specific survival and capture parameters for pups. To know if this interpretation was correct and hence if the incorporation of specific pup survivals would be an adequate treatment of the lack of fit, we examined the remaining of the capture histories once the pup observation has been taken out. The overall GOF test run on the sole juvenile and adult parts of the capture histories was no longer significant ( $\chi^2 = 37.42$ ; d.f. = 59;  $P = 0.10$ ). Hence, the lack of fit was indeed limited to the first year of life and was adequately treated by incorporating an age effect in both capture and survival parameters. The results of the root model selection are shown in the tables 1 to 4. For a greater clarity, only the models with every parameter constant, full time and sex dependent parameters and those with a non-zero AICc weight are presented. After AICc-based model selection, the root model was:  $p^s a^{*y+sex} \Phi^s a^1 *sex *log(helpm); a^{2,3} E^s a^3, p^D a^3 *y+sex \Phi^D a^3 E^D a^3 \Psi^s D a^{2,3}$ .

**Table III.6.** Model selection for the effects of age, time and sex on the recapture probabilities of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model:  $\Phi^s a^1 *sex *log(helpm) ; a^{2,3} E^s a^3, \Phi^D a^3 E^D a^3 \Psi^s D a^{2,3}$ . (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters; AICc: difference in AICc with the best model of the set;  $W_i$ : AICc weight; bold characters indicate the best model of the set).

Recapture models	Deviance	k	AICc	$\Delta$ AICc	$W_i$
$p^s a^{*y+sex}, p^D a^3 *y+sex$	<b>3625.25</b>	<b>70</b>	<b>3772.12</b>	<b>0.00</b>	<b>0.85</b>
$p^s a^{*y}, p^D a^3 *y$	3631.52	69	3776.39	4.27	0.10
$p^s a^{+y}, p^D a^3 *sex+y$	3704.44	34	3779.31	7.19	0.02
$p^s a^{+y+sex}, p^D a^3 *y+sex$	3704.91	34	3779.78	7.66	0.02
$p^s a^2+y, a^3 *sex+y, p^D a^3 *sex+y$	3703.57	35	3780.44	8.32	0.01
$p^s a^{*y} *sex, p^D a^3 *y *sex$	3558.25	125	3815.12	43.13	0.00
$p$ constant	3838.70	12	3869.57	97.45	0.00

**Table III.7.** Model selection for the effects of age, time, sex and number of male helpers on survival probabilities of Alpine marmots marked from 1990 to 2010 ; all other parameters' constraint structure fixed as in the global model :  $p^s a^* y + sex$  ,  $a^{2,3}$   $E^s a^3$  ,  $p^D a^3 * y + sex$  ,  $E^D a^3$  ,  $\Psi^{SD} a^{2,3}$  (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters; AICc: difference in AICc with the best model of the set;  $W_i$ : AICc weight; bold characters indicate the best model of the set).

Survival Models	Deviance	k	AICc	$\Delta$ AICc	$W_i$
$\Phi^s a^1 * sex * log(helpm)$ , $a^{2,3}$ , $\Phi^D a^3$	<b>3625.25</b>	<b>70</b>	<b>3772.12</b>	<b>0.00</b>	<b>0.95</b>
$\Phi^s a^1 * log(helpm)$ , $a^{2,3}$ , $\Phi^D a^3$	3636.12	68	3778.99	6.87	0.03
$\Phi^s a^1 * helpm$ , $a^{2,3}$ , $\Phi^D a^3$	3638.12	68	3780.99	8.87	0.01
$\Phi^s a$ , $\Phi^D a^3$	3698.78	67	3839.65	67.53	0.00
$\Phi$ constant	3766.92	64	3901.79	129.67	0.00
$\Phi^s a^* y * sex$ , $\Phi^D a^3 * y * sex$	3549.29	201	3958.16	186.04	0.00

**Table III.8.** Model selection for the effects of age, time and sex on the probability to become dominant of Alpine marmots marked from 1990 to 2010 ; all other parameters' constraint structure fixed as in the global model :  $p^s a^* y + sex$  ,  $\Phi^s a^1 * sex * log(helpm)$ ,  $a^{2,3}$   $E^s a^3$  ,  $p^D a^3 * y + sex$  ,  $\Phi^D a^3$  ,  $E^D a^3$  . (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters; AICc: difference in AICc with the best model of the set;  $W_i$ : AICc weight; bold characters indicate the best model of the set).

Transition models	Deviance	k	AIC	$\Delta$ AICc	$W_i$
$\Psi^{SD} a^{2-3}$	<b>3625.25</b>	<b>70</b>	<b>3772.12</b>	<b>0.00</b>	<b>0.49</b>
$\Psi^{SD} a^{2-3} * sex$ , $a^3$	3625.11	71	3773.98	1.86	0.19
$\Psi^{SD} a^{2-3}$ , $a^3 * sex$	3625.23	71	3774.10	1.98	0.18
$\Psi^{SD} a^{2-3} * sex$	3625.09	72	3775.96	3.84	0.07
$\Psi^{SD} a^{2-3} + sex$	3625.16	72	3776.03	3.91	0.07
$\Psi^{SD} a^{2-3} * y * sex$	3552.12	139	3836.99	64.87	0.00
$\Psi$ constant	3739.20	69	3886.07	113.95	0.00

**Table III.9.** Model selection for the effects of age, time and sex on annual reproduction probabilities of Alpine marmots marked from 1990 to 2010 ; all other parameters' constraint structure fixed as in the global model :  $p^s a^y + sex$  ,  $\Phi^s a^l * sex * \log(helpm)$ ,  $a^{2,3}$ ,  $p^D a^3 * y + sex$  ,  $\Phi^D a^3$  ,  $\Psi^{SD} a^{2,3}$ . (n = 806 individuals; AICc: Akaike Information Criterion corrected for small sample sizes; k: number of identifiable parameters; AICc: difference in AICc with the best model of the set;  $W_i$ : AICc weight; bold characters indicate the best model of the set).

Event models	Deviance	k	AIC	$\Delta$ AICc	$W_i$
$E^s a^3$ , $E^D a^3$	<b>3625.25</b>	<b>70</b>	<b>3772.12</b>	<b>0.00</b>	<b>0.44</b>
$E^s a^3$ , $E^D a^3 * sex$	3624.08	71	3772.95	0.83	0.29
$E^s a^3 * sex$ , $E^D a^3$	3625.24	71	3774.14	1.99	0.16
$E^s a^3 * sex$ , $E^D a^3 * sex$	3624.07	72	3774.94	2.82	0.11
$E^s a^3 + y$ , $E^D a^3 + y$	3597.41	88	3780.28	8.16	0.01
$E^s a^3 * y * sex$ , $E^D a^3 * y * sex$	3561.23	139	3846.10	73.98	0.00
E constant	4516.36	70	4663.23	891.11	0.00







# Chapter IV.A

## Sociality & Dispersal

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### Joint estimation of natal dispersal, inheritance and true survival in the Alpine marmot

**Abstract:** Natal dispersal has long been recognised as one of the main driver of population dynamics and evolution of species. However, studying dispersal in natural populations has always proved difficult since dispersing individuals may leave the study area and never be re-encountered. In this situation, demographic parameters estimated using Capture Recapture (CR) methods only account for the processes occurring within the study area and survival estimates, for example, are only “apparent survival”, *i.e.* the probability of an individual to survive *and* not emigrate outside the study area between two capture occasions. Similarly, dispersal estimates obtained from most CR studies are “apparent dispersal” that under-estimate the true dispersal probability since individuals settling outside the study area when dispersing are undistinguishable from dead individuals.

Here, we elaborated on recent methodological advances in population ecology to build an integrated multi-event dispersal model. This model was designed to account for permanent emigration outside the study area and simultaneously estimate true survival, inheritance, natal dispersal probability and natal dispersal distances distribution. We tested for the ability of our model to return unbiased estimates as the mean dispersal distance increases using simulated data sets and compared it to a classical multi-event model and a two-step model that was proposed as a solution to the “apparent survival” problem. To illustrate the usefulness of our model, we present an analysis of the sex-specific dispersal in the Alpine marmot as a case study.

Our model returned unbiased estimates of survival, dispersal probability and mean dispersal distance for a large range of dispersal patterns. The analysis of the Alpine marmot data set indicates higher levels of philopatry in females compared to males. We further discuss the validity and limits of these results and propose future developments.

**Keywords:** Capture-Recapture · Integrated Population Models · Sex-biased dispersal · Bayesian modelling · Dispersal distance distribution ·

Dupont, P., Allainé, D. & Pradel, R. (2016). An Integrated Multi-Event Dispersal model to assess true survival and natal dispersal in the Alpine marmot (*Marmota marmota*). (Draft)



## 8.1. Introduction

Capture Recapture (CR) models are now widely recognized as powerful and essential tools in many fields of biological sciences (Thomson *et al.* 2009). The main advantage of CR methods resides in the possibility to disentangle biological processes, *e.g.* survival (Tavecchia *et al.* 2001b), dispersal (Bennetts *et al.* 2001) or reproduction (Rivalan *et al.* 2005), from detection processes. In the most classic CR model, the Cormack-Jolly-Seber model (CJS model: Cormack 1964; Jolly 1965; Seber 1965), the repetition of capture occasions allows to estimate the proportion of individuals actually dead among those no longer captured. In other words, it allows to estimate the survival probability separately from the detection probability. Because of the power of such an approach, many developments have appeared to account for the complexity of both biological and detection processes. Models accounting for individual heterogeneity in survival (Choquet *et al.* 2011) and/or in recapture probabilities (Bonner 2008b), for instance, have been proposed allowing to answer more complex questions in a more accurate way.

One currently remaining limitation of CR methods is the well-known “apparent survival” problem. During dispersal, some individuals may leave the study area and settle permanently outside its boundaries. These emigrating individuals are then never recaptured and are undistinguishable from dead individuals. In this situation, survival estimates returned by CR models correspond in fact to the probability to survive *and* not leave the study area, which has been called “apparent survival” (Lebreton *et al.* 1992b). Despite this recognised limitation, most studies use apparent survival to draw conclusions about the biology of the species under study (Hagen *et al.* 2005; Blake & Loiselle 2008). This limitation is even more salient in studies on dispersal. Since only a fraction of dispersing individuals can be recaptured inside the study area, any dispersal measure obtained in these conditions is an “apparent dispersal”, which underestimates true dispersal. Even in the case of CR data including multiple sites, dispersal estimates only concern transitions between the monitored sites and all individuals dispersing elsewhere will be confused with dead individuals if no additional information is available (*e.g.* recoveries of dead individuals or count surveys; Péron *et al.* 2010).

Yet, as emphasized by Dobson (2013), dispersal, and especially natal dispersal, is one of the most fundamental and widespread process in biology. All organisms are faced with the “decision” to move and spread, or to stay and try to access reproduction on their

natal site. This “decision” entails strong fitness consequences and understanding the causes and consequences of natal dispersal is thus of prime importance in evolution and population dynamics studies (Bowler & Benton 2005). It is therefore crucial to deal with the issue of “apparent dispersal” in CR studies to study natal dispersal efficiently.

In most CR studies, ancillary information about dispersal is readily available, since the location of an individual is generally recorded when recaptured. This source of information is usually neglected but the emergence of integrated population models (IPM: Schaub & Abadi 2011) and/or spatial capture-recapture models (S-CR models: Borchers & Efford 2008) together with the democratisation of highly flexible software for Bayesian analyses using Markov Chain Monte Carlo (MCMC) methods (BUGS: Lunn *et al.* (2000), JAGS: Plummer (2003)) recently motivated several attempts to use this additional information in order to solve the problem of “apparent survival”.

Among these attempts, two different approaches can be distinguished: (i) the two-step approach in which residency probability, *i.e.* the probability for an individual to remain within the study area when dispersing, is first estimated from the dispersal data only, either at the individual (Gilroy *et al.* 2012) or at the population level (Taylor *et al.* 2015), and then used to correct the apparent survival estimated using traditional CR models (Gilroy *et al.* 2012; Taylor *et al.* 2015); (ii) the integrated approach, developed in a CJS framework by Schaub & Royle (2014) and in a spatial-robust-design framework by Ergon & Gardner (2014), where the phenomena of dispersal and survival are modelled simultaneously. In this latter approach, the location of a surviving individual is modelled at each time step to determine if it is currently inside or outside the study area.

Here, we elaborated on these previous studies to propose an integrated CR model that estimates natal dispersal by correcting for permanent emigration outside the study area. To do so, we conceived a multi-event dispersal model based on the life cycle of the Alpine marmot. Because natal dispersal in this species is a single event and because it is associated to a change in social status, Alpine marmot is a perfectly suited model to study natal dispersal. We started by comparing three different implementations of this multi-event approach and assessed their relative performances in a simulation study. The first implementation is an ordinary multi-event model returning only “apparent dispersal” and “apparent survival” estimates. The second implementation takes up the two-step approach of Gilroy *et al.* (2012) while the last one is inspired by the integrated

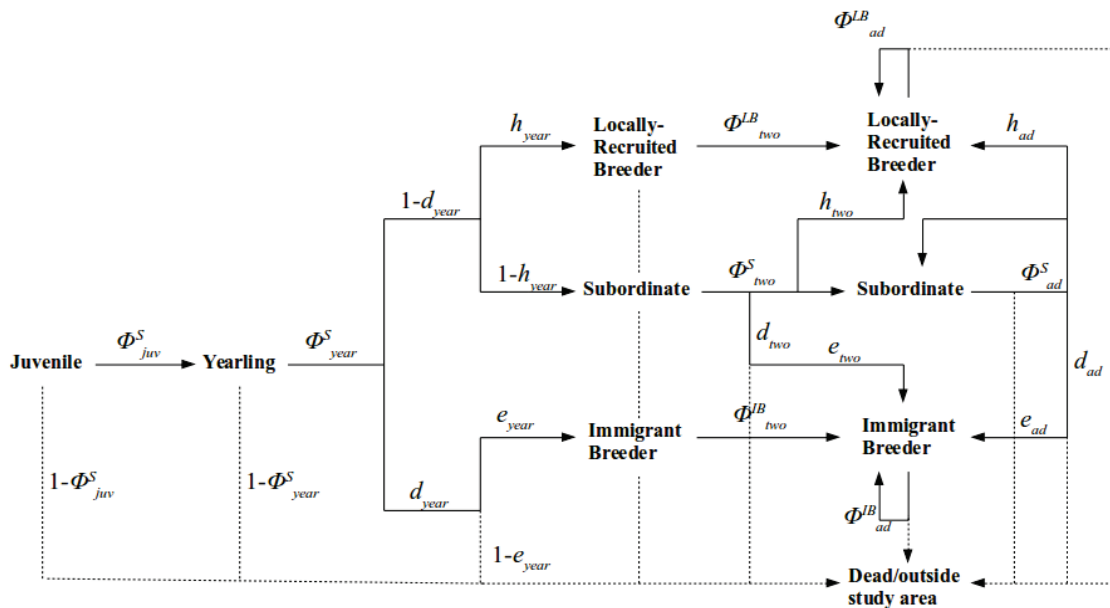
approach of Ergon & Gardner (2014) and Schaub & Royle (2014). In a second time, we ran the best implementation of the three on a long term data set of Alpine marmots to perform an analysis of the sex-specific natal dispersal of this monogamous mammal. Finally, we discuss the advantages and limitations of the different approaches, propose further developments and discuss their ability to detect sex differences in both survival and dispersal patterns.

## 8.2. Material & Methods

### 8.2.1. Multi-event marmot models

*Alpine marmot's life cycle.* All along this study, we considered the life cycle of Alpine marmots (Fig.IV.1). The Alpine marmot is a hibernating, territorial and cooperatively breeding mammal living in family groups composed of a dominant couple, adult subordinates (age > 2), yearlings and pups born that year. In each family, reproduction is monopolized by the dominant couple (with the exception of few subordinate males reproducing through extra-pair copulation (Hackländer *et al.* 2003; Cohas *et al.* 2006), and therefore, reproductive status is generally confounded with dominance status. Offspring produced by the dominant couple stay on their natal territory at least until sexual maturity at two years of age. From this age, they can either stay as subordinate and help raise subsequent pups produced by the dominant couple, or disperse (Stephens *et al.* 2002b). Subordinates that stay in the family group can get a dominant status by inheriting the position in the natal territory after the death of the same-sex dominant while dispersers reach dominance by evicting the same-sex dominant in another territory. A third possibility is the creation of a new territory by a couple of dispersing individuals (but this is highly unlikely in the saturated population under study). Once a subordinate “decided” to disperse, it cannot come back to its natal territory nor be accepted as a subordinate in another family group. Thus, in case of failure in reaching the dominant status, it becomes a floater, *i.e.* a wandering individual forced to hibernate alone and thus exposed to a very high risk of mortality (Magnolon & Jacques 1999). Because family territories are highly variable in size, we considered dispersal distances as the number of territories in straight line between the natal site and settlement territory (discrete distance) instead of the linear distance between the centres of the natal and settlement territory. Once the dominant position secured, a marmot stays dominant until death or eviction by a new incomer. Dispersal in the Alpine marmot is

therefore exclusively natal dispersal. When evicted, the dominant individual becomes a floater and is thus subject to a very high risk of mortality too (Grimm *et al.* 2003b).



**Figure IV.1.** Schematic representation of the Alpine marmot’s life cycle as used in the multi-event model. Solid lines indicate transitions between observable states while dotted lines indicate transitions to un-observable states (dead or outside of the study area). Complementary parameters (*i.e.*  $1-x$  for parameter  $x$ ) are not indicated for two-years and adult age-classes for readability reasons.

*Multi-event models.* To fit the life cycle of Alpine marmots, we constructed a multi-event model (Pradel 2005) with four states; a subordinate state  $S$  (encompassing pups, yearlings and subordinate adults), a locally-recruited-breeder state  $LB$  (individuals that became dominant on their natal territory by inheritance), an immigrant-breeder state  $IB$  (individuals that became dominant inside the study area after dispersal), and a dead state  $D$ .

Since individuals cannot always be observed, or observations may be incomplete, the state of an individual cannot always be determined with certainty (*e.g.* if an individual was seen a given year but its dominance status could not be determined) and the data at hand is thus composed of observable events instead of true state records. The goal of multi-event models is to infer the underlying state (and ultimately the demographic parameters related to this state) from a sequence of observed events recorded on the field. To do so, each observable event was given a number: 1 when the focal individual was captured and identified as a subordinate, 2 when it was captured and identified as a locally-recruited-breeder, 3 when it was captured and identified as an

immigrant breeder and 4 when no information about the focal individual was available. This type of encoding allowed us to construct capture-histories for all individuals captured at least once during the study duration, *e.g.* 1141443343 for an individual captured and marked as a subordinate for the first time on the first year of the study, recaptured as a subordinate on the second and fourth years, recaptured as an immigrant breeder on the seventh, eighth and tenth years and not recaptured on the third, fifth, sixth and ninth years.

Multi-event models can be decomposed in a state-transition and an observation process. The state-transition process models the transition of an individual between states from one capture occasion to the next while the observation process links the observed event at a given capture occasion to the underlying state of the individual. These state-transition and observation processes can be represented by two matrices containing the different parameters of the model (Pradel 2005). In the following sections, we describe these matrices and the parameters they contain for the three different models we wish to compare.

*The Apparent Dispersal model (AD).* In this model, emigration outside the study area is not taken into account and only apparent natal dispersal and apparent survival parameters can be estimated for subordinate individuals. Because dominant individuals no longer disperse, their survival estimates are not biased and are thus true survival estimates. The state-transition process of the model can be described by a four by four matrix with departure states in rows and arrival states in columns, where  $\Phi_{i,t}^S$  is the probability that a subordinate individual  $i$  at time  $t$  survived *and* did not leave the study area between  $t$  and  $t+1$ ,  $\Phi_{i,t}^{LB}$  is the survival probability of the locally recruited breeder  $i$  between  $t$  and  $t+1$ ,  $\Phi_{i,t}^{IB}$  is the survival probability of the immigrant breeder  $i$  between  $t$  and  $t+1$ ,  $d_{i,t}$  is the probability (conditional on survival) that subordinate individual  $i$  dispersed, became a dominant *and* did not leave the study area between  $t$  and  $t+1$  and  $h_{i,t}$  the probability (conditional on survival *and* non-dispersal) that subordinate individual  $i$  accessed dominance on its natal territory between  $t$  and  $t+1$ .



$$\begin{bmatrix} & S & LB & IB & D \\ \begin{bmatrix} S \\ LB \\ IB \\ D \end{bmatrix} & \begin{bmatrix} \Phi_{app}^S (1-d_{app}) \cdot (1-h) & \Phi_{app}^S (1-d_{app}) \cdot h & \Phi_{app}^S \cdot d_{app} & (1-\Phi_{app}^S) \\ 0 & \Phi^{LB} & 0 & 1-\Phi^{LB} \\ 0 & 0 & \Phi^{IB} & 1-\Phi^{IB} \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{bmatrix}$$

Since four different observable events were retained, the observation matrix is also a four by four matrix where the rows represent the underlying states and columns represent the observable events. The observation parameter is  $p^x_{i,t}$  the recapture probability of individual  $i$  in state  $x$  at time  $t$ :

$$\begin{bmatrix} & 1 & 2 & 3 & 4 \\ \begin{bmatrix} S \\ LB \\ IB \\ D \end{bmatrix} & \begin{bmatrix} p^S & 0 & 0 & 1-p^S \\ 0 & p^{LB} & 0 & 1-p^{LB} \\ 0 & 0 & p^{IB} & 1-p^{IB} \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{bmatrix}$$

*The Two-step Dispersal model (TD).* This model takes up the approach developed by Gilroy *et al.* (2012). The apparent dispersal ( $d_{app}$ ) of subordinates in the previous AD model is in fact a composite-parameter. It can be expressed as the product of the dispersal ( $d_{cor}$ ) and residency probability ( $r_{cor}$ ), *i.e.* the probability to not emigrate outside the study area when dispersing to become dominant:  $d_{app} = d_{cor} * r_{cor}$ . We can then construct a new model with a modified state-transition matrix (*SM*):

$$\begin{bmatrix} & S & LB & IB & D \\ \begin{bmatrix} S \\ LB \\ IB \\ D \end{bmatrix} & \begin{bmatrix} \Phi_{cor}^S \cdot (1-d_{cor}) \cdot (1-h) & \Phi_{cor}^S \cdot (1-d_{cor}) \cdot h & \Phi_{cor}^S \cdot d_{cor} \cdot r_{cor} & (1-\Phi_{cor}^S) + \Phi_{cor}^S \cdot d_{cor} \cdot (1-r_{cor}) \\ 0 & \Phi^{LB} & 0 & 1-\Phi^{LB} \\ 0 & 0 & \Phi^{IB} & 1-\Phi^{IB} \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{bmatrix}$$

However, because no information in the data allows differentiating between dead and emigrated individuals,  $r_{cor}$ ,  $\Phi_{cor}^S$  and  $d_{cor}$  parameters are not separately identifiable under this parametrisation and these probabilities cannot be estimated from capture-recapture data only. The residency probability thus needs to be estimated in a first step before being used in the CR model to allow the estimation of survival and dispersal parameters.

The residency probability of an individual depends on: (i) the direction of dispersal; (ii) the location of the natal territory of the individual relative to the edge of the study area and (iii) the distance travelled during dispersal (Gilroy *et al.* 2012). To simplify, we considered dispersal as homogeneous in direction, *i.e.* individuals have the same probability to choose any direction when dispersing. Given that the location of the natal site  $s_i$  was known for all individuals born within the study area, the only missing information was the individual dispersal distance, measured as the number of territories crossed between the natal territory and the territory where the individual became dominant. This distance was only recorded for individuals that settled inside the study area and had to be inferred for individuals that emigrated and became dominant outside the study area. To estimate this individual dispersal distance  $l_{cor,i}$ , we used the known dispersal distances recorded inside the study area and construct a vector  $L$  of length  $l_{max}$ , the longest distance between two territories inside the study area, containing the frequencies of observed dispersal distances. The distance an individual travelled during natal dispersal was then sampled from this observed distribution:

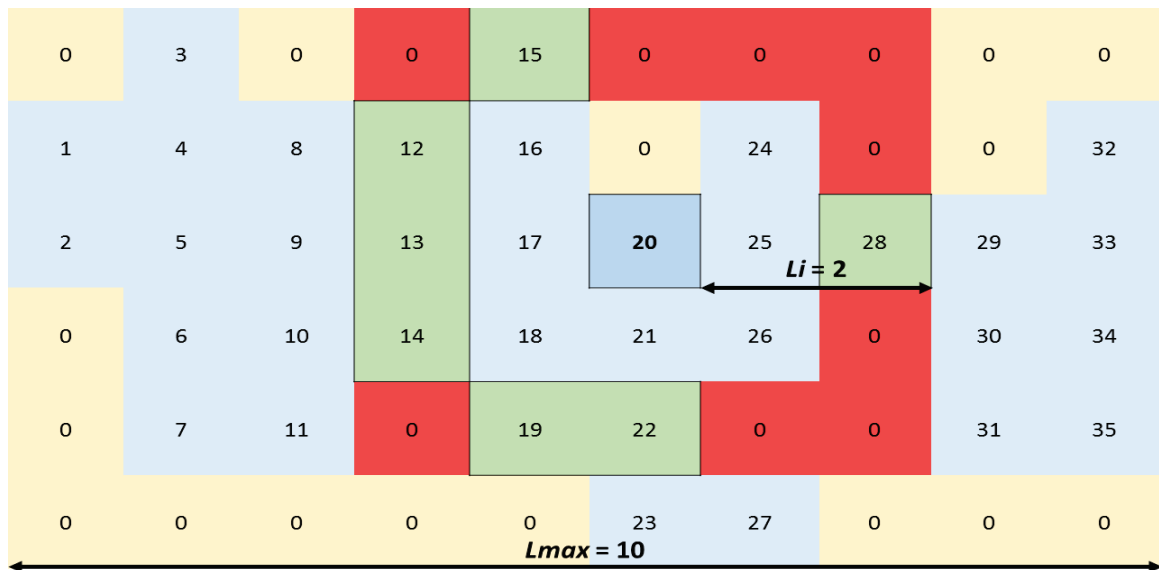
$$l_{cor,i} \sim \text{dcat}(L)$$

The individual residency probability was then easily calculated as:

$$r_{cor,i} = \frac{n_{s_i,l_i}}{N_{s_i,l_i}} = \frac{n_{s_i,l_i}}{8 * l_{cor,i}}$$

where  $n_{s_i,l_i}$  is the number of territories inside the study area situated at a distance  $l_{cor,i}$  from the natal territory  $s_i$  and  $N_{s_i,l_i}$  is the total number of territories situated at a distance  $l_{cor,i}$  from the natal territory  $s_i$ . Because we considered territories as discretely and homogeneously distributed both inside and outside the study area, the total number of territories situated at a distance  $l_i$  from any territory  $s_i$  was  $N_{s_i,l_i} = 8 * l_{cor,i}$ . In other words, the residency probability for an individual dispersing a given distance  $l_i$  was equal to the proportion of territories situated at a distance  $l_i$  from its natal site  $s_i$  that are situated

within the study area. This proportion was determined based on a grid map  $M$  of the study area (Fig.IV.2). Because the maximum dispersal distance observable inside the study area is equal to  $l_{max}$ , the distribution of dispersal distances contained in  $L$  was truncated and biased towards short distances (Taylor et al., 2015). The dispersal distance  $l_{cor,i}$  was then under-estimated and the residency probability  $r_{cor}$  was in turn over-estimated. Hence, the survival and natal dispersal estimates returned by this model are not true but only corrected estimates. The remaining part of the TD model, *i.e.* the observation process, was identical to the AD model.



**Figure IV.2** Example of a study area map as used in the simulation study. The study area is represented by the light blue and green areas. Each number represents a family group territory where trapping occurs. Yellow and red areas represent territories outside the study area. The residency probability of an individual born on territory 20 crossing two territories when dispersing is equal to  $7/16 = 0.44$  (of all 16 territories situated at a distance of two (red and green territories), seven belong to the study area (green territories)).

*The Integrated Dispersal model (ID).* This last implementation is based on the integrated approach of Ergon & Gardner (2014) and Schaub & Royle (2014). It aims at estimating *simultaneously* the dispersal kernel and the demographic parameters and thus solving the problem of truncated dispersal distances of the two-step model. The only difference with the TD parametrisation presented above is that individual dispersal distance is integrated in the model as a random variable whose distributional parameters are to be estimated. In other words, instead of using the observed and biased dispersal kernel, the dispersal distances distribution becomes part of the model and has to be estimated. Since dispersal distance in the Alpine marmot is discrete and strictly positive,

we used a Poisson distribution. The Poisson distribution also presents the advantage of requiring only one parameter, its mean  $\tau$ . The individual dispersal distance is described by:

$$l_i \sim \text{dpois}(\tau) + 1$$

Because non-dispersing individuals (*i.e.* dispersal distance of zero) are modelled elsewhere in the model (with the  $S$  and  $LB$  states), the minimal dispersal distance possible is one territory, hence the addition of one to the random Poisson sample. The state-transition matrix of the model is identical to the TD formulation, but the interpretation of the parameters is slightly different. Provided the Poisson distribution used to describe the dispersal distances is representative of the reality (a limitation common to all dispersal distribution studies), the parameters of this formulation are now the true subordinate survival (noted  $\Phi^S$ ), true natal dispersal ( $d$ ) and true residency ( $r$ ) probabilities:

$$\begin{array}{c} \left[ \begin{array}{c} S \\ LB \\ IB \\ D \end{array} \right] \left[ \begin{array}{cccc} S & LB & IB & D \\ \Phi^S.(1-d).(1-h) & \Phi^S.(1-d).h & \Phi^S. d.r & (1-\Phi^S)+ \Phi^S. d.(1-r) \\ 0 & \Phi^{LB} & 0 & 1-\Phi^{LB} \\ 0 & 0 & \Phi^{IB} & 1-\Phi^{IB} \\ 0 & 0 & 0 & 1 \end{array} \right] \end{array}$$

The observation process is identical to the one in the AD and TD model (see supplementary material 8.5.1.1 for BUGS scripts of the different models).

*Model implementation.* The different models were then fitted using Markov Chain Monte Carlo (MCMC) simulations with the computer program JAGS (Plummer 2003) called through R3.2.5 (R core team 2016) with the R package jagsUI (Kellner 2014). At each iteration, the underlying state of an individual  $i$  at the following time step  $t+1$ ,  $z_{i,t+1}$  is sampled in the categorical distribution defined by the probability vector contained in the row of the state-transition matrix ( $SM$ ) corresponding to the current state,  $z_{i,t}$ . The associated observable event, as recorded in the capture history,  $y_{i,t+1}$  is sampled from the categorical distribution defined by the row of the observation matrix ( $OM$ ) corresponding to the underlying state  $z_{i,t+1}$ :

$$z_{i,t+1} \sim \text{dcat} ( SM [z_{i,t}, ] )$$

$$y_{i,t+1} \sim \text{dcat} ( OM [z_{i,t+1}, ] )$$

All parameter priors were chosen to be un-informative. All survival, dispersal, inheritance and recapture probabilities were given uniform priors,  $\text{dunif}(0,1)$ . Prior for the Poisson mean in the ID model was given a vague gamma distribution  $\text{dgamma}(0.0001,0.0001)$ . Because convergence was obtained faster for simulated data sets compared to the Alpine marmot data set, all models in the simulation study were fitted by running three chains independently for 10000 iterations with a burning period of 6000 iterations and a thinning rate of 1 while for the case study on Alpine marmots, three chains of 15000 iterations were needed with a burning period of 10000 iterations.

### 8.2.2. Simulation study

To compare the different models, we constructed several data sets with increasing mean dispersal distance. We considered a simple situation where the survival probability was equal and high for both breeder states ( $\Phi^{IB} = \Phi^{LB} = 0.95$ ), slightly lower for subordinates ( $\Phi^S = 0.85$ ) and recapture probabilities differed between dominants and subordinates ( $p^{IB} = p^{LB} = 0.65$  and  $p^S = 0.95$ ). Finally, dispersal probability  $d$  was fixed to 0.4 and inheritance probability  $h$  to 0.12. To avoid effects due to its shape, the study area was randomly generated by sampling 35 different cells in a  $10 \times 6$  grid for each simulated data set, *i.e.* 35 territories where trapping occurs were randomly selected out of 60 possible locations for each simulated data set. Each individual's initial location was then randomly sampled among the 35 territories. We considered the landscape as homogeneous, *i.e.* the habitat was suitable for settlement anywhere inside or outside the study area. Based on this map, a matrix containing the residency probabilities for each territory and dispersal distance was constructed (see supplementary material 8.5.1.2 for the script used to generate the residency probability matrix). Because dispersal was limited to a single transition from the  $S$  to the  $IB$  state, individual dispersal distance was sampled *a priori* for all individuals from a Poisson distribution. Given its natal territory and individual dispersal distance, each individual was then assigned a residency probability  $r_i$  from the residency probability matrix. State-transition and observation matrices similar to those in the ID model were then filled with these different probabilities. Individuals capture histories were constructed by sampling the individual underlying state and observed event for each time step in the corresponding state-transition and observation process matrix based on its previous state. The initial location

was known for all simulated individuals but dispersal distances were kept only for individuals that did not disperse outside the study area to mimic true capture-recapture data (see supplementary material 8.5.1.3 for a data simulation script).

We simulated data sets with increasing mean dispersal distance  $\tau$  from 0 to 12 territories with steps 0.5 and repeated the simulation process 100 times for each value of  $\tau$ , leading to a total of 2500 simulated data sets. Each data set was composed of twenty capture occasions, with 40 individuals entering the data set at each occasion (except for the last one), leading to a total of 760 individuals per data set.

### *8.2.3. Sex-specific dispersal in the Alpine marmot*

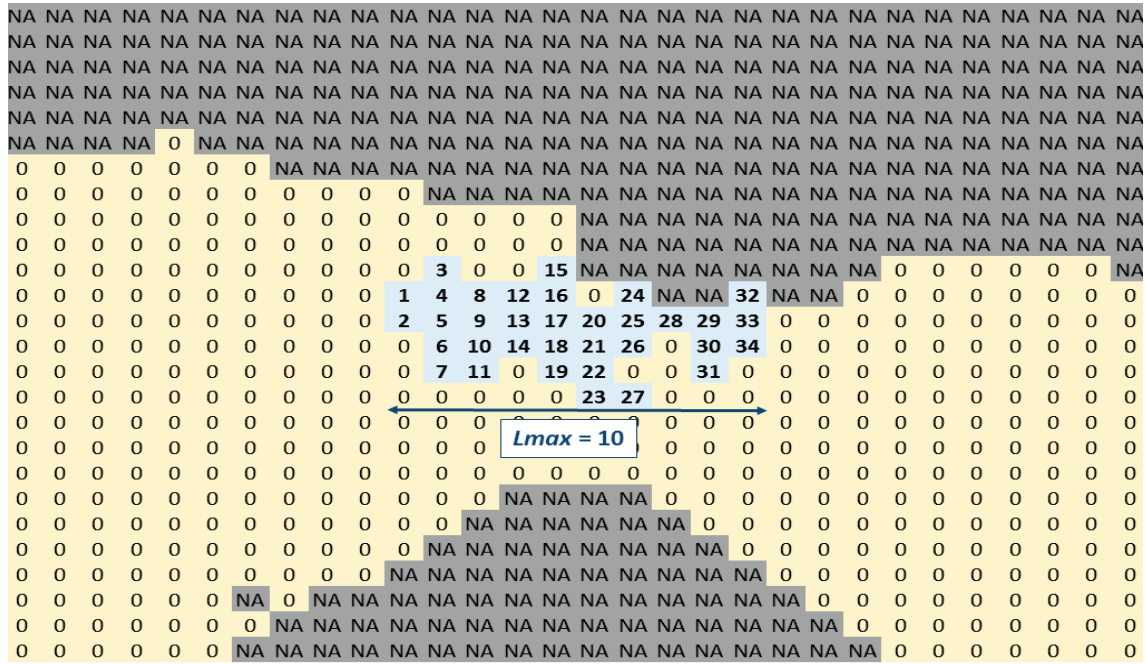
Finally, we applied the integrated dispersal model to a real Alpine marmot data set to obtain estimates of sex-specific survival and dispersal. The data set was composed of 1270 individuals captured over 26 years (from 1990 to 2015) in the Grande Sassière nature reserve (Parc National de la Vanoise, France). During this period, 172 dispersal events were recorded with a maximum dispersal distance of six territories crossed. In the same time, the study area increased and the number of family territories under study changed from 13 to 35 (Fig.IV.3). Consequently, the probability for an individual to emigrate outside the study area decreased and the probability to observe a dispersal event inside the study area increased simultaneously. To account for this change in the study area size and shape, we used annual maps representative of the territories relative positions for each time step.

Also, because the study area is situated at the bottom of a small valley surrounded by high altitude mountain tops, where habitat is unsuitable for Alpine marmots (snow, rocks and very little vegetation), the landscape could not be considered as homogeneous and dispersal was not equally possible in all directions. Because the structure of the landscape outside the study area strongly influences survival and dispersal estimates (see supplementary material 8.5.2 for a simulation study of the impact on survival and dispersal estimates of the heterogeneity of the landscape), we used a satellite picture to construct the maps of the study area and its surroundings and discarded rocky and high altitude areas from the potential settlement territories (see Fig.IV.4 for an example of grid map with 34 territories and unsuitable habitat discarded from the possible dispersal locations).



**Figure IV.3.** Schematic map of the family territories under study in the Grande Sassière nature reserve for the period 2012-2014 (2340 m a.s.l., French Alps, 45°29'N, 6°59'E) Orange area is followed since 1990. Yellow territories were added in 2013.

Following the results of previous CR studies on the same population (Dupont *et al.* 2015b; Berger *et al.* 2016; Rézouki *et al.* 2016), we incorporated time as a factor with additive age and sex effects on the recapture probabilities. In addition to the sex-effect in which we were interested, we accounted for age-specific subordinate survival and transitions probabilities by considering four age classes: juvenile (from zero to one-year-old), yearling (from one to two), two-year (from two to three) and adult (three years old and older). Since it has been shown to be an important driver of juvenile survival, we incorporated an effect of the logarithm of the number of male helpers on the juvenile survival (Allainé & Theuriau 2004; Dupont *et al.* 2015). Because no individual attained a dominant status before two years old, only the two last age classes were used for dominant individuals. In addition, we considered sex-specific dispersal patterns, *i.e.* two distinct Poisson distributions with sex-specific mean. The parameters of the model were then  $p_{t,age,sex}$  the time, age and sex-specific recapture probabilities,  $\Phi^{LB}_{age,sex}$  and  $\Phi^{LB}_{age,sex}$  the age and sex-specific survival probabilities of dominant individuals,  $\Phi^S_{age,sex}$  the age and sex-specific survival probabilities of subordinate individuals,  $d_{age,sex}$  the age and sex-specific dispersal probabilities,  $h_{age,sex}$  the age and sex-specific inheritance probabilities and  $\tau_{sex}$  the sex-specific means of the dispersal distances distribution for the integrated model.



**Figure IV.4.** Study area map of the Grande Sassière nature reserve based on a satellite picture. Light blue colour represents the study area. Numbers represent family territories where trapping occurs. Yellow area stands for territories outside the study area suitable for Alpine marmots. Grey area represents unsuitable habitat (rocky and snowy areas).

### 8.3. Results

#### 8.3.1. Simulation study

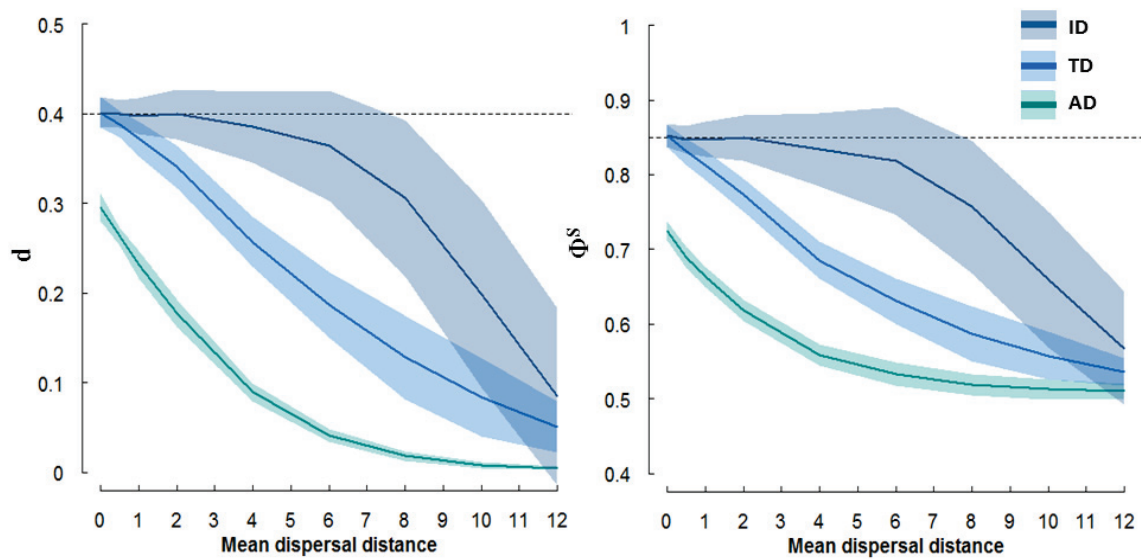
The posterior means  $\pm$  se obtained using all three models were very similar and unbiased for recapture probabilities (AD model:  $p^S = 0.95 \pm 0.01$  and  $p^{IB} = p^{LB} = 0.65 \pm 0.02$ ; TD:  $p^S = 0.95 \pm 0.01$  and  $p^{IB} = p^{LB} = 0.65 \pm 0.02$ ; ID:  $p^S = 0.95 \pm 0.01$  and  $p^{IB} = p^{LB} = 0.65 \pm 0.02$ ), inheritance probability (AD:  $h = 0.12 \pm 0.01$ ; TD:  $h = 0.12 \pm 0.01$ ; ID:  $h = 0.12 \pm 0.12$ ) and breeder survival probabilities (AD:  $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$ ; TD:  $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$ ; IS:  $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$ ), under all scenarios.

Subordinate survival and dispersal estimates, on the other hand, varied considerably among the three models. Both posterior mean estimates given by the AD model were much lower than the simulated values and this difference increased with the mean simulated dispersal distance (Fig.IV.5) until a lower plateau was reached for values of mean dispersal distance higher than the maximum length of the study area  $l_{max}$ . The difference between the simulated value and the posterior mean of the apparent dispersal probability  $d_{app}$  increased from 26% to 99% of the simulated value when mean dispersal distance increased from 0 to 12 territories, while the difference between the simulated and the apparent subordinate survival estimate  $\Phi_{app}^S$  varied from 15% to 40%



of the simulated value in the same interval. Notably, at the extreme, when the mean simulated dispersal distance was higher than  $l_{max}$ , the apparent dispersal probability estimates tended towards zero.

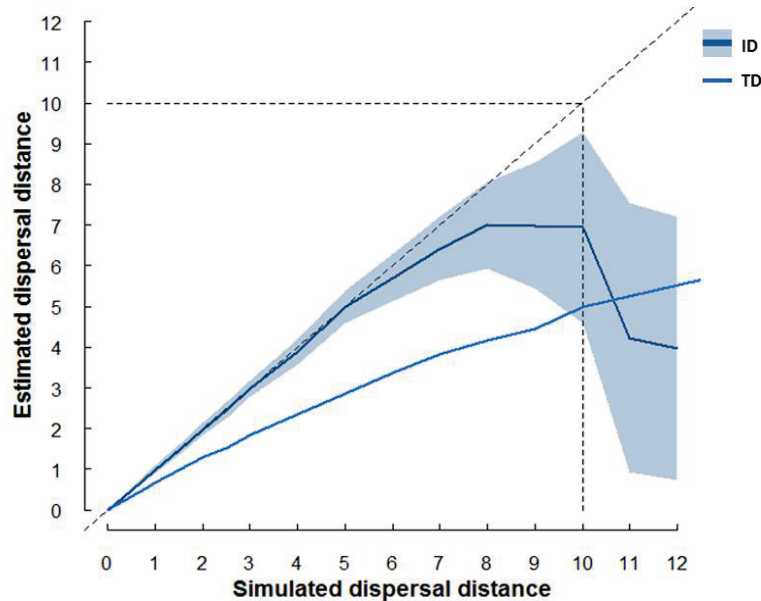
Negative bias was also observed but to a lesser extent for both the two-step and integrated models. For the TD model, the difference between  $d_{cor}$  and the simulated value of  $d$  varied from 0% to 87% of the simulated value and the difference between  $\Phi^S_{cor}$  and the simulated survival value varied from 0% to 36%. For the ID model, observed differences were always lower, varying from 0% to 84% for the dispersal probability and from 0% to 30% for the subordinate survival estimate.



**Figure IV.5.** Estimates of dispersal probability (left) and subordinate survival probability (right) given by the three different models; ID: Integrated Dispersal model, TD: Two-step Dispersal model and AD: Apparent Dispersal model. Coloured lines represent the mean estimates, shaded areas represent the standard error of the mean associated to each parameter and dashed lines represent simulated values.

Most importantly, the difference between estimated and simulated values obtained with the ID model was virtually null for mean dispersal distances lower than half of the study area length (difference between simulated and estimated value of  $d < 1\%$  and difference between the simulated and estimated value of  $\Phi^S < 1\%$  of the simulated value) and relatively small (under 10%) for mean dispersal distances lower than 75% of the study area length. In comparison, the difference between simulated and estimated values of both dispersal and subordinate survival was always higher than 10% for the AD model. For the TD model, this difference was higher than 10% as soon as mean dispersal distance exceeded one territory. This difference is also visible for the

mean dispersal distance  $\tau$ . The integrated model was able to return the true mean dispersal distance for a large range of simulated values while the difference between the simulated and observed mean dispersal distance used in the two-step model continuously increased (Fig.IV.6). Interestingly, the estimated value of mean dispersal distance  $\tau$  returned by the integrated model decreased dramatically when the mean simulated dispersal distance was higher than the maximum length of the study area.

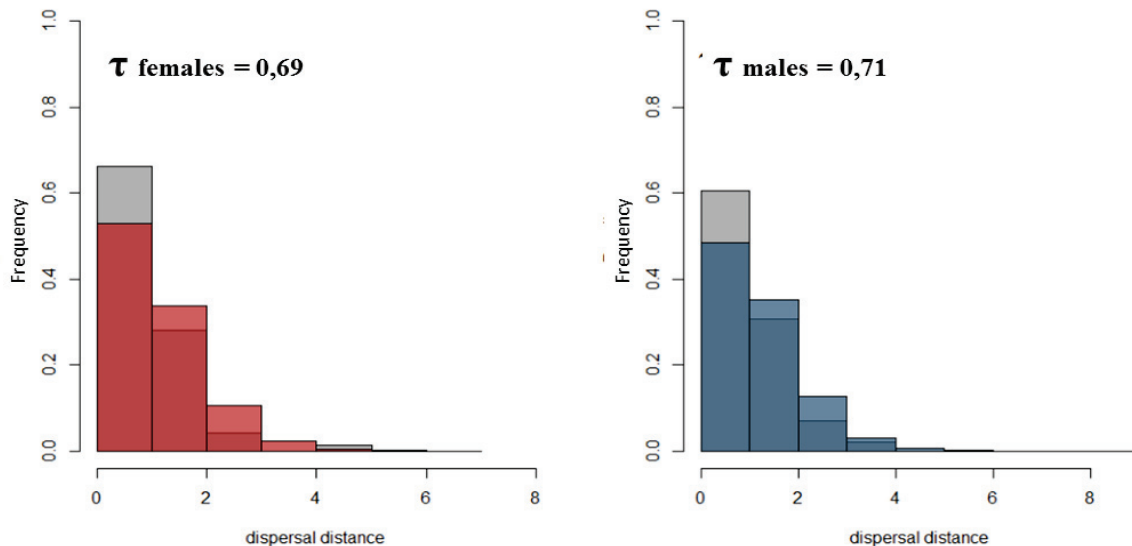


**Figure IV.6.** Mean dispersal distance as used in the Two-step Dispersal (TD: observed values inside the study area) and estimated by the Integrated Dispersal (ID: estimated mean value  $\pm$  se of the mean) models for increasing values of simulated mean dispersal distance. Horizontal and vertical dashed lines indicates the longest distance between two territories inside the study area.

### 8.3.2. Sex-specific dispersal in the Alpine marmot

The 95% confidence intervals of the posterior mean estimates returned by the ID model indicated that recapture probabilities varied with time and decreased with age (difference in recapture probabilities between yearlings and two-years  $\Delta p_{two} = -1.40$  [-1.91; -0.94] and difference between yearlings and adults  $\Delta p_{ad} = -1.90$  [-2.37; -1.50] on the logit scale). The recapture probabilities were also higher for females than for males (difference in recapture probabilities between females and males  $\Delta p_{sex} = -0.28$  [-0.55; -0.02] on the logit scale). The dispersal distances distribution did not differ between males and females (mean dispersal distance for females  $l_{females} = 1.69$  [1.55; 1.85] and mean dispersal distance for males  $l_{males} = 1.71$  [1.56; 1.86], see Fig IV.7). Juvenile subordinate survival increased with the logarithm of the number of male subordinates

present during hibernation for both sexes ( $\beta_{help\_m} = 0.41$  [0.33; 0.49] for females and 0.53 [0.44; 0.61] for males on the logit scale). Subordinate survival increased with age but did not vary significantly between sexes although two-year subordinate males tended to have a lower survival than females (Fig. IV.8 upper panel and Table IV.1). Dispersal probabilities increased with age similarly for both sexes (Fig. IV.8 middle panel and Tab.IV.1). Inheritance probabilities also varied with age and a sex difference was found for the two-year age class (Fig. IV.8 lower panel and Table IV.1). Because inheritance is conditional on survival and dispersal, this indicates that females in their third year of life had more chances to inherit a dominant position than males. To summarize these results, the fate of subordinate individuals in the population was represented as the cumulative proportions of subordinate individuals in each state predicted by the model (Fig IV.9). For dominants, survival probabilities of young dominants, *i.e.* two-year age class, were higher than those of adults but no sex difference was evidenced for both locally recruited and immigrant breeders (Table IV.1). In addition, no difference between locally recruited and immigrant breeders was evidenced (difference in survival between locally recruited and immigrant two-year breeders  $\Delta\Phi_{sub}^{LB} = 10.43$  [-34.32; 64.69] on a logit scale) and older dominants (difference in survival between locally recruited and immigrant adult breeders  $\Delta\Phi_{ad}^{LB} = 0.14$  [-0.36; 0.63] on a logit scale).



**Figure IV.7.** Histogram of observed (grey) and estimated (coloured) dispersal distances distribution for female (red) and male (blue) Alpine marmots.  $\tau$  represents the sex-specific mean of the estimated Poisson distribution, the mean number of territories crossed for a sex during dispersal is equal to  $1 +$  mean of the sex-specific Poisson distribution.

**Table IV.1.** Mean posterior estimates (standard deviation) of survival, dispersal and inheritance probabilities for the ID model. Overlap indicates whether the credible interval of the difference between males and females for this parameter includes 0, *i.e.* it indicates if the parameter does not differ significantly between sexes.

parameters	females	males	overlap
$\Phi_{juv}^S$	0.56 (0.03)	0.55 (0.02)	YES
$\Phi_{year}^S$	0.71 (0.04)	0.74 (0.04)	YES
$\Phi_{two}^S$	0.97 (0.05)	0.84 (0.11)	YES
$\Phi_{ad}^S$	0.99 (0.01)	0.99 (0.01)	YES
$\Phi_{two}^{LB}$	0.99 (0.04)	0.99 (0.07)	YES
$\Phi_{ad}^{LB}$	0.78 (0.03)	0.70 (0.04)	YES
$\Phi_{two}^{IB}$	0.99 (0.06)	0.99 (0.10)	YES
$\Phi_{ad}^{IB}$	0.80 (0.03)	0.77 (0.03)	YES
$d_{juv}$	0.00 (0.00)	0.00 (0.00)	YES
$d_{year}$	0.10 (0.03)	0.11 (0.03)	YES
$d_{two}$	0.58 (0.06)	0.57 (0.06)	YES
$d_{ad}$	0.58 (0.06)	0.58 (0.05)	YES
$h_{juv}$	0.00 (0.00)	0.00 (0.00)	YES
$h_{year}$	0.01 (0.01)	0.01 (0.01)	YES
<b><math>h_{two}</math></b>	<b>0.32 (0.06)</b>	<b>0.09 (0.04)</b>	<b>NO</b>
$h_{ad}$	0.59 (0.09)	0.58 (0.07)	YES

## 8.4. Discussion

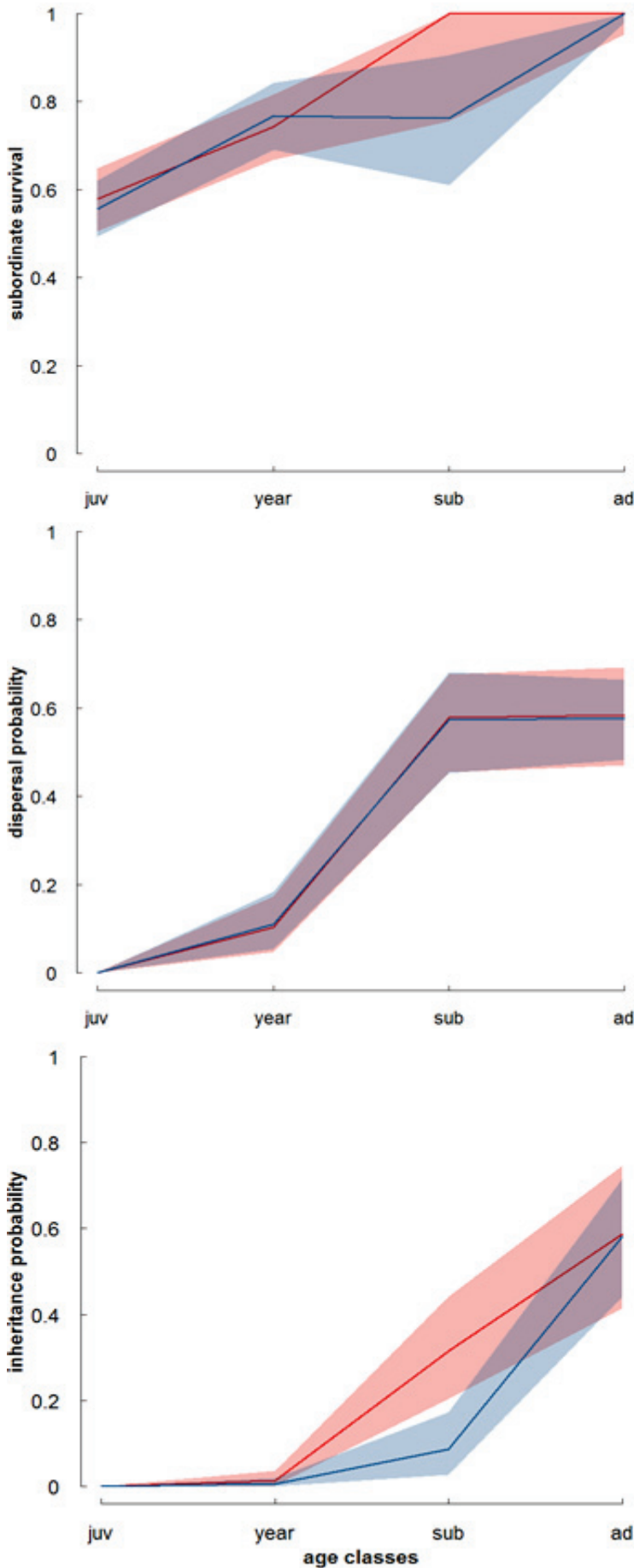
### 8.4.1. Approaches comparison

The results of the different simulations indicated that the AD model strongly underestimated both survival and dispersal even in the case of short dispersal distance. The two-step model of Gilroy *et al.* (2012) allowed to severely decrease this bias but not to delete it. The integrated approach proposed by Ergon & Gardner (2014) and Schaub & Royle (2014) on the other hand, returned unbiased estimates of both survival and dispersal as long as the coverage of the study area is relatively large compared to the mean dispersal distance.

Our results confirm and complete previous studies on the problematic of “apparent survival” in different ways (Gilroy *et al.* 2012; Ergon & Gardner 2014; Schaub & Royle 2014; Taylor *et al.* 2015). In these previous studies, authors compared

either a two-step model or an integrated model to a classical CJS model, but none of them compared all three approaches together. Here, we showed that incorporating information about dispersal, as Gilroy *et al.* (2012) or Taylor *et al.* (2015) did, is a good way to reduce the bias in the different demographic parameters but it does not allow to reach the true values of the demographic parameters. It is known that the underestimation of survival and dispersal is directly linked to the proportion of the dispersal distances distribution sampled in the dispersal data (Gilroy *et al.*, 2012), but this proportion remains unknown to researchers most of the time. Using such models can be tricky since it gives estimates of demographic parameters in between the “apparent value”, for which we have a clear definition, and “true value”. In such situation, we therefore know that estimates are biased but not to what extent. To overcome this problem, Taylor *et al.* (2015) proposed to correct the observed dispersal distances distribution before using it to calculate residency probabilities by applying a Barrowclough correction (Barrowclough 1978). However, this correction is based on the assumption of a homogeneous and circular study area, a disposition highly unlikely in natural conditions. To draw conclusions on the evolution of dispersal in a species or to propose population management recommendations based on such models is thus highly risky and should be avoided.

The integrated approach on the other hand provides reliable estimates of both survival (Ergon & Gardner 2014; Schaub & Royle 2014) and natal dispersal (this study). In addition, as noted by Schaub & Royle (2014), modelling the dispersal process within a CR model allows estimating the error associated to the dispersal kernel. We therefore obtain at the same time a good description of the true dispersal pattern and a quantification of the uncertainty associated to this dispersal pattern given the data at hand. The integrated approach is thus more rigorous and more accurate from a statistical point of view. However, the integrated approach still has some limitations. First, it returns accurate estimates of true survival and dispersal only to a certain extent. Notably, the performance of the model is related to the ratio of the size of the study area relative to the mean dispersal distance. Indeed, when the number of dispersal events observed within the study area compared to the total number of dispersal events becomes too small, the model is not able to correctly identify the parameters of the dispersal distance distribution, and demographic parameters are also misestimated. This problem is truly



**Figure IV.8.**

Mean posterior estimates of subordinate survival (top panel), dispersal probability (middle panel) and inheritance probability (lower panel) returned by the ID model for both females (red lines) and males (blue lines) and for the different age classes: juveniles (juv), yearlings (year), subadults (sub) and adults (ad). Shaded areas represent the associated 95% confidence interval.

the problem of the quality of the data available and, as noted by Schaub & Royle (2014): “if censoring becomes too strong (dispersal distances very large relative to the size of the study area), [the] model is not successful anymore in correctly estimating dispersal and consequently survival. But it is hard to imagine that any model would succeed in obtaining meaningful estimates in this case.” A second limitation of this kind of integrated models (but also true for the two-step models) lies in the specification of the dispersal kernel. By extrapolating on the dispersal events observed inside the study area, we may miss an important part of the dispersal kernel. Long distance dispersal events, for example, will be likely missed in the observed dispersal events despite their recognised importance for population dynamics (Nathan 2005). Hence, the dispersal distribution has to be chosen *a priori* based on the knowledge about dispersal in the species under study but, to our knowledge, no test exists to determine whether the chosen distribution is representative of the true dispersal process. This was also stressed out by the other studies on the same topic: “inferences about true survival will always be model-dependent to some degree” (Ergon & Gardner 2014).

#### 8.4.2. Integrated Multi-Event Dispersal model

Although they share the same general approach, our formulation of the ID model presents several differences with the other integrated models, *i.e.* the Robust-Design Spatial-Capture-Recapture model (RD-SCR: Ergon & Gardner, 2014) and the Spatial Cormack-Jolly-Seber (S-CJS: Schaub & Royle, 2014), making it more suited to the study of natal dispersal. In studies mentioned above, dispersing and non-dispersing individuals were not differentiated and thus shared the same demographic parameters. In practice, this means that the distribution of dispersal distances contains zero values to account for individuals that did not move between two time steps. For this reason, Schaub and Royle used a Normal distribution centred on zero as dispersal kernel. This represents a strong assumption because, given the shape of the Normal distribution, the proportion of non-dispersers (individuals with dispersal distances between -1 and 1 in their model) is related to the distance travelled by dispersers and vice-versa. In other words, the dispersal probability of an individual is made dependent on the distance travelled by other individuals. Ergon & Gardner (2014) circumvented this problem by using zero-inflated distributions for the dispersal kernel. The proportion of non-dispersing individuals (related to the value of the inflation parameter) is then independent of the dispersal distance distribution. However, the dispersal probability of

an individual is not explicitly modelled and the assumption of identical survival between dispersers and non-dispersers holds despite numerous evidence that dispersers are not a random sample of the population (Clobert *et al.* 2009). Dispersers are thus highly likely to possess specific demographic parameters. Here we took these different possibilities into account by modelling natal dispersal as a transition between two states in a multi-event context. Hence, our formulation allows (i) natal dispersal probability to be explicitly modelled and easily related to covariates of interest if needed, and (ii) different survival probabilities to be estimated and compared for subordinates before dispersal, philopatric dominants and dominant individuals that dispersed. The main advantage of our approach is thus its completeness and its flexibility. Any incorporation of age, sex, spatial or any type of individual covariates is straightforward, the number of dispersing individuals (given by the dispersal probability) is estimated independently of the dispersal kernel, and separate demographic parameters can be estimated and compared for dispersers and non-dispersers.

Finally, another advantage resides in the way residency probabilities are calculated. In the models of Schaub & Royle (2014) or Ergon & Gardner (2014), the position of each individual at each time step is modelled and compared one by one with all possible locations in the study area to check if the individual is still inside the study area. Instead, we calculated the residency probability matrix beforehand based on a map of the study area and therefore only needed to model the dispersal distance for each individual, thus drastically load-lightening the model.

#### 8.4.3. *Further developments*

The integrated dispersal model we developed here was constructed to study natal dispersal only with dispersal being limited to a single transition between the subordinate and locally-recruited-breeder state. By comparison, dispersal is allowed between each recapture occasions in Schaub & Royle (2014) and between each primary occasions in Ergon & Gardner (2014). However, our model can be easily modified to incorporate this kind of breeding dispersal. The only modification concerns the state-transition matrix with the addition of two parameters: one allowing for the transition from the *LB* state to the *IB* state indicating the individual dispersed between two successive reproductive events, and a second transition parameter from *IB* to *LB* indicating the individual stayed on the same site between two reproductive events. Such model would be rather complete



for the study of dispersal since it would give access simultaneously to the natal dispersal probability (transition from  $S$  to  $IB$ ), the dispersal probability of previously dispersed individuals (transition from  $IB$  to  $IB$ ), the probability to stay on the same site for a previously dispersed individual (transition from  $IB$  to  $LB$ ), the dispersal probability of an individual that did not move during the previous time step (transition from  $LB$  to  $IB$ ) and the probability to stay on the same site for an individual that did not move during the previous time step (transition from  $LB$  to  $LB$ ).

In addition, the multi-event formulation ensures straightforward incorporation of state uncertainty and/or additional information. It can be easily implemented by modifying the observation process matrix (see Pradel (2005) for an example of state uncertainty and Dupont *et al.* (2015) for the incorporation of additional information about the reproductive state). Our formulation also allowed relaxing both assumptions of homogeneous dispersal direction and homogeneous landscape. It is very easy to incorporate the spatial structure outside the study area such as unsuitable habitat patches or preferred dispersal corridors, in the dispersal estimation. It only requires modifying the map of the study area by specifying different weights for the different territories and then recalculating the residency probabilities:

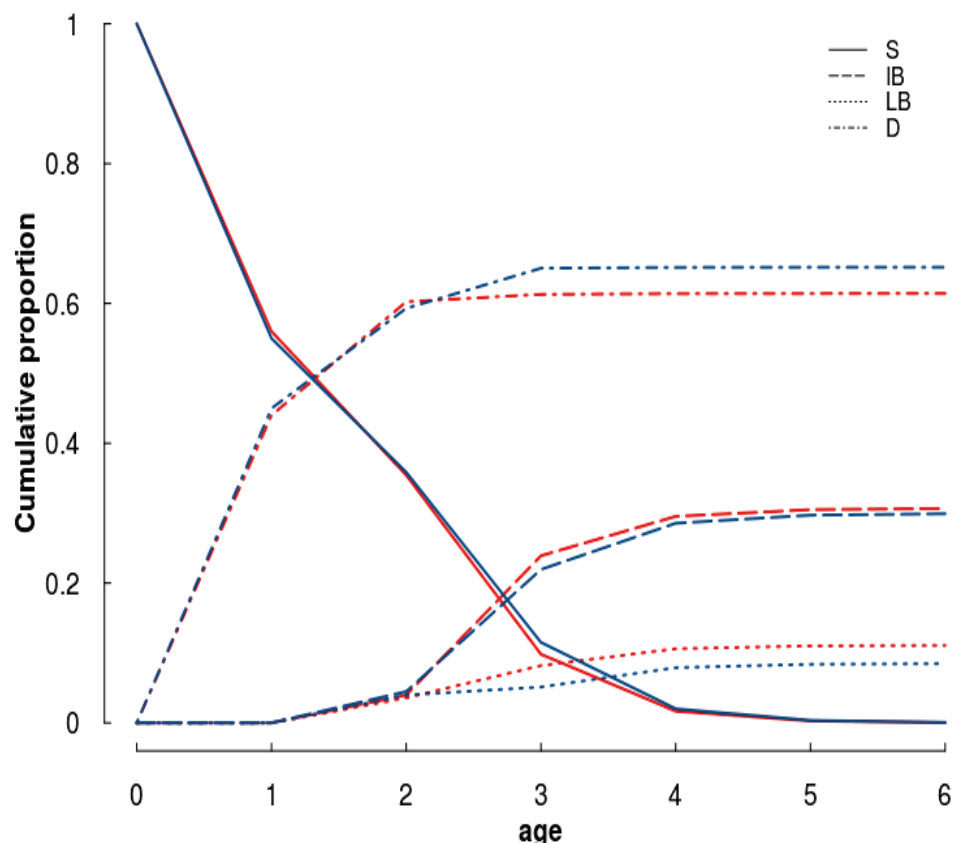
$$r_{s,l} = \frac{\sum_{k=1}^K w_{(k,s,l)}}{W_{s,l}}$$

where  $w_{k,s,l}$  is the weight of the  $k_{ieth}$  site situated inside the study area at a distance  $l$  from site  $s$ ,  $K$  is the total number of sites situated inside the study area at a distance  $l$  from site  $s$ , and  $W_{s,l}$  is the sum of weights of all sites situated at a distance  $l$  from site  $s$ . Attributing unsuitable sites a weight of zero is then equivalent to not consider them as potential settlement territory for a dispersing individual (see supplementary material 8.5.2. for a simulation study of the impact of landscape structure outside the study area on survival and dispersal estimates), and attributing a given site a weight higher than one is equivalent to consider it as favoured over other territories situated at the same distance (e.g. because of the presence of large quantities of food and/or mating opportunities).

#### 8.4.4. Sex-specific dispersal in the Alpine marmot

The application of the ID model to the Grande Sassi re data set revealed the ‘‘true’’ natal dispersal and survival pattern of Alpine marmots. As expected from the results of the simulation study, the estimates of recapture probabilities, juvenile survival and dominant

survival we obtained were consistent with the results of previous studies on the same population that did not take into account emigration outside the study area (e.g. Cohas *et al.* 2009; Dupont *et al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016). By contrast, our results shed light on the natal dispersal and inheritance processes in the Alpine marmot and gave new insights on the survival of subordinate individuals. It appears the low apparent subordinate survival of previous studies (e.g. 0.53 in Dupont *et al.* 2015) is almost entirely due to dispersal outside the study area of two-year individuals (Fig.IV.8).



**Figure IV.9.** Cumulative proportions of subordinate individuals in each state (S: subordinates, IB: immigrant breeders, LB: locally-recruited breeders, D: dead) according to sex (blue: males; red: females) and age as predicted by the integrated dispersal (ID) model.

The annual probability to become dominant was also lower in previous studies (0.45 in Rézouki *et al.* 2016) in spite of the fact that no difference was made between inheritance and dispersal. Our results indicate that the vast majority of subordinate individuals are in fact able to become dominant once they survived their two first winters. In addition, the probability to become dominant did not differ between sexes but we were able to identify a difference in inheritance between two-year males and females,

with females having a probability to inherit the dominant position of their mother more than three times the inheritance probability of males.

Contrary to what is generally reported in the literature for mammals, neither the proportion of dispersers (*i.e.* the age-specific dispersal probability) nor the dispersal pattern (*i.e.* the mean dispersal distance) differed between sexes (Dobson 2013). This absence of sex-specific dispersal pattern is not so surprising for a monogamous and monomorphic mammal such as the Alpine marmot (Lukas & Clutton-Brock 2012). However, this absence of sex-difference in dispersal probability should be considered with caution, given that in the formulation of our model, dispersal probability only reflects successful dispersal, *i.e.* individuals that dispersed *and* became dominant in another territory. Hence, it does not reflect the dispersal “decision”, *i.e.* the probability that an individual leaves its natal territory, independently of the success of this dispersal. This probability cannot be estimated using our model because no information was available about dispersing individuals that failed to become dominant. These unsuccessful dispersers disappeared from the data set and most likely died in the process (Lardy et al. 2011). The difference observed in the proportion of dead males and females (Fig.IV.9) likely reflect this fact, and thus would tend to indicate that a greater number of males leave their natal territory after their second winter compared to females. It would also indicate a lower probability of success and therefore a higher cost of dispersal for males. This alleged male-biased dispersal, although unexpected for a monogamous mammal, might be explained in Alpine marmots by the possibility of extra-pair paternities. In agreement with this hypothesis, Cohas *et al.* (2008) found that most extra-pair paternities in the Grande Sassièrè population were produced due to dispersing individuals (80% of litters containing extra-pair young). Because of this possibility for males to access reproduction through extra-pair copulation even when failing to secure a dominant position, the expected fitness of dispersing males will be higher than that of females. Accordingly, the lower two-year subordinate survival of males may indicate higher levels of competition among males to disperse and access reproduction. Finally, the higher proportion of females inheriting the dominant position from their mother (Fig.IV.9) also supposes female-biased philopatry (and therefore male-biased dispersal) in the Alpine marmot. However, further research on the dispersal decision and costs in this species is needed to confirm these predictions.

To determine whether males truly dispersed more than females would require to take into account the success of the dispersal event for each individual, *i.e.* disentangle “natural mortality” from “dispersal related mortality”. Such model would require additional information about the state of individuals during dispersal (*e.g.* a robust-design framework where mortality between primary occasions would refer to “natural survival” while mortality within primary occasions would refer to “dispersal related mortality”) or about the fate of individuals (*e.g.* spatial dead-recovery data where the dispersal status of individuals could be confirmed when individuals are found dead away from their natal territory). In the absence of such data, a last possibility, inspired by the work of Barthold *et al.* (2016) would be to assess the dispersal-related mortality by making the assumption that subordinate and dominant individuals follow the same age-related survival pattern. Constraining subordinate survival this way would allow the dispersal-based mortality to be estimated as the difference between the observed mortality (as in our model) and the “natural mortality” (as constrained by the age-related pattern).

In the end, the integrated multi-event dispersal model we presented here is a new step towards a more complete (and less biased) assessment of dispersal and its drivers for which biologists of many fields have a great interest. As all models, it presents some limitations, but, with a clear understanding of its limitations in mind, it allows to considerably increase the knowledge about the central phenomenon in population biology that is dispersal, and opens new research and development areas.



## 8.5. Supplementary material

### 8.5.1. Dispersal models & Simulation scripts

#### 8.5.1.1. Dispersal models BUGS scripts

```
#####  
## Apparent Dispersal model ##  
#####  
sink("AD.bug")  
cat("  
model  
{  
# Priors and constraints  
for (i in 1:nind)  
  {  
    for (t in f[i]:(n.occ-1))  
      {  
        phiS[i,t] <- mean.phiS  
        phiB[i,t] <- mean.phiB  
        d[i,t] <- mean.d  
        h[i,t] <- mean.h  
        pS[i,t] <- mean.pS  
        pB[i,t] <- mean.pB  
      }  
    }  
mean.phiS ~ dunif(0,1)  
mean.phiB ~ dunif(0,1)  
mean.d ~ dunif(0,1)  
mean.h ~ dunif(0,1)  
mean.pS ~ dunif(0,1)  
mean.pB ~ dunif(0,1)  
  
# Define state-transition and observation matrices  
for (i in 1:nind)  
  {  
    for (t in f[i]:(n.occ-1))  
      {  
        # Define probabilities of state S(t+1) given S(t)  
        ps[1,i,t,1] <- phiS[i,t] * (1-d[i,t]) * (1-h[i,t])  
        ps[1,i,t,2] <- phiS[i,t] * (1-d[i,t]) * h[i,t]  
        ps[1,i,t,3] <- phiS[i,t] * d[i,t]  
        ps[1,i,t,4] <- 1-phiS[i,t]  
        ps[2,i,t,1] <- 0  
        ps[2,i,t,2] <- phiB[i,t]  
        ps[2,i,t,3] <- 0  
        ps[2,i,t,4] <- (1-phiB[i,t])  
        ps[3,i,t,1] <- 0
```

```

        ps[3,i,t,2] <- 0
        ps[3,i,t,3] <- phiB[i,t]
        ps[3,i,t,4] <- (1-phiB[i,t])
        ps[4,i,t,1] <- 0
        ps[4,i,t,2] <- 0
        ps[4,i,t,3] <- 0
        ps[4,i,t,4] <- 1

        # Define probabilities of O(t) given S(t)
        po[1,i,t,1] <- pS[i,t]
        po[1,i,t,2] <- 0
        po[1,i,t,3] <- 0
        po[1,i,t,4] <- 1-pS[i,t]
        po[2,i,t,1] <- 0
        po[2,i,t,2] <- pB[i,t]
        po[2,i,t,3] <- 0
        po[2,i,t,4] <- 1-pB[i,t]
        po[3,i,t,1] <- 0
        po[3,i,t,2] <- 0
        po[3,i,t,3] <- pB[i,t]
        po[3,i,t,4] <- 1-pB[i,t]
        po[4,i,t,1] <- 0
        po[4,i,t,2] <- 0
        po[4,i,t,3] <- 0
        po[4,i,t,4] <- 1
    }
}
# Likelihood
for (i in 1:nind)
{
    z[i,f[i]] ~ dcat(y[i,f[i]])
    for (t in (f[i]+1):n.occ)
    {
        z[i,t] ~ dcat(ps[z[i,t-1], i, t-1, ])
        y[i,t] ~ dcat(po[z[i,t], i, t-1, ])
    }
}
},fill = TRUE)
sink()

#####
#####
##    Two-step Dispersal model    ##
#####
sink("TD.bug")
cat("

```

```

model
{
# Priors and constraints
for (i in 1:nind){
  dist[i] ~ dcat(L[])    ## L: vector of observed dispersal distances frequencies
  D[i] <- step(dmax-dist[i])+1
  DIST[i,1] <- dmax
  DIST[i,2] <- dist[i]
  for (t in f[i]:(n.occ-1)) {
    phiS[i,t] <- mean.phiS
    phiB[i,t] <- mean.phiB
    d[i,t] <- mean.d
    h[i,t] <- mean.h
    pS[i,t] <- mean.pS
    pB[i,t] <- mean.pB
    r[i,t] <- prob.mat[site[i],DIST[i,D[i]]]
  }
}
mean.phiS ~ dunif(0,1)
mean.phiB ~ dunif(0,1)
mean.d ~ dunif(0,1)
mean.h ~ dunif(0,1)
mean.pS ~ dunif(0,1)
mean.pB ~ dunif(0,1)

# Define state-transition and observation matrices
for (i in 1:nind)
{
  for (t in f[i]:(n.occ-1))
  {
    # Define probabilities of state S(t+1) given S(t)
    ps[1,i,t,1] <- phiS[i,t] * (1-d[i,t]) * (1-h[i,t])
    ps[1,i,t,2] <- phiS[i,t] * (1-d[i,t]) * h[i,t]
    ps[1,i,t,3] <- phiS[i,t] * d[i,t] * r[i,t]
    ps[1,i,t,4] <- 1-phiS[i,t] + phiS[i,t] * d[i,t] * (1-r[i,t])
    ps[2,i,t,1] <- 0
    ps[2,i,t,2] <- phiB[i,t]
    ps[2,i,t,3] <- 0
    ps[2,i,t,4] <- (1-phiB[i,t])
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- phiB[i,t]
    ps[3,i,t,4] <- (1-phiB[i,t])
    ps[4,i,t,1] <- 0
    ps[4,i,t,2] <- 0
    ps[4,i,t,3] <- 0
    ps[4,i,t,4] <- 1
  }
}

```



```

# Define probabilities of O(t) given S(t)
po[1,i,t,1] <- pS[i,t]
po[1,i,t,2] <- 0
po[1,i,t,3] <- 0
po[1,i,t,4] <- 1-pS[i,t]
po[2,i,t,1] <- 0
po[2,i,t,2] <- pB[i,t]
po[2,i,t,3] <- 0
po[2,i,t,4] <- 1-pB[i,t]
po[3,i,t,1] <- 0
po[3,i,t,2] <- 0
po[3,i,t,3] <- pB[i,t]
po[3,i,t,4] <- 1-pB[i,t]
po[4,i,t,1] <- 0
po[4,i,t,2] <- 0
po[4,i,t,3] <- 0
po[4,i,t,4] <- 1
}
}
# Likelihood
for (i in 1:nind)
{
z[i,f[i]] ~ dcat(y[i,f[i]])
for (t in (f[i]+1):n.occ)
{
z[i,t] ~ dcat(ps[z[i,t-1], i, t-1, ])
y[i,t] ~ dcat(po[z[i,t], i, t-1, ])
}
}
}
",fill = TRUE)
sink()
#####
#####
##    Integrated Dispersal model    ##
#####
sink("ID.bug")
cat("
model
{
# Priors and constraints
for (i in 1:nind)
{
dist[i] ~ dpois(tau)
DD[i] <- step(dmax-(dist[i]+1))
D[i] <- DD[i]+1

```

```

DIST[i,1] <- dmax
DIST[i,2] <- dist[i]+1
for (t in f[i]:(n.occ-1))
  {
    phiS[i,t] <- mean.phiS
    phiB[i,t] <- mean.phiB
    d[i,t] <- mean.d
    h[i,t] <- mean.h
    pS[i,t] <- mean.pS
    pB[i,t] <- mean.pB
    r[i,t] <- prob.mat[site[i],DIST[i,D[i]]]
  }
}
mean.phiS ~ dunif(0,1)
mean.phiB ~ dunif(0,1)
mean.d ~ dunif(0,1)
mean.h ~ dunif(0,1)
mean.pS ~ dunif(0,1)
mean.pB ~ dunif(0,1)
tau ~ dgamma(0.01,0.01)|(0.00001,100)

# Define state-transition and observation matrices
for (i in 1:nind)
  {
    for (t in f[i]:(n.occ-1))
      {
        # Define probabilities of state S(t+1) given S(t)
        ps[1,i,t,1] <- phiS[i,t] * (1-d[i,t]) * (1-h[i,t])
        ps[1,i,t,2] <- phiS[i,t] * (1-d[i,t]) * h[i,t]
        ps[1,i,t,3] <- phiS[i,t] * d[i,t] * r[i,t]
        ps[1,i,t,4] <- 1-phiS[i,t] + phiS[i,t]*d[i,t]*(1-r[i,t])
        ps[2,i,t,1] <- 0
        ps[2,i,t,2] <- phiB[i,t]
        ps[2,i,t,3] <- 0
        ps[2,i,t,4] <- (1-phiB[i,t])
        ps[3,i,t,1] <- 0
        ps[3,i,t,2] <- 0
        ps[3,i,t,3] <- phiB[i,t]
        ps[3,i,t,4] <- (1-phiB[i,t])
        ps[4,i,t,1] <- 0
        ps[4,i,t,2] <- 0
        ps[4,i,t,3] <- 0
        ps[4,i,t,4] <- 1

        # Define probabilities of O(t) given S(t)
        po[1,i,t,1] <- pS[i,t]
        po[1,i,t,2] <- 0

```

```

        po[1,i,t,3] <- 0
        po[1,i,t,4] <- 1-pS[i,t]
        po[2,i,t,1] <- 0
        po[2,i,t,2] <- pB[i,t]
        po[2,i,t,3] <- 0
        po[2,i,t,4] <- 1-pB[i,t]
        po[3,i,t,1] <- 0
        po[3,i,t,2] <- 0
        po[3,i,t,3] <- pB[i,t]
        po[3,i,t,4] <- 1-pB[i,t]
        po[4,i,t,1] <- 0
        po[4,i,t,2] <- 0
        po[4,i,t,3] <- 0
        po[4,i,t,4] <- 1
    }
}

# Likelihood
for (i in 1:nind)
{
  z[i,f[i]] ~ dcat(y[i,f[i]])
  for (t in (f[i]+1):n.occ)
  {
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1, ])
    y[i,t] ~ dcat(po[z[i,t], i, t-1, ])
  }
}
},fill = TRUE)
sink()
#####

```

### 8.5.1.2. Residency probability matrix generation function

```
n.site <- 35                ## Number of territories
x <- 6                    ## Width of the study area
y <- 10                   ## Length of the study area
pos <- sample(x*y,n.site,replace=F) ## Random sample of territories coordinates
pos <- pos[sort.list(pos)]
SA <- matrix(0,x,y)
SA[pos] <- 1:n.site       ## Map of the study area

## Create study area and residence proba matrix
P.DIST <- function(SA)
{
  SA[is.na(SA)==T] <- 0
  S <- max(SA)            ## Number of territories on the map
  Dmax <- max(dim(SA))   ## Maximum length of the study area
  ## Create an enlarged map with Dmax territories on each side of the study area
  pos <- as.data.frame(which(SA != 0, arr.ind = TRUE))
  X <- pos[,1]+Dmax+1
  Y <- pos[,2]+Dmax+1
  grid.mat <- matrix(0,max(X)+Dmax+1,max(Y)+Dmax+1)
  for (i in 1:S)
  {
    grid.mat[X[i],Y[i]] <- i
  }
  ## Create the residence probabilities matrix
  prob.mat <- matrix(NA, S, Dmax)
  n <- 8*(1:Dmax)
  for (s in 1:S)
  {
    for (d in 1:Dmax)
    {
      Xmax <- which(grid.mat[X[s]+d,(Y[s]-d):(Y[s]+d-1)]!= 0)
      Xmin <- which(grid.mat[X[s]-d,(Y[s]-d+1):(Y[s]+d)]!= 0)
      Ymax <- which(grid.mat[(X[s]-d+1):(X[s]+d),Y[s]+d]!= 0)
      Ymin <- which(grid.mat[(X[s]-d):(X[s]+d-1),Y[s]-d]!= 0)
      around <-c(Xmax,Xmin,Ymax,Ymin)
      prob.mat[s,d] <- length(around)/n[d]
    }
  }
  return(prob.mat)
}
prob.mat <- P.DIST(SA)
#####
```

### 8.5.1.3. Data simulation script

```
# General parameters
n.occ <- 20                ## Number of capture occasions
n.states <- 4              ## Number of states
n.obs <- 4                 ## Number of events (observable states)
marked <- rep(40, n.occ-1) ## Marked individuals at each occasion
n <- sum(marked)           ## Total number of individuals
f <- rep(1:length(marked),marked) ## Vector of first capture occasions

#CR parameters
phiS <- 0.85              ## Non-breeder survival
phiB <- 0.95              ## Breeder survival
h <- 0.12                 ## Inheritance probability
d <- 0.4                  ## Dispersal probability
pS <- 0.90                ## Non-breeder recapture probability
pD <- 0.65                ## Breeder recapture probability

#Dispersal parameters
tau <- 2                  ## Mean dispersal distance
D <- r <- rep(NA,1)
for (i in 1:n)
  {
    D[i] <- rpois(1,tau)+1 ## Individual dispersal distance
    r[i] <- ifelse(D[i]<= dim(prob.mat)[2],prob.mat[site[i],D[i]],0)
    ## Associated individual residence probability
  }

# 1. State process matrix
PSI.STATE <- array(NA, dim=c(n.states, n.states, n, n.occ-1))
for (i in 1:n)
  {
    for (t in 1:(n.occ-1))
      {
        PSI.STATE[ , ,i,t] <- matrix(c(
          phiS*(1-d)*(1-h), phiS*(1-d)*h , phiS*d*r[i] , 1-phiS+phiS*d*(1-r[i]) ,
          0 , phiD , 0 , 1-phiD ,
          0 , 0 , phiD , 1-phiD ,
          0 , 0 , 0 , 1
        ), nrow = n.states, byrow = TRUE)
      }
  }

# 2.Observation process matrix
PSI.OBSERV <- array(NA, dim=c(n.states, n.obs, n, n.occ-1))
for (i in 1:n)
  {
```

```

    for (t in 1:(n.occ-1))
    {
      PSI.OBSERV[ , ,i,t] <- matrix(c(
        pS, 0 , 0 , (1-pS),
        0 , pD , 0 , (1-pD),
        0 , 0 , pD , (1-pD),
        0 , 0 , 0 , 1
      ), nrow = n.states, byrow = TRUE)
    }
  }

## Simulation function
simul.disp.me <- function(PSI.STATE, PSI.OBS, marked, prob.mat, site)
{
  n.occ <- dim(PSI.STATE)[4] + 1
  n <- sum(marked)
  f <- rep(1:length(marked),marked)
  CH <- CH.TRUE <- matrix(NA, ncol = n.occ, nrow = n)
  for (i in 1:n)
  {
    # Initial state
    CH[i,f[i]] <- CH.TRUE[i,f[i]] <- 1
    for (t in (f[i]+1):n.occ)
    {
      if (f[i]== n.occ) next
      state <- which(rmultinom(1, 1, PSI.STATE[CH.TRUE[i,t-1],,i,t-1])==1)
      CH.TRUE[i,t] <- state
      event <- which(rmultinom(1, 1, PSI.OBS[CH.TRUE[i,t],,i,t-1])==1)
      CH[i,t] <- event
    }
  }
  CH[is.na(CH)] <- dim(PSI.OBS)[2]
  Dprim <- rep(NA,n)
  Dprim[which(CH==3,arr.ind=TRUE)[,1]] <- D[which(CH==3,arr.ind=TRUE)[,1]]
  return(list(CH=CH, CH.TRUE=CH.TRUE,site = site, f=f, D=Dprim, e=e))
  # CH: capture histories to be used
  # CH.TRUE: capture histories with perfect detection
  # site: birth site
  # D: vector of known dispersal distances
  # r: vector of individual residence probabilities
  # f: vector of first capture occasions
}
#####

```

## 8.5.2. Landscape heterogeneity analysis

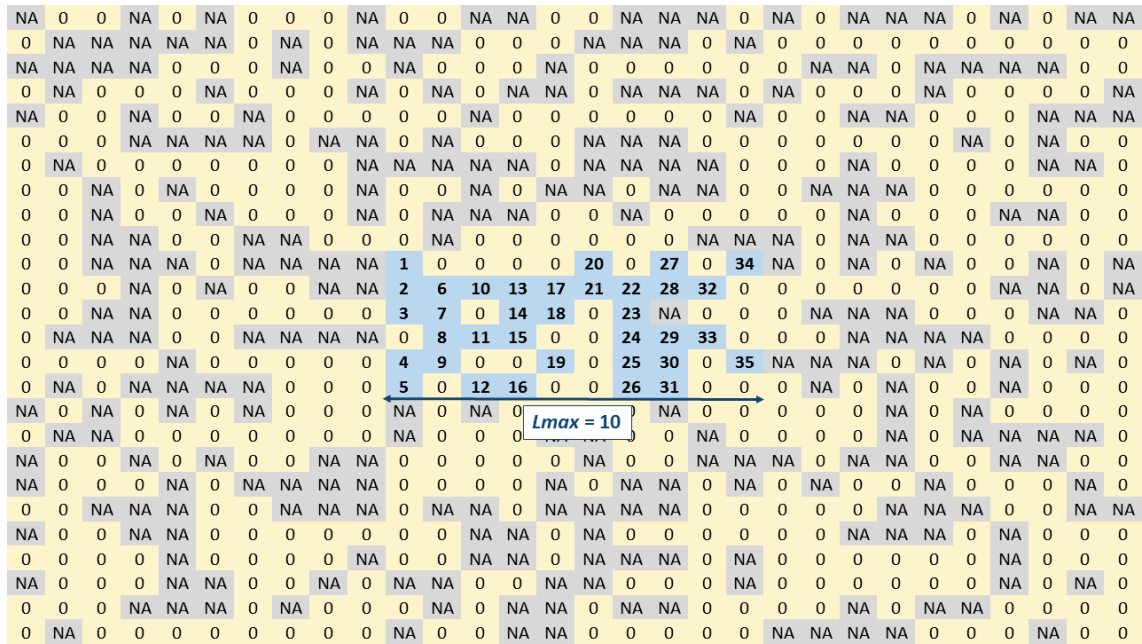
### 8.5.2.1. Simulation study

We performed this additional analysis to determine the consequences of ignoring the landscape structure when using the Integrated Dispersal model (ID). Indeed, if the landscape is heterogeneous outside the study area, with certain patches of habitat unsuitable for the organism under study, this will impact the residency probabilities of dispersers and consequently the estimation of the other demographic parameters when compared to a homogeneous landscape. However, to what degree these demographic parameters will be impacted is not clear. To answer this question, we simulated and analysed with the ID model different data sets with varying landscape structures.

The landscape for each simulation was constructed in two steps. First, we constructed a study area by randomly sampling 35 cells in a  $10 \times 6$  grid. Because any individual dispersing further than the largest distance inside the study area ( $l_{max}$ ) will never be recaptured, residency probabilities need not be calculated for distances larger than  $l_{max}$ . Thus, calculating the different residency probabilities only requires knowledge of the landscape in a radius of  $l_{max}$  around the study area. The second step of the landscape simulation therefore consisted in creating an enlarged grid map with  $l_{max}$  territories added on each side of the study area. We thus obtained a grid map of dimensions  $30 \times 26$  cells centred on the territories composing the study area (Fig IV.10.). Territories outside the study area were then randomly assigned as suitable or unsuitable following the proportion of unsuitable habitat to be tested. The residency probability matrix was constructed based on the simulated landscape, and filled with  $r_{si,li}$

$$r_{si,li} = \frac{n_{si,li}}{N_{si,li}}$$

where  $n_{si,li}$  is the number of territories inside the study area situated at a distance  $l_i$  from territory  $s_i$  and  $N_{si,li}$  is the total number of suitable habitat territories situated at a distance  $l_i$  from territory  $s_i$ . Each individual was randomly attributed one of the territories inside the study area as its natal territory. The individual dispersal distance was then sampled from a Poisson distribution. We fixed the mean of the Poisson distribution to one because we know from previous simulations (simulation study above) that the ID model performs well for such mean dispersal distance. Finally, given its natal territory and individual dispersal distance, each individual was assigned a residency probability  $r_{si,li}$  from the residency probability matrix.



**Figure IV.10.** Example of a randomly generated study area map as used in the simulation study. The study area is represented by the light blue area. Each number represents a territory where trapping occurs. Yellow area represents suitable habitat patches outside the study area and grey area represents unsuitable territories.

All other parameters of the simulation were fixed, with values close to those obtained by previous studies on Alpine marmots (Dupont *et al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016). Breeders survival was set to  $\Phi^{IB} = \Phi^{LB} = 0.95$  and subordinate survival to  $\Phi^S = 0.85$ . Recapture probabilities differed between dominants and subordinates ( $p^{IB} = p^{LB} = 0.65$  and  $p^S = 0.95$ ). Dispersal probability was set to  $d = 0.4$  and inheritance probability to  $h = 0.12$ .

The capture histories were constructed by sampling the individual underlying state and observed event at each time capture occasion in the corresponding state-transition and observation process matrix of the ID model. The location of the natal territory was kept for all individuals but dispersal distances were kept only for individuals that did not disperse outside the study area to mimic true capture-recapture data. Each simulated data set consisted of 20 capture occasions with 40 individuals marked at each occasion (except for the last one), leading to a total of 760 capture histories per data set.

We simulated data sets with increasing proportion of unsuitable habitat outside the study area ( $P$ ) from 0 to 0.9 with steps 0.1. The simulation process was repeated 100 times for each value of  $P$ , leading to a total of 1000 simulated data sets. We then fitted two different models to each data set, one with the true residency probability matrix as

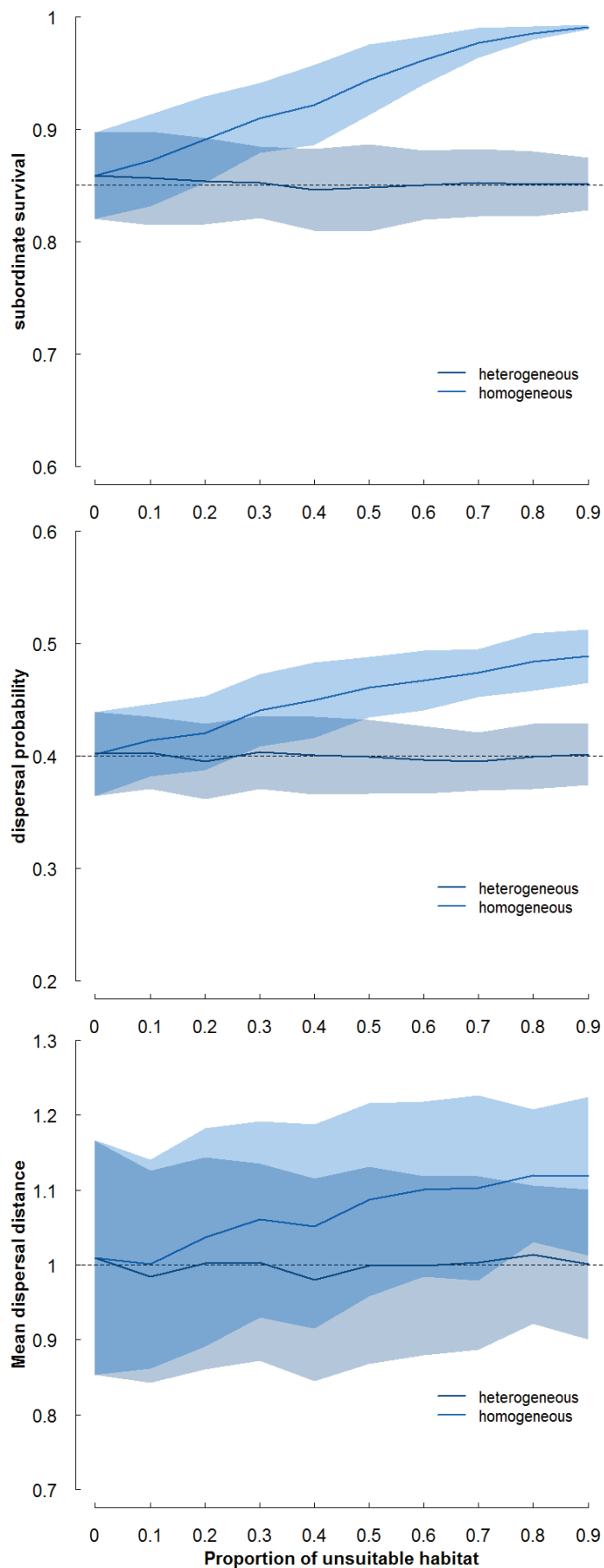


generated in the simulation process (the heterogeneity model) and one with the residency probability matrix ignoring the heterogeneity of the habitat (*i.e.* with all territories outside the study area considered as suitable: the homogeneity model). All models were fitted using Markov Chain Monte Carlo (MCMC) simulations with the computer program JAGS (Plummer 2003) through R3.2.5 (R core team 2016) with the R package jagsUI (Kellner 2014). Three chains were run independently for 10000 iterations with a burning period of 6000 iterations and a thinning rate of 1.

#### 8.5.1.2. Results

The posterior means  $\pm$  se of the different recapture, dominant survival and inheritance probabilities were identical and equal to the simulated values for both models and for all values of  $P$  (heterogeneous model:  $p^S = 0.95 \pm 0.01$ ;  $p^{IB} = p^{LB} = 0.65 \pm 0.02$ ;  $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.02$ ;  $h = 0.12 \pm 0.01$  and homogeneous model:  $p^S = 0.95 \pm 0.01$ ;  $p^{IB} = p^{LB} = 0.65 \pm 0.02$ ;  $\Phi^{IB} = \Phi^{LB} = 0.95 \pm 0.01$ ;  $h = 0.12 \pm 0.02$ ). As expected, the amount of unsuitable habitat outside the study area impacted both the subordinate survival and dispersal estimates but also the mean dispersal distance (Fig.IV.11). Because the number of territories available for settlement were over-estimated when the landscape was supposed homogeneous, the residency probabilities were artificially under-estimated and survival, dispersal and mean dispersal distance were in turn over-estimated. Subordinate survival was over-estimated by as much as 18% of the simulated value when a large part of the landscape outside the study area was unsuitable. This bias was up to 25% for the dispersal probability and much lower with only 10% for the mean dispersal distance. It is to be noticed that the lower bias observed in the mean dispersal distance was associated to a large variance of the estimate. In addition, the standard error of the mean seems to slightly decreased when the proportion of unsuitable habitat increases, and that both for the homogeneous and heterogeneous models.

These results demonstrate the importance of taking into account the structure of the landscape outside the study area when using spatial capture-recapture models. Indeed, if the landscape structure is unknown and homogeneity is supposed, the estimates returned by such models will be over-estimations of the true demographic parameters. This can have important consequences, especially in studies with population management purposes where misestimating dispersal or survival probabilities can lead to deleterious management decisions being taken.



**Figure IV.11.** Subordinate survival (upper panel), dispersal (middle panel) and mean dispersal distance (lower panel) for increasing proportions of unsuitable habitat outside the study area returned by the Integrated Survival model under the assumption of homogeneous (light blue) and heterogeneous (dark blue) landscapes. Shaded areas represent the associated standard error of the mean.

Although these models are very efficient and allow to estimate otherwise unattainable estimates of true survival and dispersal parameters, which are of primary importance for a large range of studies in evolution and population dynamics, they rely on strong assumptions concerning both the shape of the dispersal kernel (*e.g.* in Gilroy *et al.* 2012; Ergon & Gardner 2014 or Schaub & Royle 2014) and the structure of the landscape outside the study area (this study). The limitations imposed by the shape of the dispersal kernel might be severely reduced, if not suppressed when the study area is large enough to observe a large number of dispersal events but the structure of the landscape obligatory requires additional information collected outside the study area. As a conclusion, although we highly encourage the use of integrated models because of their accuracy and ability to return true demographic parameters, we also recommend to be very cautious when using such models. In particular, we advise users to fully acknowledge the information available in their data sets and therefore the underlying assumptions and limitations of their model.





# Chapter IV.B

## Sociality & Dispersal

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### Dominance change and group dynamics in the cooperatively breeding Alpine marmot

**Abstract:** In cooperatively breeding species, individual demographic rates result from the balance between costs and benefits in terms of fitness for the different group members according to their age, sex and social status, but also according to the composition of the group they live in. The characteristics of the group (*i.e.* group size and sex composition) are thus expected to strongly influence the group dynamics in such species. But the group dynamics may also arise from the interaction of social groups among them inside the population. However, to date, very few studies looked at the influence of dispersal between social groups on both individual demographic rates and resulting group dynamics.

In this chapter, I used the Integrated Multi-Event Dispersal model developed earlier to study the consequences of immigration into the family group by a new dominant on survival, dispersal and reproduction and inferred the consequences of such changes for the group dynamics.

I found that both survival and dispersal of subordinate individuals were strongly impacted by the arrival of an un-related dominant into the family group. Specifically, immigration of a new dominant led to the majority of same-sex subordinates leaving the group, resulting in a strong decrease in group size and a strong modification of the group sex-composition. This crash in the group dynamic is likely to result also from the suppression of reproduction following the arrival of a new dominant but our model failed to detect such effect.

I conclude by discussing the potential implications of such group dynamics pattern for the overall population dynamics and the different limits of the approach, as well as future developments.

**Keywords:** Cooperative breeder · Capture-Mark-Recapture · Dispersal · Integrated Population Models · Social dominance ·

*(Preliminary results)*



## 9.1. Introduction

Nowadays, the paradigm in population dynamics states that the patterns observed at the population level arise from the combination of individuals' capacity to survive, disperse and reproduce (Sutherland 1996). To understand the mechanisms responsible for the overall population dynamics, one should therefore work at the individual level to identify the factors responsible for the variation in individuals' demographic rates and characterize the ways in which they affect these rates (Benton *et al.* 2006).

In social, group-living species, population dynamics is expected to differ from this framework. In these species, population is often highly structured in age and sex classes but also in hierarchical states due to dominance relationships (Bateman *et al.* 2013). In addition, individuals interact preferentially with some conspecifics rather than others according to the associated fitness gain they can expect, thus leading to the formation of distinct social groups in the population (Trivers 1985). The resulting imbalance between interactions among group members and interactions between members of different groups will lead social groups to display dynamics of their own. Presented in such a manner, group-living species dynamics is very much alike metapopulations dynamics (Hanski & Gilpin 1991). In group-living animals, population dynamics therefore cannot be inferred solely from the combination of individual demographic rates because of the intermediate level of structuration in the population, *i.e.* the group level. Instead, as in metapopulations, the combination of individual vital rates will be responsible mainly for the social group/local population dynamics and the overall population dynamics will emerge from the combination of the different social groups/local populations dynamics. Thus, to understand the population dynamics of group living species, one must (i) understand the factors affecting the group dynamics and (ii) understand how groups interact to produce the overall dynamic (Bateman 2013).

Most research on social species until now focused on the evolution of the different social systems. Extensive bibliography is therefore available on the relative fitness costs and benefits of group living (*e.g.* McGuire *et al.* 2002; Covas *et al.* 2006; Silk 2007; Armitage 2014). These costs/benefits were most of the time expressed in terms of survival, reproduction and, to a lesser extent, dispersal of individuals, and related to the size and/or composition of social groups, sometimes in interactions with other drivers of population dynamics (*e.g.* climate: Rézouki *et al.* 2016; predation:



Marino 2010). For example, Covas *et al.* (2008) found that reproductive performance in the cooperatively breeding sociable weavers (*Philetairus socius*) depended mostly on nests predation and rainfall, but that the negative effect of rainfall was lowered by a social factor, *i.e.* the presence of non-reproductive helpers. Although these studies did not specifically use a population dynamics approach, their results are very relevant to the question of group dynamics since they quantified the influence of different social factors on individual vital rates (although not considered as such but rather as fitness components). Among the exceptions, we can cite the study by Bateman *et al.* (2012) on the influence of group size on the social group dynamics in meerkats (*Suricata suricatta*). In this paper, they explicitly tackled the question of density-dependence in social group dynamics and found that group growth rate decreased with increasing group size especially after years of low rainfall.

By contrast, interactions between social groups were largely overlooked. These interactions between groups, mediated through dispersal, are nevertheless likely to have important effects on the group dynamics and ultimately on the population dynamics, as exemplified by studies on metapopulations that highlighted the importance of the connectivity between local populations, and the importance of emigration (dispersal decision) and immigration (settlement after dispersal) in these processes (Hanski 1991). While most studies on dispersal in social species were interested in revealing factors affecting the decision to leave the group and eventually their impact on the group dynamics (*e.g.* Armitage *et al.* 2011; Bateman *et al.* 2013; McGuire *et al.* 2013), the consequences of immigration of new individuals into a social group are still poorly understood.

Here, we try to fill this gap by looking at the consequences of immigration into a social group on individual demographic rates in the Alpine marmot (*Marmota marmota*). Alpine marmots are cooperative breeders living in family groups where the reproduction is monopolized by a couple of dominant individuals. Subordinate individuals, and particularly male subordinates, are considered as helpers because of their role in increasing survival of younger relatives during hibernation (Arnold 1988; Allainé & Theuriau 2004). Alpine marmots provide an excellent model to investigate this question: (i) groups are highly territorial and do not overlap allowing movements between groups to be easily determined, (ii) immigration in a social group in this species is limited to the immigrant taking over the dominant position thus entailing potentially important

consequences and (iii) a detailed long-term individual based dataset is available for this species. Based on this data set, we constructed an integrated multi-event dispersal model to test for the consequences of a new dominant arrival on survival, dispersal and reproduction in Alpine marmots' social groups. Two alternative (but not exclusive) scenarios may be considered: (i) because the new dominant (hereafter the immigrant) is most likely un-related to other group members, relatedness between subordinate individuals of the group and subsequent offspring will be lowered. Following kin selection theory (Hamilton 1964a,b), the inclusive fitness benefits of subordinates obtained through the increased survival of the dominant's offspring will also be lowered (divided by two). This will increase the likelihood that subordinates, and especially males, the helping sex, are more inclined to disperse rather than helping half-sibs, and then try to maximize their direct fitness by reaching a dominant position on their own. Under this scenario, we expect dispersal probabilities of subordinates of both sexes to increase following the arrival of an immigrant. We also expect subordinate males to be more prone to dispersal because of the higher cost of helping they endure during hibernation (Arnold 1988); (ii) because of intra-sexual competition, the presence of same-sex subordinates has been shown to be costly for dominant individuals. Dominance tenure, for example, decreases when the number of same-sex subordinates increases (Lardy *et al.* 2012a, 2013) and the risk of losing paternities to extra-pair copulations increases in the same time for dominant individuals (Cohas *et al.* 2006; Lardy *et al.* 2012a). The immigrant dominant is thus expected to expel same-sex individuals out of the group in order to maximize its dominance tenure, its reproduction and ultimately its fitness. In such case, a higher dispersal probability should be detected for subordinate individuals but only of the same-sex that the immigrant dominant. In addition, replacement of one of the dominant in Alpine marmots is associated to an absence of reproduction that year, due to infanticide (Lardy *et al.* 2011). Thus, we expect reproduction probability to be much lower following the arrival of an immigrant dominant for both sexes.

## **9.2. Material and methods**

### *9.2.1. Alpine marmots, dispersal & dominance change*

The Alpine marmot is a socially monogamous and territorial mammal living in family groups composed of up to 20 individuals. Each family group is composed of a dominant

couple, adult subordinates (age > 2), yearlings and pups born that year (Allainé 2000a). In each family, reproduction is monopolized by the dominant couple but some subordinate males may access reproduction via extra-pair copulation (Hackländer *et al.* 2003; Cohas *et al.* 2006). Offspring produced by the dominant couple stay on their natal territory at least until sexual maturity at two years of age. From this age, natal dispersal occurs in both sexes. Dispersal rate increases until the age of three when around 58 % of subordinates of both sexes reach a dominant position by dispersing to a neighbouring territory (mean dispersal distance = 1.7 territories ; chapter IV.A). Dispersers can secure a dominant position either by immigrating in an existing family group and evicting the same-sex dominant or by creating a new territory. However, the latter is quite rare in the saturated population under study (only 5 territory creations in 25 years). Once a subordinate “decided” to disperse, it cannot come back to its natal territory nor being accepted as a subordinate in another family group. Thus, in case of failure, it becomes a floater, *i.e.* a wandering individual forced to hibernate alone and thus being exposed to a very high risk of mortality (Magnolon 1999). Subordinates that delayed dispersal can also become dominant by inheriting the position in their natal territory after the death of the same-sex dominant (32 % of three year-old females *vs.* 9 % of three year-old males). Once the dominant position secured, an Alpine marmot stays dominant until death or eviction by a new incomer. Dispersal in the Alpine marmot is therefore exclusively natal dispersal. When evicted, the dominant individual becomes a floater and is thus subject to a very high risk of mortality too (Grimm *et al.* 2003b).

### 9.2.2. Study site and data collection

The data set was composed of 1270 individuals captured in the Alpine marmot population located in the Grande Sassièrè nature reserve (2340 m a.s.l., French Alps, 45°29'N, 6°59'E) between 1990 and 2015. Marmots from up to 34 territories were monitored, from mid-May to mid-July each year, using both a capture–recapture protocol and behavioural observations. Because Alpine marmots are highly territorial, the main burrows of each family group are easily determined by observation. Traps were placed near the entrance of these burrows so that all individuals captured at a given trap are automatically assigned to their family group. All pups were captured by hand and marked at weaning *i.e.* at their first emergence from the burrows, approximately 40 days after their birth. Captured animals were tranquillized with Zoléttil 100 and marked with a

transponder (Trovan™, Germany) and a numbered ear tag. At each capture, marmots were aged from their size in four age classes (pups, yearlings, two-years and adults), sexed and their social status was determined according to scrotal development for males and teats development for females (Hackländer & Arnold 1999; Hackländer *et al.* 2003). The exact size and composition (sex and age class) of all family groups was assessed by behavioural observations. Notably, scent-marking behaviour was used to confirm the identity of the dominant pair (Bel *et al.* 1995). This allowed us to determine when a new individual (the immigrant) managed to evict one of the dominants (the resident). Hair and blood samples collected at capture allowed for kinship analyses (details on the different genetic analyses can be found elsewhere; Cohan *et al.* 2006; Ferrandiz-Rovira 2015). Based on these kinship analyses, parents of all pups captured at weaning could be identified, determining which individuals successfully reproduced each year.

### 9.2.3. *The Alpine marmot integrated model*

We used an integrated multi-event model designed to analyse the influence of the replacement of a dominant by an immigrating individual on the vital rates of social group members in Alpine marmots. Our integrated model is composed of two sub-models combined through the construction of a joint likelihood (Schaub & Abadi 2011). The integration of both sub-models allows the estimation of demographic parameters otherwise unidentifiable. Here, we were able to account for emigration outside the study area and therefore estimate true survival and dispersal probabilities instead of apparent estimates (see chapter IV.A) The first component models dispersal distance travelled by an individual during dispersal and the second component is a multi-event capture-recapture model (Pradel 2005) designed to fit the Alpine marmot's life cycle.

*The dispersal model.* This component models the movement realized by an individual Alpine marmot when dispersing. Since we considered dispersal to be equally likely in any direction, we only needed to model the distance travelled during dispersal. Dispersal distance in the Alpine marmot is measured as the number of territories in straight lines between the natal and settlement territories. Because of the discrete nature of the measure, we used a Poisson distribution to describe it. The dispersal distance of an individual ( $l_i$ ) was then simply a random realization of a Poisson process (plus one because this is the minimal dispersal distance possible) whose mean  $\tau$  needed to be estimated:

$$l_i \sim \text{dpois}(\tau) + 1$$

*The multi-event model.* To account for the different possibilities in the life cycle of Alpine marmots, our multi-event model contained four states; a subordinate state *S* (encompassing pups, yearlings and subordinate adults), a locally-recruited-breeder state *LB* (individuals that became dominant on their natal territory by inheritance), an immigrant-breeder state *IB* (individuals that became dominant after dispersal), and a dead state *D*. Thanks to the genetic analyses, we were able to determine with certainty whether an individual successfully reproduced inside the study area a given year (Cohas *et al.* 2008; Ferrandiz-Rovira *et al.* 2016), even if the individual was not captured that year. Because reproduction is highly correlated to the dominance status in Alpine marmots, we incorporated this additional source of information in the model to precise the state of the individuals. The different observations available from the data set allowed us to consider 9 events, numbered as follow: 1 when the focal individual was not captured but reproduced on its natal territory, 2 when it was not captured but reproduced on another territory, 3 when it was captured as a subordinate and did not reproduce, 4 when it was captured as a subordinate and reproduced on its natal territory, 5 when it was captured as locally-recruited-breeder but did not reproduce, 6 when it was captured as locally-recruited-breeder and reproduced on its natal territory, 7 when it was capture as immigrant breeder but did not reproduce, 8 when it was captured as immigrant breeder and reproduced on another territory and 9 when no information about the focal individual was available. This type of encoding allowed us to construct capture-histories for all individuals captured at least once during the study duration, *e.g.* 993397898899 for an individual captured and marked as a subordinate for the first time on the third year of the study, recaptured as subordinate on the fourth year, recaptured as an immigrant breeder that did not reproduce on the sixth year, recaptured as an immigrant breeder that reproduced on the seventh, ninth and tenth years and not recaptured, nor reproduced on the fifth, eighth, eleventh and twelfth years.

The multi-event model can be described using two matrices. The first one represents the state-transition process from one capture occasion to the next and the second one represents the observation process at a given capture occasion, *i.e.* the possible associations between the observed event and the underlying state of an individual at that same capture occasion. The state-transition matrix reads as state at time

$t$  in rows and state a time  $t+1$  in column. It contains the demographic parameters in which we are interested:  $\Phi^x_{i,t}$  the probability that individual  $i$  in state  $x$  at time  $t$  survived to time  $t+1$ ,  $d_{i,t}$  the probability (conditional on survival) that individual  $i$  dispersed and became dominant between  $t$  and  $t+1$ ,  $h_{i,t}$  the probability (conditional on non-dispersal) that individual  $i$  inherited a dominant position on its natal territory between  $t$  and  $t+1$  and  $r_{i,l_i}$  the probability that individual  $i$  did not leave the study area when dispersing, given the distance  $l_i$  travelled.

$$\begin{bmatrix} S \\ LB \\ IB \\ D \end{bmatrix} \begin{bmatrix} S & LB & IB & D \\ \Phi^S.(1-d).(1-h) & \Phi^S.(1-d).h & \Phi^S.d.r & (1-\Phi^S)+\Phi^S.d.(1-r) \\ 0 & \Phi^{LB} & 0 & 1-\Phi^{LB} \\ 0 & 0 & \Phi^{IB} & 1-\Phi^{IB} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

The observation matrix reads as state at time  $t$  in rows and possible observable events at time  $t$  in columns. It contains the recapture and reproduction parameters:  $p^x_{i,t}$  the probability that individual  $i$  in state  $x$  was captured at time  $t$  and  $\psi^x_{i,t}$  the probability that individual  $i$  in state  $x$  successfully reproduced between  $t$  and  $t+1$ .

$$\begin{bmatrix} S \\ LB \\ IB \\ D \end{bmatrix} \begin{bmatrix} 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 \\ 0 & (1-p^S).\psi^S & p^S.(1-\psi^S) & p^S.\psi^S & 0 & 0 & 0 & 0 & (1-p^S).(1-\psi^S) \\ 0 & (1-p^{LB}).\psi^{LB} & 0 & 0 & p^{LB}.(1-\psi^{LB}) & p^{LB}.\psi^{LB} & 0 & 0 & (1-p^{LB}).(1-\psi^{LB}) \\ (1-p^{IB}).\psi^{IB} & 0 & 0 & 0 & 0 & 0 & p^{IB}.(1-\psi^{IB}) & p^{IB}.\psi^{IB} & (1-p^{IB}).(1-\psi^{IB}) \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

To take into account the variation in recapture probabilities from one year to the other, and following results of previous CR studies on the same population (Dupont *et al.* 2015; Berger *et al.* 2016; Rézouki *et al.* 2016), we considered time, age and sex effects on the recapture probabilities. To account for the age structure in the population, we considered four age-classes: juvenile (from zero to one-year-old), yearling (from one to two), two-year (from two to three) and adult (three years old and older) for all

survival, dispersal, inheritance and reproduction probabilities. Following previous results (see chapter IV.A) we considered the same survival probability for locally-recruited and immigrant breeders ( $\Phi^{LB} = \Phi^{IB} = \Phi^B$ ) and used a single Poisson distribution to model the dispersal distances distribution of both sexes.

#### 9.2.4. Dominance change consequences

In order to study if the eviction of a resident dominant by an immigrant individual affected the group dynamics, we tested for the effect of immigration on the different vital rates of group members. To test the validity of the different scenarios we proposed, we compared three models.

*Kin selection model:* because their genetic relatedness with subsequent offspring produced by the immigrant dominant will be much lower (and consequently their inclusive fitness expectation), we expect subordinate individuals to leave their natal territory and try to gain a dominant position in another territory in order to maximize their direct fitness. Because un-successful dispersers most likely die the following winter (Magnolon 1999; Grimm *et al.* 2003b), they are never re-encountered and are indistinguishable from individuals dying during hibernation. Given our data, it is therefore impossible to estimate the probability to leave the natal territory and our model only returns estimates of successful dispersal. The hypothetical increase in the numbers of dispersing individuals may therefore translate into an increased in dispersal probability (if most individuals succeed) and/or a decrease in survival probability (if they fail). Additionally, it has been shown that subordinate males suffered from the presence of pups during hibernation, in terms of increased weight loss (Arnold 1993). Because of this additional cost, male subordinates are expected to disperse more than females when one of the dominants is replaced. In order to take these different possibilities into account, we constructed a model with different dispersal and survival probabilities between cases where an immigrant arrived in the group and cases where the dominant pair did not change. In addition, we considered sex-specific dispersal and survival probabilities of subordinates in both cases to determine whether subordinate males dispersed more than females following the arrival of an immigrant dominant. Because of the occurrence of infanticides and the impossibility to produce a second litter a given year, the reproduction probability of the newly formed dominant couple should be lower following an immigration event. We therefore implemented different dominant

reproduction probabilities whether an immigrant arrived or not. Parameters of the model were then  $p_{t,age,sex}$  the time, age and sex-specific recapture probabilities,  $\Phi^B_{age,sex}$  the age and sex-specific survival probabilities of dominant individuals,  $\Phi^S_{age,sex,kin}$  the age and sex-specific survival probabilities of subordinate individuals in the presence and in the absence of immigration,  $d_{age,sex,kin}$  the age and sex-specific dispersal probabilities in the presence and absence of immigration,  $h_{age,sex}$  the age and sex-specific inheritance probabilities,  $r^S_{age,sex,kin}$  the age and sex-specific reproductive success probability of subordinate individuals in the presence and in the absence of immigration and  $r^B_{age,sex,kin}$  the age and sex-specific reproductive success of dominant individuals in the presence and in the absence of immigration.

*Intra-sexual competition:* because of increasing sex-specific competition, dominant individuals in Alpine marmots are more likely to lose dominance when the number of same-sex subordinates increases in the family group (Lardy *et al.* 2012a, 2013). An immigrant dominant should thus avoid this risk by expelling same-sex subordinates when taking over a new family group. In this scenario, subordinate dispersal is not a choice and should translate in higher levels of dispersal and/or lower levels of survival only for subordinates of the same sex than the immigrant. Concerning the reproduction probability, the expected outcome of a new dominant take-over is similar to the previous model. The parameters of the models were then  $p_{t,age,sex}$  the time, age and sex-specific recapture probabilities,  $\Phi^B_{age,sex}$  the age and sex-specific survival probabilities of dominant individuals,  $\Phi^S_{age,sex,comp}$  the age and sex-specific survival probabilities of subordinate individuals in the presence and in the absence of immigration by a same-sex dominant,  $d_{age,sex,comp}$  the age and sex-specific dispersal probabilities in the presence and in the absence of immigration by a same-sex dominant,  $h_{age,sex}$  the age and sex-specific inheritance probabilities,  $r^S_{age,sex,comp}$  the age and sex-specific reproductive success probability of subordinate individuals in the presence and in the absence of immigration and  $r^B_{age,sex,comp}$  the age and sex-specific reproductive success of dominant individuals in the presence and in the absence of immigration.

These models were then compared to a simple model with no effect of the immigration of a new dominant (*the root model*). All three models were run using JAGS *via* R with the package jagsUI and models were compared based on the Deviance Information Criterion (Spiegelhalter *et al.* 2002a). To ensure full convergence, models

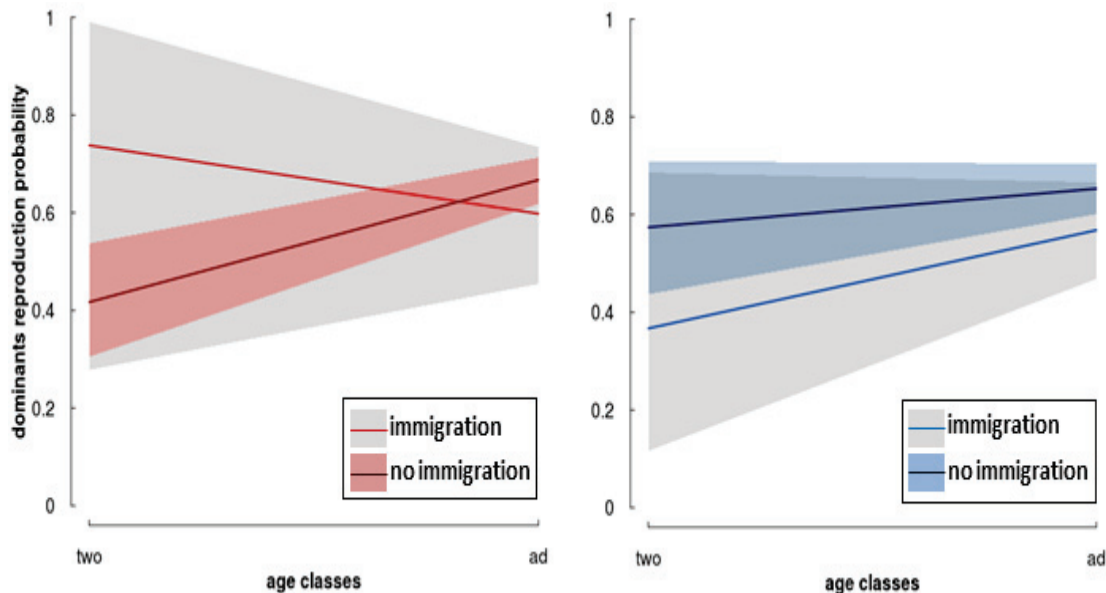


were fitted by running three chains independently for 100000 iterations with a burning period of 10000 iterations and a thinning rate of 1.

### 9.3. Results

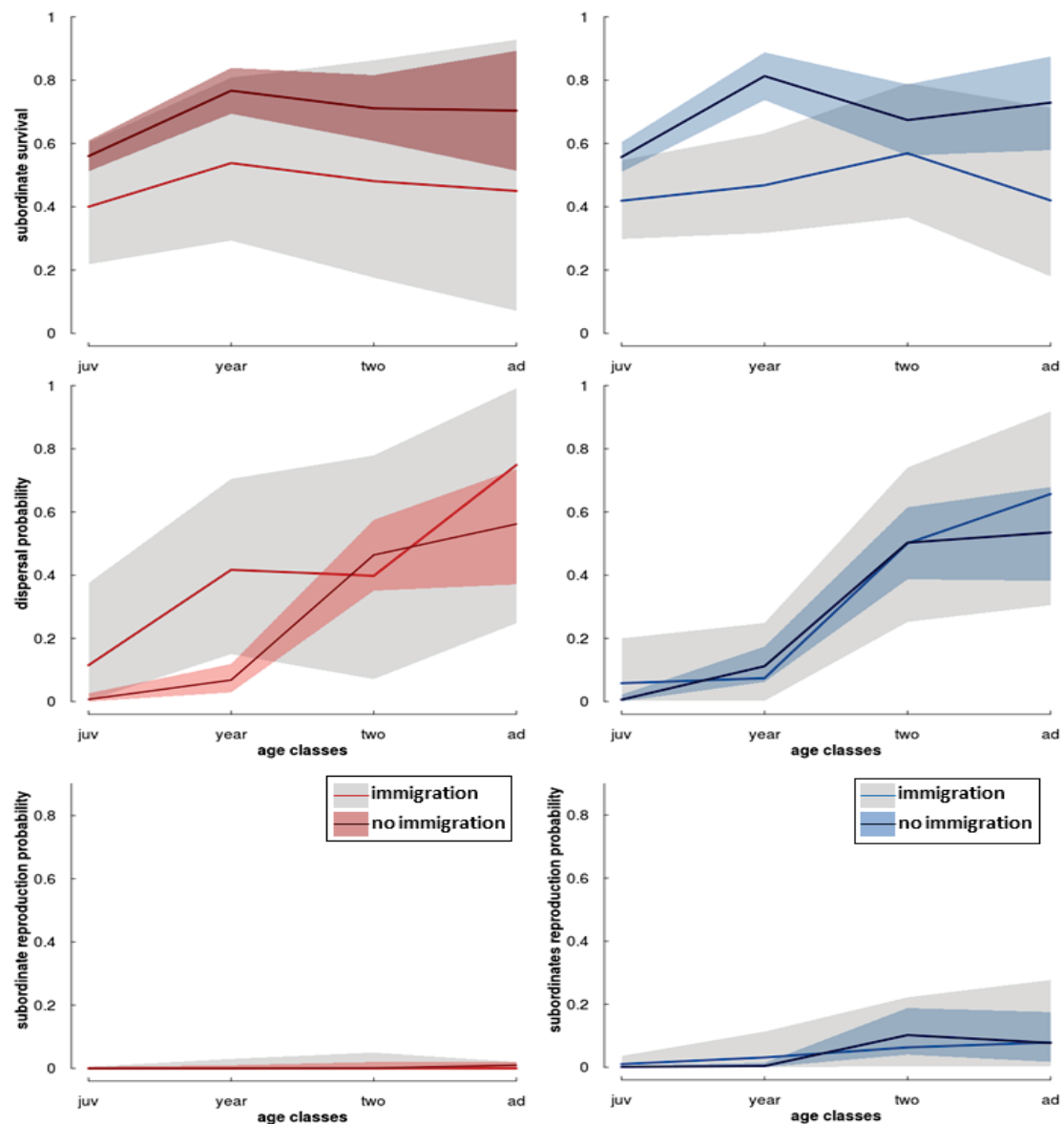
The intra-sexual competition model was the best of the set according to DIC (*intra-sexual competition model*: deviance = 3958.6; DIC = 5379.9) and the kin-selection model ranked last (*kin-selection model*: deviance = 3971.8; DIC = 5514.3; *root model*: deviance = 3973.2; DIC = 5401.9). Because the kin-selection model was so poorly supported, in the following section we focus on the results obtained with the intra-sexual competition model only (see Supporting Material 9.5 for detailed results of all three models).

Recapture probabilities varied with the year of study (between 1.36 [0.44; 2.2] and 4.39 [3.46; 5.49] on a logit scale for female yearlings), decreased with age (difference in recapture probabilities between yearlings and two-year individuals  $\Delta p_{two} = -1.41 [-1.85; -0.90]$  and difference between yearlings and adults  $\Delta p_{ad} = -1.88 [-2.25; -1.62]$  on a logit scale). Recapture probabilities were also higher for females than for males (difference in recapture probabilities between females and males  $\Delta p_{sex} = -0.27 [-0.45; -0.12]$  on the logit scale).



**Figure IV.12.** Dominant reproduction probabilities in the presence or absence of immigration by a same-sex new dominant for all dominant age classes. Left panel represents female dominants and right panels, males. Coloured lines represent the mean estimates and shaded areas represent the associated confidence interval.

Dominant survival varied with age and sex. Two-year old dominants had a lower survival than adults for both sexes ( $\Phi^B_{two, females} = 0.76 \pm 0.12$  and  $\Phi^B_{ad, females} = 0.81 \pm 0.02$ ;  $\Phi^B_{two, males} = 0.71 \pm 0.12$  and  $\Phi^B_{ad, males} = 0.76 \pm 0.02$ ). Reproduction probabilities tended to be lower for males when an immigrant individual took the dominant position while two-year dominant females seemed to have a higher reproduction probability in the same situation (Fig.IV.12). However, the very large confidence interval associated to the reproduction of two-year dominant individuals of both sexes in the presence of immigration (most likely because very few individuals are in such situation) forces us to consider these results with caution.



**Figure IV.13.** Subordinate survival, dispersal and reproduction probabilities in the presence or absence of immigration by a new same-sex dominant for all age classes. Left panels represent female subordinates and right panels, males. Coloured lines represent the mean estimates and shaded areas represent the associated confidence interval.

The influence of same-sex immigration on subordinate survival differed both with sex and age. Mean subordinate survival was always lower when a same-sex immigrant settled in the group and this difference was more pronounced for male yearlings (Fig.IV.13, upper panels). Male dispersal probability was not affected by immigration in all age classes. For females, dispersal probability increased strongly for juveniles and yearlings but not for two-years and adults (Fig.IV.13, middle panels). Reproduction probability was never different from zero for females while it was at the highest for two-year old subordinate males ( $r_{two,males}^S = 0.10 \pm 0.04$  and Fig.IV.13 lower panels) but immigration had no significant effect. Finally, inheritance probability increased with age and it was highest for two-year females ( $h_{two,females} = 0.32 \pm 0.06$  vs.  $h_{two,males} = 0.10 \pm 0.04$ ;  $h_{ad,females} = 0.15 \pm 0.09$  vs.  $h_{ad,males} = 0.21 \pm 0.07$ ).

## 9.4. Discussion

Our results demonstrate that the immigration of a new dominant individual and associated eviction of one of the resident dominants has important consequences, both for the fate of individual group members and for the group dynamics. The fact that the kin-selection model performed poorly compared to the root model and intra-sexual competition model tend to indicate that consequences of immigration by a new dominant are sex-specific according to our second hypothesis.

### 9.4.1. Individual vital rates

*Dominants.* The first consequence of immigration by a new dominant is obviously the eviction of the previous dominant. However, our model did not test for this effect because of its parametrization. Indeed, we investigated the consequences of immigration and therefore considered an effect on demographic rates *after* the immigrating individual took over the dominant position. To test for the capacity of an evicted dominant individual to survive and become dominant again in another group would instead require testing for an effect of immigration on the resident dominant survival during the *previous* time interval. Although a very low survival of evicted dominants is always assumed in studies on Alpine marmots (*e.g.* Stephens *et al.* 2002; Grimm *et al.* 2003), to our knowledge no study was able to estimate precisely the capacity of evicted dominants to survive and secure a new dominant position. Our model provides a good framework for testing such effects and further investigations will be conducted on this aspect.

Contrary to what was expected, the reproduction probability of dominant individuals did not strongly decrease following immigration. The reason for this surprising result actually lies in a lousy parametrization of this part of the model. Instead of testing for the effect of any change in the dominant couple on the remaining dominant reproduction probability, we tested for the effect of male immigration on male reproduction only and for the effect of female immigration on female reproduction only (see the scripts in the supplementary material 9.5.1). Because of that, the “no-immigration” situation of a male, for example, encompasses both situations where no immigration occurred and situations where the female dominant was evicted, and conversely for females. The immigration situation is also quite irrelevant since it actually confounds the reproduction probability of both the immigrating and evicted individuals. New analyses are thus required to truly determine the effect of immigration in the social group on reproduction, and more generally for dominants.

*Subordinates.* When a new male immigrated in a social group and evicted the resident dominant, this was accompanied by a decrease in the survival of male subordinates, especially important for yearlings. Successful dispersal probability of subordinate males, on the other hand, was not affected by immigration. Taken together, the survival and dispersal patterns of subordinate males tell us precisely about the effect produced by the immigration of a new dominant male within the social group. The decline in survival, particularly important in yearlings, suggests that the majority of subordinate males will be forced to leave the territory even if they do not have the necessary physical condition to acquire dominant status after dispersal. Since in the Alpine marmot adult size is not reached before the emergence from the third hibernation (two-year-olds having survived), yearlings generally remain in their natal territory at least until that time (Arnold 1990 and chapter IV.A). Here, the much lower survival of yearlings following immigration indicates that a vast majority of these yearlings will still disperse despite the very low chances of success, thus giving hints that dispersal is not voluntary but rather forced by the new dominant male. In addition, our model provides information about extra-pair copulations, indicating that most subordinate males that produced pups did so at the age of two when most individuals disperse, confirming that dispersing subordinate males may access to reproduction even if they do not access to the dominant status (Cohas *et al.* 2006).

As for males, female subordinate survival strongly decreased when an immigrating female took over the dominant position and, unlike males, successful dispersal probability of female subordinates was also affected. It was especially true for female yearlings, in which successful dispersal sharply increased following the immigration of a new dominant female. In the same way as for males, patterns of survival and dispersal of subordinate females tend to show that it is indeed the immigrating dominant female that forces subordinate females to leave their natal territory. It is particularly interesting to note that female yearlings have a higher probability of becoming dominant by dispersing following immigration by a new dominant female. It would then appear that subordinate females delay dispersal as much as they can, even if they possess the physical capacities to disperse and become dominant. This confirms previous results (chapter IV.A) which indicated that females were likely to be more philopatric than males in the Alpine marmot. A potential explanation for the higher level of female philopatry is that differences in dispersal patterns between males and females result from the impossibility for female subordinates to access reproduction through extra-pair copulations, as evidenced here by the null reproduction probability of subordinate females.

Altogether, the results tend to confirm our second proposal, *i.e.* the immigrating dominant will evict not only the resident dominant but also the subordinates of the same sex to avoid intra-sexual competition. This pattern of eviction by the new dominant individual is not unusual in singular breeders and it is well explained by the costs incurred by dominant individuals in the presence of same-sex rivals related to higher levels of competition for reproduction, breeding sites or other resources (Clutton-Brock & Huchard 2013a,b). In meerkats for example, dominant females commonly evict temporarily subordinate females from the social group (Young & Clutton-Brock 2006). The benefits associated to these evictions for dominant females are two-fold: (i) in meerkats, pregnant females regularly kill pups born to other females in the days following parturition. By evicting subordinate pregnant females, the dominant female thus avoids the risk of infanticide on its pups; (ii) following eviction, pregnant females frequently abort and may subsequently participate in suckling pups born to the dominant female, therefore increasing benefits to the dominant. In Alpine marmots also, high levels of intra-sexual competition can be very costly for dominant individuals. More precisely, dominance tenure and reproduction monopolization (for dominant males) was

found to be negatively related to the number of same-sex subordinates present in the social group (Lardy *et al.* 2012a, 2013). It is therefore not surprising that the new dominant chases same-sex subordinates out of the group. On the contrary, this raises the question of why previous dominants tolerated many same-sex subordinates when it was shown to be highly costly. The answer is likely to be related to kin-selection theory (Hamilton 1964b) since subordinates in Alpine marmot family groups are most often offspring of the resident dominant (Allainé 2000a). It is indeed expected from kin-selection theory that dominants should be more tolerant towards their subordinates if they are kin-related (Smith 2014). This was found to be true in many mammal species (Clutton-Brock & Huchard 2013b) and, accordingly, Arnold & Dittami (1997) found that dominant male Alpine marmots were more aggressive with unrelated subordinates. This higher tolerance towards relatives clearly accounts for the pattern observed in marmots and explains the difference in dispersal observed after immigration.

However, the reasons for this higher tolerance of kin-related subordinates are still unclear and different hypotheses may be advanced. Dominants may tolerate the presence of subordinate males because of their strong positive effect on juvenile survival during hibernation compensating partly for the cost of losing dominance and paternities (Allainé & Theuriau 2004). However, this explanation would be valid only if subordinate males helped preferentially related juveniles. Accordingly, Arnold (1990) found that pups mortality was lower in groups where all subordinates were potentially full sibs. However, this does not explain the tolerance of the dominant female towards subordinate females. Alternatively, dominant individuals may tolerate a large number of subordinates to allow them time to become competitive enough and thus increase the probability that they become dominant in turn. The direct costs of having numerous subordinates in the group would then be compensated by later high fitness benefits provided by an offspring becoming dominant. This scenario is highly probable in Alpine marmots because of the time required to complete growth (marmots only reach their adult size when three years old) and because dispersal is very costly (Arnold 1990b) but further research is needed to clearly identify the mechanisms responsible for increased social tolerance towards kins in Alpine marmots.

#### 9.4.2. Group dynamics implications

Because of the implications for subordinate demographic rates, the group dynamics will also be strongly impacted by immigration. To illustrate this fact, we can look at the mean probabilities to stay in the social group after the arrival of an immigrating dominant for individuals of each sex and age class and compare them to the estimates when no change of dominant occurred. To do so, we only need to multiply the survival probability and the probability to not disperse in each situation ( $\Phi \cdot (1-d)$ ).

When no change occurs, 56% of male and female juveniles will survive and remain in the social group the following year, 72% of female and male yearlings, 38% of two-year-old females, 34% of two-year-old males, 31 % of females 3 years and older and 34% of males 3 years and older. Depending on the age-structure of the group, the group growth rate is thus highly likely to vary a lot. However, given the high probability of producing a litter each year (around 0.65 for dominants three years and older) and the mean litter size in the population ( $4.15 \pm 0.05$  pups; Dupont *et al.* 2015), group growth rate is much likely to be positive.

By comparison, when a new dominant female immigrates into the social group, only 35% of female juveniles will survive and stay in the group the following year, 31% of female yearlings, 29% of two-year-old females and 11% of females three years and older. In case it is a dominant male that immigrates, 39% of male juveniles will remain in the group, 43% of yearlings, 29% of two-year-old males and 14% of males of three years and more. In total, more than 50% of individuals of all age classes will leave the social group (or die). Adding to these low proportions, the very low probability to produce a litter when a dominance change happens (Lardy *et al.* 2011; sadly not evidenced using our model yet), it becomes obvious that the group size will suffer a drastic decrease following the arrival of a new dominant.

Put together, our results outline the following group dynamics in Alpine marmots: after the settlement of a new dominant, the family group will likely grow until one of the resident dominants is evicted again, after which the group will undergo a dramatic decrease due to the eviction of the majority of subordinates of one sex. This cyclic dynamic is quite different from what was evidenced in other cooperative species.

In meerkats, for example, the group dynamics was shown to be mainly driven by group density dependence in interaction with climatic factors. More precisely, the group growth rate declined with increasing group size and this negative effect of group size was stronger in years of low rainfalls. Because of the increase in intra-sexual competition with subordinate numbers in Alpine marmots, group size is also likely to play a role in Alpine marmots' group dynamics and further studies should investigate the influence of group size and composition on group dynamics.

#### *9.4.3 Conclusion*

Our results shed light on the consequences of immigration by a new dominant into the social group, both at the individual and group level. At the individual level, it appears that resident dominants tolerate a much higher number of same-sex subordinates than immigrating individuals, probably because of the relatedness between the resident dominant and associated subordinates. It is likely to be advantageous for the dominant to tolerate a large number of same-sex subordinates until they are fit enough to disperse and become dominant, thus providing the dominant with fitness benefits, rather than chasing them away earlier in order to avoid the costs related to intra-sexual competition.

At the group level, we highlighted the importance of group interactions on group dynamics of cooperatively breeding species. More specifically, we identified a potential mechanism responsible for large modifications in the group composition and swift declines in group size without the action of any biotic factors. Our results stress out the fact that in social species, groups are not isolated entities and interactions between these groups may be very important for the overall population dynamics of the species.



## 9.5. Supporting Material

### 9.5.1 Root model script and results

```
sink("IMED_ROOT.bug")
> cat("
+ model
+ {
+ # Priors and constraints
+ for (i in 1:nind)
+ {
+ dist[i] ~ dpois(tau)
+ DD[i] <- step(dmax -(dist[i]+1))
+ D[i] <- DD[i]+1
+ DIST[i,1] <- dmax
+ DIST[i,2] <- dist[i]+1
+
+ for (t in f[i]:(n.occ-1))
+ {
+ pi[i,t] <- mean.pi[age[i,t]]
+ pS1[i,t] <- mean.pS1[sex[i]]
+ pD1[i,t] <- mean.pD1[sex[i]]
+ phiS[i,t] <- mean.phiS[sex[i],age[i,t]]
+ phiD[i,t] <- mean.phiD[sex[i],age[i,t]]
+ d[i,t] <- mean.d[sex[i],age[i,t]]
+ h[i,t] <- mean.h[sex[i],age[i,t]]
+ p[i,t] <- mean.p[age[i,t+1], sex[i], t]
+ rDS[i,t] <- mean.rDS[sex[i], age[i,t]]
+ rDB[i,t] <- mean.rDB[sex[i], age[i,t]]
+ r[i,t] <- prob.mat[site[i],DIST[i,D[i]]]
+ }
+ }
+ tau ~ dgamma(0.01,0.01)|(0.00001,100)
+
+ mean.pi[1] ~ dunif(0,1)
+ mean.pi[2] ~ dunif(0,1)
+ mean.pi[3] ~ dunif(0,1)
+ mean.pi[4] ~ dunif(0,1)
+
+ mean.pS1[1] ~ dunif(0,1)
+ mean.pS1[2] ~ dunif(0,1)
+
+ mean.pD1[1] ~ dunif(0,1)
+ mean.pD1[2] ~ dunif(0,1)
+
+ for (a in 1:4)
+ {
```

```

+ mean.phiS[1,a] ~ dunif(0,1)
+ mean.phiS[2,a] ~ dunif(0,1)
+
+ mean.phiD[1,a] ~ dunif(0,1)
+ mean.phiD[2,a] ~ dunif(0,1)
+
+ mean.d[1,a] ~ dunif(0,1)
+ mean.d[2,a] ~ dunif(0,1)
+
+ mean.h[1,a] ~ dunif(0,1)
+ mean.h[2,a] ~ dunif(0,1)
+
+ mean.rDS[1,a] ~ dunif(0,1)
+ mean.rDS[2,a] ~ dunif(0,1)
+
+ mean.rDB[1,a] ~ dunif(0,1)
+ mean.rDB[2,a] ~ dunif(0,1)
+ }
+
+ for (t in 1:(n.occ-1))
+ {
+ logit(mean.p[2,1,t]) <- P[t]
+ logit(mean.p[2,2,t]) <- P[t]+d.P
+ logit(mean.p[3,1,t]) <- P[t]+d.trois
+ logit(mean.p[3,2,t]) <- P[t]+d.P+d.trois
+ logit(mean.p[4,1,t]) <- P[t]+d.quatre
+ logit(mean.p[4,2,t]) <- P[t]+d.P+d.quatre
+ P[t] ~ dnorm(0,0.001)
+ }
+ d.trois ~ dnorm(0,0.001)
+ d.quatre ~ dnorm(0,0.001)
+ d.P ~ dnorm(0,0.001)
+
+ # Define state-transition and observation matrices
+ for (i in 1:nind)
+ {
+ for (t in f[i]:(n.occ-1))
+ {
+ # Define probabilities of state S at first capture
+ ps1[i,t,1] <- pi[i,t]
+ ps1[i,t,2] <- 0
+ ps1[i,t,3] <- 1-pi[i,t]
+
+ # Define probabilities of O given S at first capture
+ po1[1,i,t,1] <- (1-ps1[i,t])*rDS[i,t]
+ po1[1,i,t,2] <- 0
+ po1[1,i,t,3] <- ps1[i,t]*(1-rDS[i,t])

```

```

+ po1[1,i,t,4] <- pS1[i,t]*rDS[i,t]
+ po1[1,i,t,5] <- 0
+ po1[1,i,t,6] <- 0
+ po1[1,i,t,7] <- 0
+ po1[1,i,t,8] <- 0
+ po1[1,i,t,9] <- 0
+ po1[2,i,t,1] <- (1-pD1[i,t])*rDB[i,t]
+ po1[2,i,t,2] <- 0
+ po1[2,i,t,3] <- 0
+ po1[2,i,t,4] <- 0
+ po1[2,i,t,5] <- pD1[i,t]*(1-rDB[i,t])
+ po1[2,i,t,6] <- pD1[i,t]*rDB[i,t]
+ po1[2,i,t,7] <- 0
+ po1[2,i,t,8] <- 0
+ po1[2,i,t,9] <- 0
+ po1[3,i,t,1] <- 0
+ po1[3,i,t,2] <- (1-pD1[i,t])*rDB[i,t]
+ po1[3,i,t,3] <- 0
+ po1[3,i,t,4] <- 0
+ po1[3,i,t,5] <- 0
+ po1[3,i,t,6] <- 0
+ po1[3,i,t,7] <- pD1[i,t]*(1-rDB[i,t])
+ po1[3,i,t,8] <- pD1[i,t]*rDB[i,t]
+ po1[3,i,t,9] <- 0
+
+ # Define probabilities of state S(t+1) given S(t)
+ ps[1,i,t,1] <- phiS[i,t] * (1-d[i,t]) * (1-h[i,t])
+ ps[1,i,t,2] <- phiS[i,t] * (1-d[i,t]) * h[i,t]
+ ps[1,i,t,3] <- phiS[i,t] * d[i,t] * r[i,t]
+ ps[1,i,t,4] <- 1-phiS[i,t] + phiS[i,t]*d[i,t]*(1-r[i,t])
+ ps[2,i,t,1] <- 0
+ ps[2,i,t,2] <- phiD[i,t]
+ ps[2,i,t,3] <- 0
+ ps[2,i,t,4] <- (1-phiD[i,t])
+ ps[3,i,t,1] <- 0
+ ps[3,i,t,2] <- 0
+ ps[3,i,t,3] <- phiD[i,t]
+ ps[3,i,t,4] <- (1-phiD[i,t])
+ ps[4,i,t,1] <- 0
+ ps[4,i,t,2] <- 0
+ ps[4,i,t,3] <- 0
+ ps[4,i,t,4] <- 1
+
+ # Define probabilities of O(t) given S(t)
+ po[1,i,t,1] <- (1-p[i,t])*rDS[i,t]
+ po[1,i,t,2] <- 0
+ po[1,i,t,3] <- p[i,t]*(1-rDS[i,t])

```

```

+ po[1,i,t,4] <- p[i,t]*rDS[i,t]
+ po[1,i,t,5] <- 0
+ po[1,i,t,6] <- 0
+ po[1,i,t,7] <- 0
+ po[1,i,t,8] <- 0
+ po[1,i,t,9] <- (1-p[i,t])*(1-rDS[i,t])
+ po[2,i,t,1] <- (1-p[i,t])*rDB[i,t]
+ po[2,i,t,2] <- 0
+ po[2,i,t,3] <- 0
+ po[2,i,t,4] <- 0
+ po[2,i,t,5] <- p[i,t]*(1-rDB[i,t])
+ po[2,i,t,6] <- p[i,t]*rDB[i,t]
+ po[2,i,t,7] <- 0
+ po[2,i,t,8] <- 0
+ po[2,i,t,9] <- (1-p[i,t])*(1-rDB[i,t])
+ po[3,i,t,1] <- 0
+ po[3,i,t,2] <- (1-p[i,t])*rDB[i,t]
+ po[3,i,t,3] <- 0
+ po[3,i,t,4] <- 0
+ po[3,i,t,5] <- 0
+ po[3,i,t,6] <- 0
+ po[3,i,t,7] <- p[i,t]*(1-rDB[i,t])
+ po[3,i,t,8] <- p[i,t]*rDB[i,t]
+ po[3,i,t,9] <- (1-p[i,t])*(1-rDB[i,t])
+ po[4,i,t,1] <- 0
+ po[4,i,t,2] <- 0
+ po[4,i,t,3] <- 0
+ po[4,i,t,4] <- 0
+ po[4,i,t,5] <- 0
+ po[4,i,t,6] <- 0
+ po[4,i,t,7] <- 0
+ po[4,i,t,8] <- 0
+ po[4,i,t,9] <- 1
+ }
+ }
+ # Likelihood
+ for (i in 1:nind)
+ {
+ z[i,f[i]] ~ dcat(ps1[i,f[i],])
+ y[i,f[i]] ~ dcat(po1[z[i,f[i]], i, f[i], ])
+ for (t in (f[i]+1):n.occ)
+ {
+ z[i,t] ~ dcat(ps[z[i,t-1], i, t-1, ])
+ y[i,t] ~ dcat(po[z[i,t], i, t-1, ])
+ } } }
+ ",fill = TRUE)
> sink()

```

**Table IV.2.** parameter estimates from the root model

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat
mean.pi[1]	0.999	0.001	0.996	0.999	1.000	FALSE	1.000	1
mean.pi[2]	0.984	0.011	0.955	0.986	0.998	FALSE	1.000	1
mean.pi[3]	0.939	0.041	0.837	0.948	0.992	FALSE	1.000	1
mean.pi[4]	0.288	0.043	0.209	0.287	0.375	FALSE	1.000	1
mean.pS1[1]	0.762	0.180	0.345	0.799	0.992	FALSE	1.000	1
mean.pS1[2]	0.845	0.127	0.532	0.877	0.995	FALSE	1.000	1
mean.pD1[1]	0.659	0.086	0.486	0.662	0.818	FALSE	1.000	1
mean.pD1[2]	0.852	0.059	0.721	0.859	0.947	FALSE	1.000	1
mean.phiS[1,1]	0.549	0.024	0.502	0.549	0.597	FALSE	1.000	1
mean.phiS[2,1]	0.539	0.023	0.495	0.539	0.583	FALSE	1.000	1
mean.phiS[1,2]	0.750	0.036	0.679	0.750	0.821	FALSE	1.000	1
mean.phiS[2,2]	0.757	0.036	0.687	0.757	0.827	FALSE	1.000	1
mean.phiS[1,3]	0.692	0.053	0.590	0.692	0.796	FALSE	1.000	1
mean.phiS[2,3]	0.654	0.052	0.553	0.653	0.757	FALSE	1.000	1
mean.phiS[1,4]	0.678	0.093	0.495	0.678	0.860	FALSE	1.000	1
mean.phiS[2,4]	0.661	0.068	0.528	0.661	0.795	FALSE	1.000	1
mean.phiD[1,1]	0.502	0.288	0.026	0.502	0.975	FALSE	1.000	1
mean.phiD[2,1]	0.500	0.289	0.025	0.500	0.975	FALSE	1.000	1
mean.phiD[1,2]	0.671	0.234	0.163	0.713	0.988	FALSE	1.000	1
mean.phiD[2,2]	0.497	0.288	0.025	0.495	0.975	FALSE	1.000	1
mean.phiD[1,3]	0.789	0.115	0.533	0.802	0.971	FALSE	1.000	1
mean.phiD[2,3]	0.700	0.123	0.441	0.708	0.913	FALSE	1.000	1
mean.phiD[1,4]	0.808	0.018	0.772	0.809	0.842	FALSE	1.000	1
mean.phiD[2,4]	0.763	0.020	0.724	0.764	0.801	FALSE	1.000	1
mean.d[1,1]	0.007	0.007	0.000	0.005	0.024	FALSE	1.000	1
mean.d[2,1]	0.005	0.005	0.000	0.004	0.020	FALSE	1.000	1
mean.d[1,2]	0.088	0.025	0.045	0.086	0.142	FALSE	1.000	1
mean.d[2,2]	0.103	0.027	0.057	0.101	0.161	FALSE	1.000	1
mean.d[1,3]	0.454	0.056	0.343	0.454	0.564	FALSE	1.000	1
mean.d[2,3]	0.499	0.054	0.391	0.500	0.604	FALSE	1.000	1
mean.d[1,4]	0.600	0.090	0.415	0.603	0.764	FALSE	1.000	1
mean.d[2,4]	0.554	0.070	0.414	0.555	0.687	FALSE	1.000	1
mean.h[1,1]	0.004	0.004	0.000	0.003	0.014	FALSE	1.000	1
mean.h[2,1]	0.003	0.003	0.000	0.002	0.013	FALSE	1.000	1
mean.h[1,2]	0.038	0.016	0.012	0.036	0.075	FALSE	1.000	1
mean.h[2,2]	0.010	0.007	0.001	0.009	0.028	FALSE	1.000	1
mean.h[1,3]	0.323	0.061	0.210	0.321	0.447	FALSE	1.000	1
mean.h[2,3]	0.102	0.039	0.038	0.098	0.191	FALSE	1.000	1
mean.h[1,4]	0.152	0.091	0.022	0.136	0.367	FALSE	1.000	1
mean.h[2,4]	0.208	0.073	0.085	0.201	0.369	FALSE	1.000	1
P[1]	3.319	0.706	2.069	3.272	4.843	FALSE	1.000	1
P[2]	1.341	0.456	0.451	1.340	2.238	FALSE	0.998	1
P[3]	2.676	0.449	1.830	2.665	3.589	FALSE	1.000	1

P[4]	2.574	0.355	1.898	2.568	3.289	FALSE	1.000	1
P[5]	3.107	0.371	2.404	3.098	3.857	FALSE	1.000	1
P[6]	2.478	0.358	1.797	2.471	3.203	FALSE	1.000	1
P[7]	3.639	0.444	2.813	3.623	4.554	FALSE	1.000	1
P[8]	1.850	0.348	1.182	1.845	2.545	FALSE	1.000	1
P[9]	2.289	0.336	1.648	2.283	2.965	FALSE	1.000	1
P[10]	1.981	0.329	1.351	1.976	2.641	FALSE	1.000	1
P[11]	2.441	0.350	1.769	2.435	3.145	FALSE	1.000	1
P[12]	2.105	0.346	1.441	2.100	2.800	FALSE	1.000	1
P[13]	1.782	0.331	1.144	1.778	2.441	FALSE	1.000	1
P[14]	1.828	0.322	1.210	1.824	2.472	FALSE	1.000	1
P[15]	1.019	0.304	0.429	1.016	1.622	FALSE	1.000	1
P[16]	2.584	0.314	1.985	2.577	3.216	FALSE	1.000	1
P[17]	2.198	0.317	1.589	2.194	2.834	FALSE	1.000	1
P[18]	1.975	0.299	1.403	1.971	2.572	FALSE	1.000	1
P[19]	3.405	0.377	2.693	3.395	4.172	FALSE	1.000	1
P[20]	3.299	0.357	2.619	3.292	4.022	FALSE	1.000	1
P[21]	3.716	0.439	2.897	3.700	4.616	FALSE	1.000	1
P[22]	3.738	0.433	2.936	3.722	4.632	FALSE	1.000	1
P[23]	4.247	0.489	3.352	4.225	5.272	FALSE	1.000	1
P[24]	4.418	0.516	3.489	4.389	5.512	FALSE	1.000	1
P[25]	3.494	0.394	2.762	3.481	4.301	FALSE	1.000	1
d.P	-0.261	0.125	-0.506	-0.261	-0.016	FALSE	0.982	1
d.trois	-1.511	0.244	-1.997	-1.508	-1.042	FALSE	1.000	1
d.quatre	-1.838	0.212	-2.266	-1.835	-1.434	FALSE	1.000	1
mean.rDS[1,1]	0.001	0.001	0.000	0.001	0.004	FALSE	1.000	1
mean.rDS[2,1]	0.001	0.001	0.000	0.001	0.004	FALSE	1.000	1
mean.rDS[1,2]	0.009	0.008	0.000	0.008	0.029	FALSE	1.000	1
mean.rDS[2,2]	0.003	0.003	0.000	0.002	0.012	FALSE	1.000	1
mean.rDS[1,3]	0.014	0.014	0.000	0.010	0.052	FALSE	1.000	1
mean.rDS[2,3]	0.084	0.032	0.032	0.080	0.156	FALSE	1.000	1
mean.rDS[1,4]	0.036	0.035	0.001	0.025	0.130	FALSE	1.000	1
mean.rDS[2,4]	0.060	0.033	0.013	0.055	0.139	FALSE	1.000	1
mean.rDB[1,1]	0.476	0.288	0.021	0.464	0.971	FALSE	1.000	1
mean.rDB[2,1]	0.488	0.289	0.023	0.482	0.974	FALSE	1.000	1
mean.rDB[1,2]	0.470	0.114	0.253	0.468	0.694	FALSE	1.000	1
mean.rDB[2,2]	0.328	0.113	0.133	0.319	0.569	FALSE	1.000	1
mean.rDB[1,3]	0.433	0.059	0.320	0.432	0.550	FALSE	1.000	1
mean.rDB[2,3]	0.541	0.066	0.412	0.541	0.671	FALSE	1.000	1
mean.rDB[1,4]	0.660	0.023	0.614	0.660	0.704	FALSE	1.000	1
mean.rDB[2,4]	0.635	0.024	0.588	0.635	0.681	FALSE	1.000	1
tau	0.604	0.067	0.480	0.602	0.743	FALSE	1.000	1
deviance	3973.180	53.456	3871.893	3972.086	4081.250	FALSE	1.000	1

### 9.5.2. Kin-selection model script and results

```
sink("IMED_KIN.bug")
> cat("
+ model
+ {
+ # Priors and constraints
+ for (i in 1:nind)
+ {
+ dist[i] ~ dpois(tau)
+ DD[i] <- step(dmax -(dist[i]+1))
+ D[i] <- DD[i]+1
+ DIST[i,1] <- dmax
+ DIST[i,2] <- dist[i]+1
+
+ for (t in f[i]:(n.occ-1))
+ {
+ pi[i,t] <- mean.pi[age[i,t]]
+ pS1[i,t] <- mean.pS1[sex[i]]
+ pD1[i,t] <- mean.pD1[sex[i]]
+ phiS[i,t] <- mean.phiS[sex[i], age[i,t], chg[i,t] ]
+ phiD[i,t] <- mean.phiD[sex[i], age[i,t]]
+ d[i,t] <- mean.d[sex[i], age[i,t], chg[i,t] ]
+ h[i,t] <- mean.h[sex[i], age[i,t]]
+ p[i,t] <- mean.p[age[i,t+1], sex[i], t]
+ rDS[i,t] <- mean.rDS[sex[i], age[i,t], chg[i,t] ]
+ rDB[i,t] <- mean.rDB[sex[i], age[i,t], chg[i,t] ]
+ r[i,t] <- prob.mat[site[i],DIST[i,D[i]]]
+ } }
+ tau ~ dgamma(0.01,0.01)I(0.00001,100)
+
+ mean.pi[1] ~ dunif(0,1)
+ mean.pi[2] ~ dunif(0,1)
+ mean.pi[3] ~ dunif(0,1)
+ mean.pi[4] ~ dunif(0,1)
+
+ mean.pS1[1] ~ dunif(0,1)
+ mean.pS1[2] ~ dunif(0,1)
+
+ mean.pD1[1] ~ dunif(0,1)
+ mean.pD1[2] ~ dunif(0,1)
+
+ for (a in 1:4)
+ {
+ mean.phiS[1,a,1] ~ dunif(0,1)
+ mean.phiS[2,a,1] ~ dunif(0,1)
+ mean.phiS[1,a,2] ~ dunif(0,1)
```

```

+ mean.phiS[2,a,2] ~ dunif(0,1)
+
+ mean.phiD[1,a] ~ dunif(0,1)
+ mean.phiD[2,a] ~ dunif(0,1)
+
+ mean.d[1,a,1] ~ dunif(0,1)
+ mean.d[1,a,2] ~ dunif(0,1)
+ mean.d[2,a,1] ~ dunif(0,1)
+ mean.d[2,a,2] ~ dunif(0,1)
+
+ mean.h[1,a] ~ dunif(0,1)
+ mean.h[2,a] ~ dunif(0,1)
+
+ mean.rDS[1,a,1] <-0
+ mean.rDS[2,a,1] ~ dunif(0,1)
+ mean.rDS[1,a,2] <-0
+ mean.rDS[2,a,2] ~ dunif(0,1)
+
+ mean.rDB[1,a,1] ~ dunif(0,1)
+ mean.rDB[2,a,1] ~ dunif(0,1)
+ mean.rDB[1,a,2] ~ dunif(0,1)
+ mean.rDB[2,a,2] ~ dunif(0,1)
+ }
+
+ for (t in 1:(n.occ-1))
+ {
+ logit(mean.p[2,1,t]) <- P[t]
+ logit(mean.p[2,2,t]) <- P[t]+d.P
+ logit(mean.p[3,1,t]) <- P[t]+d.trois
+ logit(mean.p[3,2,t]) <- P[t]+d.P+d.trois
+ logit(mean.p[4,1,t]) <- P[t]+d.quatre
+ logit(mean.p[4,2,t]) <- P[t]+d.P+d.quatre
+ P[t] ~ dnorm(0,0.001)
+ }
+ d.trois ~ dnorm(0,0.001)
+ d.quatre ~ dnorm(0,0.001)
+ d.P ~ dnorm(0,0.001)
+
+ # Define state-transition and observation matrices
+ for (i in 1:nind)
+ {
+ for (t in f[i]:(n.occ-1))
+ {
+ # Define probabilities of state S at first capture
+ ps1[i,t,1] <- pi[i,t]
+ ps1[i,t,2] <- 0
+ ps1[i,t,3] <- 1-pi[i,t]

```



```

+
+ # Define probabilities of O given S at first capture
+ po1[1,i,t,1] <- (1-pS1[i,t])*rDS[i,t]
+ po1[1,i,t,2] <- 0
+ po1[1,i,t,3] <- pS1[i,t]*(1-rDS[i,t])
+ po1[1,i,t,4] <- pS1[i,t]*rDS[i,t]
+ po1[1,i,t,5] <- 0
+ po1[1,i,t,6] <- 0
+ po1[1,i,t,7] <- 0
+ po1[1,i,t,8] <- 0
+ po1[1,i,t,9] <- 0
+ po1[2,i,t,1] <- (1-pD1[i,t])*rDB[i,t]
+ po1[2,i,t,2] <- 0
+ po1[2,i,t,3] <- 0
+ po1[2,i,t,4] <- 0
+ po1[2,i,t,5] <- pD1[i,t]*(1-rDB[i,t])
+ po1[2,i,t,6] <- pD1[i,t]*rDB[i,t]
+ po1[2,i,t,7] <- 0
+ po1[2,i,t,8] <- 0
+ po1[2,i,t,9] <- 0
+ po1[3,i,t,1] <- 0
+ po1[3,i,t,2] <- (1-pD1[i,t])*rDB[i,t]
+ po1[3,i,t,3] <- 0
+ po1[3,i,t,4] <- 0
+ po1[3,i,t,5] <- 0
+ po1[3,i,t,6] <- 0
+ po1[3,i,t,7] <- pD1[i,t]*(1-rDB[i,t])
+ po1[3,i,t,8] <- pD1[i,t]*rDB[i,t]
+ po1[3,i,t,9] <- 0
+
+ # Define probabilities of state S(t+1) given S(t)
+ ps[1,i,t,1] <- phiS[i,t] * (1-d[i,t]) * (1-h[i,t])
+ ps[1,i,t,2] <- phiS[i,t] * (1-d[i,t]) * h[i,t]
+ ps[1,i,t,3] <- phiS[i,t] * d[i,t] * r[i,t]
+ ps[1,i,t,4] <- 1-phiS[i,t] + phiS[i,t]*d[i,t]*(1-r[i,t])
+ ps[2,i,t,1] <- 0
+ ps[2,i,t,2] <- phiD[i,t]
+ ps[2,i,t,3] <- 0
+ ps[2,i,t,4] <- (1-phiD[i,t])
+ ps[3,i,t,1] <- 0
+ ps[3,i,t,2] <- 0
+ ps[3,i,t,3] <- phiD[i,t]
+ ps[3,i,t,4] <- (1-phiD[i,t])
+ ps[4,i,t,1] <- 0
+ ps[4,i,t,2] <- 0
+ ps[4,i,t,3] <- 0
+ ps[4,i,t,4] <- 1

```

```

+
+ # Define probabilities of O(t) given S(t)
+ po[1,i,t,1] <- (1-p[i,t])*rDS[i,t]
+ po[1,i,t,2] <- 0
+ po[1,i,t,3] <- p[i,t]*(1-rDS[i,t])
+ po[1,i,t,4] <- p[i,t]*rDS[i,t]
+ po[1,i,t,5] <- 0
+ po[1,i,t,6] <- 0
+ po[1,i,t,7] <- 0
+ po[1,i,t,8] <- 0
+ po[1,i,t,9] <- (1-p[i,t])*(1-rDS[i,t])
+ po[2,i,t,1] <- (1-p[i,t])*rDB[i,t]
+ po[2,i,t,2] <- 0
+ po[2,i,t,3] <- 0
+ po[2,i,t,4] <- 0
+ po[2,i,t,5] <- p[i,t]*(1-rDB[i,t])
+ po[2,i,t,6] <- p[i,t]*rDB[i,t]
+ po[2,i,t,7] <- 0
+ po[2,i,t,8] <- 0
+ po[2,i,t,9] <- (1-p[i,t])*(1-rDB[i,t])
+ po[3,i,t,1] <- 0
+ po[3,i,t,2] <- (1-p[i,t])*rDB[i,t]
+ po[3,i,t,3] <- 0
+ po[3,i,t,4] <- 0
+ po[3,i,t,5] <- 0
+ po[3,i,t,6] <- 0
+ po[3,i,t,7] <- p[i,t]*(1-rDB[i,t])
+ po[3,i,t,8] <- p[i,t]*rDB[i,t]
+ po[3,i,t,9] <- (1-p[i,t])*(1-rDB[i,t])
+ po[4,i,t,1] <- 0
+ po[4,i,t,2] <- 0
+ po[4,i,t,3] <- 0
+ po[4,i,t,4] <- 0
+ po[4,i,t,5] <- 0
+ po[4,i,t,6] <- 0
+ po[4,i,t,7] <- 0
+ po[4,i,t,8] <- 0
+ po[4,i,t,9] <- 1
+ }
+ }
+
+ # Likelihood
+ for (i in 1:nind)
+ {
+ z[i,f[i]] ~ dcat(ps1[i,f[i],])
+ y[i,f[i]] ~ dcat(po1[z[i,f[i]], i, f[i], ])
+ for (t in (f[i]+1):n.occ)

```

```

+ {
+ z[i,t] ~ dcat(ps[z[i,t-1], i, t-1, ])
+ y[i,t] ~ dcat(po[z[i,t], i, t-1, ])
+ }
+ }
+ }
+ ",fill = TRUE)
> sink()

```

**Table IV.3.** parameter estimates from the kin-selection model.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat
mean.pi[1]	0.999	0.001	0.996	0.999	1.000	FALSE	1.000	1.000
mean.pi[2]	0.984	0.012	0.954	0.986	0.998	FALSE	1.000	1.000
mean.pi[3]	0.940	0.041	0.839	0.948	0.992	FALSE	1.000	1.000
mean.pi[4]	0.288	0.043	0.208	0.287	0.376	FALSE	1.000	1.000
mean.pS1[1]	0.829	0.139	0.489	0.863	0.995	FALSE	1.000	1.000
mean.pS1[2]	0.873	0.108	0.599	0.902	0.996	FALSE	1.000	1.000
mean.pD1[1]	0.654	0.087	0.478	0.656	0.814	FALSE	1.000	1.000
mean.pD1[2]	0.848	0.060	0.714	0.854	0.946	FALSE	1.000	1.000
mean.phiS[1,1,1]	0.586	0.026	0.535	0.586	0.637	FALSE	1.000	1.000
mean.phiS[2,1,1]	0.568	0.025	0.519	0.567	0.616	FALSE	1.000	1.000
mean.phiS[1,2,1]	0.809	0.037	0.735	0.810	0.881	FALSE	1.000	1.000
mean.phiS[2,2,1]	0.815	0.039	0.739	0.815	0.890	FALSE	1.000	1.000
mean.phiS[1,3,1]	0.736	0.061	0.617	0.736	0.854	FALSE	1.000	1.000
mean.phiS[2,3,1]	0.684	0.060	0.567	0.684	0.803	FALSE	1.000	1.000
mean.phiS[1,4,1]	0.667	0.112	0.449	0.666	0.885	FALSE	1.000	1.000
mean.phiS[2,4,1]	0.746	0.079	0.588	0.747	0.897	FALSE	1.000	1.000
mean.phiS[1,1,2]	0.384	0.058	0.274	0.382	0.500	FALSE	1.000	1.000
mean.phiS[2,1,2]	0.420	0.053	0.319	0.419	0.526	FALSE	1.000	1.000
mean.phiS[1,2,2]	0.464	0.081	0.313	0.461	0.629	FALSE	1.000	1.000
mean.phiS[2,2,2]	0.503	0.075	0.362	0.502	0.654	FALSE	1.000	1.000
mean.phiS[1,3,2]	0.615	0.091	0.441	0.614	0.795	FALSE	1.000	1.000
mean.phiS[2,3,2]	0.574	0.094	0.397	0.572	0.764	FALSE	1.000	1.000
mean.phiS[1,4,2]	0.613	0.156	0.316	0.611	0.919	FALSE	1.000	1.000
mean.phiS[2,4,2]	0.438	0.119	0.225	0.432	0.687	FALSE	1.000	1.000
mean.phiD[1,1,1]	0.500	0.289	0.024	0.500	0.975	FALSE	1.000	1.000
mean.phiD[2,1,1]	0.499	0.288	0.025	0.499	0.974	FALSE	1.000	1.000
mean.phiD[1,2,1]	0.671	0.235	0.161	0.713	0.988	FALSE	1.000	1.000
mean.phiD[2,2,1]	0.498	0.288	0.025	0.497	0.975	FALSE	1.000	1.000
mean.phiD[1,3,1]	0.709	0.147	0.396	0.721	0.954	FALSE	1.000	1.000
mean.phiD[2,3,1]	0.798	0.119	0.528	0.814	0.979	FALSE	1.000	1.000
mean.phiD[1,4,1]	0.810	0.021	0.767	0.811	0.850	FALSE	1.000	1.000
mean.phiD[2,4,1]	0.769	0.024	0.721	0.769	0.813	FALSE	1.000	1.000
mean.phiD[1,1,2]	0.499	0.289	0.024	0.497	0.975	FALSE	1.000	1.000
mean.phiD[2,1,2]	0.500	0.289	0.025	0.500	0.975	FALSE	1.000	1.000

mean.phiD[1,2,2]	0.497	0.289	0.025	0.496	0.974	FALSE	1.000	1.000
mean.phiD[2,2,2]	0.496	0.289	0.024	0.495	0.975	FALSE	1.000	1.000
mean.phiD[1,3,2]	0.828	0.144	0.467	0.866	0.995	FALSE	1.000	1.000
mean.phiD[2,3,2]	0.394	0.205	0.064	0.375	0.823	FALSE	1.000	1.000
mean.phiD[1,4,2]	0.801	0.039	0.720	0.803	0.873	FALSE	1.000	1.000
mean.phiD[2,4,2]	0.745	0.042	0.659	0.747	0.824	FALSE	1.000	1.000
mean.d[1,1,1]	0.008	0.008	0.000	0.005	0.028	FALSE	1.000	1.000
mean.d[2,1,1]	0.006	0.006	0.000	0.004	0.022	FALSE	1.000	1.000
mean.d[1,2,1]	0.075	0.025	0.033	0.072	0.131	FALSE	1.000	1.000
mean.d[2,2,1]	0.113	0.030	0.061	0.111	0.178	FALSE	1.000	1.000
mean.d[1,3,1]	0.555	0.062	0.429	0.556	0.672	FALSE	1.000	1.000
mean.d[2,3,1]	0.509	0.061	0.389	0.510	0.626	FALSE	1.000	1.000
mean.d[1,4,1]	0.603	0.111	0.373	0.608	0.801	FALSE	1.000	1.000
mean.d[2,4,1]	0.570	0.078	0.412	0.572	0.716	FALSE	1.000	1.000
mean.d[1,1,2]	0.049	0.046	0.001	0.035	0.170	FALSE	1.000	1.000
mean.d[2,1,2]	0.040	0.038	0.001	0.029	0.140	FALSE	1.000	1.000
mean.d[1,2,2]	0.235	0.096	0.075	0.226	0.444	FALSE	1.000	1.000
mean.d[2,2,2]	0.102	0.066	0.013	0.089	0.261	FALSE	1.000	1.000
mean.d[1,3,2]	0.231	0.090	0.080	0.224	0.425	FALSE	1.000	1.000
mean.d[2,3,2]	0.468	0.110	0.253	0.469	0.679	FALSE	1.000	1.000
mean.d[1,4,2]	0.473	0.163	0.156	0.476	0.776	FALSE	1.000	1.000
mean.d[2,4,2]	0.510	0.151	0.210	0.514	0.790	FALSE	1.000	1.000
mean.h[1,1,1]	0.004	0.004	0.000	0.003	0.016	FALSE	1.000	1.000
mean.h[2,1,1]	0.004	0.004	0.000	0.003	0.015	FALSE	1.000	1.000
mean.h[1,2,1]	0.025	0.015	0.003	0.023	0.061	FALSE	1.000	1.000
mean.h[2,2,1]	0.011	0.008	0.001	0.009	0.030	FALSE	1.000	1.000
mean.h[1,3,1]	0.363	0.080	0.215	0.360	0.525	FALSE	1.000	1.000
mean.h[2,3,1]	0.099	0.044	0.031	0.093	0.199	FALSE	1.000	1.000
mean.h[1,4,1]	0.244	0.130	0.041	0.228	0.534	FALSE	1.000	1.000
mean.h[2,4,1]	0.226	0.084	0.086	0.218	0.411	FALSE	1.000	1.000
mean.h[1,1,2]	0.034	0.033	0.001	0.024	0.121	FALSE	1.000	1.000
mean.h[2,1,2]	0.025	0.025	0.001	0.018	0.092	FALSE	1.000	1.000
mean.h[1,2,2]	0.138	0.073	0.030	0.126	0.310	FALSE	1.000	1.000
mean.h[2,2,2]	0.044	0.039	0.001	0.032	0.147	FALSE	1.000	1.000
mean.h[1,3,2]	0.285	0.092	0.126	0.279	0.481	FALSE	1.000	1.000
mean.h[2,3,2]	0.126	0.082	0.017	0.110	0.327	FALSE	1.000	1.000
mean.h[1,4,2]	0.142	0.123	0.004	0.109	0.455	FALSE	1.000	1.000
mean.h[2,4,2]	0.253	0.149	0.036	0.230	0.596	FALSE	1.000	1.000
P[1]	3.197	0.701	1.951	3.150	4.710	FALSE	1.000	1.000
P[2]	1.308	0.457	0.414	1.307	2.210	FALSE	0.998	1.000
P[3]	2.600	0.449	1.751	2.588	3.513	FALSE	1.000	1.000
P[4]	2.543	0.357	1.860	2.535	3.262	FALSE	1.000	1.000
P[5]	3.074	0.376	2.363	3.066	3.838	FALSE	1.000	1.000
P[6]	2.368	0.357	1.689	2.360	3.090	FALSE	1.000	1.000
P[7]	3.546	0.444	2.717	3.531	4.460	FALSE	1.000	1.000

P[8]	1.857	0.350	1.185	1.852	2.558	FALSE	1.000	1.000
P[9]	2.214	0.340	1.565	2.207	2.898	FALSE	1.000	1.000
P[10]	1.933	0.329	1.302	1.928	2.589	FALSE	1.000	1.000
P[11]	2.390	0.351	1.719	2.384	3.097	FALSE	1.000	1.000
P[12]	2.013	0.345	1.351	2.007	2.702	FALSE	1.000	1.000
P[13]	1.752	0.333	1.111	1.749	2.417	FALSE	1.000	1.000
P[14]	1.787	0.322	1.170	1.783	2.429	FALSE	1.000	1.000
P[15]	0.972	0.302	0.389	0.969	1.570	FALSE	0.999	1.000
P[16]	2.520	0.313	1.922	2.515	3.149	FALSE	1.000	1.000
P[17]	2.221	0.323	1.601	2.216	2.868	FALSE	1.000	1.000
P[18]	1.897	0.303	1.313	1.892	2.500	FALSE	1.000	1.000
P[19]	3.313	0.379	2.595	3.304	4.081	FALSE	1.000	1.000
P[20]	3.217	0.361	2.529	3.209	3.944	FALSE	1.000	1.000
P[21]	3.605	0.442	2.782	3.590	4.516	FALSE	1.000	1.000
P[22]	3.692	0.435	2.887	3.676	4.595	FALSE	1.000	1.000
P[23]	4.201	0.491	3.301	4.178	5.228	FALSE	1.000	1.000
P[24]	4.338	0.516	3.412	4.309	5.438	FALSE	1.000	1.000
P[25]	3.376	0.392	2.645	3.362	4.183	FALSE	1.000	1.000
mean.rDS[1,1,1]	0.001	0.001	0.000	0.001	0.005	FALSE	1.000	1.000
mean.rDS[2,1,1]	0.001	0.001	0.000	0.001	0.005	FALSE	1.000	1.000
mean.rDS[1,2,1]	0.014	0.010	0.001	0.012	0.038	FALSE	1.000	1.000
mean.rDS[2,2,1]	0.004	0.004	0.000	0.003	0.014	FALSE	1.000	1.000
mean.rDS[1,3,1]	0.022	0.022	0.001	0.015	0.081	FALSE	1.000	1.000
mean.rDS[2,3,1]	0.055	0.029	0.013	0.050	0.125	FALSE	1.000	1.000
mean.rDS[1,4,1]	0.056	0.054	0.001	0.040	0.200	FALSE	1.000	1.000
mean.rDS[2,4,1]	0.057	0.038	0.007	0.049	0.151	FALSE	1.000	1.000
mean.rDS[1,1,2]	0.008	0.008	0.000	0.006	0.031	FALSE	1.000	1.000
mean.rDS[2,1,2]	0.007	0.007	0.000	0.005	0.025	FALSE	1.000	1.000
mean.rDS[1,2,2]	0.032	0.031	0.001	0.023	0.116	FALSE	1.000	1.000
mean.rDS[2,2,2]	0.024	0.023	0.001	0.017	0.085	FALSE	1.000	1.000
mean.rDS[1,3,2]	0.044	0.042	0.001	0.031	0.156	FALSE	1.000	1.000
mean.rDS[2,3,2]	0.223	0.094	0.069	0.213	0.432	FALSE	1.000	1.000
mean.rDS[1,4,2]	0.097	0.089	0.003	0.071	0.333	FALSE	1.000	1.000
mean.rDS[2,4,2]	0.124	0.082	0.016	0.108	0.325	FALSE	1.000	1.000
tau	0.617	0.068	0.492	0.614	0.757	FALSE	1.000	1.001
deviance	3987.792	55.255	3882.818	3986.716	4099.130	FALSE	1.000	1.000

### 9.5.3. Intra-sexual competition model script and results

```
sink("IMED_INTRA_SEX.bug")
> cat("
+ model
+ {
+ # Priors and constraints
+ for (i in 1:nind)
+ {
+ dist[i] ~ dpois(tau)
+ DD[i] <- step(dmax -(dist[i]+1))
+ D[i] <- DD[i]+1
+ DIST[i,1] <- dmax
+ DIST[i,2] <- dist[i]+1
+
+ for (t in f[i]:(n.occ-1))
+ {
+ pi[i,t] <- mean.pi[age[i,t]]
+ pS1[i,t] <- mean.pS1[sex[i]]
+ pD1[i,t] <- mean.pD1[sex[i]]
+ phiS[i,t] <- mean.phiS[sex[i], age[i,t], chg[i,t,sex[i]] ]
+ phiD[i,t] <- mean.phiD[sex[i], age[i,t]]
+ d[i,t] <- mean.d[sex[i], age[i,t], chg[i,t,sex[i]] ]
+ h[i,t] <- mean.h[sex[i], age[i,t]]
+ p[i,t] <- mean.p[age[i,t+1], sex[i], t]
+ rDS[i,t] <- mean.rDS[sex[i], age[i,t], chg[i,t,sex[i]] ]
+ rDB[i,t] <- mean.rDB[sex[i], age[i,t], chg[i,t,sex[i]] ]
+ r[i,t] <- prob.mat[site[i],DIST[i,D[i]]]
+ }
+ }
+
+ tau ~ dgamma(0.01,0.01)|(0.00001,100)
+
+ mean.pi[1] ~ dunif(0,1)
+ mean.pi[2] ~ dunif(0,1)
+ mean.pi[3] ~ dunif(0,1)
+ mean.pi[4] ~ dunif(0,1)
+
+ mean.pS1[1] ~ dunif(0,1)
+ mean.pS1[2] ~ dunif(0,1)
+
+ mean.pD1[1] ~ dunif(0,1)
+ mean.pD1[2] ~ dunif(0,1)
+
+ for (a in 1:4)
+ {
+ mean.phiS[1,a,1] ~ dunif(0,1)
```

```

+ mean.phiS[2,a,1] ~ dunif(0,1)
+ mean.phiS[1,a,2] ~ dunif(0,1)
+ mean.phiS[2,a,2] ~ dunif(0,1)
+
+ mean.phiD[1,a] ~ dunif(0,1)
+ mean.phiD[2,a] ~ dunif(0,1)
+
+ mean.d[1,a,1] ~ dunif(0,1)
+ mean.d[1,a,2] ~ dunif(0,1)
+ mean.d[2,a,1] ~ dunif(0,1)
+ mean.d[2,a,2] ~ dunif(0,1)
+
+ mean.h[1,a] ~ dunif(0,1)
+ mean.h[2,a] ~ dunif(0,1)
+
+ mean.rDS[1,a,1] <-0
+ mean.rDS[2,a,1] ~ dunif(0,1)
+ mean.rDS[1,a,2] <-0
+ mean.rDS[2,a,2] ~ dunif(0,1)
+
+ mean.rDB[1,a,1] ~ dunif(0,1)
+ mean.rDB[2,a,1] ~ dunif(0,1)
+ mean.rDB[1,a,2] ~ dunif(0,1)
+ mean.rDB[2,a,2] ~ dunif(0,1)
+ }
+
+ for (t in 1:(n.occ-1))
+ {
+   logit(mean.p[2,1,t]) <- P[t]
+   logit(mean.p[2,2,t]) <- P[t]+d.P
+   logit(mean.p[3,1,t]) <- P[t]+d.trois
+   logit(mean.p[3,2,t]) <- P[t]+d.P+d.trois
+   logit(mean.p[4,1,t]) <- P[t]+d.quatre
+   logit(mean.p[4,2,t]) <- P[t]+d.P+d.quatre
+   P[t] ~ dnorm(0,0.001)
+ }
+ d.trois ~ dnorm(0,0.001)
+ d.quatre ~ dnorm(0,0.001)
+ d.P ~ dnorm(0,0.001)
+
+ # Define state-transition and observation matrices
+ for (i in 1:nind)
+ {
+   for (t in f[i]:(n.occ-1))
+   {
+     # Define probabilities of state S at first capture
+     ps1[i,t,1] <- pi[i,t]

```

```

+ ps1[i,t,2] <- 0
+ ps1[i,t,3] <- 1-pi[i,t]
+
+ # Define probabilities of O given S at first capture
+ po1[1,i,t,1] <- (1-pS1[i,t])*rDS[i,t]
+ po1[1,i,t,2] <- 0
+ po1[1,i,t,3] <- pS1[i,t]*(1-rDS[i,t])
+ po1[1,i,t,4] <- pS1[i,t]*rDS[i,t]
+ po1[1,i,t,5] <- 0
+ po1[1,i,t,6] <- 0
+ po1[1,i,t,7] <- 0
+ po1[1,i,t,8] <- 0
+ po1[1,i,t,9] <- 0
+ po1[2,i,t,1] <- (1-pD1[i,t])*rDB[i,t]
+ po1[2,i,t,2] <- 0
+ po1[2,i,t,3] <- 0
+ po1[2,i,t,4] <- 0
+ po1[2,i,t,5] <- pD1[i,t]*(1-rDB[i,t])
+ po1[2,i,t,6] <- pD1[i,t]*rDB[i,t]
+ po1[2,i,t,7] <- 0
+ po1[2,i,t,8] <- 0
+ po1[2,i,t,9] <- 0
+ po1[3,i,t,1] <- 0
+ po1[3,i,t,2] <- (1-pD1[i,t])*rDB[i,t]
+ po1[3,i,t,3] <- 0
+ po1[3,i,t,4] <- 0
+ po1[3,i,t,5] <- 0
+ po1[3,i,t,6] <- 0
+ po1[3,i,t,7] <- pD1[i,t]*(1-rDB[i,t])
+ po1[3,i,t,8] <- pD1[i,t]*rDB[i,t]
+ po1[3,i,t,9] <- 0
+
+ # Define probabilities of state S(t+1) given S(t)
+ ps[1,i,t,1] <- phiS[i,t] * (1-d[i,t]) * (1-h[i,t])
+ ps[1,i,t,2] <- phiS[i,t] * (1-d[i,t]) * h[i,t]
+ ps[1,i,t,3] <- phiS[i,t] * d[i,t] * r[i,t]
+ ps[1,i,t,4] <- 1-phiS[i,t] + phiS[i,t]*d[i,t]*(1-r[i,t])
+ ps[2,i,t,1] <- 0
+ ps[2,i,t,2] <- phiD[i,t]
+ ps[2,i,t,3] <- 0
+ ps[2,i,t,4] <- (1-phiD[i,t])
+ ps[3,i,t,1] <- 0
+ ps[3,i,t,2] <- 0
+ ps[3,i,t,3] <- phiD[i,t]
+ ps[3,i,t,4] <- (1-phiD[i,t])
+ ps[4,i,t,1] <- 0
+ ps[4,i,t,2] <- 0

```



```

+   ps[4,i,t,3] <- 0
+   ps[4,i,t,4] <- 1
+
+   # Define probabilities of O(t) given S(t)
+   po[1,i,t,1] <- (1-p[i,t])*rDS[i,t]
+   po[1,i,t,2] <- 0
+   po[1,i,t,3] <- p[i,t]*(1-rDS[i,t])
+   po[1,i,t,4] <- p[i,t]*rDS[i,t]
+   po[1,i,t,5] <- 0
+   po[1,i,t,6] <- 0
+   po[1,i,t,7] <- 0
+   po[1,i,t,8] <- 0
+   po[1,i,t,9] <- (1-p[i,t])*(1-rDS[i,t])
+   po[2,i,t,1] <- (1-p[i,t])*rDB[i,t]
+   po[2,i,t,2] <- 0
+   po[2,i,t,3] <- 0
+   po[2,i,t,4] <- 0
+   po[2,i,t,5] <- p[i,t]*(1-rDB[i,t])
+   po[2,i,t,6] <- p[i,t]*rDB[i,t]
+   po[2,i,t,7] <- 0
+   po[2,i,t,8] <- 0
+   po[2,i,t,9] <- (1-p[i,t])*(1-rDB[i,t])
+   po[3,i,t,1] <- 0
+   po[3,i,t,2] <- (1-p[i,t])*rDB[i,t]
+   po[3,i,t,3] <- 0
+   po[3,i,t,4] <- 0
+   po[3,i,t,5] <- 0
+   po[3,i,t,6] <- 0
+   po[3,i,t,7] <- p[i,t]*(1-rDB[i,t])
+   po[3,i,t,8] <- p[i,t]*rDB[i,t]
+   po[3,i,t,9] <- (1-p[i,t])*(1-rDB[i,t])
+   po[4,i,t,1] <- 0
+   po[4,i,t,2] <- 0
+   po[4,i,t,3] <- 0
+   po[4,i,t,4] <- 0
+   po[4,i,t,5] <- 0
+   po[4,i,t,6] <- 0
+   po[4,i,t,7] <- 0
+   po[4,i,t,8] <- 0
+   po[4,i,t,9] <- 1
+   }
+ }
+
+ # Likelihood
+ for (i in 1:nind)
+ {
+   z[i,f[i]] ~ dcat(ps1[i,f[i],])

```

```

+   y[i,f[i]] ~ dcat(po1[z[i,f[i]], i, f[i], ])
+   for (t in (f[i]+1):n.occ)
+     {
+       z[i,t] ~ dcat(ps[z[i,t-1], i, t-1, ])
+       y[i,t] ~ dcat(po[z[i,t], i, t-1, ])
+     }
+   }
+ }
+ ",fill = TRUE)
> sink()

```

**Table IV.4.** Parameter estimates from the intra-sexual competition model.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat
mean.pi[1]	0.999	0.001	0.996	0.999	1.000	FALSE	1.000	1.000
mean.pi[2]	0.984	0.011	0.955	0.986	0.998	FALSE	1.000	1.000
mean.pi[3]	0.939	0.041	0.838	0.948	0.992	FALSE	1.000	1.000
mean.pi[4]	0.288	0.043	0.208	0.287	0.375	FALSE	1.000	1.000
mean.pS1[1]	0.499	0.288	0.025	0.499	0.975	FALSE	1.000	1.000
mean.pS1[2]	0.873	0.108	0.600	0.902	0.996	FALSE	1.000	1.000
mean.pD1[1]	0.656	0.086	0.480	0.658	0.816	FALSE	1.000	1.000
mean.pD1[2]	0.848	0.060	0.713	0.854	0.946	FALSE	1.000	1.000
mean.phiS[1,1,1]	0.560	0.025	0.512	0.560	0.609	FALSE	1.000	1.000
mean.phiS[2,1,1]	0.557	0.024	0.510	0.557	0.604	FALSE	1.000	1.000
mean.phiS[1,2,1]	0.767	0.037	0.694	0.767	0.839	FALSE	1.000	1.000
mean.phiS[2,2,1]	0.813	0.038	0.737	0.813	0.888	FALSE	1.000	1.000
mean.phiS[1,3,1]	0.711	0.053	0.608	0.711	0.816	FALSE	1.000	1.000
mean.phiS[2,3,1]	0.674	0.057	0.562	0.673	0.787	FALSE	1.000	1.000
mean.phiS[1,4,1]	0.704	0.097	0.514	0.705	0.893	FALSE	1.000	1.000
mean.phiS[2,4,1]	0.729	0.076	0.579	0.730	0.875	FALSE	1.000	1.000
mean.phiS[1,1,2]	0.400	0.099	0.218	0.396	0.603	FALSE	1.000	1.000
mean.phiS[2,1,2]	0.419	0.064	0.298	0.418	0.547	FALSE	1.000	1.000
mean.phiS[1,2,2]	0.538	0.133	0.293	0.534	0.808	FALSE	1.000	1.000
mean.phiS[2,2,2]	0.468	0.081	0.317	0.466	0.632	FALSE	1.000	1.000
mean.phiS[1,3,2]	0.481	0.178	0.176	0.467	0.863	FALSE	1.000	1.000
mean.phiS[2,3,2]	0.569	0.109	0.366	0.565	0.790	FALSE	1.000	1.000
mean.phiS[1,4,2]	0.450	0.234	0.071	0.428	0.928	FALSE	1.000	1.000
mean.phiS[2,4,2]	0.420	0.138	0.180	0.411	0.713	FALSE	1.000	1.000
mean.phiD[1,1]	0.500	0.289	0.025	0.500	0.975	FALSE	1.000	1.000
mean.phiD[2,1]	0.501	0.289	0.025	0.502	0.976	FALSE	1.000	1.000
mean.phiD[1,2]	0.673	0.234	0.165	0.714	0.988	FALSE	1.000	1.000
mean.phiD[2,2]	0.498	0.289	0.025	0.496	0.975	FALSE	1.000	1.000
mean.phiD[1,3]	0.760	0.116	0.507	0.771	0.952	FALSE	1.000	1.000
mean.phiD[2,3]	0.701	0.124	0.440	0.709	0.917	FALSE	1.000	1.000
mean.phiD[1,4]	0.808	0.018	0.772	0.808	0.842	FALSE	1.000	1.000
mean.phiD[2,4]	0.763	0.020	0.723	0.763	0.801	FALSE	1.000	1.000
mean.d[1,1,1]	0.007	0.007	0.000	0.005	0.026	FALSE	1.000	1.000

mean.d[2,1,1]	0.006	0.006	0.000	0.004	0.022	FALSE	1.000	1.000
mean.d[1,2,1]	0.068	0.023	0.029	0.065	0.119	FALSE	1.000	1.000
mean.d[2,2,1]	0.112	0.029	0.062	0.110	0.174	FALSE	1.000	1.000
mean.d[1,3,1]	0.464	0.057	0.351	0.464	0.575	FALSE	1.000	1.000
mean.d[2,3,1]	0.503	0.058	0.387	0.503	0.615	FALSE	1.000	1.000
mean.d[1,4,1]	0.562	0.094	0.371	0.565	0.736	FALSE	1.000	1.000
mean.d[2,4,1]	0.535	0.076	0.382	0.537	0.679	FALSE	1.000	1.000
mean.d[1,1,2]	0.115	0.101	0.003	0.087	0.375	FALSE	1.000	1.000
mean.d[2,1,2]	0.058	0.054	0.002	0.042	0.200	FALSE	1.000	1.000
mean.d[1,2,2]	0.417	0.146	0.150	0.413	0.705	FALSE	1.000	1.000
mean.d[2,2,2]	0.074	0.067	0.002	0.054	0.249	FALSE	1.000	1.000
mean.d[1,3,2]	0.398	0.191	0.071	0.388	0.779	FALSE	1.000	1.000
mean.d[2,3,2]	0.501	0.127	0.252	0.503	0.741	FALSE	1.000	1.000
mean.d[1,4,2]	0.749	0.205	0.248	0.802	0.992	FALSE	1.000	1.000
mean.d[2,4,2]	0.657	0.162	0.305	0.674	0.918	FALSE	1.000	1.000
mean.h[1,1]	0.004	0.004	0.000	0.003	0.014	FALSE	1.000	1.000
mean.h[2,1]	0.003	0.003	0.000	0.002	0.013	FALSE	1.000	1.000
mean.h[1,2]	0.047	0.016	0.021	0.045	0.083	FALSE	1.000	1.000
mean.h[2,2]	0.010	0.007	0.001	0.008	0.028	FALSE	1.000	1.000
mean.h[1,3]	0.322	0.061	0.209	0.320	0.447	FALSE	1.000	1.000
mean.h[2,3]	0.102	0.039	0.038	0.097	0.191	FALSE	1.000	1.000
mean.h[1,4]	0.148	0.088	0.022	0.133	0.355	FALSE	1.000	1.000
mean.h[2,4]	0.207	0.073	0.085	0.200	0.369	FALSE	1.000	1.000
P[1]	3.247	0.697	2.005	3.201	4.743	FALSE	1.000	1.000
P[2]	1.336	0.460	0.440	1.335	2.241	FALSE	0.998	1.000
P[3]	2.644	0.451	1.793	2.633	3.561	FALSE	1.000	1.000
P[4]	2.585	0.357	1.906	2.577	3.307	FALSE	1.000	1.000
P[5]	3.126	0.374	2.420	3.117	3.885	FALSE	1.000	1.000
P[6]	2.423	0.356	1.745	2.415	3.141	FALSE	1.000	1.000
P[7]	3.602	0.443	2.775	3.586	4.513	FALSE	1.000	1.000
P[8]	1.878	0.351	1.204	1.872	2.582	FALSE	1.000	1.000
P[9]	2.274	0.339	1.625	2.268	2.955	FALSE	1.000	1.000
P[10]	1.970	0.330	1.336	1.965	2.632	FALSE	1.000	1.000
P[11]	2.413	0.352	1.741	2.407	3.119	FALSE	1.000	1.000
P[12]	2.067	0.346	1.401	2.061	2.761	FALSE	1.000	1.000
P[13]	1.782	0.334	1.140	1.778	2.444	FALSE	1.000	1.000
P[14]	1.808	0.324	1.187	1.803	2.456	FALSE	1.000	1.000
P[15]	1.001	0.304	0.411	0.999	1.607	FALSE	1.000	1.000
P[16]	2.566	0.315	1.963	2.561	3.199	FALSE	1.000	1.000
P[17]	2.228	0.320	1.611	2.223	2.868	FALSE	1.000	1.000
P[18]	1.956	0.301	1.378	1.952	2.557	FALSE	1.000	1.000
P[19]	3.352	0.380	2.634	3.342	4.126	FALSE	1.000	1.000
P[20]	3.286	0.360	2.601	3.279	4.015	FALSE	1.000	1.000
P[21]	3.652	0.439	2.840	3.636	4.555	FALSE	1.000	1.000
P[22]	3.749	0.437	2.938	3.732	4.653	FALSE	1.000	1.000

P[23]	4.220	0.491	3.323	4.196	5.246	FALSE	1.000	1.000
P[24]	4.389	0.517	3.463	4.358	5.486	FALSE	1.000	1.000
P[25]	3.463	0.394	2.731	3.451	4.277	FALSE	1.000	1.000
mean.rDS[1,1,1]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,1,1]	0.001	0.001	0.000	0.001	0.005	FALSE	1.000	1.000
mean.rDS[1,2,1]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,2,1]	0.004	0.004	0.000	0.003	0.014	FALSE	1.000	1.001
mean.rDS[1,3,1]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,3,1]	0.102	0.038	0.040	0.098	0.188	FALSE	1.000	1.000
mean.rDS[1,4,1]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,4,1]	0.077	0.041	0.017	0.070	0.175	FALSE	1.000	1.000
mean.rDS[1,1,2]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,1,2]	0.010	0.010	0.000	0.007	0.036	FALSE	1.000	1.000
mean.rDS[1,2,2]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,2,2]	0.031	0.031	0.001	0.022	0.113	FALSE	1.000	1.000
mean.rDS[1,3,2]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,3,2]	0.063	0.060	0.002	0.045	0.222	FALSE	1.000	1.000
mean.rDS[1,4,2]	0.000	0.000	0.000	0.000	0.000	FALSE	1.000	NA
mean.rDS[2,4,2]	0.079	0.074	0.002	0.057	0.277	FALSE	1.000	1.000
mean.rDB[1,1,1]	0.470	0.287	0.021	0.454	0.970	FALSE	1.000	1.000
mean.rDB[2,1,1]	0.488	0.288	0.024	0.482	0.973	FALSE	1.000	1.000
mean.rDB[1,2,1]	0.460	0.117	0.242	0.457	0.695	FALSE	1.000	1.000
mean.rDB[2,2,1]	0.331	0.113	0.135	0.323	0.571	FALSE	1.000	1.000
mean.rDB[1,3,1]	0.417	0.059	0.305	0.416	0.537	FALSE	1.000	1.000
mean.rDB[2,3,1]	0.574	0.070	0.437	0.575	0.709	FALSE	1.000	1.000
mean.rDB[1,4,1]	0.667	0.024	0.618	0.667	0.713	FALSE	1.000	1.000
mean.rDB[2,4,1]	0.653	0.026	0.601	0.653	0.704	FALSE	1.000	1.000
mean.rDB[1,1,2]	0.497	0.289	0.025	0.495	0.975	FALSE	1.000	1.000
mean.rDB[2,1,2]	0.490	0.288	0.024	0.485	0.973	FALSE	1.000	1.000
mean.rDB[1,2,2]	0.654	0.181	0.270	0.671	0.944	FALSE	1.000	1.000
mean.rDB[2,2,2]	0.464	0.287	0.021	0.446	0.969	FALSE	1.000	1.000
mean.rDB[1,3,2]	0.738	0.198	0.278	0.781	0.991	FALSE	1.000	1.000
mean.rDB[2,3,2]	0.367	0.149	0.116	0.354	0.686	FALSE	1.000	1.000
mean.rDB[1,4,2]	0.598	0.072	0.454	0.599	0.735	FALSE	1.000	1.000
mean.rDB[2,4,2]	0.568	0.051	0.468	0.568	0.666	FALSE	1.000	1.000
tau	0.614	0.068	0.488	0.611	0.753	FALSE	1.000	1.000
deviance	3958.565	53.319	3857.937	3957.301	4066.803	FALSE	1.000	1.000



# Chapter V.A

## Sociality, Group contribution & Fitness

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### Testing determinants of the annual individual fitness: an overall-mean mixture-model for de-lifing data

**Abstract:** The de-lifing method (Coulson *et al.* 2006), though very promising for studying ecological and evolutionary changes, has yet to be used to identify factors influential on fitness. Through simulations representative of a variety of iteroparous species, we establish that a two-component normal mixture usually provides a much better representation of de-lifing data than the single normal distribution assumed in linear models. To analyse factors acting on de-lifing data, we propose the Overall Mean Mixture Model (O3M), a mixture model parameterized in terms of the overall mean, the measure of annual individual fitness on which we seek to examine the influence of social status, sex, age... We compare the performances and accuracy of the O3M with that of a classical linear model on simulated finite normal mixture distributions for different regression shapes and variance structure, and apply it to a real data set to study how the annual individual fitness varies with age in Alpine marmots. The O3M improves considerably the precision of the estimates and the power of the analysis. We discuss the adaptation of the O3M model to more complex distributions and advise on its use.

**Keywords:** Ecology and Evolution · Fitness · Mixture modelling · Multi-modal distributions · Linear modelling

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## 10.1. Introduction

When working on evolution and/or selection in natural conditions, most studies either use generation-based proxies for fitness, such as Lifetime Reproductive Success (LRS: Clutton-Brock 1988), or fitness-related traits, such as age-state specific survival or reproductive rates, clutch size, life expectancy, age at first reproduction and so on (see Kingsolver *et al.* 2001 for a review). However, such measures present theoretical and empirical pitfalls. Fitness related traits, for instance, may not be impacted with the same strength and in the same direction by a given factor (Lande 1982). Because trade-offs occur between traits, one can hardly extrapolate conclusions regarding one trait to general conclusions regarding evolutionary changes. LRS, on the other hand, does incorporate both survival and fecundity but it has been shown to suffer from other problems in species with overlapping generations or when ecological variation occurs during the lifespan of an individual (Coulson *et al.* 2003). In addition, LRS requires to record individual performance for the entire lifespan, which makes it hard to collect sufficient and comparable data, especially for long-lived species.

To overcome such problems, different non-generational fitness measures have been proposed, including de-lifing (Coulson *et al.* 2006a). This recent method, derived from the jackknife technique (Miller 1974), estimates an individual's contribution to the population growth rate over a period of time shorter than a generation. This contribution to population growth rate can be considered as the realized fitness of an individual during this time interval, usually a year, and offers great opportunities to empirically study ecological and evolutionary changes in stochastic environments (Coulson *et al.* 2006a). This method offers both theoretical and practical advantages. First, contrary to fitness related traits it integrates both survival and reproduction. Second, contrary to LRS based approaches, it offers the possibility to calculate fitness for individuals with incomplete life histories. Lastly but most importantly, it allows for the consideration that selection is a continuous process acting at any time and that the realized fitness of an individual is inherently relative to the changes in environment and to the performance of potential competitors, *i.e.* relative to the population size and composition at any given time. It is then possible to calculate selection gradients by regressing the values of a trait of interest on the individual fitness values, and thus determine how this trait might evolve and be an important fitness determinant when accounting for variations in the population during the time interval under study.



Despite the original paper being largely cited (114 citations registered on Web of Science<sup>tm</sup> as of June 2016), the method was scarcely applied to actual data. Fifteen studies only were able to calculate and analyse the individuals' contributions to growth rate of wild populations (Tab.V.1). The need for detailed long-term survival, reproductive data and population size estimates might be responsible for the rarity of studies using this powerful tool. However, such datasets exist and the method is applicable to incomplete data. Instead, we believe that analytical difficulties might prevent researchers from using this method. Indeed, in many cases, the individual fitness data display a strong bimodal distribution. Therefore, commonly used statistical tools from the generalized linear model family (linear models in a broad sense, including but not limited to glm, glmm, gamm...) cannot be used without considerable violations of the underlying assumptions, potentially leading to invalid diagnoses and biased estimates, hence leading to inaccurate conclusions (Jarque & Bera 1987).

Here, we propose a linear model derived from the mixture modelling framework (McLachlan & Peel 2004), called the Overall Mean Mixture Model (O3M). It was specifically designed to study the determinants of individual fitness, calculated as the individual contribution to population growth rate, in wild populations. Mixture models have already proven very useful in ecological and evolutionary studies where individuals are often distributed among different unrecorded or unobserved states (e.g. zero-inflated ecological data, Martin *et al.* 2005; uncertain class of abundance for amphibians, Royle & Link 2005; different growth trajectories of roe deer, Hamel *et al.* 2016). However, our aim here is quite different. We believe the multimodality of the de-lifing data is an inherent distributional property of this fitness metric and does not reflect biologically relevant clusters of individuals. That is to say, the different modes of the fitness distribution do not represent distinct classes of individuals in different states but are contingent on random events in a given year. Hence, we do not wish to identify how the individuals in the population are distributed among different clusters and independently impacted by a set of covariates (as already implemented mixture models do, *i.e.* *FlexMix* R package, Leisch 2004). Instead, we wish to estimate how the annual fitness expectancy of an individual in the population, hence the overall mean of the bimodal distribution, covaries with a set of independent variables while accounting for the bimodality of the data.

**Table V.1.** Publications to use the de-lifing method. NA means the individual annual fitness were calculated for descriptive reasons, but were not analysed using any statistical model.

Publication	Type of model	Explanatory variables	Study species
(Cockburn <i>et al.</i> 2008)	glm & gam	Week in year nuptial plumage attained	Superb fairy wrens ( <i>Malurus cyaneus</i> )
(Di Fonzo <i>et al.</i> 2011)	multiple regression	Body weight, Fecal eggs count Heterozygosity & year	Soay sheep ( <i>Ovis aries</i> )
(Ezard <i>et al.</i> 2007)	gamm & glmm	Laying date, arrival date & mass	Common terns ( <i>Sterna hirundo</i> )
(Foerster <i>et al.</i> 2007)	bivariate animal model	Relatedness	Red deer ( <i>Cervus elaphus</i> )
(Grange <i>et al.</i> 2009)	glm	Population size	Camargue horses ( <i>Equus caballus</i> )
(Gratten <i>et al.</i> 2008)	animal model	Relatedness & presence/absence of alleles	Soay sheep ( <i>Ovis aries</i> )
(Höner <i>et al.</i> 2010)	glm	Population size & rank of the mother	Spotted hyenas ( <i>Crocuta crocuta</i> )
(Höner <i>et al.</i> 2012)	NA	NA	Spotted hyenas ( <i>Crocuta crocuta</i> )
(Moyes <i>et al.</i> 2009)	PCA	NA	Red deer ( <i>Cervus elaphus</i> )
(Nicolai <i>et al.</i> 2014)	NA	NA	Black brant geese ( <i>Branta bernicla nigricans</i> )
(Pelletier <i>et al.</i> 2007a)	gam	Body weight, hind leg length & birth weight	Soay sheep ( <i>Ovis aries</i> )
(Pelletier <i>et al.</i> 2007b)	gam	Body mass	Bighorn sheep ( <i>Ovis canadensis</i> )
(Schroeder <i>et al.</i> 2011)	MCMC glmm	Pit treatment, sex, age & year (random)	House sparrow ( <i>Passer domesticus</i> )
(Schroeder <i>et al.</i> 2012)	MCMC glmm	Age & year	House sparrow ( <i>Passer domesticus</i> )
(Stopher <i>et al.</i> 2008b)	NA	NA	Red deer ( <i>Cervus elaphus</i> )

We start by presenting a simulation study to show that a two-class mixture distribution better describes de-lifing data than a single Gaussian one. Then we present the O3M model and compare it to a classical linear model to demonstrate its usefulness. To do so, we simulated data sets following different scenarios where the mean of a two-components normal mixture distribution was dependent on a hypothetical variable, and we compared the results obtained by the O3M and a classical linear model. Finally, we illustrate the usefulness of our model on real data with an analysis of the relationship between annual realized fitness calculated using the de-lifing method and age in a cooperatively breeding mammal, the Alpine marmot (*Marmota marmot*). We end by discussing the strengths and limitations of our approach, by providing general advice on how and when to use it, and discussing further developments.

## 10.2. Material and methods

### 10.2.1. De-lifing data distribution

According to (Coulson *et al.* 2006a), the annual individual fitness of individual  $i$  is measured by its contribution  $p_{ti}$  to the growth rate of the population between  $t$  and  $t+1$ .

$$p_{ti} = \frac{S_{ti} - \bar{S}_t}{N_t - 1} + \frac{F_{ti} - \bar{F}_t}{N_t - 1} \quad (1)$$

where  $S_{ti}$  is the survival of individual  $i$  between  $t$  and  $t+1$  (1 if it survived and 0 otherwise),  $\bar{S}_t$  is the mean survival rate in the population between  $t$  and  $t+1$ ;  $F_{ti}$  is the fecundity of individual  $i$  defined as the number of offspring born between  $t$  and  $t+1$  and still alive at  $t+1$ ;  $\bar{F}_t$  is the mean fecundity in the population between  $t$  and  $t+1$  and  $N_t$  is the population size at  $t$ .

In order to analyse the distributional properties of individual fitness calculated using the de-lifing method, we simulated several data sets under different parameterizations. These parameterizations covered a wide range of biological scenarios on the slow-fast continuum (Gaillard *et al.* 2005), from species with high survival, high reproductive skew and small litter size to species with low survival, evenly distributed reproduction and large number of offspring. For each simulation, individual annual survival ( $S_{ti}$ ) and reproductive status ( $R_{ti}$ ) were sampled from a Bernoulli with different rates (low = 0.2, medium = 0.5 or high = 0.8). The number of recruits per individual ( $NR_{ti}$ ) that survive to the next time step were sampled either from a Gaussian or Poisson

distribution (mean = 1 or 6 and standard deviation = 0.05 or 2 for the Gaussian). The fecundity used in the calculation ( $F_{ti}$ ) was calculated as the product  $R_{ti} * NR_{ti}$ . To account for between-year population size fluctuation, the annual population size ( $N_t$ ) was sampled from a Gaussian distribution with mean 20 and standard deviation of 0.2 (stable population) or 2 (fluctuating population). Finally, we calculated the individual fitness values  $p_{ti}$  following equation 1 for 20 years for each scenario leading to a mean of 400 individual.year per data set. Each simulation scenario was repeated ten times leading to a total of 1080 simulated data sets.

We then fitted a two-component mixture of normal distributions to each simulated data set and compared it to a single normal distribution to test if  $p_{ti}$  distributions were best approximated by a mixture of two normal distributions or by a single normal distribution. Both distributions were fitted with a burning period of 6000 and a total number of iterations of 10000 (see supplementary material 10.6.1 for the simulation and distributions fitting R-scripts).

### 10.2.2. Overall-Mean Mixture Model

The classical linear model can be described by:

$$N(y|\mu, \sigma^2) \text{ with } \mu = \alpha + \beta.x \quad (2)$$

where  $y$  is the random variable we wish to explain, *i.e.* the annual fitness in our case,  $\mu$  and  $\sigma^2$  are respectively the mean and variance of the normal conditional density of  $y$ ,  $x$  is the vector of independent variables we wish to relate  $y$  to,  $\alpha$  is the intercept and  $\beta$  is the vector of variable-specific coefficients. Here, we replace the normal distribution with a mixture of two normal distributions:

$$h(y|\mu_1, \mu_2, \pi, \sigma_1^2, \sigma_2^2) = \pi.N(y|\mu_1, \sigma_1^2) + (1 - \pi).N(y|\mu_2, \sigma_2^2) \quad (3)$$

where  $\pi$  is the mixture weight of the first component and  $\mu_k$  and  $\sigma_k^2$  are the mean and variance of the  $k^{th}$  component.

Following Everitt (1981), the mean and variance of the normal mixture are:

$$\mu = \pi.\mu_1 + (1 - \pi).\mu_2 \quad (4.1)$$

$$\sigma^2 = \pi.[\sigma_1^2 + (\mu_1 - \mu)^2] + (1 - \pi).[ \sigma_2^2 + (\mu_2 - \mu)^2] \quad (4.2)$$

The mean of the mixture distribution  $\mu$  is thus the weighted mean of the different component-specific means and the variance of the mixture distribution  $\sigma^2$  is the sum of the mean of the component-specific variances and the variance of the component-specific means. We refer to this mean and variance as the “overall mean” and “overall variance” of the mixture distribution.

Here we aim at estimating the overall mean of the mixture distribution  $\mu$  and see how it relates to a set of independent covariates. To do so, we express  $\mu$  as a linear combination of the independent covariates and express the component-specific means as functions of the overall mean  $\mu$ , the mixture weight  $\pi$ , and the difference between the two component-specific means  $\Delta$ :

$$\mu = \alpha + \beta \cdot x \quad (5.1)$$

$$\mu_1 = \mu - (1 - \pi) \cdot \Delta \quad (5.2)$$

$$\mu_2 = \mu + \pi \cdot \Delta \quad (5.3)$$

$$\text{with } \Delta = \mu_2 - \mu_1$$

The same reasoning could be applied to obtain a linear expression of the overall variance  $\sigma^2$ , by expressing the two component-specific variances as (slightly more complicated) expressions of the overall variance, the mixture weight, the difference between the component-specific variances, the overall mean and the component-specific means. However, we did not consider this case in our model since we had no *a priori* hypotheses about the overall variance. For full flexibility, we consider the case where  $\Delta$  and  $\pi$  are allowed to vary with the same set of independent variables  $x$  as  $\mu$ . Since  $\pi$  is a probability, we use a logit-linear relationship to relate  $\pi$  and  $x$ . To avoid a common practical problem in mixture modelling known as “label switching”(Lunn *et al.* 2012), we constrain one component-specific variance to be larger than the second one by specifying a positive difference between the two:

$$h(y | \mu, \Delta, \pi, \sigma_1^2, \sigma_2^2) = \pi \cdot N(y | \mu, \Delta, \sigma_1^2) + (1 - \pi) \cdot N(y | \mu, \Delta, \sigma_2^2) \quad (6.1)$$

$$\text{with } \mu = \alpha + \beta \cdot x \quad (6.2)$$

$$\text{logit}(\pi) = \alpha_\pi + \beta_\pi \cdot x \quad (6.3)$$

$$\Delta = \alpha_\Delta + \beta_\Delta \cdot x \quad (6.4)$$

$$\text{with } \sigma_1^2 > \sigma_2^2$$

The parameters of the model are then the different intercepts  $\alpha$ ,  $\alpha_\pi$ ,  $\alpha_\Delta$ , the regression coefficients  $\beta$ ,  $\beta_\pi$ ,  $\beta_\Delta$  and the two component-specific variance parameters  $\sigma_2^2$  and  $\sigma_1^2$ .

### 10.2.3. Parameters estimation

Specifying the mixture normal rather than a simple normal distribution entails a price in terms of number of parameters and model complexity. To test whether the gain was worth the additional complexity, we compared the performance of the O3M to a linear model on simulated two-component normal mixture distributions. The data sets were simulated to mimic the distribution of de-lifing-like data driven by a covariate (*e.g.* discrete age classes in our case). The data simulation process was as follow. First, we sampled a covariate value  $x_i$  from a Poisson distribution with a mean of 4 for each of 1000 simulated individuals. Given this value, the individual probability  $\pi_i$  to belong to the first component of the mixture was calculated as  $\pi_i = \text{logit}^{-1}(\alpha_\pi + \beta_\pi \cdot x_i)$  and the component to which the individual belonged was sampled from a Bernoulli distribution  $C_i = \text{Bern}(\pi_i)$ . Conditionally on  $C_i$ , the fitness value of an individual was sampled from the corresponding normal;  $N(\mu_1, \sigma_1^2)$  if  $C_i = 0$  (individual  $i$  belongs to the first component of the mixture) with  $\mu_1 = \mu_i - \pi_i \cdot \Delta_i$  and  $\sigma_1^2$  the first component-specific variance, and  $N(\mu_2, \sigma_2^2)$  if  $C_i = 1$  with  $\mu_2 = \mu_i + (1 - \pi_i) \cdot \Delta_i$  and  $\sigma_2^2$  the second component-specific variance, where  $\mu_i$  is the general mean of the mixture distribution  $\mu_i = \alpha + \beta \cdot x_i$  and  $\Delta_i$  is the difference between the mean of the two components. For a given value of  $x_i$ ,  $\Delta_i = \alpha_\Delta + \beta_\Delta \cdot x_i$ .

We produced different data sets of increasing complexity to cover a wide range of possibilities, from constant overall mean  $\mu$ , mixture weight  $\pi$  and difference  $\Delta$  (*i.e.* no effect of the variable  $x_i$ ) to quadratic relationships between  $\mu$  and  $x$ , linearly increasing  $\Delta$  and logit-linearly increasing  $\pi$  (Tab.V.2). We then fitted the O3M model and a classical linear model independently ten times for each scenario with a burning period of 6000 and a total number of iterations of 10000 to determine the accuracy of the parameter estimates (see supplementary material 10.6.2 for the simulation and O3M scripts). To be able to analyse the results from the different simulations together, we worked on the difference between the simulated and the estimated value of the regression parameters of the mean for each run of each simulation for both the O3M and the linear model. To determine whether the linear model was able to recover the simulated parameters although the specified distribution violates the linear models assumptions, we tested if

these differences between the simulated values and the estimated parameters were significantly different between the O3M and the linear model using Wilcoxon signed rank tests. We then tested if the precision of the estimates differed between the two models by testing if the standard deviations associated to the different regression parameters differed between the O3M and the linear model using Wilcoxon signed rank tests.

**Table V.2.** Summary of parameters used in the simulations for the second analysis.

A - CLUSTERING PARAMETERS			
1 - Component-means difference			
Slight difference	$\alpha_{\Delta} = 2$		
Large difference	$\alpha_{\Delta} = 10$		
Variable difference	$\alpha_{\Delta} = 2$	$\beta_{\Delta} = 1$	
2 - Component-specific standard deviation			
Identical	$\sigma_1 = \sigma_2 = 1$		
Component-specific	$\sigma_1 = 1.5$	$\sigma_2 = 0.5$	
3 - Proportion of individuals in each cluster			
Balanced	$\alpha_{\pi} = 0$		$(\pi = 0.5)$
Unbalanced	$\alpha_{\pi} = 1$		$(\pi = 0.27)$
Variable	$\alpha_{\pi} = -0.6$	$\beta_{\pi} = 0.9$	$(\pi \in [0.35; 1])$
B - REGRESSION PARAMETERS			
Constant	$\alpha = 0$		
Linear	$\alpha = 0$	$\beta = 1$	
Quadratic	$\alpha = 0$	$\beta = 1$	$\beta^2 = -0.1$

#### 10.2.4. Real data application: Fitness variation with age in the Alpine marmot

To illustrate the usefulness of our model in evolutionary studies, we applied it to data from a long-term field study on Alpine marmots. We studied how the individual annual fitness calculated with the de-lifing method varies with age using the O3M, and compared our results to those obtained with a classical linear model. From 1990, individuals from the population located in the Grande Sassièrè Nature Reserve (Vanoise, France) were captured each summer between May 15<sup>th</sup> and July 15<sup>th</sup>. At first capture, individuals were permanently marked using both pit-tags and metal ear tags for later identification by recapture and/or resighting (Cohas *et al.* 2008b). Each individual's annual survival ( $S_{it}$ ) and reproductive status ( $R_{it}$ ) was determined either from capture-recapture data or from observations. The annual number of recruits per individual ( $NR_{it}$ ) was estimated as the number of offspring produced per individual (determined by

genetic kinship analyses) that survived the first hibernation. Because the study area and the recapture pressure increased during the study period, and for the de-lifing calculation to be coherent with time, we limited our analysis to a subset of the complete data set, *i.e.* the data concerning the central location of the study area during the years 1994-2014, leading to a total sample size of 1417 individual.years. More details on the study species, the study area, and the genetic analyses can be found elsewhere (Allainé & Theuriau 2004; Cohas *et al.* 2007; Ferrandiz-Rovira *et al.* 2016 and chapter II).

We calculated the annual individual fitness  $p_{ti}$  following equation 1 and tested whether the annual fitness of Alpine marmots varied with age. We expected annual fitness to increase in the first years of age because of low juvenile survival and progressive access to reproduction (marmots are sexually mature at 2 years of age, Allainé & Theuriau 2004) and to decrease in older ages because of senescence (Berger *et al.* 2016). Therefore, we accounted for a quadratic effect of age on fitness in our model. Social status is strongly differentiated in Alpine marmots (dominant individuals monopolize reproduction for example, Goossens *et al.* 1998) and sex differences in fitness are most likely to exist (male dominants turn-over is higher than females' one and male subordinates may access reproduction *via* extra-pair paternities (Cohas *et al.* 2007; Lardy *et al.* 2012). We then included both factors in the model. For the same reasons, we expected the distribution of fitness to vary with the social status and sex. Therefore, we incorporated different variance structures according to sex and status in our model:

$$p_{ti} = \alpha_{(Status,Sex)} + \beta_{(Status,Sex)} \cdot age_{ti} + \beta^2_{(Status,Sex)} \cdot (age_{ti})^2 + \varepsilon_{ti}$$

$$\text{with } \varepsilon_{ti} \sim \pi \cdot N(0, \sigma_1^2) + (1 - \pi) \cdot N(0, \sigma_2^2)$$

Thus, the O3M model was:

$$h(p_{ti} | age, Status, Sex) = \pi \cdot N(p_{ti} | \mu_{ti}, \Delta, \sigma_1^2_{(Status,Sex)}) + (1 - \pi) \cdot N(p_{ti} | \mu_{ti}, \Delta, \sigma_2^2_{(Status,Sex)})$$

$$\text{with } \mu_{ti} = \alpha_{(Status,Sex)} + \beta_{(Status,Sex)} \cdot age_{ti} + \beta^2_{(Status,Sex)} \cdot (age_{ti})^2$$

$$\text{logit}(\pi) = \alpha_{\pi(Status,Sex)} + \beta_{\pi(Status,Sex)} \cdot age_{ti}$$

$$\text{and } \Delta = \alpha_{\Delta(Status,Sex)} + \beta_{\Delta(Status,Sex)} \cdot age_{ti}$$

For comparison, the linear model was:

$$N(p_{ti} | \lambda_{ti}, \sigma^2)$$

$$\text{with } \lambda_{ti} = \alpha_{(Status,Sex)} + \beta_{(Status,Sex)} \cdot age_{ti} + \beta^2_{(Status,Sex)} \cdot (age_{ti})^2$$



We calculated the residuals of both models to check *a posteriori* if the underlying assumptions of both models were respected. In the case of the linear models, the residuals  $\varepsilon_{i,t} = \mu_{ti} - p_{ti}$  are supposed to be normally distributed. In the case of the O3M, residuals are calculated according to each component  $\varepsilon_{i,t} = \mu_{k,ti} - p_{ti}$  and are thus normally distributed only within each component. Thus, if we look at the overall distribution of the O3M residuals, we should obtain a mixture of two normal distributions centered on zero with a mixing proportion  $\pi$ .

All simulations and statistical tests were conducted using R 3.2.5 (R Development Core Team 2008). The different models (O3Ms and linear models) were written using the BUGS language and parameters estimation was performed using jags (Plummer 2003b) from R with the jagsUI package (Kellner 2014). Model selection was done based on DIC values (Spiegelhalter *et al.* 2002b).

### 10.3. Results

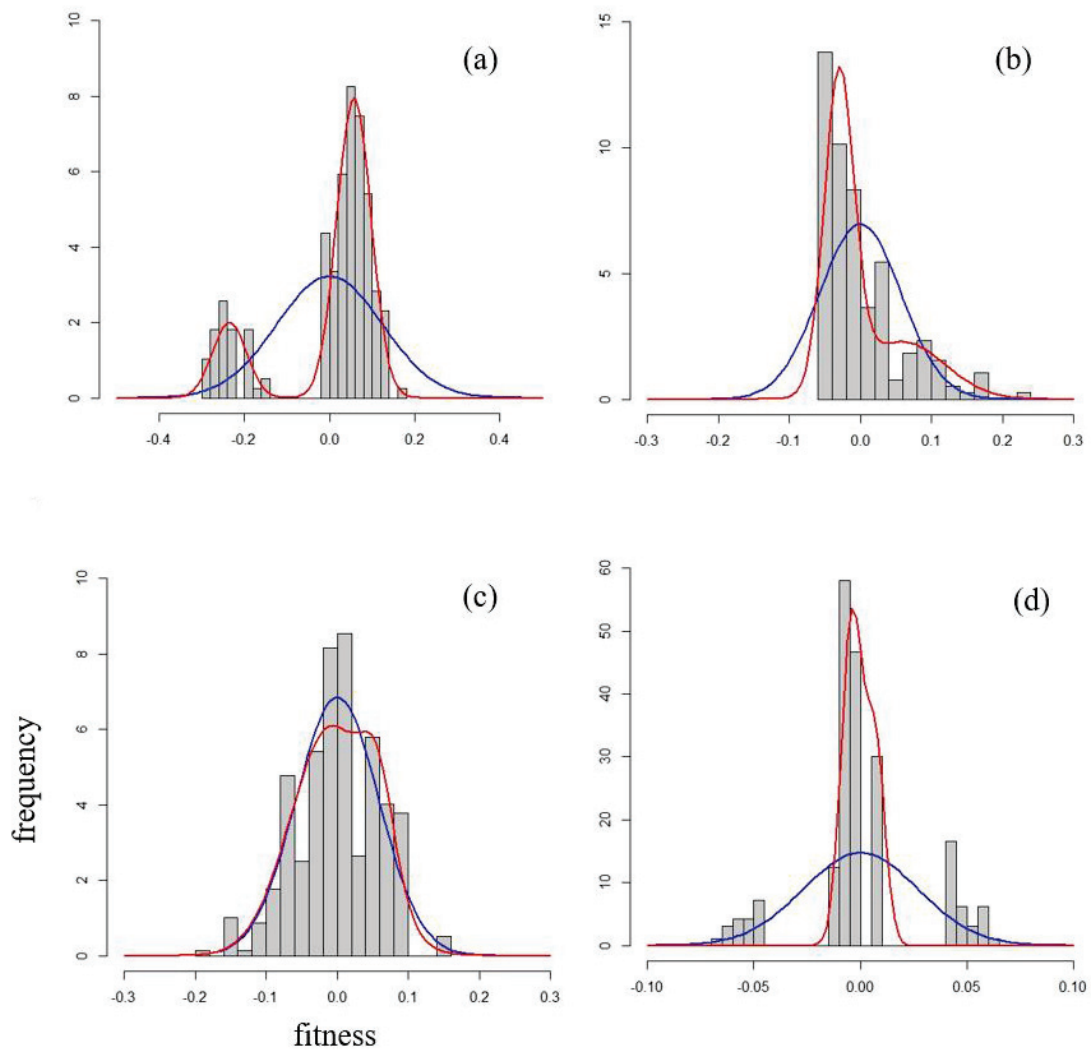
#### 10.3.2. De-lifing data distribution

According to the DIC, the two-component normal mixture distribution fitted best the simulated de-lifing data under almost every scenario (Fig.V.1a and V.1b). In 91% of the simulations, the DIC difference was larger than two supporting the O3M as the best of the two models (see supplementary material 10.6.3 for a table with complete results). A single normal distribution better approximated de-lifing data in only 10 out of the 108 simulated data sets. Although no clear pattern emerged when looking at the relationships between the parameters in the simulations and the DIC difference between the two models (Fig.V.2), data sets better fitted by a Normal distribution corresponded to one of two situations. First, when de-lifing data tended to be uni-modally and normally distributed (Fig.V.1c), second when individual fitness data presented three distinct modes (Fig.V.1d).

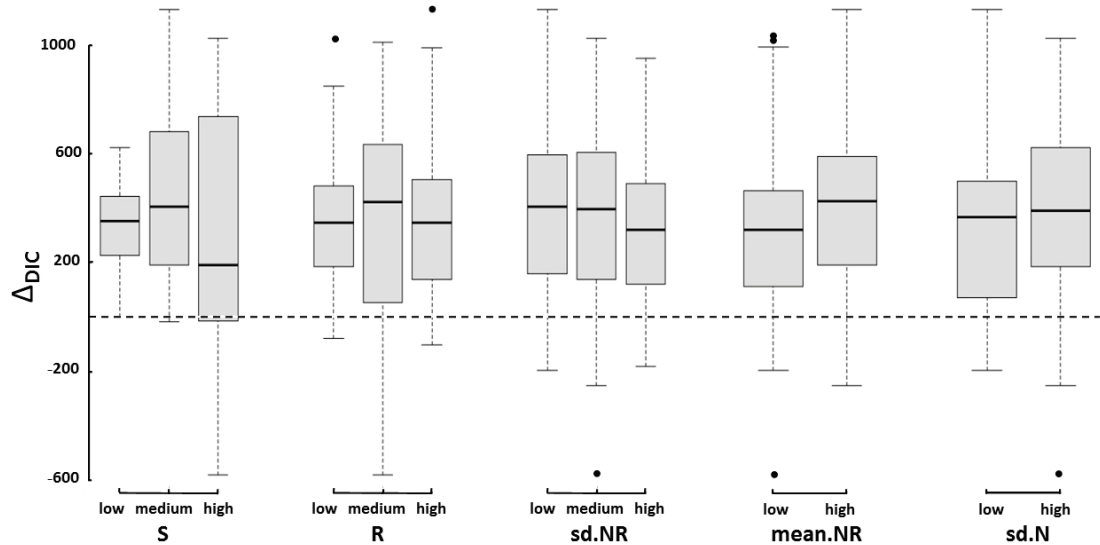
#### 10.3.3. Parameters estimation

As expected, for all simulated data sets, the O3M gave unbiased estimates of the parameters of interest, *i.e.* the regression parameters of the overall mean ( $\alpha$ ,  $\beta$  and  $\beta^2$ , Fig.V.3). More surprising, the linear model also gave unbiased regression coefficients. Indeed, the mean estimates did not significantly differ between both models (Wilcoxon signed rank tests for  $\alpha$ :  $W = 1212$ ,  $p\text{-value} = 0.131$ ;  $\beta$ :  $W = 1595$ ,  $p\text{-value} = 0.403$ ;  $\beta^2$ :  $W$

= 1529, p-value = 0.666). However, the variance in the estimates of the regression parameters was always lower using the O3M model. Most importantly, the standard deviation associated to each of the three regression parameters was always smaller using the O3M (Fig.V.4) as demonstrated by the one-sided Wilcoxon signed rank tests between the standard deviations of the different regression parameters ( $sd_{b0}$ :  $W = 64$ , p-value < 0.001;  $sd_{b1}$ :  $W = 7$ , p-value < 0.001;  $sd_{b2}$ :  $W = 2$ , p-value < 0.001).



**Figure V.1.** Histogram of simulated data and models fit. Blue curves represent the fitted Normal distribution; Red curves represent the fitted O3M. (a) and (b) represent cases where the two-normal mixture distribution has the best fit; (c) and (d) represent cases where the normal distribution has the best fit.



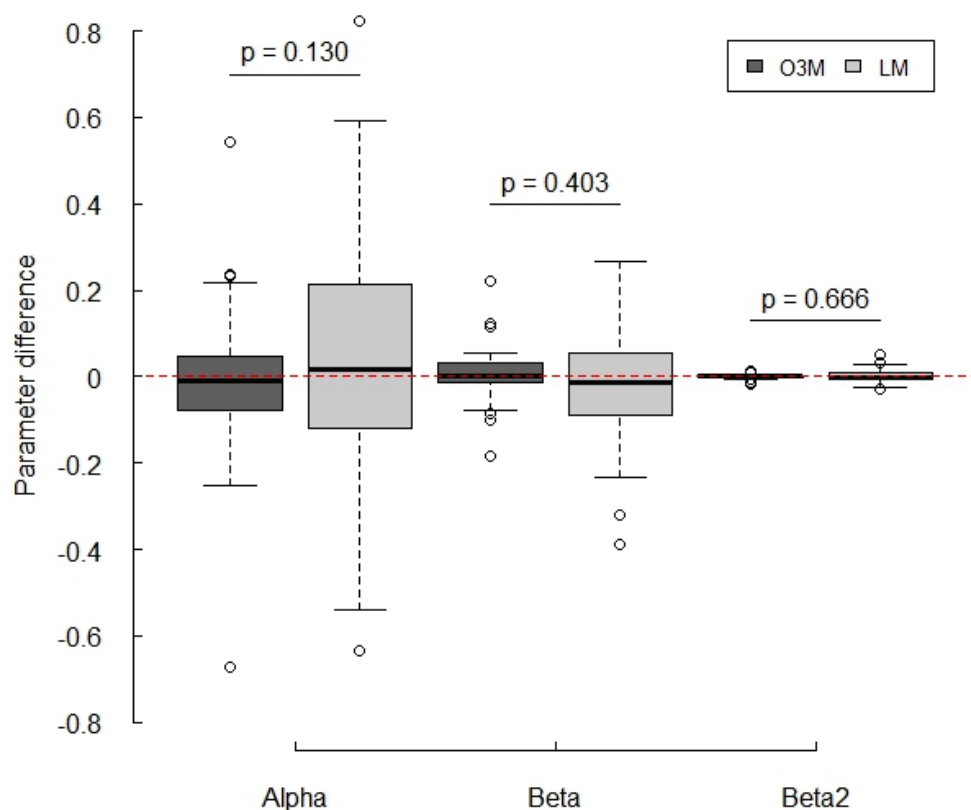
**Figure V.2.** Boxplots of DIC difference between the two-component normal mixture distribution and the Normal model. A positive  $\Delta_{\text{DIC}}$  indicates the two-component normal mixture fits the data better than the linear model. S: survival probability (low: 0.2, medium: 0.5, high: 0.8); R: reproductive success probability (low: 0.2, medium: 0.5, high: 0.8); sd.NR: standard deviation of the number of recruits produced (low: 0.05 or high: 2 for the Gaussian distribution,  $\text{sd} = \sqrt{\text{mean}}$  for the Poisson); mean.NR: mean number of recruits per individual. $\text{year}^{-1}$ ; sd.N: standard deviation of the annual population size (low: 0.2 or high: 2).

#### 10.3.4. Fitness variation with age in the Alpine marmot

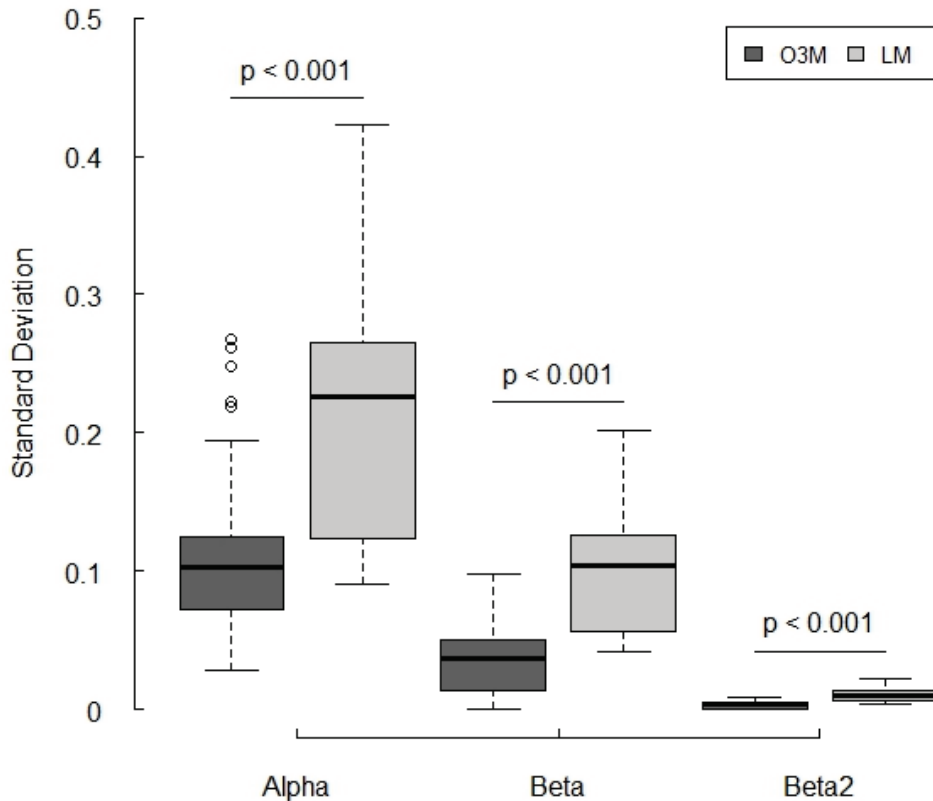
The O3M performed better than the classical linear model as indicated by the DIC (DIC difference between the linear model and the O3M = 186). We analysed the residuals of the models to check the assumption of normality. The residuals for dominants departed from the assumed normal distribution when using the linear model (Fig.V.5b and V.5d; Shapiro-Wilk tests, dominant males:  $W = 0.986$ ,  $p\text{-value} = 0.023$  and dominant females:  $W = 0.991$ ,  $p\text{-value} = 0.045$ ). This departure was especially apparent for subordinate individuals as can be visually asserted given the bimodality of these residuals (Fig.V.5f and V.5h, Shapiro-Wilk tests, subordinate males:  $W = 0.913$ ,  $p\text{-value} < 0.0001$  and subordinate females:  $W = 0.911$ ,  $p\text{-value} < 0.0001$ ). On the contrary, residuals for the O3M seemed to fit well the underlying two-component normal distributions assumed by the model (Fig.V.5a, V.5c, V.5e and V.5g).

Following our previous results, the estimates obtained using the O3M and the linear model were not qualitatively different and only little quantitatively different. However, the standard deviations associated to the different parameters in the model

were always smaller with the O3M (Tab.V.3 and V.4). Both male and female dominants' annual fitness significantly increased with age until approximately seven years of age and decreased thereafter (Fig.V.6a and V.6b). For female subordinates, both the linear and quadratic terms were not significantly different from zero contrary to the intercept, indicating that the annual fitness was constant with age and always negative (Fig.V.6c). For male subordinates, the intercept and the quadratic terms were significantly different from zero, indicating an increase in fitness accelerating with age (Fig.V.6d). Note that the linear model gave qualitatively different (although quantitatively close) estimates for the subordinate males. The linear effect for subordinate males was negative and different from zero with the linear model (Tab.V.4), thus indicating a significant decrease in fitness in the first years of life followed by an accelerating increase after 3 years of age. On the contrary, it was null with the O3M indicating no decrease in the first years of age (Tab.V.3).



**Figure V.3.** Boxplot of the regression parameter differences between the simulated value and the estimated value for both the Overall Mean Mixture Model (O3M) and a classical linear model (LM). A parameter difference of zero indicates the value of the parameter estimates exactly equals the value of the parameter used in the simulation.



**Figure V.4.** Standard deviation associated to the regression parameters estimated for both the Overall Mean Mixture Model (O3M) and the classical linear model (LM).

## 10.4. Discussion

### 10.4.2. Overall Mean Mixture Model

Our results indicate that the O3M is a powerful and well-designed model for analysing fitness data calculated using the de-lifing method. Our simulations show that the distribution of such fitness data are most often bimodal, thus violating the underlying assumptions of classical regression models such as the generalized linear model family. We also showed that these distributions could be approximated by a finite mixture of Gaussian distributions and therefore analysed in a mixture modelling framework using the Overall-Mean Mixture Model.

When de-lifing data follow a mixture of two normal distributions, as is most often the case (as demonstrated in the first analysis and in the example on Alpine marmots), the O3M was able to accurately recover the different parameters used in the simulations. Contrary to our expectations, the linear model also gave good estimations of the simulated values. However, the O3M estimates were much more precise than the linear model ones, *i.e.* the confidence intervals associated to the regression parameters were always smaller with the O3M.

**Table V.3.** JAGS Output for the Alpine marmot individual fitness with age analysis using the O3M. Rhat indicates convergence (inferior to 1.1), n.eff is a measure of effective sample size, overlap0 checks if 0 falls in the parameter's 95% credible interval, f is the proportion of the posterior with the same sign as the mean; i.e., our confidence that the parameter is positive or negative.

parameter	mean	sd	2.5%	50%	97.5%	overlap0	f	R <sub>hat</sub>	n.eff
$\alpha_{\text{Dom}}^{\text{♀}}$	0.139	0.202	-0.253	0.139	0.532	TRUE	0.753	1.017	123
$\alpha_{\text{Dom}}^{\text{♂}}$	0.165	0.181	-0.186	0.161	0.526	TRUE	0.817	1.020	103
$\alpha_{\text{Sub}}^{\text{♀}}$	-0.572	0.091	-0.752	-0.570	-0.401	FALSE	1.000	1.007	309
$\alpha_{\text{Sub}}^{\text{♂}}$	-0.555	0.126	-0.808	-0.553	-0.310	FALSE	1.000	1.006	322
$\beta_{\text{Dom}}^{\text{♀}}$	0.240	0.079	0.090	0.240	0.397	FALSE	0.999	1.016	133
$\beta_{\text{Dom}}^{\text{♂}}$	0.174	0.071	0.037	0.175	0.310	FALSE	0.993	1.009	233
$\beta_{\text{Sub}}^{\text{♀}}$	-0.092	0.077	-0.245	-0.092	0.057	TRUE	0.884	1.001	1281
$\beta_{\text{Sub}}^{\text{♂}}$	-0.235	0.127	-0.487	-0.233	0.011	TRUE	0.967	1.003	689
$\beta^2_{\text{Dom}}^{\text{♀}}$	-0.020	0.007	-0.033	-0.020	-0.007	FALSE	0.999	1.012	184
$\beta^2_{\text{Dom}}^{\text{♂}}$	-0.015	0.006	-0.027	-0.015	-0.002	FALSE	0.989	1.002	856
$\beta^2_{\text{Sub}}^{\text{♀}}$	0.007	0.017	-0.026	0.007	0.040	TRUE	0.660	1.003	772
$\beta^2_{\text{Sub}}^{\text{♂}}$	0.066	0.028	0.014	0.065	0.123	FALSE	0.996	1.001	1979
$\alpha_{\text{P}}^{\text{Dom}}^{\text{♀}}$	-0.177	0.287	-0.750	-0.176	0.374	TRUE	0.732	1.014	212
$\alpha_{\text{P}}^{\text{Dom}}^{\text{♂}}$	-0.202	0.301	-0.787	-0.200	0.386	TRUE	0.746	1.009	548
$\alpha_{\text{P}}^{\text{Sub}}^{\text{♀}}$	0.002	0.204	-0.418	0.004	0.384	TRUE	0.508	1.007	283
$\alpha_{\text{P}}^{\text{Sub}}^{\text{♂}}$	0.293	0.202	-0.081	0.288	0.707	TRUE	0.934	1.018	124
$\beta_{\text{P}}^{\text{Dom}}^{\text{♀}}$	0.372	0.081	0.222	0.367	0.548	FALSE	1.000	1.023	96
$\beta_{\text{P}}^{\text{Dom}}^{\text{♂}}$	0.427	0.094	0.251	0.423	0.628	FALSE	1.000	1.008	611
$\beta_{\text{P}}^{\text{Sub}}^{\text{♀}}$	0.013	0.104	-0.192	0.011	0.215	TRUE	0.543	1.021	104
$\beta_{\text{P}}^{\text{Sub}}^{\text{♂}}$	-0.442	0.125	-0.701	-0.433	-0.215	FALSE	1.000	1.020	231
$\alpha_{\Delta}^{\text{Dom}}^{\text{♀}}$	-0.109	0.226	-0.588	-0.096	0.290	TRUE	0.661	1.044	58
$\alpha_{\Delta}^{\text{Dom}}^{\text{♂}}$	-0.120	0.230	-0.587	-0.117	0.321	TRUE	0.683	1.057	41
$\alpha_{\Delta}^{\text{Sub}}^{\text{♀}}$	0.102	0.118	-0.135	0.110	0.315	TRUE	0.796	1.048	69
$\alpha_{\Delta}^{\text{Sub}}^{\text{♂}}$	0.416	0.119	0.159	0.421	0.634	FALSE	1.000	1.045	60
$\beta_{\Delta}^{\text{Dom}}^{\text{♀}}$	0.010	0.047	-0.074	0.006	0.116	TRUE	0.554	1.069	42
$\beta_{\Delta}^{\text{Dom}}^{\text{♂}}$	-0.040	0.050	-0.146	-0.036	0.050	TRUE	0.783	1.065	36
$\beta_{\Delta}^{\text{Sub}}^{\text{♀}}$	0.100	0.049	0.005	0.101	0.194	FALSE	0.982	1.043	59
$\beta_{\Delta}^{\text{Sub}}^{\text{♂}}$	-0.173	0.066	-0.302	-0.174	-0.045	FALSE	0.996	1.046	52
$\text{sd}_{\text{Dom}}^{\text{♀}1}$	0.223	0.038	0.160	0.221	0.307	FALSE	1.000	1.005	559
$\text{sd}_{\text{Dom}}^{\text{♂}1}$	0.178	0.038	0.101	0.177	0.258	FALSE	1.000	1.008	1231
$\text{sd}_{\text{Sub}}^{\text{♀}1}$	0.753	0.058	0.647	0.751	0.878	FALSE	1.000	1.005	622
$\text{sd}_{\text{Sub}}^{\text{♂}1}$	0.959	0.048	0.871	0.957	1.059	FALSE	1.000	1.003	599
$\text{sd}_{\text{Dom}}^{\text{♀}2}$	1.610	0.071	1.480	1.607	1.755	FALSE	1.000	1.001	1700
$\text{sd}_{\text{Dom}}^{\text{♂}2}$	1.602	0.070	1.471	1.600	1.749	FALSE	1.000	1.001	6000
$\text{sd}_{\text{Sub}}^{\text{♀}2}$	0.199	0.014	0.170	0.200	0.226	FALSE	1.000	1.007	370
$\text{sd}_{\text{Sub}}^{\text{♂}2}$	0.173	0.013	0.149	0.173	0.200	FALSE	1.000	1.001	2645
deviance	2929.1	54.37	2825.02	2929.43	3035.60	FALSE	1.000	1.004	729
DIC	4403.7								

**Table V.4.** JAGS Output for the Alpine marmot individual fitness with age analysis using a classical linear model. Rhat indicates convergence (inferior to 1.1), n.eff is a measure of effective sample size, overlap0 checks if 0 falls in the parameter's 95% credible interval, f is the proportion of the posterior with the same sign as the mean; i.e., our confidence that the parameter is positive or negative.

parameter	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
$\alpha_{\text{Dom}}^{\text{♀}}$	-0.190	0.225	-0.634	-0.193	0.249	TRUE	0.797	1.000	5760
$\alpha_{\text{Dom}}^{\text{♂}}$	-0.099	0.222	-0.533	-0.102	0.340	TRUE	0.669	1.000	6000
$\alpha_{\text{Sub}}^{\text{♀}}$	-0.551	0.173	-0.897	-0.550	-0.204	FALSE	1.000	1.001	2734
$\alpha_{\text{Sub}}^{\text{♂}}$	-0.409	0.172	-0.739	-0.409	-0.065	FALSE	0.992	1.000	6000
$\beta_{\text{Dom}}^{\text{♀}}$	0.363	0.079	0.216	0.362	0.511	FALSE	1.000	1.000	6000
$\beta_{\text{Dom}}^{\text{♂}}$	0.276	0.077	0.126	0.277	0.429	FALSE	1.000	1.000	6000
$\beta_{\text{Sub}}^{\text{♀}}$	-0.071	0.173	-0.409	-0.071	0.268	TRUE	0.659	1.001	2216
$\beta_{\text{Sub}}^{\text{♂}}$	-0.393	0.170	-0.720	-0.394	-0.059	FALSE	0.989	1.000	6000
$\beta^2_{\text{Dom}}^{\text{♀}}$	-0.029	0.006	-0.040	-0.029	-0.018	FALSE	1.000	1.000	6000
$\beta^2_{\text{Dom}}^{\text{♂}}$	-0.022	0.006	-0.035	-0.022	-0.010	FALSE	1.000	1.000	6000
$\beta^2_{\text{Sub}}^{\text{♀}}$	-0.007	0.039	-0.084	-0.007	0.071	TRUE	0.573	1.001	2243
$\beta^2_{\text{Sub}}^{\text{♂}}$	0.101	0.037	0.030	0.102	0.172	FALSE	0.996	1.000	6000
sd	1.217	0.023	1.172	1.217	1.262	FALSE	1.000	1.001	4245
deviance	4577.000	5.002	4568.941	4576.415	4588.346	FALSE	1.000	1.000	6000
DIC	4589.509								

This result is very important since all tests or indicators for decision-making are based on such confidence intervals of the estimators. In a Bayesian context, for example, one will look at the confidence interval of a slope estimate associated to a covariate to determine if that covariate has an effect. The covariate will not be retained in the model, or not considered as having a significant effect, if its confidence interval overlaps zero. Hence, in such situation one may retain and discuss the effect of a tested covariate when using the O3M while dismissing it if using a classical linear model. Using a classical linear model instead of the O3M model to study bimodally distributed fitness data can therefore lead not to detect an effect because of a lack of power.

However, and even though the two-normal mixture distribution fitted best the simulated data in almost every cases, it appeared that the O3M was not always necessary. In some cases, individual fitness data are unimodal and their distribution approaches a Gaussian one. Hence, in this situation, a two-component mixture distribution is over-parameterized and therefore useless. Based on the results of our first simulation study it is difficult to determine in which conditions such a situation arises but it seems that de-living data are more likely to be unimodal and tend to follow a single

normal distribution when the variance in the different demographic parameters is large and population size highly variable. On the contrary, individual fitness data sometimes present three distinct modes. This situation occurs when population size varies little between years and the number of recruited offspring per individual is close to one. Then, these three modes correspond to the three possible outcomes for an individual a given year: either an individual will survive and produce one offspring, in which case its fitness will be positive, or it will die before reproducing, in which case its fitness will be negative. Finally, it can either survive and not reproduce, or reproduce but not survive, in which case the outcome will be the same and its fitness will be close to zero. The mean survival and reproductive rates determined the relative height of the three modes. In this situation, and even though a two-components normal mixture distribution is preferred over a single normal, both distributions are a poor fit and a three-components mixture distribution should be tested. It is therefore very important to check the distribution of the data to be analysed to decide what kind of model to use. In some cases, visual inspection of the data might be sufficient to determine whether the data are distributed following one, two or three modes, but in most cases, a careful inspection of the fit of the model *a posteriori* is recommended. Such inspection can be done using the residuals of the models. If the data are distributed in accordance with the model assumptions (*i.e.* a two-component normal mixture distribution in our case), then the residuals should be unimodal and centred on zero. As soon as the residuals are multimodal, this indicates that the data do not follow the assumed Gaussian distribution. A more complex O3M with more than two components should then be considered. However, the development of such a model is not straightforward and requires the model to be reformulated since the weight of the second component cannot be simply written as the complement of the first one. Similarly, the definition of delta, the difference between the two components means is no longer valid and needs to be re-considered. Hopefully, de-lifing data are most often bimodal and the O3M with two components should be sufficient most of the time.

Finally, some practical downsides are to be taken into account. First and foremost, the Gibbs samplers we used, either in BUGS (Lunn *et al.* 2009) or JAGS (Plummer 2003b), are not algorithms specifically designed for such mixture models. Thus, the O3M model converges slower than conventional linear models and the model failed to converge in certain situations, because of local maxima or absorbing states (*e.g.*



when all individuals are randomly assigned to the same component during one iteration). This can be circumvented in most cases by using informative priors, notably priors for the component assignment probability  $\pi$ . It can easily be constrained to be different from 0 or 1 by stating a uniform distribution ranging from 0.01 to 0.99 for example. This is easily done when  $\pi$  is constant but much more complicated when the proportion of individuals varies with the variables considered in the model. We therefore recommend being very cautious when choosing the priors distributions and run several replicates of the same model with different initial values to ensure “true” convergence. In the near future, some mixture-model specific algorithms (such as the Expectation-Maximization algorithm used in the FlexMix package, Leisch 2004) could be modified to fit the O3M and thus improve both the convergence efficiency and speed. However, even in the current configuration, we believe the time lost during slow converging MCMC runs, or in hard-writing an overall mean mixture model specific to the research question one wants to address is largely compensated by the gain in power and the precision of the results provided by the flexibility of the O3M.

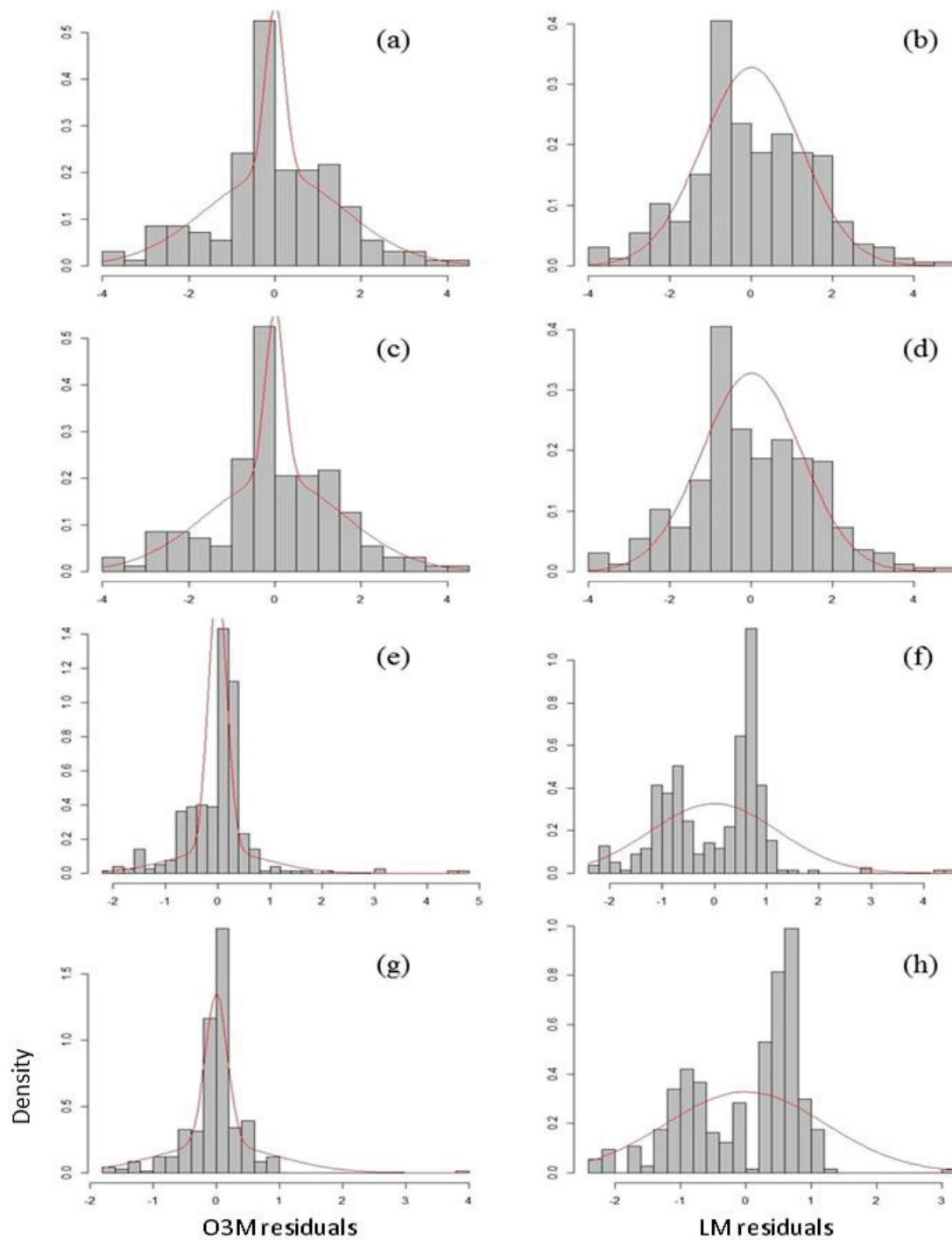
#### *10.4.3. Fitness variation with age in the Alpine marmot*

The de-lifing method is really well adapted to study how fitness varies with age. To our knowledge, it is the only fitness metric including both survival and reproduction that takes into account the current environment (represented by the population size here), and calculated on a yearly basis. Our results indicate that in our population of Alpine marmots, annual fitness does not follow a Gaussian distribution, and is largely influenced by age, sex and social status.

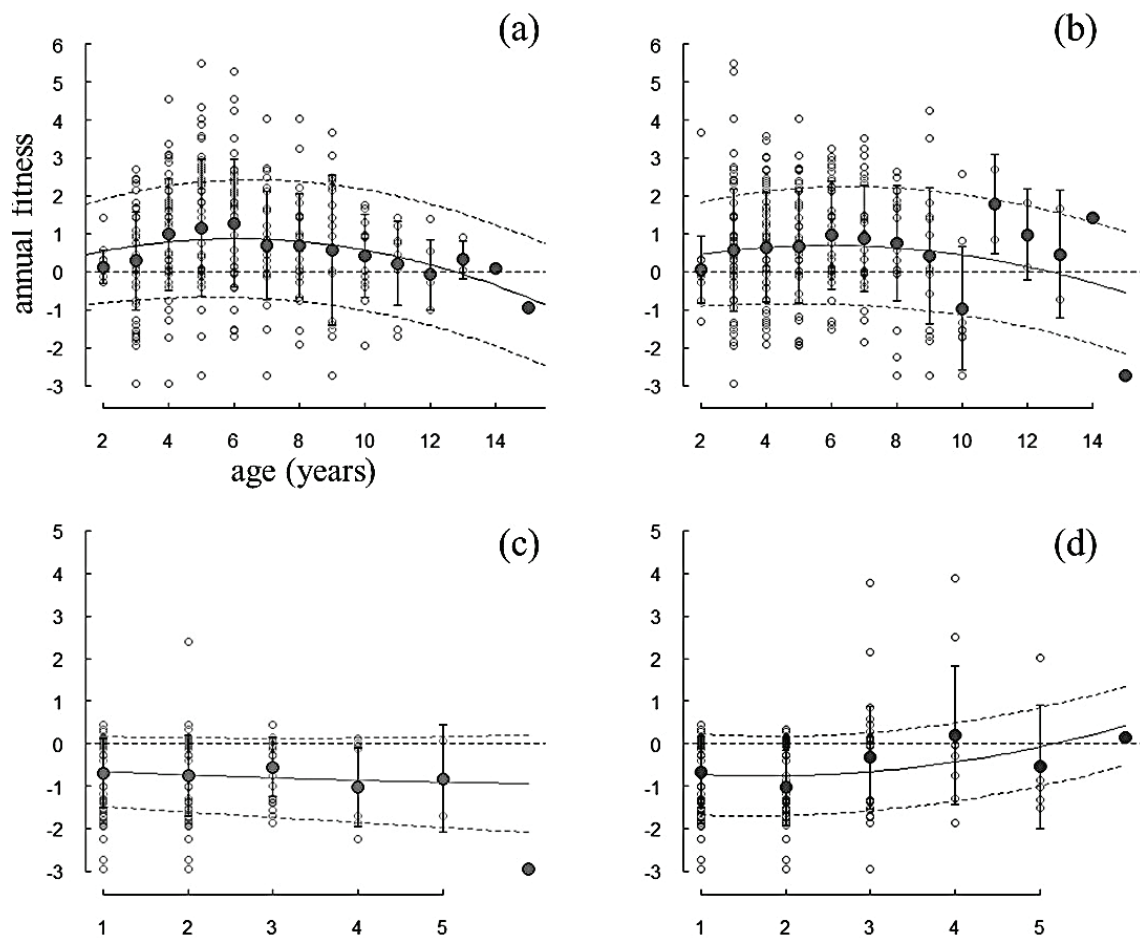
The residuals of the linear model clearly indicate that the distribution of fitness is not normal, especially in subordinate individuals. This is easily understandable given that subordinates never (females) or very rarely (males) reproduce (Goossens *et al.* 1998; Cohas *et al.* 2007). Subordinates contribution to the population growth rate is only through their own survival (positive contribution) or death (negative contribution). The extent to which a subordinate survival will affect the population and thus its fitness then depends on the population size and on the mean survival rate that year. It is therefore not surprising that subordinate fitness display a strong bimodality. In opposition, the distribution of annual fitness of dominant individuals is unimodal, although not normal. This distribution presents a narrow peak around the mean most likely representing the

dominant individuals that survive but do not reproduce. Those individuals are numerous since dominant survival is really high (around 0.8) in Alpine marmots and around 65% of the dominant individuals reproduce each year (King & Allainé 2002; Dupont *et al.* 2015). The rest of the distribution represents the individuals who reproduced and/or died a given year. This part of the distribution is less skewed because of various possible sources of variation (litter size variation, juvenile survival variation, population size variation, yearly mean survival and reproduction variation...). The O3M correctly captures this variation, thanks to the two components, and the estimates we obtain are thus trustworthy.

As expected, annual fitness presents a quadratic pattern for dominant individuals of both sexes, with the fitness increasing until approximately 7 years of age and decreasing thereafter. The senescence in fitness observed after 7 years of age is in agreement with actuarial senescence occurring between 6 and 8 years of age (Berger *et al.* 2016). The curvature seems to be slightly steeper for dominant females than for dominant males, with the annual dominant females' fitness increasing faster but also decreasing faster than males'. This suggests a faster rate of senescence in fitness in dominant females. However, no sex effect occurs in actuarial senescence (Berger *et al.* 2016). Then, competing models specifically designed to test this possible sex-difference in senescence in fitness are needed before drawing any conclusion. For subordinate individuals, the fitness/age pattern was also sex-specific. The fitness expectancy of subordinate females was negative and constant across all ages while it increased for males. This difference could result from the possibility for male subordinates to access reproduction *via* extra-pair copulations (Goossens *et al.* 1998) while subordinate females do not reproduce (with the exception of one subordinate female in 1995, Fig.V.6c) (Hackländer *et al.* 2003; Cohan *et al.* 2007). Then, they contribute little to the population growth rate and relatively less than dominant individuals, a fact explaining their constant negative fitness. The increase in fitness with age observed in subordinate males suggests that the probability to gain extra-pair paternity increases with age. Young subordinate males (sexual maturity is reached at two years old) are likely unable to gain extra-pair paternity probably because they are less competitive than older experienced males.



**Figure V.5.** Histograms of the residuals of the O3M (left panel) and the linear model (right panel) for the different social status and sexes. (a) and (b): dominant males, (c) and (d): dominant females, (e) and (f): subordinate males and (g) and (h): subordinate females. Red curves indicate the residuals distributions assumed by the models.



**Figure V.6.** Individual fitness as a function of age in Alpine marmots for both sexes and social status. (a) dominant females; (b) dominant males; (c) subordinate females; (d) subordinate males. Lines represent the predictions of the O3M. Dashed lines represent the associated standard errors. Open circles represent raw data and filled circles with error bars represent the mean fitness value per age with the associated standard deviation.

Due to viability selection, the proportion of high quality individuals gradually increases with age and only high quality individuals are responsible for the survival pattern at old ages (Péron *et al.* 2010a). This likely also occurs when considering the pattern of fitness with age. Thus, it is of primary importance to incorporate individual random effects on the intercepts and/or on the slopes to account for the differences in individual quality and subsequent differences in trajectories. This could be easily implemented in the O3M by stating that the intercept and slopes of the overall mean differ between individuals and are actually sampled from a normal distribution. The mean of this normal distribution will then be the mean estimate for the population and its

associated standard deviation will give an idea of the difference in individual quality that exists in the population.

### **10.5. Conclusion**

The O3M proved to be very useful and powerful for studying fitness data calculated with the de-lifing method. More generally, this relatively new, theoretically sound, fitness metric, combined with the appropriate modelling framework opens new perspectives in ecological and evolutionary studies. It is especially well fitted for microevolution studies by allowing for smaller scale and theoretically coherent analyses. In the context of ongoing climatic changes for example, we believe such metrics might be of great importance to study how populations respond to rapid changes in their environment in terms of fitness and therefore how species will be able to adapt (or not). We therefore encourage its use in a variety of contexts, from theoretical evolution to applied conservation studies.

## 10.6. Supplementary Material

### 10.6.1. De-lifing distribution analysis; R and jags scripts

```
## De-lifing data simulation
pt <- NULL ## Vector of individual fitness
St.mean<- 0.5 ## Mean survival probability
Rt.mean<- 0.5 ## Mean reproduction probability
NRt.mean <- 6 ## Mean number of recruits per reproducer
Nt.mean <- 20 ## Mean population size
Nt.sd <- 2 ## Population size standard deviation
for (t in 1:20) ## Loop over 20 time steps
  {
    Nt <- trunc(rnorm(1,Nt.mean,Nt.sd)) ## Sample of population size at t
    Sti <- rbinom(Nt,1,St.mean) ## Sample of individual survival
    S.bar <- mean(Sti) ## Mean survival between t and t+1
    Rti <- rpois(Nt,NRt.mean) ## Sample of the number of recruits
    Fti <- rbinom(Nt,1,Rt.mean)*Rti ## Individual reproductive success
    F.bar <- mean(Fti) ## Mean reproductive success
    pti <- ((Sti-St.bar)+(Fti-F.bar))/(Nt-1) ## Individual fitness
    pt <- c(pt,pti) ## Pools the different time steps together
  }
#####
## Normal distribution fitting
cat(file = "Normal.txt", " ## Specify model in BUGS language
model
{
sd ~ dunif(0,100) ## standard deviation prior
tau <- 1/pow(sd,2) ## link between sd and precision
mu ~ dunif(-100,100) ## prior for the mean of the normal
for (i in 1:N) ## Loop over individuals
  {
    pt[i] ~ dnorm(mu,tau) ## Individual fitness sampled from
  } ## a normal distribution
}")
data <- list(pt = pt, N = length(pt)) ## Bundle data
inits <- function() list(sd = runif(1,0,100), mu = runif(1,-100,100)) ## Initial values
params <- c("mu","sd") ## Parameters
ni <- 10000 ; nt <- 1 ; nb <- 6000 ; nc <- 3 ## MCMC settings
## Call Jags from R
library(jagsUI)
normal <- jags(data, inits, params, "Normal.txt", n.chains = nc, n.thin = nt, n.iter = ni,
              n.burnin = nb, debug = TRUE)
print(normal, digits = 3) ## prints the results
#####
```

```

## Two-component normal mixture distribution fitting
cat(file = "MixNorm.txt", "                               # Specify model in BUGS language
model
{
pi ~ dunif(0,1)                                           ## Prior probability for component 1
lambda[1] ~ dnorm(0, 0.1)                                  ## Mean of component 1
specification
delta ~ dunif(0,100)                                       ## Prior for difference of means
lambda[2] <- lambda[1] + delta                             ## Mean of component 2
specification
sd[1] ~ dunif(0,100)                                       ## Component 1 standard deviation
sd[2] ~ dunif(0,100)                                       ## Component 2 standard deviation
tau[1] <- 1/pow(sd[1],2)                                    ## Component 1 precision
tau[2] <- 1/pow(sd[2],2)                                    ## Component 2 precision
for (i in 1:N)                                             ## Loop over individuals
  {
    pt[i] ~ dnorm(mu[i], theta[i])                          ## individual fitness sample
    T[i] ~ dbern(pi)                                         ## Component sample (0 or 1)
    component[i] <- T[i]+1                                   ## Component identifier (1 or 2)
    mu[i] <- lambda[component[i]]                           ## Individual mean and precision are
    theta[i] <- tau[component[i]]                           ## conditional on its component
  }
} ")
data <- list(pt = pt, N = length(pt))
inits <- function() list(pi = runif(1,0,1), delta = runif(1,0,10),sd = runif(2,0,5))
params <- c("p", "lambda","sd")
ni <- 10000 ; nt <- 1 ; nb <- 6000 ; nc <- 3
## Call Jags from R
library(jagsUI)
MixNorm <- jags(data, inits, params, "MixNorm.txt", n.chains = nc, n.thin = nt, n.iter =
ni, n.burnin = nb, debug = TRUE)
print(MixNorm, digits = 3)
#####

```

### 10.6.2. Overall Mean Mixture Model.

The two-component normal mixture distributions simulation and Overall-Mean Mixture Model fitting R and jags script. The fitness data are simulated such that the mean of the distribution (MU) is linearly related to a hypothetical covariate (cov).

#### ##Data simulation : creation of the binorm function

```
binorm <- function(N=1000, a=0, b=0, b2=0, aP=0, bP=0, aD=0, bD=0, mean.cov=0,
sd1=1, sd2=1)
{
cov <- rpois(N,mean.cov)          ## Sample of the individual covariate value
p <- 1/(1+exp(-aP-bP*cov))      ## Definition of the prior probability  $\pi$ 
class <- rbinom(N,1,p)          ## Sample of the component
delta <- aD + bD*cov            ## Definition of the between-components
difference
MU <- a + b*cov + b2*(cov^2)    ## Definition of the overall mean
mu2 <- MU +(1-p)*delta         ## first component mean
mu1 <- mu2 - delta              ## second component mean
mu <- ifelse(class==0,mu1,mu2)
sd <- ifelse(class==0,sd1,sd2)
pt <- rnorm(N,mu,sd)           ## sample of the individual fitness value

return(list(cov = cov, p = p, class = class, delta = delta, MU = MU, mu1 = mu1, mu2 =
mu2, pt = pt, aP = aP, bP = bP, aD = aD, bD = bD, a = a, b = b, b2 = b2, sd1 = sd1, sd2 =
sd2))
}
bin <- binorm(N=1000, a=0, b=1, b2=-0.1, aD=4, bD=2, aP=-0.5, bP=1.2,
sd1=0.5,sd2=0.3, mean.cov=4)
#####
## Overall-Mean Mixture Model
# Specify model in BUGS language
cat(file = "O3M.txt","model {
# Priors
    aP ~ dnorm(0,0.01)          ## prior for the intercept of  $\pi$ 
    bP ~ dnorm(0,0.01)          ## prior for the slope of  $\pi$ 
    aD ~ dnorm(0,0.01)          ## prior for the intercept of  $\Delta$ 
    bD ~ dnorm(0,0.01)          ## prior for the slope of  $\Delta$ 
    alpha ~ dnorm(0,0.01)       ## prior for the intercept of  $\mu$ 
    beta ~ dnorm(0,0.01)        ## prior for the slope of  $\mu$ 
    beta2 ~ dnorm(0,0.01)       ## prior for the quadratic slope of  $\mu$ 
    sd[1] ~ dunif(0,100)         ## prior for the first component standard deviation
    diff ~ dunif(0,100)         ## prior for the difference in standard deviation
    sd[2] <- sd[1] + diff        ## second component standard deviation
    tau[1] <- 1/pow(sd[1],2)
    tau[2] <- 1/pow(sd[2],2)

## Likelihood
for (i in 1:N)                  ## loop over individuals (N)
```



```

    {
      pt[i] ~ dnorm(mu[i],theta[i])          ## sample of the individual
fitness
      T[i] ~ dbern(pi[i])                   ## sample of the individual's
component
      component[i] <- T[i]+1                ## component identifier

      mu[i] <- lambda[i,component[i]]       ## component specific mean

      theta[i] <- tau[component[i]]         ## component specific
precision
      MU[i] <- alpha + beta*cov[i] +beta2*pow(cov[i],2) ## overall mean
      lambda[i,1] <- lambda[i,2] - delta[i] ## component 1 mean
      lambda[i,2] <- MU[i] + (1-p[i])*delta[i] ## component 2 mean
      pi[i] <- 1/(1+exp(-rateP[i]))         ## individual  $\pi$ 
      rateP[i] <- aP + bP*cov[i]           ## rate of  $\pi$ 
      delta[i] <- aD + bD*cov[i]           ## individual  $\Delta$ 
      residuals[i] <- pt[i] - mu[i]         ## residuals of the model
    }
  })
# Bundle Data
data <- list(pt = bin$pt, N = length(bin$pt), cov = bin$cov)
# Initial values
inits <- function() list(alpha=rnorm(1,0,0.1), beta=rnorm(1,0,0.1), beta2=rnorm(1,0,0.1),
aD=rnorm(1,0,0.1), bD= , aP = rnorm(1,0,0.1), bP = rnorm(1,0,0.1))
# Parameters monitored
params <- c("alpha", "beta", "beta2", "aP", "bP", "aD", "bD", "sd", "residuals")
# MCMC settings
ni <- 10000 ; nt <- 1 ; nb <- 6000 ; nc <- 3
## Call jags from R
O3M <- jags(data, inits, params, "O3M.txt", n.chains = nc, n.thin = nt, n.iter = ni,
n.burnin = nb)
print(O3M, digits = 3)          ## prints the results
plot(O3M)                       ## to visualise the convergence of the chains and the
                                parameters distributions
#####
## Classical Linear Model (Gaussian) for comparison
cat(file = "LM.txt", "model {
# Priors
      ALPHA ~ dnorm(0,0.1)
      BETA ~ dnorm(0,0.1)
      BETA2~ dnorm(0,0.1)
      sd ~ dunif(0,100)
      tau <- 1/pow(sd,2)
# Likelihood
for (i in 1:N)
  {

```

```

    pt[i] ~ dnorm(mu[i],tau)
    mu[i] <- ALPHA + BETA*cov[i] + BETA2*pow(cov[i],2)
    residuals[i] <- pt[i] - mu[i]
  }
})
# Bundle Data
data <- list(pt = bin$pt, N = length(bin$pt),cov = bin$cov)
# Initial values
inits <- function() list(ALPHA = rnorm(1,0,0.1), BETA = rnorm(1,0,0.1), BETA2 =
rnorm(1,0,0.1), sd = rnorm(1,0,0.1))
# Parameters monitored
params <- c("ALPHA", "BETA", "BETA2", "sd")
# MCMC settings
ni <- 10000 ; nt <- 1 ; nb <- 6000 ; nc <- 3
## Call jags from R
LM <- jags(data, inits, params, "LM.txt", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin =
nb)
print(LM, digits = 3)
plot(LM)
#####

```

10.6.3. De-lifing distribution analysis; Simulation results

**Table V.5.** De-lifing simulated data sets analysis. The parameters averaged over ten replicates for each simulation are given as well as the deviance and DIC for both the Normal distribution fit ( $Dev_{Norm}$  and  $DIC_{Norm}$ ) and the O3M fit ( $Dev_{O3M}$  and  $DIC_{O3M}$ ).  $\Delta DIC$  is the mean difference between the DIC for the normal distribution and the O3M specification. Simulations that were best fitted by the normal distribution are in bold.

$S_{it}$	$R_{it}$	$NR_{it}$	$sd(NR_{it})$	$N_t$	$sd(N_t)$	$Dev_{Norm}$	$DIC_{Norm}$	$Dev_{O3M}$	$DIC_{O3M}$	$\Delta DIC$
0.2	0.2	1.0	0.05	20.0	0.2	-861.9	-860.0	-1301.3	-1286.0	426.0
0.2	0.2	1.0	0.05	20.0	2.0	-848.3	-846.1	-1205.6	-1121.4	275.3
0.2	0.2	1.0	2.0	20.0	0.2	-821.8	-819.8	-1171.0	-1074.1	254.3
0.2	0.2	1.0	2.0	20.0	2.0	-855.5	-853.6	-1482.1	-1477.2	623.6
0.2	0.2	1.0	Pois.	20.0	0.2	-254.8	-252.7	-819.4	-815.1	562.4
0.2	0.2	1.0	Pois.	20.0	2.0	-788.7	-786.8	-1221.1	-1114.2	327.4
0.2	0.2	6.0	0.05	20.0	0.2	-262.1	-260.0	-704.3	-699.7	439.7
0.2	0.2	6.0	0.05	20.0	2.0	-236.9	-234.9	-753.1	-748.9	514.0
0.2	0.2	6.0	2.0	20.0	0.2	-554.7	-552.7	-807.6	-623.7	71.0
0.2	0.2	6.0	2.0	20.0	2.0	-633.8	-631.9	-959.8	-873.2	241.3
0.2	0.2	6.0	Pois.	20.0	0.2	-699.3	-697.3	-893.9	-748.2	50.9
0.2	0.2	6.0	Pois.	20.0	2.0	-210.6	-208.6	-667.8	-660.3	451.7
0.2	0.5	1.0	0.05	20.0	0.2	-199.2	-197.2	-628.7	-622.3	425.1
0.2	0.5	1.0	0.05	20.0	2.0	-271.9	-269.8	-627.1	-474.7	204.9
0.2	0.5	1.0	2.0	20.0	0.2	-215.4	-213.2	-570.05	-475.1	261.9
0.2	0.5	1.0	2.0	20.0	2.0	-309.6	-307.7	-732.0	-725.4	417.7
0.2	0.5	1.0	Pois.	20.0	0.2	-794.1	-792.1	-1196.8	-1136.4	344.3
0.2	0.5	1.0	Pois.	20.0	2.0	-872.9	-871.0	-1307.5	-1337.0	466.0
0.2	0.5	6.0	0.05	20.0	0.2	-838.0	-835.9	-1073.0	-900.9	65.0
0.2	0.5	6.0	0.05	20.0	2.0	-798.2	-796.0	-1282.3	-1216.5	420.5
0.2	0.5	6.0	2.0	20.0	0.2	-260.3	-258.4	-763.8	-759.6	501.2
0.2	0.5	6.0	2.0	20.0	2.0	-272.8	-270.7	-806.6	-802.2	531.5
0.2	0.5	6.0	Pois.	20.0	0.2	-324.2	-322.2	-743.8	-739.3	417.1
0.2	0.5	6.0	Pois.	20.0	2.0	-288.2	-286.3	-844.2	-840.05	553.8
0.2	0.8	1.0	0.05	20.0	0.2	-696.6	-694.5	-860.6	-695.1	0.6
0.2	0.8	1.0	0.05	20.0	2.0	-661.08	-659.2	-1389.8	-1072.1	412.9
0.2	0.8	1.0	2.0	20.0	0.2	-699.2	-697.1	-901.0	-775.2	78.1
0.2	0.8	1.0	2.0	20.0	2.0	-688.5	-686.5	-935.7	-826.7	140.2
0.2	0.8	1.0	Pois.	20.0	0.2	-238.8	-236.7	-713.9	-704.9	468.2
0.2	0.8	1.0	Pois.	20.0	2.0	-768.3	-766.2	-1134.2	-1013.0	246.8
0.2	0.8	6.0	0.05	20.0	0.2	-215.4	-213.3	-656.3	-648.5	435.2
0.2	0.8	6.0	0.05	20.0	2.0	-287.4	-285.3	-669.8	-648.0	362.7
0.2	0.8	6.0	2.0	20.0	0.2	-727.1	-725.2	-1004.5	-862.2	137.0
0.2	0.8	6.0	2.0	20.0	2.0	-649.1	-647.2	-1034.2	-979.0	331.8
0.2	0.8	6.0	Pois.	20.0	0.2	-673.3	-671.3	-1052.1	-884.1	212.8
0.2	0.8	6.0	Pois.	20.0	2.0	-286.3	-284.2	-653.3	-547.0	262.8
0.5	0.2	1.0	0.05	20.0	0.2	-246.5	-244.5	-656.0	-637.9	393.4

0.5	0.2	1.0	0.05	20.0	2.0	-195.4	-193.3	-554.9	-548.0	354.7
0.5	0.2	1.0	2.0	20.0	0.2	-208.4	-206.5	-653.9	-644.9	438.4
0.5	0.2	1.0	2.0	20.0	2.0	-181.8	-179.7	-566.2	-522.3	342.6
0.5	0.2	1.0	Pois.	20.0	0.2	-788.6	-786.5	-1220.0	-1104.9	318.4
0.5	0.2	1.0	Pois.	20.0	2.0	-921.6	-919.6	-1221.4	-1103.9	184.3
0.5	0.2	6.0	0.05	20.0	0.2	-768.4	-766.4	-1133.9	-1014.8	248.4
0.5	0.2	6.0	0.05	20.0	2.0	-695.5	-693.5	-1019.3	-870.8	177.3
0.5	0.2	6.0	2.0	20.0	0.2	-210.7	-208.8	-667.8	-660.05	451.3
0.5	0.2	6.0	2.0	20.0	2.0	-253.4	-251.5	-670.0	-627.3	375.8
0.5	0.2	6.0	Pois.	20.0	0.2	-286.4	-284.4	-654.1	-550.4	266.0
0.5	0.2	6.0	Pois.	20.0	2.0	-280.2	-278.2	-689.7	-683.5	405.3
0.5	0.5	1.0	0.05	20.0	0.2	-1557.7	-1555.6	-2308.5	-2131.5	575.9
0.5	0.5	1.0	0.05	20.0	2.0	-1578.0	-1576.0	-2170.5	-1762.8	186.8
0.5	0.5	1.0	2.0	20.0	0.2	-467.9	-465.8	-1481.6	-1477.1	1011.3
0.5	0.5	1.0	2.0	20.0	2.0	-478.6	-476.5	-1449.2	-1445.0	968.5
0.5	0.5	1.0	Pois.	20.0	0.2	-1279.0	-1276.9	-1579.7	-1299.5	22.6
<b>0.5</b>	<b>0.5</b>	<b>1.0</b>	<b>Pois.</b>	<b>20.0</b>	<b>2.0</b>	<b>-1207.5</b>	<b>-1205.6</b>	<b>-1430.9</b>	<b>-1190.0</b>	<b>-15.7</b>
0.5	0.5	6.0	0.05	20.0	0.2	-492.3	-490.3	-1174.4	-996.5	506.2
0.5	0.5	6.0	0.05	20.0	2.0	-478.2	-476.3	-1226.1	-1096.2	620.0
0.5	0.5	6.0	2.0	20.0	0.2	-1560.7	-1558.6	-2229.0	-2018.9	460.3
0.5	0.5	6.0	2.0	20.0	2.0	-1554.7	-1552.8	-2148.7	-1745.1	192.3
0.5	0.5	6.0	Pois.	20.0	0.2	-500.6	-498.5	-1349.3	-1344.6	846.1
0.5	0.5	6.0	Pois.	20.0	2.0	-418.4	-416.4	-1374.8	-1370.3	953.9
0.5	0.8	1.0	0.05	20.0	0.2	-1221.3	-1219.3	-1480.0	-1265.2	45.9
0.5	0.8	1.0	0.05	20.0	2.0	-1183.3	-1181.3	-1472.0	-1293.7	112.4
0.5	0.8	1.0	2.0	20.0	0.2	-383.5	-381.5	-1192.3	-1183.1	801.5
0.5	0.8	1.0	2.0	20.0	2.0	-469.9	-468.1	-1277.3	-1261.8	793.8
0.5	0.8	1.0	Pois.	20.0	0.2	-1555.2	-1553.2	-2219.1	-1963.4	410.2
0.5	0.8	1.0	Pois.	20.0	2.0	-1566.0	-1563.8	-2422.5	-2307.4	743.6
0.5	0.8	6.0	0.05	20.0	0.2	-328.8	-326.8	-1463.9	-1459.7	1132.8
0.5	0.8	6.0	0.05	20.0	2.0	-358.2	-356.2	-1354.6	-1348.7	992.5
0.5	0.8	6.0	2.0	20.0	0.2	-478.0	-475.9	-1224.9	-1067.0	591.1
0.5	0.8	6.0	2.0	20.0	2.0	-1223.5	-1221.6	-1483.2	-1415.9	194.3
0.5	0.8	6.0	Pois.	20.0	0.2	-323.2	-321.2	-946.2	-835.9	514.7
0.5	0.8	6.0	Pois.	20.0	2.0	-246.5	-244.4	-736.6	-332.4	88.0
0.8	0.2	1.0	0.05	20.0	0.2	-1583.8	-1581.6	-2048.1	-1712.5	130.9
0.8	0.2	1.0	0.05	20.0	2.0	-1552.1	-1550.05	-1995.4	-1632.3	82.2
0.8	0.2	1.0	2.0	20.0	0.2	-376.0	-373.7	-1232.7	-1211.8	838.1
0.8	0.2	1.0	2.0	20.0	2.0	-348.6	-346.7	-1378.5	-1374.3	1027.6
<b>0.8</b>	<b>0.2</b>	<b>1.0</b>	<b>Pois.</b>	<b>20.0</b>	<b>0.2</b>	<b>-908.8</b>	<b>-906.7</b>	<b>-1106.6</b>	<b>-829.4</b>	<b>-77.3</b>
0.8	0.2	1.0	Pois.	20.0	2.0	-921.6	-919.6	-1221.9	-1106.9	187.3
0.8	0.2	6.0	0.05	20.0	0.2	-332.0	-329.9	-1091.1	-1050.0	720.0
0.8	0.2	6.0	0.05	20.0	2.0	-216.1	-214.1	-1079.1	-1064.8	850.7
0.8	0.2	6.0	2.0	20.0	0.2	-1483.2	-1481.1	-1919.7	-1600.7	119.6
0.8	0.2	6.0	2.0	20.0	2.0	-328.3	-326.2	-1355.5	-1351.6	1025.4

<b>0.8</b>	<b>0.2</b>	<b>6.0</b>	<b>Pois.</b>	<b>20.0</b>	<b>0.2</b>	<b>-1066.1</b>	<b>-1064.1</b>	<b>-1321.5</b>	<b>-1024.2</b>	<b>-39.9</b>
0.8	0.2	6.0	Pois.	20.0	2.0	-302.5	-300.4	-965.1	-884.0	583.6
<b>0.8</b>	<b>0.5</b>	<b>1.0</b>	<b>0.05</b>	<b>20.0</b>	<b>0.2</b>	<b>-1509.8</b>	<b>-1507.7</b>	<b>-1872.2</b>	<b>-1312.1</b>	<b>-195.6</b>
0.8	0.5	1.0	0.05	20.0	2.0	-366.5	-364.5	-1363.2	-1358.9	994.4
0.8	0.5	1.0	2.0	20.0	0.2	-1017.7	-1015.6	-1243.0	-1030.9	15.4
<b>0.8</b>	<b>0.5</b>	<b>1.0</b>	<b>2.0</b>	<b>20.0</b>	<b>2.0</b>	<b>-210.3</b>	<b>-208.3</b>	<b>-604.5</b>	<b>370.7</b>	<b>-579.0</b>
<b>0.8</b>	<b>0.5</b>	<b>1.0</b>	<b>Pois.</b>	<b>20.0</b>	<b>0.2</b>	<b>-1500.6</b>	<b>-1498.7</b>	<b>-1826.9</b>	<b>-1317.7</b>	<b>-181.0</b>
0.8	0.5	1.0	Pois.	20.0	2.0	-1441.4	-1439.6	-2044.4	-1484.5	44.9
0.8	0.5	6.0	0.05	20.0	0.2	-480.9	-478.8	-1264.7	-1128.9	650.05
0.8	0.5	6.0	0.05	20.0	2.0	-441.5	-439.5	-1235.9	-1194.1	754.6
<b>0.8</b>	<b>0.5</b>	<b>6.0</b>	<b>2.0</b>	<b>20.0</b>	<b>0.2</b>	<b>-1428.6</b>	<b>-1426.5</b>	<b>-1759.7</b>	<b>-1374.4</b>	<b>-52.1</b>
<b>0.8</b>	<b>0.5</b>	<b>6.0</b>	<b>2.0</b>	<b>20.0</b>	<b>2.0</b>	<b>-1550.0</b>	<b>-1548.1</b>	<b>-1937.8</b>	<b>-1295.4</b>	<b>-252.7</b>
0.8	0.5	6.0	Pois.	20.0	0.2	-524.2	-522.2	-1324.4	-1280.3	758.1
0.8	0.5	6.0	Pois.	20.0	2.0	-421.6	-419.6	-1149.4	-1113.3	693.7
0.8	0.8	1.0	0.05	20.0	0.2	-1336.0	-1334.1	-1844.9	-1731.6	397.5
0.8	0.8	1.0	0.05	20.0	2.0	-1249.3	-1247.2	-1417.5	-1286.7	39.4
0.8	0.8	1.0	2.0	20.0	0.2	-179.4	-177.4	-796.1	-639.3	461.9
0.8	0.8	1.0	2.0	20.0	2.0	-302.2	-300.05	-1114.0	-1100.9	800.8
0.8	0.8	1.0	Pois.	20.0	0.2	-1344.2	-1342.3	-1810.4	-1542.1	199.8
0.8	0.8	1.0	Pois.	20.0	2.0	-695.5	-693.5	-987.2	-848.5	155.0
0.8	0.8	6.0	0.05	20.0	0.2	-383.5	-381.5	-868.0	-521.4	139.9
0.8	0.8	6.0	0.05	20.0	2.0	-273.4	-271.3	-1164.8	-1157.1	885.8
<b>0.8</b>	<b>0.8</b>	<b>6.0</b>	<b>2.0</b>	<b>20.0</b>	<b>0.2</b>	<b>-1321.6</b>	<b>-1319.7</b>	<b>-1582.1</b>	<b>-1217.5</b>	<b>-102.2</b>
0.8	0.8	6.0	2.0	20.0	2.0	-217.7	-215.6	-833.1	-711.3	495.7
<b>0.8</b>	<b>0.8</b>	<b>6.0</b>	<b>Pois.</b>	<b>20.0</b>	<b>0.2</b>	<b>-1325.2</b>	<b>-1323.4</b>	<b>-1512.3</b>	<b>-1227.1</b>	<b>-96.3</b>
0.8	0.8	6.0	Pois.	20.0	2.0	-280.2	-278.0	-689.7	-683.6	405.6





## Chapter V.B.

# Sociality, Group contribution & Fitness

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### The more (not) the merrier? Group contribution and individual fitness in the Alpine marmot

**Abstract:** In cooperative breeders, the size and composition of the group are very important for most aspects of an individual life. It will influence its survival, reproduction and potentially dispersal. At the higher level, these variations in demographic rates are expected to contribute differently to the overall population dynamics of the species.

In this chapter, I studied the consequences of varying group size and/or composition for the group dynamics and overall population dynamics by studying how different social groups contribute to the population growth rate based on a long-term individual-based data set on Alpine marmots (*Marmota marmota*).

Surprisingly, group contribution to population growth rate steadily decreased with group size. This pattern can be explained by looking at the differences between subordinate and dominant contributions to the overall population growth rate. The increase in dominant contribution to population growth rate with the number of subordinate males in the groups we found is not sufficient to counter-balance the accumulation of subordinate negative contributions due to reproductive suppression, hence leading to the observed pattern at the group level. Further implications of this result for the population dynamics are discussed.

**Keywords:** Group contribution to population growth rate · Group dynamics · Annual individual fitness

*(Preliminary results).*





### 11.1. Introduction

In social, cooperatively breeding species, the size and composition of the group are very important for most aspects of an individual life. In these species, only a subset of individuals reproduces but the young benefit from the care provided by all (or a large part) of the group members (Clutton-Brock 2002). This is, for example, the case in meerkats (*Suricata suricatta*) where pups produced by the dominant female of the group are fed by all subordinates over 3 months of age. As a result, these pups enjoy a higher survival as the number of helpers in the group increases (Clutton-Brock *et al.* 2001). But in some species, not all individuals contribute equally to rearing the young. This is the case in Alpine marmots (*Marmota marmota*) where the presence of male subordinates (and not females) during hibernation has been shown to be associated to higher juvenile survival (Allainé & Theuriau 2004). In other cooperatively breeding species, the presence of helpers may not directly benefit the young but rather the parents by reducing the costs associated to reproduction (*i.e.* the load lightening hypothesis; Crick 1992). In sociable weavers (*Philetairus socius*), for example, dominant females produce smaller eggs when helpers are present, but the additional care provided by helpers compensate for the reduction in egg size (Paquet *et al.* 2013). This compensation mechanism ensures an equivalent fledgling mass between nestlings raised with and without helpers. Accordingly, in superb fairy wrens (*Malurus cyaneus*), female with helpers invest less in eggs and therefore increase their probability to survive to the next breeding season (Russell *et al.* 2003)).

But this kind of social system also entails different costs for individuals because of the higher level of competition for resources and mating opportunities among group members resulting from living in close proximity. These costs will notably depend on the dominance status of the individual considered (Heinsohn & Legge 1999). The most obvious cost of cooperative breeding is certainly the suppression of reproduction in subordinate individuals, imposed by dominant individuals (Arnold & Dittami 1997; O’Riain *et al.* 2000; Hackländer *et al.* 2003a). This reproductive suppression may take different forms, from behavioural harassment leading to hormonal sterilization (Creel 2001), to direct infanticide by the dominant individuals (O’Riain *et al.* 2000). In addition, costs associated to cooperative breeding for subordinate individuals are not limited to reproductive costs and may include reduced body condition, reduced survival and reduced future fecundity (Clutton-Brock 2016). Accordingly, meerkat helpers lose

weight when babysitting (looking after pups to avoid predation) and their weight loss increases as the group size decreases.

Dominant individuals will also bear variable costs depending on the characteristics of their social group. In meerkats, the probability of pups born to the dominant female to survive their first four days was considerably lower in the presence of a pregnant subordinate female, indicating that infanticide by pregnant subordinates can account for a substantial proportion of the reproductive failure suffered by dominants. In Alpine marmots, both male and female dominants have been shown to suffer from lower survival and male dominants are less likely to monopolize reproduction as the number of same-sex subordinates in the group increases, (Lardy *et al.* 2012a, 2013).

Depending on their age, sex, size and/or composition of the social group, different costs and benefits will therefore apply to individuals according to their age, sex and social status. Altogether, these studies indicate that group size and/or composition will have outstanding consequences for individuals' survival and reproduction, and consequently for their fitness (McGuire *et al.* 2002; Silk 2007; Berger *et al.* 2015). From a population dynamics perspective, this very large variation in individual vital rates according to group size/composition will most likely lead different social groups to display very different group dynamics. At the higher level, it is thus expected that social groups of various size and/or composition contribute differently to the population dynamic.

Despite its potential importance for the population dynamics of cooperatively breeding species, very few studies looked at the influence of group size and/or composition on group dynamics and at its consequences for the overall population dynamics (but see Bateman 2013). Here, we propose to study the consequences of varying group size and/or composition for the overall population dynamics by studying how different social groups contribute to the population growth rate based on a long-term dataset on Alpine marmots (*Marmota marmota*).

Answering this question can be quite challenging because social groups are not fixed entities and can vary greatly, both in size and composition, with time (Allainé & Theuriau 2004; Bateman *et al.* 2012). To overcome this limitation, we measured the contribution of social groups to the population growth rate of the population on a yearly

basis using a slightly modified version of the de-lifing method proposed by Coulson *et al.* (2006). This method was originally proposed to quantify the contribution of an individual to the population growth rate as the difference between the observed growth rate between two times steps (usually a year), and the growth rate of the same population only with the focal individual removed. Similarly, we calculated the contribution of a group a given year as the difference between the observed growth rate and a virtual growth rate calculated with all individuals of the focal group removed from the population. Additionally, we performed the same analysis at the individual level, both for dominant and subordinate individuals, in order to better understand the relationships existing between the individual level, the group level and the overall dynamic of the population.

## **11.2. Material and methods**

### *11.2.1. The Alpine marmot data set*

From 1990 on, the population of Alpine marmots situated in the Grande Sassi re nature reserve was monitored using a capture-recapture protocol. Every year between mid-May and mid-July, marmots were captured and blood and hair sampled for genetic analyses (for more details on genetic analyses see Cohas *et al.* 2008; Ferrandiz-Rovira *et al.* 2016). All pups were captured by hand within three days of their first emergence from the natal burrow and parentage analyses were performed to determine which individual successfully reproduced each year. In addition to these captures, behavioural observations allowed us to determine the size and composition of the different social groups each year. We considered group size and group composition at the end of the field season to not differ before the entrance into hibernation. The composition of the group was described as the number of subordinates of each sex present in the group at the emergence from hibernation, *i.e.* before pups' emergence. Because survival, dispersal, and reproduction of all individuals had to be known with certainty, as well as the corresponding group size and composition, we discarded the first years of the study and peripheral territories because the quality of the data was insufficient for the analysis. The dataset was then composed of 333 group.year and 1417 individual.year from 18 territories between 1994 and 2015. Population size was calculated as the sum of the group sizes each year.

### 11.2.2. Group contribution calculation

To measure how much a group contributed to the population dynamics, we used a slightly modified version of the de-lifing method (Coulson, 2006):

$$p_{tG} = (\varepsilon_{tG} - G_t \cdot \omega_t) / (N_t - G_t)$$

where  $p_{tG}$  is the contribution of group  $G$  to the population growth rate between time  $t$  and  $t+1$ ,  $\varepsilon_{tG}$  is the group performance between  $t$  and  $t+1$ , *i.e.* the number of individuals present in the group at time  $t$  and still alive at time  $t+1$  plus the number of offspring produced by group members between  $t$  and  $t+1$  that are still alive at  $t+1$ ,  $G_t$  is the group size at  $t$ ,  $\omega_t$  is the population growth rate between  $t$  and  $t+1$  ( $\omega_t = N_{t+1}/N_t$ ) and  $N_t$  is the population size at time  $t$ . To identify through which demographic rate groups contributed the most to population growth rate, group contribution to population growth rate was decomposed in its survival and recruitment components. In addition, the group survival contribution can further be decomposed in its philopatric survival and dispersal components since individuals that survive can either stay in their natal group or disperse and found or take over another group. These two different behaviours are likely to be differently influenced by social factors and are worth analysing apart. The group contribution can thus be written as the sum of the group contributions to mean survival, mean dispersal rate and mean recruitment:

$$p_{tG} = \frac{S_{tG} - G_t \cdot \acute{S}_t}{N_t - G_t} + \frac{D_{tG} - G_t \cdot \acute{D}_t}{N_t - G_t} + \frac{F_{tG} - G_t \cdot \acute{F}_t}{N_t - G_t}$$

where  $S_{tG}$  is the number of individuals present in group  $G$  at time  $t$  and still present in group  $G$  at time  $t+1$ ,  $D_{tG}$  is the number of individuals present in group  $G$  at time  $t$  that dispersed and are found alive elsewhere at time  $t+1$  and  $F_{tG}$  is the number of offspring produced between  $t$  and  $t+1$  that are still alive and recruited at time  $t+1$ .  $\acute{S}_t$ ,  $\acute{D}_t$  and  $\acute{F}_t$  are respectively the mean philopatric survival rate, mean dispersal success rate and mean recruitment in the population between time  $t$  and  $t+1$ .

### 11.2.3. Individual contribution calculation.

To further analyse the influence of group living in the Alpine marmot, we calculated individuals' contribution to population growth rate as:

$$p_{ti} = \frac{S_{ti} - \acute{S}_t}{N_t - 1} + \frac{D_{ti} - \acute{D}_t}{N_t - 1} + \frac{F_{ti} - \acute{F}_t}{N_t - 1}$$

where  $S_{it}$  is the philopatric survival of individual  $i$  (1 if it survived and stayed on its natal territory and 0 otherwise) between time  $t$  and  $t+1$ ,  $D_{it}$  is the successful dispersal of individual  $i$  (1 if it dispersed and settled as a dominant inside the study area and 0 otherwise) between time  $t$  and  $t+1$  and  $F_{it}$  is the number of offspring produced by individual  $i$  between  $t$  and  $t+1$  that are still alive at time  $t+1$  (divided by 2 because both sexes are considered).  $\bar{S}_t$ ,  $\bar{D}_t$  and  $\bar{F}_t$  still represent the mean philopatric survival rate, mean dispersal success rate and mean fecundity.

#### *11.2.4. Statistical analyses*

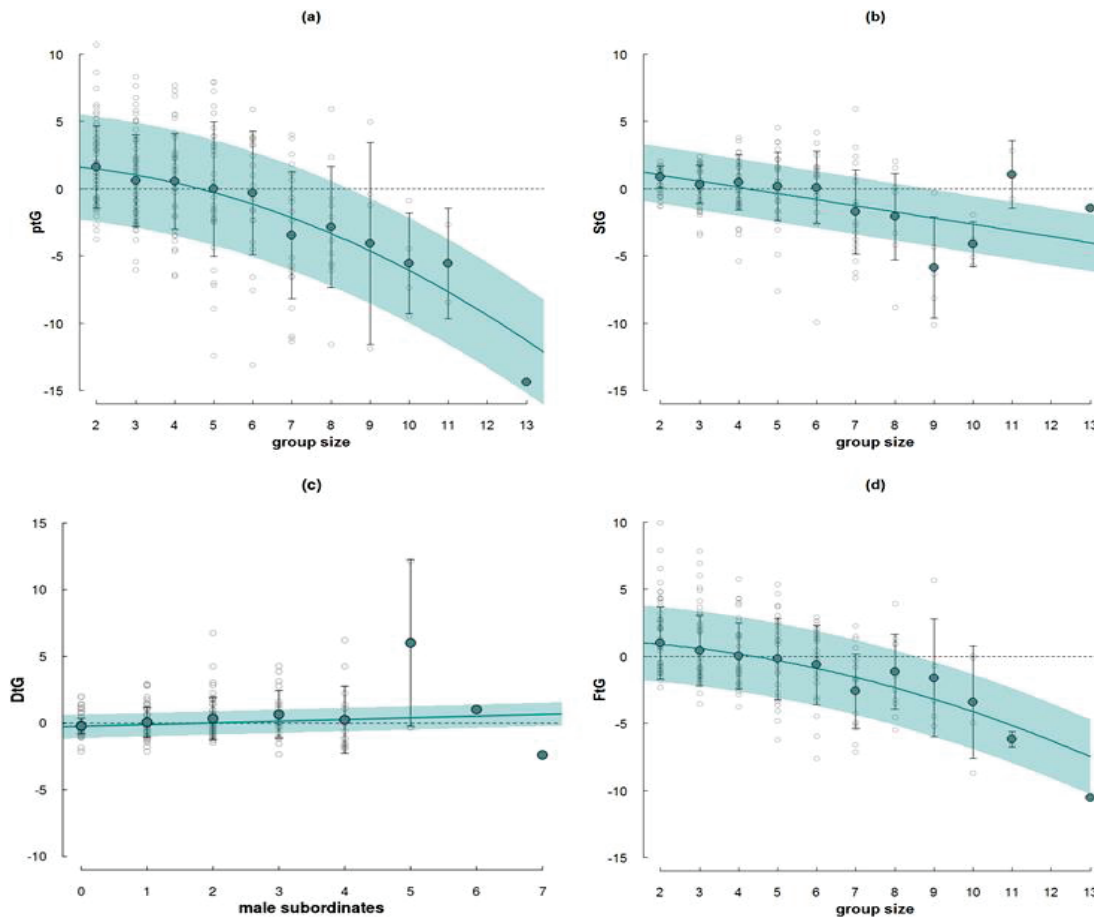
Because de-lifing data are rarely normally distributed, we used overall-mean mixture-models (O3M; see chapter V.A) to analyse how the group size and composition influenced the group and individual contributions to population growth rate (see supplementary material 11.5 for the complete model selection procedure).

### **11.3. Results**

De-lifing values distributions were better approximated by a single Gaussian and therefore modelled using a classical linear model for: group contribution to population growth rate (hereafter group contribution), group contribution to mean survival rate (hereafter group survival), group contribution to mean recruitment (hereafter group recruitment), dominant contribution to population growth rate (hereafter dominant contribution), dominant contribution to mean recruitment (hereafter dominant recruitment), subordinate contribution to population growth rate (hereafter subordinate contribution) and subordinate contribution to mean survival rate (hereafter subordinate survival). On the other hand, de-lifing values were better approximated by a mixture of two normal distributions using the O3M for: group contribution to mean dispersal rate (hereafter group dispersal), dominant contribution to mean survival rate (hereafter dominant survival), dominant contribution to mean dispersal rate (hereafter dominant dispersal), subordinate contribution to mean dispersal rate (hereafter subordinate dispersal) and subordinate contribution to mean recruitment (hereafter subordinate recruitment)(see supplementary material 11.5.1 for the complete variance-structure model selection).

### 11.3.1. Group contributions

After DIC model selection, the only covariate retained to explain variation in group contributions was group size (see supplementary material 11.5.2.1). Mean group contribution was found to be quadratically related to group size (Fig.V.7a; regression coefficients  $\pm$  sd:  $\beta = -0.077 \pm 0.422$  and  $\beta^2 = -0.072 \pm 0.038$ ). Group contribution to population growth rate was positive for all groups under 5 individuals and negative over 5 individuals. The same general pattern was found for mean group recruitment, except that the transition from positive to negative contributions took place around 4 individuals (Fig.V.7d;  $\beta = -0.086 \pm 0.301$  and  $\beta^2 = -0.045 \pm 0.027$ ). Mean group survival also decreased but linearly with group size (Fig.V.7b;  $\beta = -0.457 \pm 0.058$ ). Finally, mean group dispersal was not related to group size but slightly increased with the number of male subordinates present in the group (Fig.V.7c;  $\beta = 0.127 \pm 0.045$ ).



**Figure V.7.** Group contribution to population growth rate (a), to mean survival (b), to mean dispersal (c) and to mean recruitment (d) according to group size and/or composition. Filled dots with vertical bars represent mean observed values with associated standard deviations. Lines and shaded areas represent the models predictions with associated standard deviations. For practical reasons, contributions values were multiplied by 100 before analysis

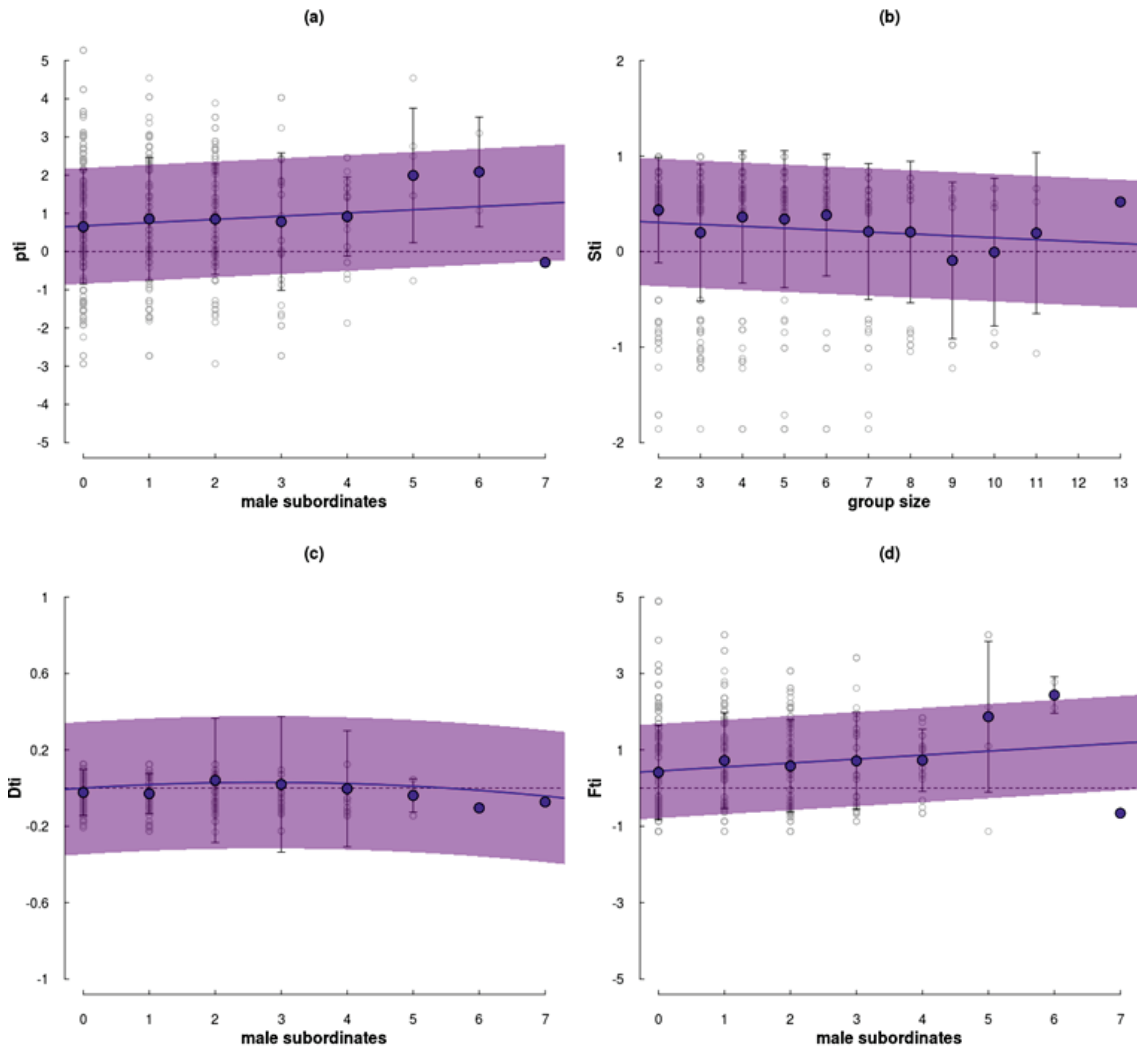
### 11.3.2. Dominant contributions

Overall, the contribution of dominant individuals to population growth rate was positive and did not differ between sexes. Dominant contribution, dominant dispersal and dominant recruitment variations were best explained by the number of subordinate males while dominant survival was found to be related to group size but not to the group composition (Fig.V.8 and see supplementary material 11.5.2.2). Mean dominant contribution increased linearly with the number of male subordinates present in the group (Fig.V.8a;  $\beta = 0.084 \pm 0.048$ ). The increase of dominant contribution with the number of male subordinates followed the pattern of dominant recruitment (Fig.V.8d;  $\beta = 0.104 \pm 0.039$ ) while mean dominant survival decreased with the number of male helpers (Fig.V.8b;  $\beta = -0.010 \pm 0.005$ ). Finally, mean dominant dispersal slightly increased until 3 male subordinates and decreased thereafter (Fig.V.8c;  $\beta = 0.036 \pm 0.010$  and  $\beta^2 = -0.006 \pm 0.002$ ).

### 11.3.3. Subordinate contributions

By contrast, subordinate contributions were not found to be related to group size or to the number of male subordinates. The only covariate retained to explain variation in subordinate contributions to growth rate, survival, dispersal and recruitment was the number of subordinate females present in the group (see supplementary material 11.5.2.3). In addition, the effect of female subordinates was found to be sex-specific for the contribution to growth rate and for the contribution to mean survival. Mean subordinate contribution decreased faster for males than for females with the number of female subordinates in the group (Fig.V.9a;  $\beta_{\text{females}} = -0.059 \pm 0.037$  and  $\beta_{\text{males}} = -0.145 \pm 0.035$ ). Contrary to group contributions and dominant contributions, the pattern of subordinate contribution did not follow the pattern of subordinate recruitment but the pattern of subordinate survival. Subordinate males' survival suffered more than females' one from the presence of subordinate females (Fig.V.9b;  $\beta_{\text{females}} = -0.057 \pm 0.035$  and  $\beta_{\text{males}} = -0.075 \pm 0.034$ ). Mean subordinate dispersal on the other hand, was found to be constant for all group sizes and compositions (Fig.V.9c; intercept =  $0.14 \pm 0.04$ ). Finally, mean subordinate recruitment slowly decreased until 3 female subordinates and increased thereafter (Fig.V.9d;  $\beta = -0.063 \pm 0.016$  and  $\beta^2 = 0.008 \pm 0.003$ ).



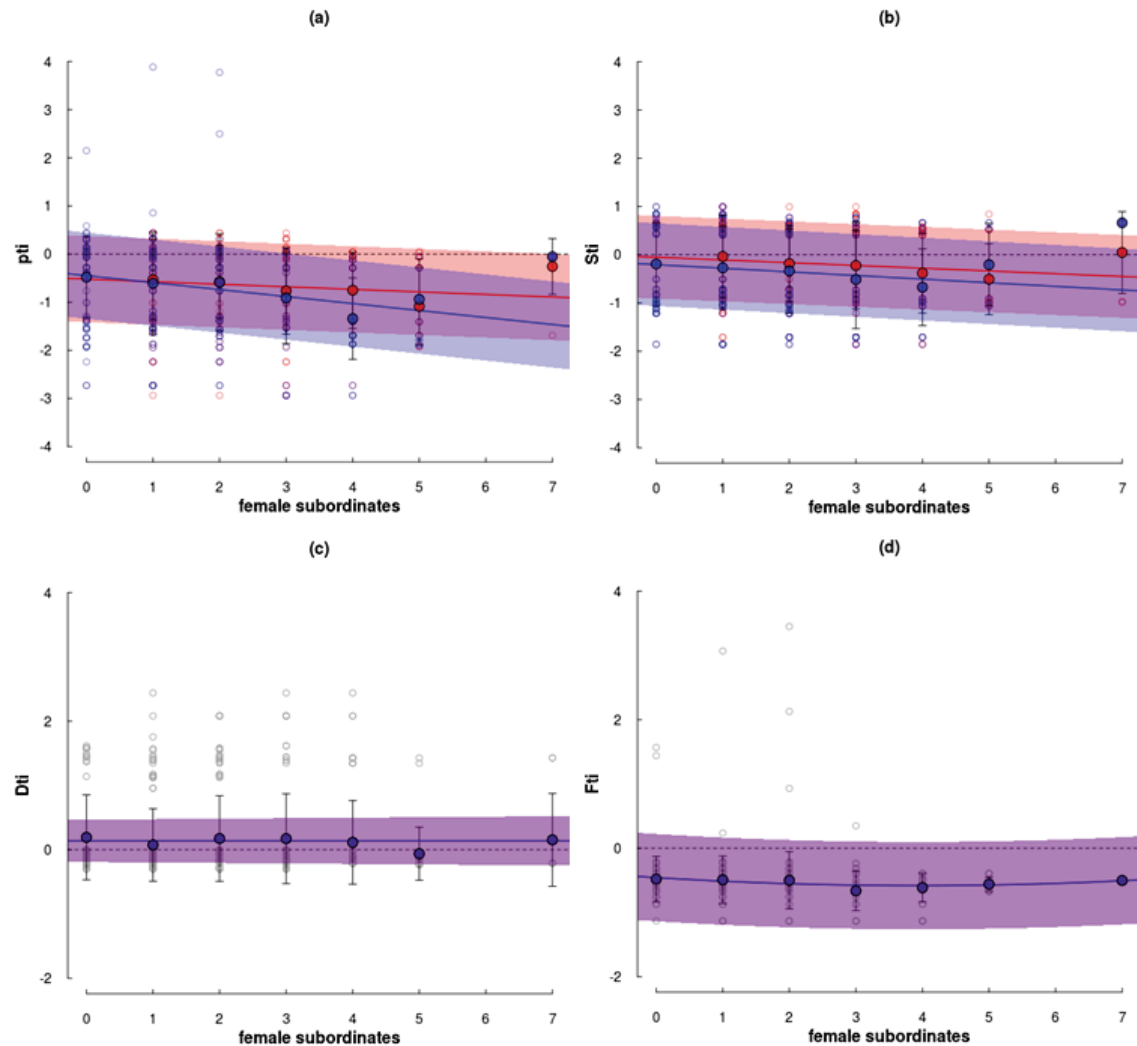


**Figure V.8.** Individual contribution of dominants to population growth rate (a), individual contribution of dominants to mean survival (b), individual contribution of dominants to mean dispersal (c) and individual contribution of dominants to mean recruitment (d) according to group size and/or composition. Grey open dots represent single dominant.year contributions. Filled dots with vertical bars represent mean observed values with associated standard deviations. Lines and shaded areas represent the models predictions with associated standard deviations. For practical reasons, contributions values were multiplied by 100 before analysis.

## 11.4. Discussion

Our results indicate that the larger the social group, the more negative its contribution to population growth rate. More specifically, groups of more than five individuals contributed negatively to growth rate, meaning that the average contribution of an individual in a family group over five individuals was below the average individual contribution in the population, *i.e.* below the population growth rate. In other words, the mean annual individual performance of an Alpine marmot living in a large group is

lower than the mean annual individual performance of a marmot living in a small group. This result seems paradoxical at first sight because sociality is expected to evolve only when it provides individuals with benefits larger than costs (Trivers 1985). To better understand this result, one needs to look at the influence of group characteristics at the individual level.



**Figure V.9.** Individual contribution of subordinates to population growth rate (a), individual contribution of subordinates to mean survival (b), individual contribution of subordinates to mean dispersal (c) and individual contribution of subordinates to mean recruitment (d) according to group size and/or composition. Blue open dots represent subordinate males, red open dots represent females and grey open dots represent single subordinate year contributions without sex differences. Filled dots with vertical bars represent the mean observed contribution values with associated standard deviations. Lines and shaded areas represent the best model prediction with associated standard deviation. For practical reasons, contributions values were multiplied by 100 before analysis.

#### 11.4.1. Group composition and individual fitness

Following previous results (Allainé & Theuriau 2004; Cohas *et al.* 2006; Lardy *et al.* 2012, 2013), the individual fitness of dominant individuals was overall positively linked to group characteristics (Fig V.8a). Dominants with a large number of male helpers benefited from higher juvenile survival (Allainé & Theuriau 2004), thus contributing to increase the mean recruitment rate in the population (Fig V.8d). Dominants in groups of intermediate sizes were most likely to become dominant again after being evicted from their group but the difference in dispersal success was too low to affect the overall contribution of a dominant individual to population growth (Fig V.8c). On the other hand, when too many individuals are present in the group, competition increases, dominants are more likely to be evicted and their survival probability decreases (Lardy *et al.* 2012a, 2013). Accordingly, we found that dominants living in large groups contributed negatively to the mean survival rate in the population (Fig V.8b). However, since survival costs increase with group size slower than recruitment benefits increase with the number of subordinate males, group size has an overall positive effect on dominants' annual contribution to population growth rate, *i.e.* dominants' annual fitness. From this result, it seems that natural selection will favour dominants in ever increasing groups which contradicts most studies on social animals that found an optimal group size and/or composition maximizing the dominant fitness (Hill *et al.* 2000; McGuire *et al.* 2002; Mosser & Packer 2009; Lardy *et al.* 2015). The discrepancy between their results and ours probably lies in the fact that we only looked at the annual fitness in relation to annual group size and composition instead of lifetime fitness proxies in relation to group characteristics averaged over the whole tenure length of the dominant (*e.g.* lifetime reproductive success). This tenure length was shown to be very important for the overall fitness in many social animals (Ellis 1995; Setchell *et al.* 2006; Lardy *et al.* 2015). Factors affecting dominant survival, while relatively un-important for the annual performance, will therefore be crucial for the lifetime fitness of an individual and trade-offs (Stearns 1992) between immediate performance and later dominance tenure might explain why we did not find an optimal group size for dominant annual fitness.

For subordinates, costs associated to sociality are quite obvious but no positive effect of sociality was evidenced (Fig V.9a). Since subordinates have little (males) or no (females) access to reproduction, their contribution to population growth rate depends

solely on their ability to survive, whether they dispersed or not. Our results show that both male and female contributions to mean survival decreased with increasing numbers of subordinate females in the family group (Fig V.9b). The negative effect of the presence of female subordinates for female subordinates is probably due to intra-sexual competition between females. On the other hand, the lower survival rate of subordinate males in the presence of many females in the group confirms previous studies which showed that the presence of subordinate females in the hibernaculum during hibernation led to a greater weight loss of males. This higher energetic cost incurred by males is due to the fact that females awaken later and produce less heat during periods of euthermia, causing the males to produce more heat and therefore spend more energy in order to survive (Arnold 1993; Allainé & Theuriau 2004). Because they do not produce any offspring, female subordinates' contribution to recruitment can only be negative (or at best null). Surprisingly, we did not find any sex difference in subordinate recruitment despite the occurrence of extra-pair paternities potentially allowing subordinate males to have a much higher recruitment value (Fig V.9d). Finally, no effect of social group size and/or composition was found on the contribution to mean dispersal rate indicating that marmots leaving large groups were not more successful when dispersing than marmots from small groups (Fig V.9c). Subordinate individuals therefore seem to suffer rather than benefit from living in large groups. These different costs result in an overall negative selective pressure on subordinates living in large groups and also reveal a conflict over group size between subordinates and dominants in Alpine marmots as is expected from theory (Vehrencamp 1983b). However, the measure of annual fitness presented here does not take into account indirect fitness benefits gained by related subordinates when the dominant individual reproduces. The evolutionary conflict between dominant and subordinate individuals over group size is then likely to be less pronounced than expected or even deleted when considering the annual fitness benefits gained by subordinates thanks to the higher contribution to recruitment of dominants living in large groups.

#### *11.4.2. Group composition and group dynamics*

From a group dynamic perspective, these differences in selective pressures between subordinates and dominants will result in the group growth rate being strongly density-dependent. Indeed, if we consider survival, the average survival rate within the group

will decrease as group size increases as a result of decreased subordinate survival with increasing numbers of females and decreasing dominant survival with increasing group size (Fig V.7a, V.8a and V.9a). Similarly, the *per capita* recruitment rate will also decrease when group size increases (Fig V.7d). Finally, the dispersal rate will increase with the number of male subordinates as males tend to disperse more than females in Alpine marmots (Fig V.7c and chapter IV). As a consequence, large groups will lose a large proportion of their members each year because of a decrease in survival and an increase in dispersal while the number of pups recruited per individual in the groups strongly decreases. The group growth rate will therefore decrease sharply as its size increases. Among the few studies that were interested in group dynamics in social species, Bateman *et al.* (2012) also found a strong negative effect of group size on group growth rate in meerkats although they hypothesized group dynamics in this species should be subjected to an Allee effect because of the positive effect of group size on individual survival (Courchamp *et al.* 1999). In Alpine marmots also, small groups were expected to perform less well because of lower rates of recruitment due to less efficient social thermoregulation during hibernation (Allainé & Theuriau 2004). Together, these results highlight the importance of taking into account the group-level processes and the idea that those processes may display conflicting patterns with individual processes.

#### *11.4.3. Group composition and population dynamics*

At the population level, it appears that large groups will contribute negatively to population growth while small groups will contribute positively. Once again, this counter-intuitive pattern can be explained by the difference in costs and benefits associated to group living between subordinate and dominant individuals. While dominant individuals' fitness gain will increase with increasing group size, subordinate costs will add up in the same time (Vehrencamp 1983b,a). In large groups, the positive effect of sociality that benefits dominants will be therefore erased by the accumulation of costs for subordinates. As a consequence, the population dynamics is expected to vary greatly according to its groups composition. Two populations with the same number of individuals but distributed differently in the social groups will likely differ in their growth rate and overall population trajectories just like populations with different age or sex structures may display different population dynamics (Tuljapurkar & Caswell 1997). To be more specific, a population composed of mainly small groups should display a

high growth rate, because of all the small groups displaying high growth rate, before showing signs of slowing down as mean group size increases in the population. Such population with synchronized group dynamics would therefore display overall density-dependence. On the other hand, if groups in the populations are highly variable, their different group dynamics are expected to compensate and the overall population may seem stationary while groups vary a lot. This discrepancy between individual benefits of sociality, group dynamics and their consequences at the population level confirms the particularity of social species population dynamics and the importance of the group structure in the population for the overall population dynamics (Bateman 2013). However, further studies are still needed to better understand the links between individual costs and benefits, group composition and population dynamics. Notably, the costs and benefits for subordinate individuals according to group characteristics should be better analysed by taking into account potentially important indirect fitness benefits when helping a related dominant to reproduce.

## 11.5. Supplementary material

### 11.5.1. Model selection

Overall-mean mixture-models (O3M) are linear models designed to account for bimodally distributed data. The variance structure in such models is modelled using a mixture of two normal distributions instead of the Gaussian distribution assumed in classical linear models. It can write as:

$$h(y|\mu, \Delta, \pi, \sigma_1^2, \sigma_2^2) = \pi.N(y|\mu, \Delta, \sigma_1^2) + (1 - \pi).N(y|\mu, \Delta, \sigma_2^2)$$

$$\text{with } \mu = \alpha + \beta \cdot x$$

$$\text{logit}(\pi) = \alpha_\pi + \beta_\pi \cdot x$$

$$\Delta = \alpha_\Delta + \beta_\Delta \cdot x$$

where  $y$  is the random variable we wish to explain, *i.e.* the group contribution to population growth rate in our case,  $\mu$  is the mean of the two-normal mixture density of  $y$ ,  $x$  is the vector of independent variables we wish to relate  $y$  to, *i.e.* the group size and composition in our case,  $\alpha$  is the intercept,  $\beta$  is the vector of variable-specific coefficients,  $\Delta$  is the difference between the means of the two components and  $\pi$  is the mixture weight of the first component.

Although linear models are very robust to non-normality, O3M are more powerful when data strongly deviate from normality (see chapter V.A.). To determine what group characteristics affected group, dominant and subordinate contributions to the population dynamics, we tested for linear and quadratic effects of group size, number of subordinate males and number of subordinate females in interaction with the sex of the focal individual. Because group size is highly correlated to the number of subordinates of both sexes, we did not include group size and subordinate numbers in the same model to avoid collinearity issues.

Model selection was performed in two steps. Based on DIC values, we first selected for the model that best accounted for the variance structure in the data by comparing models of decreasing complexity, starting from a full model where both mixture weight ( $\pi$ ) and difference between the two mixture-components' means ( $\Delta$ ) were allowed to vary with the covariate of interest. We also included a classical linear model in the comparison. In a second step, once the variance structure had been selected, we tested for all possible combinations of covariates and sex-effects and selected the best model based on DIC.

11.5.1.1. Group contributions

**Table V.6.** Variance-structure model selection for group contributions to population growth rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>1562,7</b>	<b>1566,7</b>
cst	cst	1568,8	1575,3
helpm+helpf	helpm+helpf	1569	1575,4
helpm	helpm	1569,3	1575,6
cst	helpm	1569	1575,9
helpm	helpm+helpf	1569,2	1576
helpm+helpf	helpf	1568,8	1576,4
helpf	cst	1569,3	1576,4
helpf	helpm+helpf	1569,1	1576,5
cst	helpm+helpf	1569,1	1576,6
helpf	helpm	1569	1576,6
helpm	helpf	1569	1576,6
cst	helpf	1568,8	1576,6
helpm+helpf	helpm	1568,9	1576,7
helpm+helpf	cst	1568,9	1576,8
helpm	cst	1569,1	1576,9
helpf	helpf	1569,1	1577,2
GS	cst	1537,8	1769,1
GS	GS	1422,4	1926,4
cst	GS	1459	2618,6

**Table V.7.** Variance-structure model selection for group contributions to mean survival rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>1219,3</b>	<b>1223,3</b>
cst	GS	1114,2	1232,3
GS	GS	1113,8	1238,9
GS	cst	1113	1251,2
cst	cst	1113,2	1253,3
helpf	cst	1111,2	1285,1
helpm	cst	1118,2	1292
helpf	helpm+helpf	1124,1	1293,7
helpm	helpm	1124,1	1296,7
cst	helpm+helpf	1125	1299,7
helpf	helpm	1118,7	1304
cst	helpm	1123,3	1307,3



helpm+helpf	helpm	1121,1	1307,9
helpm+helpf	cst	1114,7	1310,1
cst	helpf	1122,6	1310,8
helpf	helpf	1117,8	1311
helpm+helpf	helpf	1121	1319,5
helpm	helpf	1118,6	1339,9
helpm+helpf	helpm+helpf	1124	1345,2
helpm	helpm+helpf	1124,2	1380

**Table V.8.** Variance-structure model selection for group contributions to mean dispersal rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>helpm</b>	<b>helpf</b>	<b>697,4</b>	<b>826,1</b>
cst	helpf	697,8	828,1
helpm+helpf	helpf	697,1	828,4
helpf	helpf	698,7	829,4
cst	GS	716,7	832,8
helpm+helpf	helpm+helpf	698,8	834,7
GS	GS	716,9	835,1
helpm	helpm+helpf	699,3	835,3
cst	helpm+helpf	699,2	836,4
helpf	helpm+helpf	700,5	837,4
helpf	cst	711,8	844,4
cst	cst	710,3	854,2
helpm+helpf	cst	709,6	855,3
helpf	helpm	712,4	856,5
GS	cst	721,5	857,8
cst	helpm	711,2	866,6
helpm	helpm	711,2	866,8
helpm+helpf	helpm	709,7	867,6
helpm	cst	731,1	892
lm	lm	985,2	989,2

**Table V.9.** Variance-structure model selection for group contributions to mean fecundity.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>1373,1</b>	<b>1377,1</b>
helpf	helpm+helpf	1375,9	1382,6
helpf	helpm	1376,3	1382,6
helpm+helpf	helpf	1376,2	1382,6

helpf	helpf	1376,3	1382,6
helpm+helpf	cst	1376,8	1382,6
helpf	cst	1376,3	1382,6
helpm	helpf	1375,7	1383,6
helpm	helpm+helpf	1375,6	1383,7
cst	helpf	1376,2	1383,7
cst	cst	1376,2	1383,7
helpm	helpm	1376,2	1384
helpm+helpf	helpm+helpf	1375,3	1384,6
helpm	cst	1375,7	1385,4
cst	helpm	1376,4	1386,1
helpm+helpf	helpm	1376,3	1388,4
cst	helpm+helpf	1375,7	1390,1
GS	GS	1133	1453,5
cst	GS	1139	1464,2
GS	cst	1140,7	1472,3

### 11.5.1.2. Dominant contributions

**Table V.10.** Variance-structure model selection for dominant contributions to population growth rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>2065,7</b>	<b>2072,8</b>
cst	helpm+helpf	2065,4	2079
helpm+helpf	helpm	2063,7	2081,4
helpf	helpm+helpf	2065,7	2082,4
helpm	helpf	2065,1	2082,4
helpf	helpf	2064,9	2082,4
helpm	helpm	2065,3	2083,4
cst	helpm	2065,2	2083,8
helpm+helpf	helpf	2065,7	2085,4
cst	helpf	2065,3	2085,9
helpm	cst	2065,3	2086,8
helpm+helpf	cst	2064,2	2086,9
helpm+helpf	helpm+helpf	2064,5	2087,4
helpm	helpm+helpf	2065	2088,4
helpf	cst	2065,7	2089,2
helpf	helpm	2064,9	2090
cst	cst	2065,5	2095,9
GS	GS	1771,2	2119,7
cst	cst	1763,5	2186,3

GS	cst	1765	2188,5
cst	GS	1819,8	2292,9

**Table V.11.** Variance-structure model selection for dominant contributions to mean survival rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>GS</b>	<b>GS</b>	<b>-355,2</b>	<b>-344,3</b>
cst	cst	-356	-346,3
GS	cst	-356	-346,1
cst	GS	-355,1	-344,3
helpm+helpf	cst	-352,6	-338,7
helpf	cst	-353,6	-338,6
helpm	cst	-352,6	-338,5
helpm+helpf	helpm	-351,9	-336,8
helpf	helpm	-351,9	-336,8
helpm+helpf	helpf	-351,8	-336,8
helpm	helpf	-351,9	-336,8
helpm	helpm	-351,8	-336,7
cst	helpm	-351,7	-336,6
helpf	helpf	-351,9	-336,6
cst	helpf	-351,8	-336,6
cst	helpm+helpf	-352,1	-336,4
helpm	helpm+helpf	-353,9	-334,8
helpf	helpm+helpf	-353	-333,8
helpm+helpf	helpm+helpf	-354,2	-333,2
lm	lm	1140,5	1147,6
lm	lm	1141,3	1152,5

**Table V.12.** Variance-structure model selection for dominant contributions to mean dispersal rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>helpm+helpf</b>	<b>cst</b>	<b>-1132,4</b>	<b>-1116,3</b>
helpm	cst	-1130,5	-1114,4
helpm+helpf	helpf	-1133,4	-1114,1
cst	cst	-1121	-1110,9
helpm+helpf	helpm	-1130,7	-1110,5
GS	cst	-1121,2	-1110,2
helpm	helpf	-1130,1	-1109,3
GS	GS	-1120,7	-1106,4
helpm+helpf	helpm+helpf	-1133	-1106

cst	GS	-1120,5	-1105,9
cst	cst	-1119,5	-1104,5
helpf	cst	-1118,9	-1102,9
helpm	helpm	-1126,8	-1102,8
cst	helpf	-1121,2	-1102,7
helpf	helpf	-1120,8	-1101,4
helpm	helpm+helpf	-1128,8	-1101,1
cst	helpm	-1117,7	-1098,5
helpf	helpm	-1117,1	-1097,3
cst	helpm+helpf	-1120,5	-1095,8
helpf	helpm+helpf	-1120,4	-1093,5
lm	lm	-213,1	-201,9

**Table V.13.** Variance-structure model selection for dominant contributions to mean fecundity.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>1836,5</b>	<b>1843,7</b>
GS	GS	1668,8	1964,6
helpm	helpm	1678,4	2031,6
helpf	helpm+helpf	1544,5	2032,3
helpf	helpm	1678,7	2033,4
cst	helpm+helpf	1559,4	2033,8
helpm+helpf	helpm	1678,7	2033,8
cst	helpm	1679,1	2036,7
GS	cst	1673,8	2078,5
cst	GS	1703,9	2079,1
helpm	helpm+helpf	1543,1	2081,6
cst	cst	1674,4	2085,6
helpm+helpf	helpf	1691,8	2088,6
helpm	helpf	1692,4	2091,8
helpm	cst	1676,7	2118,8
helpf	cst	1676,7	2120,1
helpm+helpf	cst	1676,9	2123,1
helpf	helpf	1590,1	2123,4
cst	cst	1677,9	2126,8
helpm+helpf	helpm+helpf	1543,1	2178,2
cst	helpf	1693,1	2230,2

11.5.1.3. Subordinate contributions

**Table V.14.** Variance-structure model selection for subordinate contributions to population growth rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>1585,9</b>	<b>1597,3</b>
helpf	helpf	1537	1607,4
cst	cst	1531,011	1612,2
cst	helpm+helpf	1530,1	1612,3
helpm	helpm+helpf	1528,2	1615,4
helpf	helpm+helpf	1545,7	1615,5
helpf	cst	1528,5	1617,5
helpm+helpf	helpm+helpf	1525,4	1619,0
cst	helpm	1543,1	1620,0
helpm+helpf	helpf	1546,1	1620,4
helpf	helpm	1542,9	1622,4
helpm	helpm	1531,2	1629,8
helpm+helpf	helpm	1533,6	1630,3
helpm	helpf	1540,3	1632,9
cst	helpf	1534,2	1640,7
helpm	cst	1525,4	1643,3
helpm+helpf	cst	1524,8	1643,8
cst	GS	1526,3	1657,5
GS	GS	1524,9	1658,0
GS	cst	1525,5	1661,5

**Table V.15.** Variance-structure model selection for subordinate contributions to mean survival rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>lm</b>	<b>lm</b>	<b>1534,5</b>	<b>1541,6</b>
cst	helpm+helpf	1535	1546,4
cst	helpm	1535	1546,5
cst	helpf	1535	1546,5
helpf	helpf	1535	1546,9
helpm	cst	1535,4	1547,1
helpm	helpm	1535,6	1547,2
helpm+helpf	cst	1536	1547,3
helpf	helpm+helpf	1535,5	1547,5
helpm+helpf	helpm	1535,5	1547,5

helpm	helpm+helpf	1535,4	1547,6
helpm	helpf	1536,3	1547,6
helpf	helpm	1535,7	1547,7
helpm+helpf	helpf	1535,8	1547,7
cst	cst	1535,9	1547,8
helpf	cst	1536,2	1548
helpm+helpf	helpm+helpf	1535,6	1548,6
GS	GS	1008,4	1622,7
GS	cst	1028,4	1779,5
cst	GS	1021,9	1980,8

**Table V.16.** Variance-structure model selection for subordinate contributions to mean dispersal rate.  $\pi$ : mixture weight;  $\Delta$ : difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>cst</b>	<b>GS</b>	<b>-994,5</b>	<b>-984</b>
GS	GS	-994,5	-983,9
GS	cst	-990,5	-981,2
helpf	cst	-993,8	-980,3
cst	cst	-993,8	-980,3
helpm	cst	-993,9	-980,2
helpm+helpf	cst	-993,8	-980,1
helpm+helpf	helpm	-996,3	-979,9
helpm	helpf	-994,2	-979,9
helpm	helpm+helpf	-997,1	-979,8
cst	helpm	-996	-979,8
helpm+helpf	helpf	-994,3	-979,8
helpm	helpm	-996,5	-979,7
helpf	helpm	-996,2	-979,6
helpf	helpf	-994,1	-979,6
helpm+helpf	helpm+helpf	-997,1	-979,5
cst	helpf	-994,2	-979,1
cst	helpm+helpf	-996,5	-978,9
helpf	helpm+helpf	-996,7	-978,7
lm	lm	1175,4	1182,6

**Table V.17.** Variance-structure model selection for subordinate contributions to mean fecundity.  $\pi$ : mixture weight;  $\Delta$ : weight difference between the two component-specific means; cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

$\pi$	$\Delta$	deviance	DIC
<b>cst</b>	<b>cst</b>	<b>-68,7</b>	<b>-28,03</b>
cst	helpm	-67,2	-24,4

cst	helpf	-67	-24,1
helpm	helpf	-66,8	-22,2
helpf	helpm+helpf	-66,5	-19,7
cst	helpm+helpf	-65,3	-19,2
cst	GS	-62,2	-19,2
helpm	helpm+helpf	-65,4	-18,7
helpf	helpm	-66,9	-18,7
helpf	helpf	-67,1	-18,7
helpm+helpf	cst	-66,7	-17,5
helpm	cst	-66,4	-15,5
helpm+helpf	helpm+helpf	-65,6	-13,4
helpm+helpf	helpf	-64,8	-11,2
helpm+helpf	helpm	-65,6	-9,9
GS	GS	-61,6	-9,1
helpm	helpm	-65,1	-7,4
helpf	cst	-64,4	-7,3
GS	cst	-61,7	-0,8
lm	lm	475,6	482,7

### 11.5.2. Group size and composition model selection

#### 11.5.2.1. Group contributions

**Table V.18.** Group size and composition model selection for group contributions to population growth rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

covariates	deviance	DIC
<b>GS+GS<sup>2</sup></b>	<b>1562,7</b>	<b>1566,7</b>
GS	1565,2	1568,2
helpm + helpf	1568,1	1572,2
helpm <sup>2</sup> +helpf	1568,5	1573,6
helpm + helpf <sup>2</sup>	1568,6	1573,7
helpm <sup>2</sup> + helpf <sup>2</sup>	1569,1	1575,2
cst + helpf	1572,6	1575,7
cst + helpf <sup>2</sup>	1573,5	1577,5
helpm	1600,3	1603,4
helpm <sup>2</sup>	1601,2	1605,3
cst	1620,5	1622,5
cst	1620,5	1622,6

**Table V.19.** Group size and composition model selection for group contributions to mean survival rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

covariates	deviance	DIC
<b>GS</b>	<b>1218,9</b>	<b>1221,9</b>
GS+GS <sup>2</sup>	1219,3	1223,9
helpm + helpf	1225,3	1229,3

helpm <sup>2</sup> +helpf	1226,3	1231,4
helpm + helpf <sup>2</sup>	1226,3	1231,5
helpm <sup>2</sup> + helpf <sup>2</sup>	1227,3	1233,5
cst + helpf	1236,1	1239,1
cst + helpf <sup>2</sup>	1236,7	1240,8
helpm	1247,4	1250,4
helpm <sup>2</sup>	1248,2	1252,3
cst	1275,2	1277,2
cst	1275,2	1277,3

**Table V.20.** Group size and composition model selection for group contributions to mean dispersal rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>GS</b>	<b>716,7</b>	<b>832,8</b>
GS+GS <sup>2</sup>	721,1	834,5
helpm	696,2	802,8
helpm + helpf	697,2	808
helpm <sup>2</sup>	696,8	811,4
helpm <sup>2</sup> +helpf	698	815,4
cst	696,1	817,2
helpm + helpf <sup>2</sup>	697,7	818,8
cst + helpf	700,1	819,4
cst	718,1	821
cst + helpf <sup>2</sup>	701,2	821,2
helpm <sup>2</sup> + helpf <sup>2</sup>	697,8	828,1

**Table V.21.** Group size and composition model selection for group contributions to mean fecundity. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>GS+GS<sup>2</sup></b>	<b>1373,1</b>	<b>1377,1</b>
GS	1374,7	1377,7
helpm + helpf	1376,5	1380,6
helpm + helpf <sup>2</sup>	1376,3	1381,4
helpm <sup>2</sup> +helpf	1376,3	1381,5
helpm <sup>2</sup> + helpf <sup>2</sup>	1376,3	1382,4
cst + helpf	1381,7	1384,8
cst + helpf <sup>2</sup>	1382,2	1386,3
helpm	1403,8	1406,9
helpm <sup>2</sup>	1404,3	1408,4
cst	1424	1426
cst	1424	1426,1



11.5.2.3. Dominant contributions

**Table V.22.** Group size and composition model selection for dominant contributions to population growth rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>hlp_m</b>	<b>2062,1</b>	<b>2065,2</b>
hlp_m*sex	2060,8	2065,9
hlp_m+hlp_f	2062,1	2066,1
cst	2064,1	2066,1
cst	2064,1	2066,2
sex	2063,6	2066,6
sex	2063,6	2066,6
hlp_m <sup>2</sup>	2062,9	2066,9
GS	2064,5	2067,6
hlp_m <sup>2</sup> +hlp_f	2062,9	2068
hlp_f	2065,1	2068,1
hlp_m+hlp_f <sup>2</sup>	2063,1	2068,2
GS*sex	2063,9	2069
(hlp_m+hlp_f)*sex	2061,9	2069,1
GS+GS <sup>2</sup>	2065,4	2069,5
hlp_m <sup>2</sup> *sex	2062,5	2069,6
hlp_f*sex	2065,1	2070,1
hlp_f <sup>2</sup>	2066,1	2070,1
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	2063,9	2070,2
(GS+GS <sup>2</sup> )*sex	2065,7	2072,7
(hlp_m <sup>2</sup> +hlp_f)*sex	2063,5	2072,8
(hlp_m+hlp_f <sup>2</sup> )*sex	2063,8	2073,2
hlp_f <sup>2</sup> *sex	2067	2074,3
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	2065,4	2076,8

**Table V.23.** Group size and composition model selection for dominant contributions to mean survival rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>GS</b>	<b>-359,5</b>	<b>-351,9</b>
hlp_m	-359,3	-351,8
cst	-356,3	-350,8
hlp_f	-357,6	-350,3
GS+GS <sup>2</sup>	-358,7	-350,2
cst	-356,1	-349,7
hlp_f <sup>2</sup> +hlp_m	-358,6	-349,7
hlp_m <sup>2</sup>	-358,1	-349,5
hlp_f <sup>2</sup>	-357,2	-349,3

hlp_f+hlp_m	-358,8	-348,8
hlp_f+hlp_m <sup>2</sup>	-358	-348,7
GS*sex	-357,5	-347,9
sex	-355,1	-347,7
hlp_f*sex	-355,6	-347,4
sex	-355,1	-347,3
hlp_m*sex	-357,1	-346,9
hlp_f <sup>2</sup> +hlp_m <sup>2</sup>	-357,3	-346,7
(GS+GS <sup>2</sup> )*sex	-355,8	-344
(hlp_f+hlp_m)*sex	-355,9	-343,9
hlp_m <sup>2</sup> *sex	-355,4	-343,6
hlp_f <sup>2</sup> *sex	-353,9	-341,8
(hlp_f <sup>2</sup> +hlp_m)*sex	-354,5	-341,6
(hlp_f+hlp_m <sup>2</sup> )*sex	-353,8	-339,4
(hlp_f <sup>2</sup> +hlp_m <sup>2</sup> )*sex	-352,4	-336,5

**Table V.24.** Group size and composition model selection for dominant contributions to mean dispersal rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>hlp_m<sup>2</sup></b>	<b>-1137,3</b>	<b>-1126,3</b>
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	-1131,9	-1122
hlp_m <sup>2</sup> +hlp_f	-1131,7	-1121,1
cst	-1125,3	-1118,9
hlp_m+hlp_f <sup>2</sup>	-1128,8	-1117,6
cst	-1124,9	-1117,6
sex	-1124,4	-1117,2
GS	-1121,7	-1116,8
sex	-1124,2	-1116,4
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	-1132,4	-1116,3
hlp_m <sup>2</sup> *sex	-1128,9	-1115,9
GS+GS <sup>2</sup>	-1123,8	-1115,8
hlp_f <sup>2</sup>	-1126,4	-1115,7
hlp_f	-1123	-1114,4
(hlp_m <sup>2</sup> +hlp_f)*sex	-1127,9	-1113,1
hlp_m	-1124,2	-1113
GS*sex	-1122,7	-1113
hlp_m+hlp_f	-1123,4	-1112,1
(GS+GS <sup>2</sup> )*sex	-1121	-1110,9
hlp_m*sex	-1121,9	-1110,3
(hlp_m+hlp_f <sup>2</sup> )*sex	-1125,2	-1110,2
hlp_f*sex	-1121	-1109,4
hlp_f <sup>2</sup> *sex	-1123,1	-1108,7
(hlp_m+hlp_f)*sex	-1120,4	-1107

**Table V.25.** Group size and composition model selection for dominant contributions to mean fecundity. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>hlp_m</b>	<b>1831</b>	<b>1834,1</b>
hlp_m*sex	1830,5	1835,6
hlp_m+hlp_f	1831,6	1835,7
hlp_m <sup>2</sup>	1831,7	1835,8
hlp_m+hlp_f <sup>2</sup>	1832	1837,1
hlp_m <sup>2</sup> +hlp_f	1832,3	1837,5
GS	1835,2	1838,2
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	1832,7	1838,9
cst	1837,2	1839,2
(hlp_m+hlp_f)*sex	1832,1	1839,3
cst	1837,2	1839,3
hlp_m <sup>2</sup> *sex	1832,2	1839,4
GS+GS <sup>2</sup>	1835,6	1839,6
sex	1837	1840
sex	1837	1840
GS*sex	1835,1	1840,2
hlp_f	1838	1841,2
hlp_f <sup>2</sup>	1837,5	1841,7
(hlp_m+hlp_f <sup>2</sup> )*sex	1833,5	1842,7
(hlp_m <sup>2</sup> +hlp_f)*sex	1833,9	1843,2
(GS+GS <sup>2</sup> )*sex	1836,5	1843,7
hlp_f*sex	1838,6	1843,7
hlp_f <sup>2</sup> *sex	1839,1	1846,3
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	1835,3	1846,6

*11.5.2.3. Subordinate contributions*

**Table V.26.** Group size and composition model selection for subordinate contributions to population growth rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>hlp_f*sex</b>	<b>1587,7</b>	<b>1592,7</b>
hlp_f <sup>2</sup>	1589,1	1593,3
hlp_f <sup>2</sup> *sex	1586,5	1593,7
hlp_f	1591,1	1594,1
hlp_m+hlp_f <sup>2</sup>	1590	1595
(hlp_m+hlp_f)*sex	1588,3	1595,3
hlp_m <sup>2</sup> +hlp_f	1592,4	1595,4
GS	1592,6	1595,6
hlp_m+hlp_f	1591,8	1595,9

(hlp_m <sup>2</sup> +hlp_f)*sex	1586,8	1596,1
GS+GS <sup>2</sup>	1592,4	1596,5
(hlp_m+hlp_f <sup>2</sup> )*sex	1587,5	1596,6
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	1590,4	1596,6
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	1585,8	1596,9
GS+GS <sup>2</sup> *sex	1591,6	1598,7
GS*sex	1594	1599,1
cst	1603,7	1605,7
hlp_m	1604	1607
sex	1604,6	1607,6
hlp_m <sup>2</sup>	1604,9	1609
hlp_m <sup>2</sup> *sex	1603,3	1610,5
hlp_m*sex	1605,7	1610,9

**Table V.27.** Group size and composition model selection for subordinate contributions to mean survival rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

covariates	deviance	DIC
<b>hlp_f*sex</b>	<b>1535,4</b>	<b>1539,4</b>
GS+GS <sup>2</sup>	1532,8	1539,9
hlp_f <sup>2</sup> *sex	1535,2	1540,2
GS	1538,5	1541,5
GS+GS <sup>2</sup> *sex	1534,5	1541,6
GS*sex	1536,5	1541,6
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	1532	1543,4
(hlp_m+hlp_f <sup>2</sup> )*sex	1534,3	1543,5
hlp_f	1540,5	1543,7
hlp_f <sup>2</sup>	1539,7	1543,8
(hlp_m+hlp_f)*sex	1537	1544,1
(hlp_m <sup>2</sup> +hlp_f)*sex	1535,1	1544,3
sex	1541,4	1544,5
hlp_m+hlp_f	1540,8	1545
hlp_m+hlp_f <sup>2</sup>	1540,1	1545,1
cst	1543,9	1545,8
hlp_m <sup>2</sup> +hlp_f	1540,8	1546
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	1539,9	1546,1
hlp_m	1543,7	1546,7
hlp_m <sup>2</sup> *sex	1540,4	1547,4
hlp_m*sex	1542,8	1547,8
hlp_m <sup>2</sup>	1544,2	1548,3

**Table V.28.** Group size and composition model selection for subordinate contributions to mean dispersal rate. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>cst</b>	<b>-995,9</b>	<b>-990,6</b>
sex	-996,3	-990,1
hlp_f <sup>2</sup>	-995,4	-989,6
GS	-994,9	-988,6
GS+GS <sup>2</sup>	-994,5	-987,1
hlp_m+hlp_f <sup>2</sup>	-994,3	-987
hlp_f <sup>2</sup> *sex	-995,9	-986,3
GS*sex	-994,3	-986
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	-994,1	-985,6
hlp_m <sup>2</sup>	-989,5	-985,2
hlp_f	-990,4	-985
GS+GS <sup>2</sup> *sex	-994,5	-984
hlp_m	-989,6	-984
(hlp_m+hlp_f <sup>2</sup> )*sex	-995	-983,2
hlp_m+hlp_f	-989,5	-983,1
hlp_m*sex	-990,1	-982,8
hlp_f*sex	-989,5	-981,7
hlp_m <sup>2</sup> +hlp_f	-989,2	-981,7
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	-993,8	-980,3
hlp_m <sup>2</sup> *sex	-989,1	-979,6
(hlp_m+hlp_f)*sex	-988,6	-979,6
(hlp_m <sup>2</sup> +hlp_f)*sex	-987,7	-976,5

**Table V.29.** Group size and composition model selection for subordinate contributions to mean fecundity. cst: constant; helpm: number of male subordinates; helpf: number of females subordinates; GS: group size; lm: classical linear model

<b>covariates</b>	<b>deviance</b>	<b>DIC</b>
<b>hlp_f<sup>2</sup></b>	<b>-64</b>	<b>-34,7</b>
hlp_m+hlp_f <sup>2</sup>	-68,9	-33,6
(hlp_m <sup>2</sup> +hlp_f <sup>2</sup> )*sex	-69,3	-31,9
hlp_f <sup>2</sup> *sex	-64,7	-31,3
(hlp_m+hlp_f <sup>2</sup> )*sex	-67,6	-31,2
hlp_m <sup>2</sup> +hlp_f <sup>2</sup>	-68,2	-30,3
GS	-63	-28,9
GS+GS <sup>2</sup>	-63,5	-28,3
(hlp_m <sup>2</sup> +hlp_f)*sex	-63,9	-27,4
hlp_m <sup>2</sup> +hlp_f	-61,7	-26,9
hlp_m+hlp_f	-62	-26,4
GS+GS <sup>2</sup> *sex	-64,3	-26,2
hlp_f	-56,2	-24,9
GS*sex	-60,4	-24,1
(hlp_m+hlp_f)*sex	-62,3	-23,5

hlp_f*sex	-57,2	-23,4
hlp_m	-25,7	-16,7
hlp_m*sex	-52,1	-16,5
hlp_m <sup>2</sup> *sex	-53,8	-15,6
cst	-45,4	-13,4
hlp_m <sup>2</sup>	-51,6	-13,1
sex	-44,2	-11,2

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# Chapter VI.

## General Discussion, Perspectives & Conclusion

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**Population dynamics of Alpine marmots:  
beyond sociality**







## 12. Overview

Population dynamics of social species is expected to differ from the population dynamics of solitary species because of the higher level of structuration they display. In highly social species, such as cooperative breeders, populations are structured not only according to age and sex but also according to breeding status because of dominance relationships within social groups (Lukas & Clutton-Brock 2012). Because the costs and benefits of group living depend on the group characteristics, demographic rates are expected to vary with the group size/composition. These differences in individual vital rates will in turn lead to social groups displaying different group dynamics and the overall population dynamics will in turn emerge from the combination of these different social group dynamics. Understanding the population dynamics of social species thus requires understanding the mechanisms responsible for the differences in individual demographic rates responsible for the group dynamics but also the mechanisms responsible for the interactions between social groups.

In this thesis, I tried to better understand the consequences of this structuration in different hierarchical levels for social species' population dynamics. To do so, I took advantage of a detailed long term individual-based data set on Alpine marmots (*Marmota marmota*) to study the influence of sociality on population dynamics. In this cooperatively breeding species, sociality is characterized by a life in territorial family groups where the dominant couple monopolizes reproduction and subordinate individuals are most often offspring of the dominant couple. Using recently developed statistical methods, I investigated the consequences of this particular social system at all levels, from individuals to the population.

In chapter III, thanks to the duration of the population monitoring program in the Grande Sassièrè nature reserve, I was able to test for the long term influence of early-life social conditions on the probability to reach a dominant status later in life. The composition of the birth litter was shown to be a major determinant of the ability to reach dominance. Notably, the presence of numerous females was associated to lower probabilities of becoming dominant, potentially because of feminizing hormone transfers during *in utero* development. This study reveals that sociality can have long-lasting effects on individuals' capacity to reach a dominance status and therefore higher fitness values.

In chapter IV, I developed an integrated multi-event dispersal model in order to obtain true survival and natal dispersal estimates. By jointly modelling dispersal movements and demographic parameters in an integrated modelling framework, the model allowed us to accurately study the complex life cycle of Alpine marmots. This model was then used to study the interactions between social groups and their consequences for individual vital rates and subsequent group dynamics. The immigration of a new dominant resulted in the forced dispersal of most of the same-sex subordinates to avoid costs linked to intra-sexual competition between un-related individuals. This phenomenon led to a severe decrease in group size and a strong modification of the group composition. These results highlight the importance of groups' interactions not only for individuals' survival and reproduction but also for group dynamics in cooperative breeders.

In chapter V, I used the de-lifing method to analyze how the size and composition of social groups affected their contribution to the overall population dynamics. To do so, I first developed a mixture model to study variations in the mean of bimodally distributed de-lifing data and exemplified its use with an analysis of age-specific fitness variation in Alpine marmots. Group contribution to population growth was found to be negatively correlated to group size while dominant contributions were positively related to the presence of male subordinates and subordinate contributions to population growth rate were negatively related to the presence of subordinate females. By decomposing group contributions into contributions of dominant and subordinate individuals, I showed that social group dynamics were regulated through density-dependent mechanisms. At the population level, these results highlight the importance of the population composition in terms of groups of different size/compositions for the overall dynamics.

Altogether, these different results shed light on the functioning of Alpine marmots' populations and more generally on the complexity of cooperative breeders' population dynamics. Contrary to solitary species, population dynamics of group-living cannot be directly inferred from the mathematical combination of individual demographic rates and the different results presented here tend to depict population dynamics of social species as an emergent property of these populations in the sense that: "it is necessary to study not only parts and processes in isolation, but also to solve the decisive problems found in organization and order unifying them, resulting from

dynamic interaction of parts, and making the behavior of the parts different when studied in isolation or within the whole.” (Von Bertalanffy 1969). In the same way, we have found here that individual demographic rates will depend on the group characteristics (size and composition in particular; chapter III and previous studies on the same population), thus leading to social groups displaying density-dependent group dynamics. But group dynamics does not entirely depend on its own constitution and it will also be subject to the influence of neighboring groups which can strongly influence the characteristics of the focal group through dispersal events (chapter IV). The dynamic of a group studied in isolation will therefore be very different from the dynamic of the same group studied inside a given population (chapter V). Additionally, while I focused only on the consequences of sociality *per se* on social organization and group performances, the influence of sociality on individual demographic rates, group dynamics and ultimately population dynamics may also result from indirect effects involving other factors.

### **13. Perspectives**

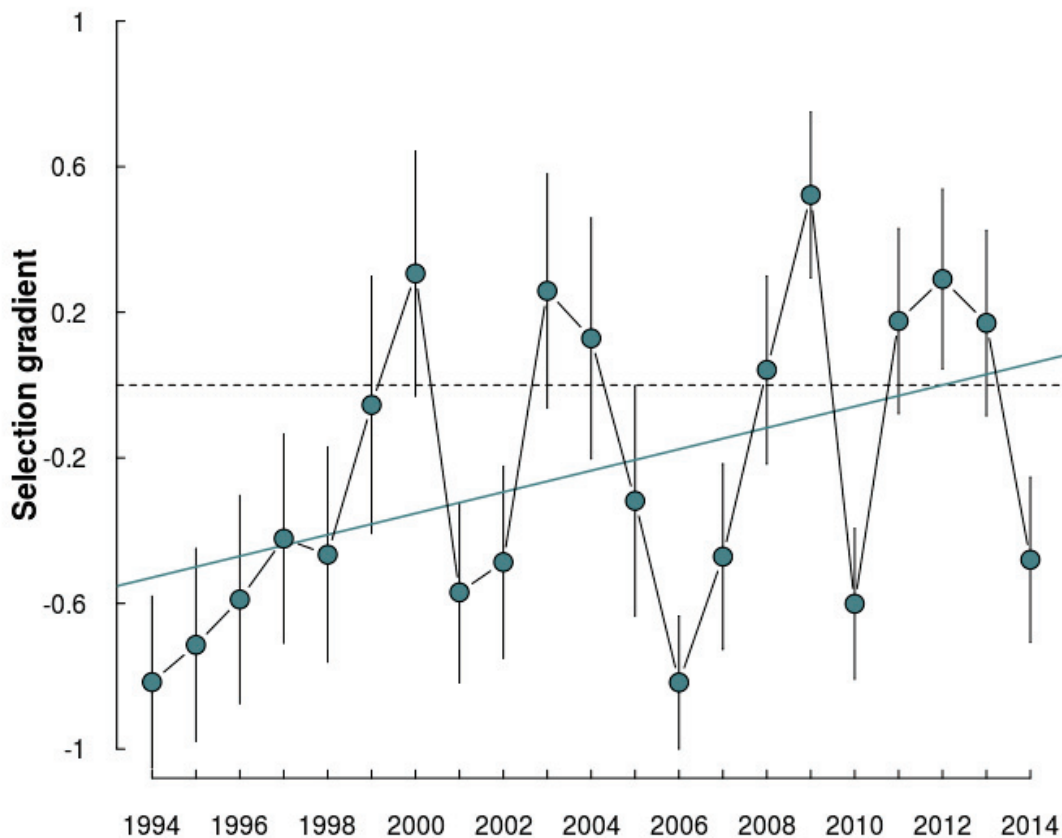
#### *13.1. Climatic factors*

Many studies on social species have shown that sociality had the potential to strongly mediate the influence of ecological factors, and particularly climatic factors. In meerkats, for example, Bateman *et al.* (2013) showed that the social structure of the population will determine the population response to environmental variation. Specifically, they found that seasons of low rainfalls were responsible for a decrease in reproductive success leading to a modification of social groups’ age structure the following years, thus increasing subordinate emigration probabilities and therefore contributing to crashes in group dynamics. In common mole rats (*Cryptomys hottentotus hottentotus*), it has been shown that the decision to leave a colony was also strongly influenced by climatic conditions in interaction with group size (Spinks *et al.* 2000). More precisely, dispersal rates increased as a function of colony size but this relationship was modulated by the aridity of the surrounding environment.

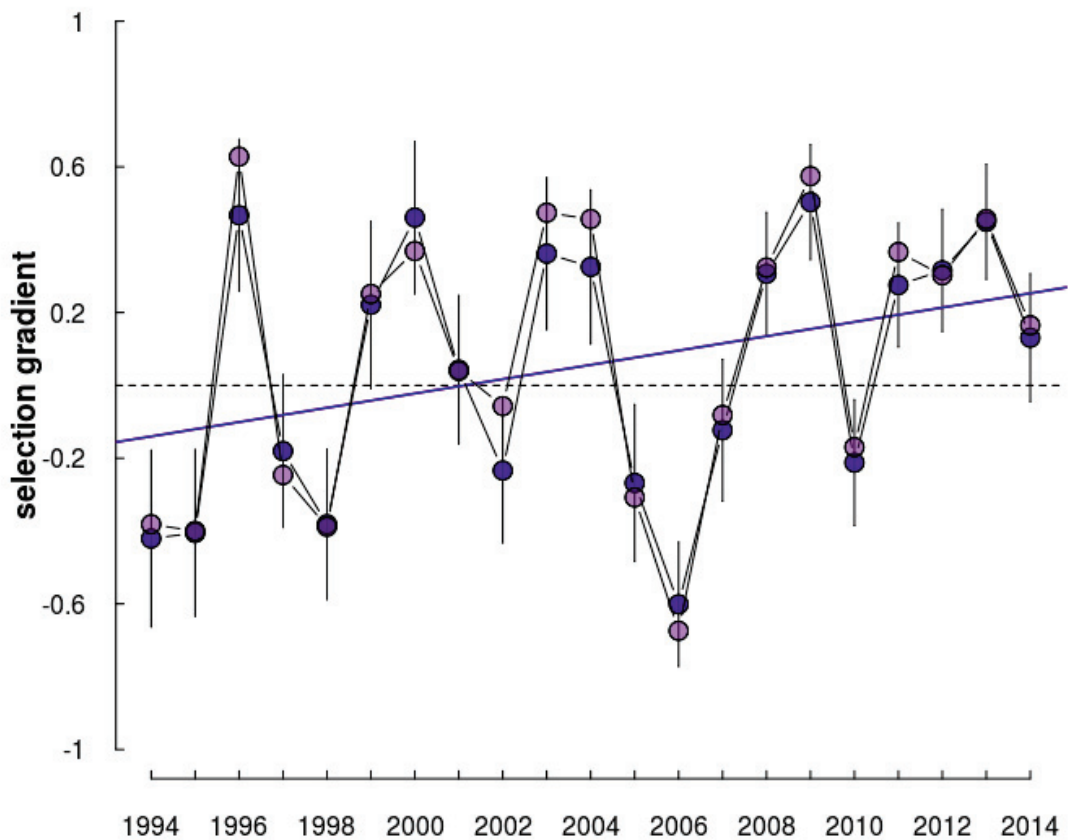
Similarly, in Alpine marmots, recent studies have highlighted the impact of changing climatic conditions on individual demographic rates and therefore on social group structure. It has been evidenced that the decreasing snow depths during winter led to a decrease in litter size (Tafani *et al.* 2013) while juvenile survival decreased between

1990 and 2012 because of the interactive effect between winter conditions and the presence of subordinate males during hibernation (Rézouki *et al.* 2016).

Climatic factors, and particularly climate change, is therefore expected to strongly affect the social structure of the Alpine marmot population and consequently its population dynamics. Accordingly, a preliminary analysis we conducted using the de-lifing method shows a strong increasing trend in the relationship between group size and group contribution to population growth rate between 1990 and 2014 (Fig.VI.1). This change in the influence of group size on group contribution to growth rate seems in turn directly related to an evolution of the relationship between dominant contributions and group size (Fig VI.2). Interestingly, we also found that dominant contribution to population growth rate was exactly matching the pattern of dominant recruitment.



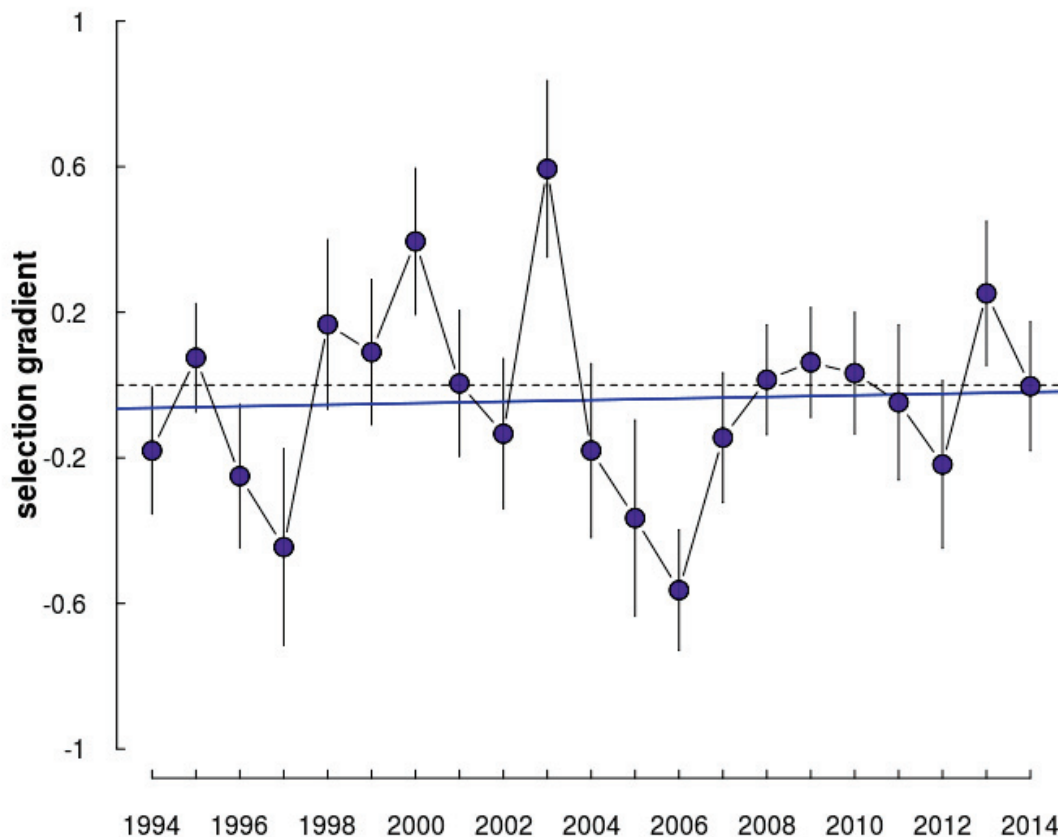
**Figure VI.1.** Time series of the effect of group size on group contribution to population growth rate between 1994 and 2014 in the Grande Sassièrè nature reserve population. Points represent the slope of the linear regression of group contribution to growth rate according to its size. Data for each year were transformed prior to analysis to have a mean of zero and a standard deviation of one.



**Figure VI.2.** Time series of the group size effect on dominant contribution to population growth rate (purple) and on dominant contribution to recruitment (blue) between 1994 and 2014 in the Grande Sassière nature reserve population. Points represent the slope of the linear regressions of group size on dominant annual fitness or recruitment. Data for each year were transformed prior to analysis to have a mean of zero and a standard deviation of one.

In the same time, the relationship between subordinate contribution to population growth rate and group size does not show any significant temporal trend. Altogether, these results indicate that the balance between cost and benefits associated to group size and composition for dominant individuals is likely to be impacted by ongoing climate change. The effect of climate change in Alpine marmots therefore seems to be mediated through the effect of sociality on demographic rates.

Further research should therefore integrate this climate change dimension in order to fully understand the population dynamics of Alpine marmots.



**Figure VI.3.** Time series of the group size effect on subordinate contribution to population growth rate between 1994 and 2014 in the Grande Sassière nature reserve population. Points represent the slope of the linear regressions of group size on dominant annual fitness or recruitment. Data for each year were transformed prior to analysis to have a mean of zero and a standard deviation of one.

### 13.2. Individual Based Model

One possible way further to better describe and understand the mechanisms driving population dynamics in Alpine marmots would be the development and use of an individual based model (Judson 1994). By combining the results of the numerous studies on Alpine marmots (*e.g.* Allainé *et al.* 2004, Cohas *et al.* 2008; Tafani *et al.* 2013; Dupont *et al.* 2015; Berger *et al.* 2016 and this thesis), we could construct a model that fully accounts for social influences on individual demographic rates and see if the resulting groups and population dynamics match the observed population dynamics. The use of individual based model is particularly fit to study social species because it allows to explicitly incorporate interactions between individuals within social groups but also

(potentially spatially explicit) interactions between social groups, two features that do not possess matrix models (Caswell 2001).

In addition, the analysis of such individual-based model would allow to quantify the relative importance of the different effects of sociality for the overall population dynamics. Indeed, the different results reported here do not take into account the effect size associated with it and some social effects might only marginally affect the overall population dynamics of Alpine marmots. By varying the values and intensity of these effects, an individual based model constructed after these results would allow us to identify and contrast the main drivers of the population dynamics. As an example, this could allow us to determine whether the effect of early-life social context (chapter III) is really important for individuals to reach dominance compared to other factors affecting dominance access like, say, dispersal (chapter IV). The results obtained in Chapter V may already give us clues as to the importance of these different factors. It seems, that the main driver of group contributions to the population growth rate is the recruitment, largely influenced by group size, and more specifically by the presence of male helpers (Allainé & Theuriau 2004), indicating that juvenile survival is probably a key process in the overall population dynamics of Alpine marmots. However, this result only holds for the yearly growth rate and does not allow for testing of delayed effects, contrary to a thorough analysis of an individual based model constructed with great caution.

#### **14. Conclusion**

In this thesis, I have presented different studies aiming at the same general goal: understanding the consequences of group-living from the individual to the population level. With these different studies (some of which are only beginning), I tried to bring together results of previous research on the Alpine marmots and provide new results about little-known aspects of this cooperative breeder. Notably, I started by highlighting the presence of long-term developmental consequences on the ability to reach a dominant status potentially entailing important fitness consequences.

A large part of my work also focused in developing new models to be able to make the most out of the long-term individual-based data set at hand in order to answer new questions. This concern about methodological issues allowed me to study the causes and consequences of dispersal in Alpine marmots, a part of its life history poorly known until now. Following this I was able to quantify the important consequences of dispersal



at both the individual and group levels. Additionally, this work has paved the way for other studies on dispersal in Alpine marmots and notably further studies should look at the influence of group composition on the probability to leave the natal territory and succeed in becoming dominant for both males and females.

I also presented the first study linking the composition of the family groups to the overall population dynamics in Alpine marmots and showed how it was related to individual demographic rates. However, further studies are required to better understand the relationship between lifetime individual fitness conditioning the decisions of dominants and subordinates and how it relates to optimal group composition and group dynamics.

Finally, understanding the relationships between individuals within groups and between groups in the Alpine marmot will help understand the reasons that led to the evolution of such social systems and how it may evolve in the future. The Alpine marmot system also provides this unique opportunity to study evolutionary changes in ecological times (to paraphrase Coulson *et al.* (2006)) and the evolutionary demography of Alpine marmots should be a very prolific field of study in the near future.

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# Appendices

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## **A. Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence**

## **B. Phylogeographic history of the Alpine marmot**

**Abstract:** In this last section, I present two additional articles published by the research team to which I contributed during my thesis.

The first article was published as part of the thesis of Dr. Berger entitled “Senescence and sociality: the example of the Alpine marmot (*Marmota marmota*)”. My contribution to this article was mainly in helping developing and analysing multi-event capture-recapture models to study the sex-specific survival trajectories of dominant Alpine marmots.

The second article was published as part of the post-doctoral project of Dr. Bichet called “Intra and inter-populations genetic diversity in the Alpine marmot (*Marmota marmota*)”. My contribution to this project was mainly in gathering data and managing the field-work team in the Aussois population in the Vanoise National Park. I also participated in revising the manuscript.

**Keywords:** Senescence patterns · Threshold models · Genetic differentiation · Phylogeographic history





## Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence

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We investigated age-specific variation in survival of dominant individuals in a long-lived and monogamous mammal, the alpine marmot (*Marmota marmota*), from a large dataset collected during a 24-year intensive monitoring of a free-ranging population. We found evidence of actuarial senescence in dominant individuals for both sexes. Survivorship was constant with age until dominant marmots were between 6 and 8 years of age and declined markedly thereafter. No between sex differences occurred in the intensity of actuarial senescence, which might be related to the weak intensity of sexual selection in this socially monogamous mammal. More investigations are needed to know whether cooperative breeding, hibernation, and monogamy, which are key features of the alpine marmot life history, could have shaped the patterns of actuarial senescence we report.

Key words: ageing, cooperative breeder, multievent models, sciurids

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Actuarial senescence is defined as the increase in annual mortality with age (Ricklefs 1998; Nussey et al. 2008). It has been argued that actuarial senescence has evolved because of the decline of natural selection forces with increasing age, as demonstrated by pioneer works (Medawar 1952; Williams 1957; Hamilton 1966). During the last century, it was believed that ageing does not occur in wild populations because individuals die before the occurrence of any sign of senescence (Medawar 1952; Comfort 1956). However, thanks to the detailed analyses of long-term individual monitoring, actuarial senescence has been widely documented in free-ranging and age-structured populations during the last 2 decades, especially in vertebrates (review in Nussey et al. 2013). In addition, there is now compelling evidence that senescence displays highly variable patterns across the tree of life (Jones et al. 2014).

As senescence is grounded into life history evolution (Jones et al. 2008; Lemaître et al. 2015), having a comprehensive view of senescence patterns allows understanding factors shaping population dynamics. To date, most senescence studies have focused on the analysis of the rate of senescence (e.g., Ricklefs 2010), which has been shown to vary greatly among individuals (Bouwhuis et al. 2010), populations (Lemaître et al. 2013), and species (Jones et al. 2008). However, variation in the age at the onset of senescence also contributes to shape senescence patterns (Péron et al. 2010; Gamelon et al. 2014). Although both Williams (1957)

and Hamilton (1966) explicitly stated that actuarial senescence should set on after the age at 1st breeding, accumulating empirical evidence indicates that it is not the case (Péron et al. 2010). For example, in alpine ibex (*Capra ibex*), the age at 1st reproduction is between 2 and 3 years old, whereas actuarial senescence only occurs from 7 years of age onward (Toïgo et al. 2007).

Studying senescence in the wild requires longitudinal data on known-aged individuals over their entire lifespan. Mammalian species that are monogamous and cooperative breeders have rarely been the target of such long-term studies, which leads our understanding of actuarial senescence in these species to be currently limited. To date, only 5 studies have investigated the age-specific variation in survival using transversal (*Alouatta palliata*—Froehlich et al. 1981, *Castor canadensis*—Bergerud and Miller 1977) or longitudinal (*Helogale parvula*—Waser et al. 1995, *Lycaon pictus*—Creel and Creel 2002, *Rhodomys pumilio*—David and Jarvis 1985, *Alouatta seniculus*—Larson et al. 2016) data. On the contrary, mammals in which only mothers care for young have been the subject of many detailed analyses of actuarial senescence (reviewed in Nussey et al. 2013). Yet, cooperative breeder species, where nonparent individuals help in raising young of dominants (Jennions and Macdonald 1994), display typical life histories with delayed age at 1st reproduction and decreased environmentally driven mortality risks that could shape senescence.



Additionally, a growing number of studies provide evidence that in mammals, sex is an important cause of variation in actuarial senescence (e.g., Loison et al. 1999; Descamps et al. 2008; Greiner et al. 2013; Gamelon et al. 2014; Tidière et al. 2015). Williams (1957) predicted that senescence should be more rapid for the sex with the highest mortality rate and argued that males should display faster actuarial senescence. Indeed, the costs associated with fights for mating, with growing large secondary sexual characteristics, and with monopolizing resources, should all be higher in males than in females. Such sex differences led Bonduriansky et al. (2008) to launch the term for male life history strategy referred to as “live fast-die young”. However, some species do not display any sex difference in ageing patterns (see Clutton-Brock and Isvaran 2007; Tidière et al. 2015 for some interspecific analyses). Our current empirical knowledge then indicates that the influence of sex on ageing patterns is more complex and is still poorly understood.

Since 1990, a free-ranging population of alpine marmots (*Marmota marmota*) has been monitored on an individual basis. The alpine marmot is a socially monogamous species breeding cooperatively (Arnold 1990). This species displays a long lifespan in the wild, as the oldest individual observed in our population was 16 years of age. Previous studies of this population have pointed out the complexity of senescence patterns in life history traits of alpine marmots. Tafani et al. (2013) found that male body mass peaks at 8 years of age and declines thereafter, whereas female body mass does not show any sign of senescence. Likewise, Berger et al. (2015) found that litter size remains constant with age until females reach 10 years of age and declines thereafter, whereas mass of pups does not show any evidence of senescence. As new evidence suggests that senescence in traits associated with individual fitness might show heterochrony (Nussey et al. 2013; Hayward et al. 2015), it is crucial to analyze both demographic and phenotypic traits to have a comprehensive view of ageing processes within a given species. However, to date, age-specific changes in survival have not been yet investigated in this species.

Using an exceptional long-term individual monitoring of an alpine marmot population, we estimated age-specific changes of survival in dominant individuals and tested for sex differences of the rate of senescence. In our population, no subordinate individual older than 6 years of age was ever observed. All subordinates either died or become dominant before being old enough to show senescence. Based on previous analyses of age-specific variation in body mass that provided evidence of sex-specific senescence pattern (Tafani et al. 2013), we expected that actuarial senescence should be more intense in males than in females, assuming that body mass is a good indicator of condition and survivorship in this species, similarly to what has been reported for other mammals (e.g., Gaillard et al. 2000 in large herbivores, Ozgul et al. 2010 in yellow-bellied marmots, *Marmota flaviventris*).

## MATERIALS AND METHODS

### *Study Species*

Alpine marmots live in family groups of 2–16 individuals composed of a dominant couple, sexually mature (individuals from 2 years of age onward) and immature subordinates of both sexes (yearlings), and offspring of the year (Allainé 2000). Alpine marmots are territorial. The territory is shared by all family members but is mainly defended by the dominant pair.

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). Dominant marmots mate during the 15 days following the emergence from hibernation (i.e., from early to late April). After 30 days of gestation, dominant females give birth to the sole litter of the year. The altricial offspring stay in the natal burrow during 40 days and once weaned emerge above ground between mid-June and mid-July (Psenner 1956, 1960). At sexual maturity (i.e., 2 years of age), an individual can stay as a subordinate in its natal group or attempt to become dominant by either inheriting the dominance status in its natal group or dispersing to gain dominance in another territory. A dispersing individual never joins a new family group as a subordinate (Magnolon 1999).

Dominant marmots monopolize reproduction by physiologically suppressing reproduction of almost all mature subordinates of both sexes (Arnold and Dittami 1997; Hackländer et al. 2003). However, when the group size increases, the control of subordinates through aggressive behaviors is less effective. Therefore, in large family groups, some subordinate males unrelated to the dominant female can escape the control of the dominant and mate with the dominant female. Moreover, when subordinate males disperse to try to reach the dominant position in another territory, they can mate during dispersal with dominant females unbeknownst to the dominant males. In these 2 cases, the dominant female can give birth to young fathered by both the subordinate or transient male and the dominant male (Cohas et al. 2006).

Hibernation is characterized by a cyclic process with alternate hypothermia and euthermia phases (Arnold 1990). Group members hibernate together from mid-October to early April, and produce heat during periodic arousal, a phenomenon called social thermoregulation (Arnold 1990). However, all members of a family group do not have the same length and rhythm of hibernation. In particular, at each cycle, subordinate males wake up earlier and have longer euthermic periods than other family members, leading them to warm the burrow more than other group members (Arnold 1993). Consequently, subordinate males act as helpers and their presence in a family group increases the probability of offspring to survive their 1st hibernation (Allainé and Theuriau 2004), while they pay the costs in terms of body mass loss (Arnold 1988).

### *Study Site and Data Collection*

Marmots were captured in a free-ranging population located in the Grande Sassièr Nature Reserve (2,340 meters above

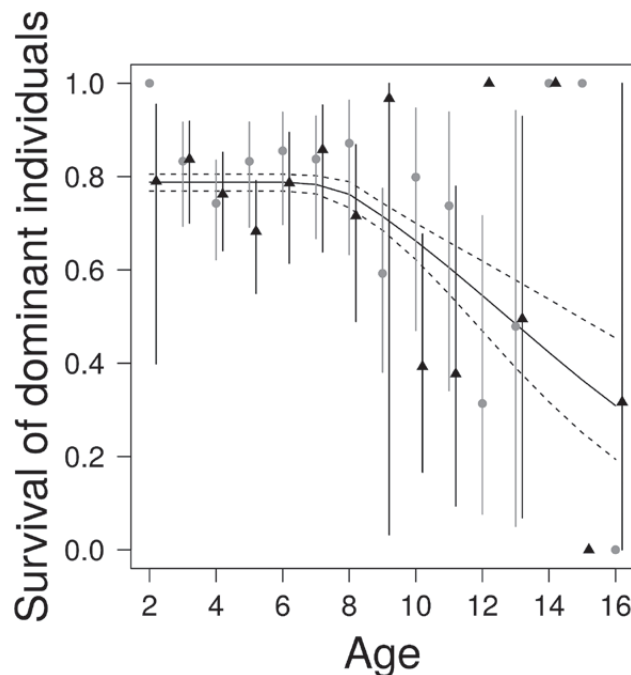
sea level, French Alps, 45°29'N, 6°59'E), from 1990 to 2013. Every year, marmots from 24 territories were monitored, from mid-April to mid-July, using both capture-mark-recapture and observations. Marmots were captured using 2-door live-capture traps baited with dandelions (*Taraxacum officinale*). Traps were placed near the entrances of the main burrows to assign easily each captured individual to its family group. Juveniles were counted and captured by hand within the 3 days following their 1st emergence from the natal burrow (i.e., approximately 40 days after their birth). Captured animals were tranquilized with Zolétil 100 (Vibrac Corporation, St. Louis, Wisconsin). At 1st capture, unmarked individuals were implanted with a PIT-tag (Trovan Ltd, [www.Trovan.com](http://www.Trovan.com), Cologne, Germany), and marked with a numbered ear tag. Tags were put on the right ear of females and on the left ear of males. In addition, a colored plastic ear tag was placed on the opposite ear of dominant marmots. At each capture, marmots were sexed and their social status was determined (assessed as dominant when testes reach the bottom of the scrotum [males] and when large mammary glands were present [females]). Daily observations were conducted and we further assessed the number of individuals of each sex and age class (pup, yearling, and adult) for each family. Scent-marking behavior was used to confirm the identity of the dominant pair (Bel et al. 1995).

We measured age (in years) from birth and assigned the age of 0 to offspring. We knew the exact age of dominant individuals born on the study site (84 females, 82 males), but not the age of immigrants (29 females, 47 males). As most marmots disperse at 2 years of age and almost never reproduce before 3 years of age (no female among the 84 females of known age, 3 males among the 82 males of known age), we assigned the age of 3 to immigrants when they first reproduce.

Genetic analyses were performed to assess the certainty of the maternity and paternity of individuals. When an individual was not captured in a given year, its survival could be accessed through genetic analyses by revealing a pup production for a given year. Details about genetic and kinship analyses are provided in Dupont et al. (2015).

#### Capture–Recapture Analysis

**Model structure.**—Between 1990 and 2013, 242 marmots were captured as dominant individuals (113 females and 129 males). We used multievent capture–recapture models (ME-CR—Pradel 2005) to investigate the influence of age on survival of dominant marmots because recapture probability of individuals was much lower than 1 (recapture probability varying from 0.380 to 0.886—Cohas et al. 2007) and not accounting for imperfect detection indeed leads to biased survival estimates (Gimenez et al. 2008). In these models, as in multistate models (Lebreton et al. 2009), each individual can only be in 1 of the 3 following states: subordinate (*s*), dominant (*D*), or dead ( $\dagger$ ). Therefore, we were able to estimate different probabilities of survival for animals in the 2 live states and of transition probabilities from one state to another (Fig. 1). In addition, multievent models allow taking into account uncertainty about the state of individuals and/or any additional information. Here, we



**Fig. 1.**—Age-specific variation in survival of dominant adult marmots (*Marmota marmota*). The solid line represents survival estimated from model averaging of the 3 competitive models (in bold in Table 2) and the dashed lines the associated standard errors. The grey circles and the associated error bars represent the age-specific survival estimates and their associated confidence intervals for females, while the black triangles and the associated error bars represent the age-specific survival estimates and their associated confidence intervals for males.

incorporated additional information about the reproductive status. Indeed, based on kinship analyses, we were able to determine whether an individual successfully reproduced (i.e., young emerging from the burrows) or not in a given year, even when the individual was not captured that year, thus allowing us to refine the survival estimates (Dupont et al. 2015). The different observable events retained were no information (event 0), individual not captured but its pups were captured (event 1), individual captured as dominant but none of its pups were captured (event 2), individual captured as dominant with its pups captured (event 3), individual captured as subordinate but none of its pups were captured (event 4), and individual captured as subordinate with its pups captured (event 5). Based on these events, capture–recapture histories were constructed for each individual.

The constructed multievent model can be summarized by a transition matrix and associated vectors of survival, capture, and successful reproduction probabilities (only the 2 live states are shown since the parameters of the dead state are fixed to  $p^\dagger = 0$ ;  $\Psi^{\dagger\dagger} = 1$ ;  $E^\dagger = 0$ , see Table 1 for the glossary of abbreviations and their meanings).

$$\begin{bmatrix} 1 - \Psi^{sD} & \Psi^{sD} \\ 0 & 1 \end{bmatrix}_r \begin{bmatrix} \Phi^s \\ \Phi^D \end{bmatrix}_r \begin{bmatrix} p^s \\ p^D \end{bmatrix}_r \begin{bmatrix} E^s \\ E^D \end{bmatrix}_r$$

where probabilities of capture ( $p$ ), survival ( $\Phi$ ), reproduction ( $E$ ) and state transition conditional on survival ( $\Psi$ ) are defined

as:  $P_t^x$ , the probability that an individual in state  $x$  was captured during the year  $t$ ;  $\Phi_t^x$ , the probability that an individual in state  $x$  in year  $t$  survived and did not permanently emigrate from the study area between  $t$  and  $t + 1$ ;  $\Psi_t^{xy}$ , the probability that an individual in state  $x$  in year  $t$  is in state  $y$  in year  $t + 1$  given that it survived and did not permanently emigrate from the study area between  $t$  and  $t + 1$  and  $E_t^x$ , the probability that an individual in state  $x$  at time  $t$  had successfully reproduced this same year. Since dominant individuals never revert to subordinate state (Grimm et al. 2003), the transition probability from the dominant state to the subordinate state was fixed to 0 ( $\Psi^{SD} = 0$ ), thus constraining the state transition probability from dominant to 1. Additionally, we fixed to 0 the transition probability from subordinate to dominant between 1 and 2 years of age and after 6 years of age.

**Model selection.**—To investigate the influence of age on survival, we followed 3 steps as proposed by Lebreton et al. (1992):

1. Goodness-of-fit tests: We 1st tested whether a general model compatible with our biological knowledge fitted our data. To this purpose, we performed goodness-of-fit (GOF) tests (Pradel et al. 2005) using the program U-CARE (Choquet et al. 2009a).
2. Obtaining a baseline model: Next, we selected the most parsimonious model, starting from a general model. Following Burnham and Anderson (2002), we built the general model by considering only a priori biological hypotheses based on literature (Arnold 1993; Farand et al. 2002; Stephens et al. 2002; Grimm et al. 2003; Cohas et al. 2008; Dupont et al. 2015). We thus considered effects of age, time, sex, and their 2-way interactions on all capture, state transition, and reproduction probabilities. For survival, we also considered the effects of time, sex, and the simplest age structure in 3 classes for subordinates (yearling, 2 years old, and aged from 2 to 6) and age structure in 2 classes for dominants (2 year old and aged from 3 to 6). In addition, we considered an effect of the number of male helpers since a high number of these latter groups appeared to be beneficial in terms of juvenile survival (Allainé and Theuriau 2004). Consequently, we denoted the most general model as follows:

$$p^s(a_2; a_{3-7}) * t * sex \Phi^s(a_1 * helpm; a_2; a_3; a_{4-7}) * t * sex \\ E^s(a_{3-7}) * t * sex p^D(a_{3-7}) * t * sex \Phi^D(a_3; a_{4-17}) * t * sex \\ E^D(a_{3-17}) * t * sex \Psi^{SD} a_1 : a_{7-17}; (a_2; a_{3-6}) * t * sex$$

Following a step-down approach, models were sequentially fitted with constrained parameterizations for recapture, survival, transitions, and reproduction probabilities, in that order. We then checked that the best model could not be improved by exploring all nested models differing by only 1 effect.

3. Testing for age-specific survival: To test for age-specific variation in survival we fitted age-specific models by

considering age as a linear or quadratic covariate, or as a categorical factor. We further fitted threshold models by holding survival constant until a threshold age, beyond which it linearly depended on age. The tested threshold age varied between 5 and 15 years. For each of these models, we also included a possible sex effect. Model selection and parameter estimation were performed using the program E-SURGE 1.8.5 (Choquet et al. 2009b). Estimates and standard errors of regression slopes reported in the result section are on the logit scale. All other parameters are given on the absolute scale. The associated standard errors were obtained by the delta method (Burnham and Anderson 2002). When several candidate models were competitive (i.e., differences in Akaike Information Criterion [AIC] less than 2), we performed a multimodel inference based on AIC weights ( $w_i$ ) to produce mean estimates averaged across the different models of interest.

*Comparing the onset of actuarial senescence estimated in marmots with the expectation based on early life history traits.*—The onset of actuarial senescence in alpine marmots has not been previously investigated. Péron et al. (2010) provided a life history model that allows predicting the onset of actuarial senescence across bird and mammal species based on their early life history traits. From a dataset included species studied using capture-mark-recapture and after accounting for potentially confounding effects of phylogeny, Péron et al. (2010) found that the onset of actuarial senescence is expected to be equal to

$$\text{Onset} = \exp(0.22 \log(A) + 1.78 / (F^{0.34} S^{0.20A}))$$

where  $A$  is the age at 1st reproduction,  $F$  the annual prime age fecundity, and  $S$  the juvenile survival (between birth and 1 year of age).

We included  $A$ ,  $F$ , and  $S$  values that we got from our studied population of alpine marmots to calculate the age at the onset of senescence expected for marmots. We then compared this expected value to the value obtained from the survival analysis of our studied population.

## RESULTS

*Goodness-of-fit tests.*—The overall goodness-of-fit (GOF) test of the Cormack–Jolly–Seber model (i.e., the fully time-dependent model) was statistically significant ( $\chi^2 = 159.58$ ,  $d.f. = 79$ ,  $P < 0.01$ ) due to transience detected by the 3SR component test or also called the Brownie–Robson test ( $\chi^2 = 93.55$ ;  $d.f. = 22$ ,  $P < 0.01$ ). Individuals considered as transients were in fact pups that did not survive to their 1st hibernation and were thus captured only once. A 2nd GOF test was thus run on a dataset from which the 1st occasion of capture for individuals caught as pups was removed. The overall GOF test was no longer statistically significant ( $\chi^2 = 28.87$ ,  $d.f. = 56$ ,  $P = 0.99$ ) nor was the transience test (test 3SR;  $\chi^2 = 21.55$ ,  $d.f. = 22$ ,  $P = 0.49$ ). Yet, taking into account age classes in the baseline model solved the initial problem of apparent transience.

*Baseline model.*—After selection using AIC (see [Supporting Information S1](#)), the baseline model was

$$p^s(a_1; a_2; a_3; a_{4-7}) + t + \text{sex } \Phi^s(a_1 * \text{helpm}; a_2; a_3; a_{4-7}) + t E^s a_3; a_4; a_{5-7} p^D(a_3; a_{4-7}) + t + \text{sex } \Phi^D(a_3; a_{4-7}) + t \Psi^{SD} a_1 : a_{7-17}; a_2; a_3; a_{4-7}$$

Survival varied over time, between status, and age classes. Dominant adults had a higher survival ( $0.773 \pm 0.016$ ) than subordinate adults ( $0.550 \pm 0.024$ ), which can result from natal dispersal of subordinates outside the study site ([Magnolon 1999](#)) that cannot be distinguished from death.

*Age-specific survival.*—Dominant alpine marmots displayed clear evidence of senescence in survival ([Table 2](#)). Both linear and quadratic models performed poorly compared to the baseline model. Our results rather showed a threshold pattern of survival where survival remained constant until a threshold age and declined thereafter ([Fig. 1](#)). Three threshold models received strong support with an age at the onset of senescence at 6, 7, and 8 years of age, respectively. As these models provided similar fit, we performed a model-averaging procedure to estimate the constant survival during early ages and the rate of actuarial senescence, and thereby age-specific survival estimates. Survival remained constant at  $0.79 \pm 0.02$  from 3 years of age until the threshold age (in females:  $0.82 \pm 0.02$ ; in males:  $0.78 \pm 0.02$ ) until 6 years of age and then declined to 0.31 at 16 years of age ( $\beta_{\text{averaged}} = -0.25$ ; [Fig. 1](#); see [Supporting Information S2](#)). Neither early adulthood survival nor the rate of senescence differed between sexes ([Table 2](#)). As expected, the

number of individuals monitored decreased with increasing age, which led error bars from the full dependent age model to be larger for old than for young individuals, especially in males.

## DISCUSSION

Survival starts to decrease from 6 to 8 years of age in dominant alpine marmots, which is quite similar to the value obtained from the model in [Péron et al. \(2010\)](#) based on the covariation among early life history traits across bird and mammal species. Indeed, model in [Péron et al. \(2010\)](#) predicts an onset of actuarial senescence of marmots at 6.5 years of age. However, as most marmots start reproducing at 3 years of age, the onset of actuarial senescence of alpine marmots is delayed compared to the theoretical assumption that actuarial senescence should start at the age at 1st reproduction ([Williams 1957](#); [Hamilton 1966](#)). Although the age-specific survival patterns we report in alpine marmots does not fit with theoretical expectations, several iteroparous species showed similar patterns (e.g., [Stolen and Barlow 2003](#); [Toïgo et al. 2007](#); [Descamps et al. 2008](#); [Bronikowski et al. 2011](#)). Our case study on alpine marmots thus contributes to the growing empirical evidence supporting that the synchrony between the age at 1st reproduction and the age at the onset of senescence is rather the exception than the rule. Finally, contrary to our expectation based on senescence patterns observed in body mass, the rate of actuarial senescence did not differ between sexes.

The absence of sex difference in the strength of actuarial senescence we report for alpine marmots does not support the expected “live fast, die young” life history strategy expected to be displayed by males ([Bonduriansky et al. 2008](#)). Indeed, our finding markedly contrasts with studies of other mammal species that reported earlier or stronger senescence in males compared to females (e.g., [Gaillard et al. 2003](#); [Lemaître and Gaillard 2013](#)). However, these studies included polygynous species for which reproductive effort is much greater in males than in females ([Clutton-Brock and Isvaran 2007](#); [Bonduriansky et al. 2008](#); but see [Greiner et al. 2013](#)). In polygynous species, the intensity of sexual selection is expected to drive the magnitude of sex differences in actuarial senescence ([Clutton-Brock and Isvaran 2007](#); but see [Tidière et al. 2014](#)). On the contrary, in monogamous species, like the alpine marmot, the intrasexual competition is similar in both sexes and sex-specific differences in ageing should not be marked in monogamous species ([Bonduriansky et al. 2008](#)), which is supported by several empirical studies ([Clutton-Brock and Isvaran 2007](#); [Larson et al. 2016](#)).

In females, the onset of actuarial senescence is consistent with the onset of senescence reported for reproductive success (approximately 8 years of age—[Berger et al. 2015](#)) but markedly differs from the senescence pattern reported in body mass (with an absence of senescence—[Tafari et al. 2013](#)). In males, no information on age-specific variation in reproduction is available but body mass starts to decrease from about 8 years of age, which is consistent with the onset of actuarial senescence we report here. Surprisingly, alpine marmots displayed

**Table 1.**—Abbreviations used in model notations.

Abbreviations	Meanings
<i>P</i>	Recapture probability
$\Phi$	Survival probability
$\Phi^D$	Survival probability of dominant individuals
$1 - \Phi$	Mortality probability (encompassing both mortality and dispersal probabilities for individuals older than 2 years of age)
$\Psi$	State transition probability (conditional on survival)
<i>E</i>	Event probability (probability of successful reproduction)
Subscript	
<i>a<sub>1</sub></i>	Age from 0 to 1 year
<i>a<sub>2</sub></i>	Age from 1 to 2 years
<i>a<sub>x,y</sub></i>	Age from <i>x</i> to <i>y</i>
<i>a<sub>x+...+y</sub></i>	Age classes <i>x</i> +...+ <i>y</i>
<i>Sex</i>	Sex
<i>T</i>	Time effect (years)
*	Interactive effects
+	Additive effects
<i>Helpm</i>	Number of male helpers present during the 1st hibernation
Superscript	
<i>S</i>	Subordinate status
<i>D</i>	Dominant status
†	Dead

**Table 2.**—Model selection for the effects of age on survival of dominant alpine marmots (*Marmota marmota*) marked from 1990 to 2013 ( $N = 242$ ).  $\Phi^D$  corresponds to survival of dominant individuals.  $T_i$  corresponds to a constant survival until the threshold age ( $i$ ) followed by a linear decline of survival with increasing age.  $\Phi_{a_2-16}^D$  corresponds to a linear decrease of survival from age 2 to age 16.  $\Phi_{a_2+\dots+a_{16}}^D$  corresponds to the full age-dependent model. All other parameters (transition, capture, and reproduction) are fixed as in the baseline model.  $AIC_c$ : Akaike Information Criterion corrected for small sample sizes;  $k$ : number of identifiable parameters;  $\Delta AIC_c$ : difference in  $AIC_c$  between the candidate model and the model of the set with the lowest  $AIC_c$ ;  $AIC_w$ :  $AIC_c$  weight. The selected model including an age effect is in bold and is highlighted with gray shading, and the competitive candidate models are in bold.

Model notation	Deviance	$k$	AIC	$\Delta AIC$	$AIC_w$
<b><math>\Phi_{T_6}^D + t</math></b>	<b>6,108.39</b>	<b>113</b>	<b>6,334.39</b>	<b>0</b>	<b>0.25</b>
<b><math>\Phi_{T_7}^D + t</math></b>	<b>6,108.48</b>	<b>113</b>	<b>6,334.48</b>	<b>0.09</b>	<b>0.24</b>
<b><math>\Phi_{T_8}^D + t</math></b>	<b>6,110.36</b>	<b>113</b>	<b>6,336.36</b>	<b>1.97</b>	<b>0.09</b>
$\Phi_{T_9}^D * sex + t$	6,106.55	115	6,336.55	2.16	0.08
$\Phi_{T_{10}}^D * sex + t$	6,106.56	115	6,336.56	2.17	0.08
$\Phi_{T_{11}}^D + t$	6,110.78	113	6,336.78	2.39	0.07
$\Phi_{T_{12}}^D * sex + t$	6,108.38	115	6,338.38	3.99	0.03
$\Phi_{T_{13}}^D + t$	6,112.54	113	6,338.54	4.15	0.03
$\Phi_{a_2-16}^D + t$	6,112.80	113	6,338.8	4.41	0.03
$\Phi_{T_{14}}^D * sex + t$	6,109.08	115	6,339.08	4.69	0.02
$\Phi_{T_{15}}^D + t$	6,113.97	113	6,339.97	5.58	0.01
$\Phi_{T_{16}}^D * sex + t$	6,110.55	115	6,340.55	6.16	0.01
$\Phi_{a_2-16}^D + \Phi_{a_2-16}^D + t$	6,110.64	115	6,340.64	6.25	0.01
$\Phi_{a_2-16}^D * sex + t$	6,110.89	115	6,340.89	6.5	< 0.01
$\Phi_{T_{17}}^D * sex + t$	6,112.42	115	6,342.42	8.03	< 0.01
$\Phi_{T_{18}}^D + t$	6,116.44	113	6,342.44	8.05	< 0.01
$\Phi_{T_{19}}^D + t$	6,117.74	113	6,343.74	9.35	< 0.01
$\Phi_{T_{20}}^D + t$	6,117.94	113	6,343.94	9.55	< 0.01
$\Phi_{T_{21}}^D + t$	6,118.39	113	6,344.39	10	< 0.01
$\Phi_{a_2-16}^D * sex + \Phi_{a_2-16}^D * sex + t$	6,108.67	118	6,344.67	10.28	< 0.01
$\Phi_{T_{22}}^D + t$	6,118.81	113	6,344.81	10.42	< 0.01
$\Phi_{T_{23}}^D * sex + t$	6,115.03	115	6,345.03	10.64	< 0.01
$\Phi_{T_{24}}^D * sex + t$	6,115.89	115	6,345.89	11.5	< 0.01
$\Phi_{T_{25}}^D * sex + t$	6,116.68	115	6,346.68	12.29	< 0.01
$\Phi_{T_{26}}^D * sex + t$	6,117.14	115	6,347.14	12.75	< 0.01
$\Phi_{T_{27}}^D * sex + t$	6,117.53	115	6,347.53	13.14	< 0.01
$\Phi_{a_2+\dots+a_{16}}^D + t$	6,097.49	127	6,351.49	17.1	< 0.01
$\Phi_{a_2+\dots+a_{16}}^D * sex + t$	6,077.17	142	6,361.17	26.78	< 0.01

sex differences in body mass senescence, which involves the decline of body mass with increasing age in males but only a last year effect in females (Tafari et al. 2013), whereas no sex difference occurred in the rate of actuarial senescence. Two possible explanations may explain this pattern. First, in the alpine marmot, the senescence in body mass is independent of the senescence in other traits, as expected if fitness-related traits show heterochrony in their senescence patterns (Nussey et al. 2013). Such variable patterns of senescence have been recently reported in Soay sheep (*Ovis aries*) across 20 phenotypic traits (Hayward et al. 2015). Second, the senescence in body mass has implications for senescence in fitness traits, but could target reproduction rather than survival in marmots. As males consume more energy than do females during hibernation (Arnold 1986, 1988), sex differences in body mass could result from highest costs of hibernation in males and one can speculate that this may potentially strengthen reproductive senescence (i.e., the decline of reproductive output, including probability

to give birth, litter size, or offspring size, with increasing age). However, in monogamous species such as the alpine marmot in which reproduction of dominant males is strongly associated to that of females and the loss of dominance (reproduction) is associated to death in both sexes (Lardy et al. 2011), it is not easy to understand why reproductive senescence could be stronger in males than in females. However, assessing sex differences in reproductive senescence is required to assess a potential heterochrony of senescence among demographic traits.

The pattern of actuarial senescence in alpine marmots we report could result from the high level of sociality of this species. In cooperative breeders, individuals in the family group help, warn, defend, or check the territory, which leads to decrease environmentally driven mortality (Komdeur 2010). Moreover, in cooperative breeders, both dispersal and reproduction are delayed for several years (Koenig et al. 1992). Additionally, helpers may contribute to decrease the reproductive effort of dominant individuals (Crick 1992). Cooperative

breeding influences biological times (i.e., by delaying age at 1st reproduction) and leads the species-specific pace of life to slow down, which might ultimately delay the onset of actuarial senescence (e.g., Jones et al. 2008). Indeed, the released energy costs of reproduction for breeders offered by helpers can be allocated in somatic maintenance and can potentially delay senescence (Bourke 2007). At the intraspecific level, the evidence for associations between sociality and actuarial senescence is scarce (e.g., Paquet et al. 2015). Although further investigation is required, we suggest that a high level of sociality should delay the onset of actuarial senescence in cooperative breeders.

Moreover, hibernation is also expected to shape the actuarial senescence pattern in alpine marmots. Hibernation is an energy-saving tactic that strongly affects life history strategies (Turbill et al. 2011). Thus, from a comparative analysis across mammals, Turbill et al. (2011) showed that hibernation slows down the pace of life. In particular, they found that small hibernating mammals have longer maximum longevity (50% greater), survive better over the winter (by 15%), reproduce at slower rates, mature at older ages, and have longer generation times than nonhibernating mammals of similar size. In other words, hibernation slows down the pace of life. As senescence is strongly linked with the pace of life (Jones et al. 2008), hibernation should also strongly impact senescence patterns. In Alpine marmots, all members of the family group hibernate altogether. Males enter first at each cycle in eutheria phases and warm the hibernaculum, providing heat for the other members of the family group. The phenomenon is called social thermoregulation (sensu—Arnold 1990). The energy saved during the winter through social thermoregulation during hibernation could thus be reallocated into somatic maintenance. Social thermoregulation during hibernation could thus also shape senescence in alpine marmots. However, further research is required to know whether such reallocation mechanisms allowed by hibernation takes place in the alpine marmot.

We showed that actuarial senescence does occur in dominant alpine marmots of both sexes from about 6 years of age. The alpine marmot displays a delayed senescence relatively to the age at 1st reproduction that might come from the sociality of this species and/or the social thermoregulation during hibernation, an energy-saving strategy. The absence of sex differences in senescence patterns we report on alpine marmots could be associated with the weak intensity of sexual selection experienced by monogamous species.

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#### SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online ([jmmammal.oxfordjournals.org](http://jmmammal.oxfordjournals.org)). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

**Supporting Information S1.**—Alpine marmot’s life cycle and selection of the multievent baseline model.

**Supporting Information S2.**—Model averaging.

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# 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; Sjöberg 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 (Tafari 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.

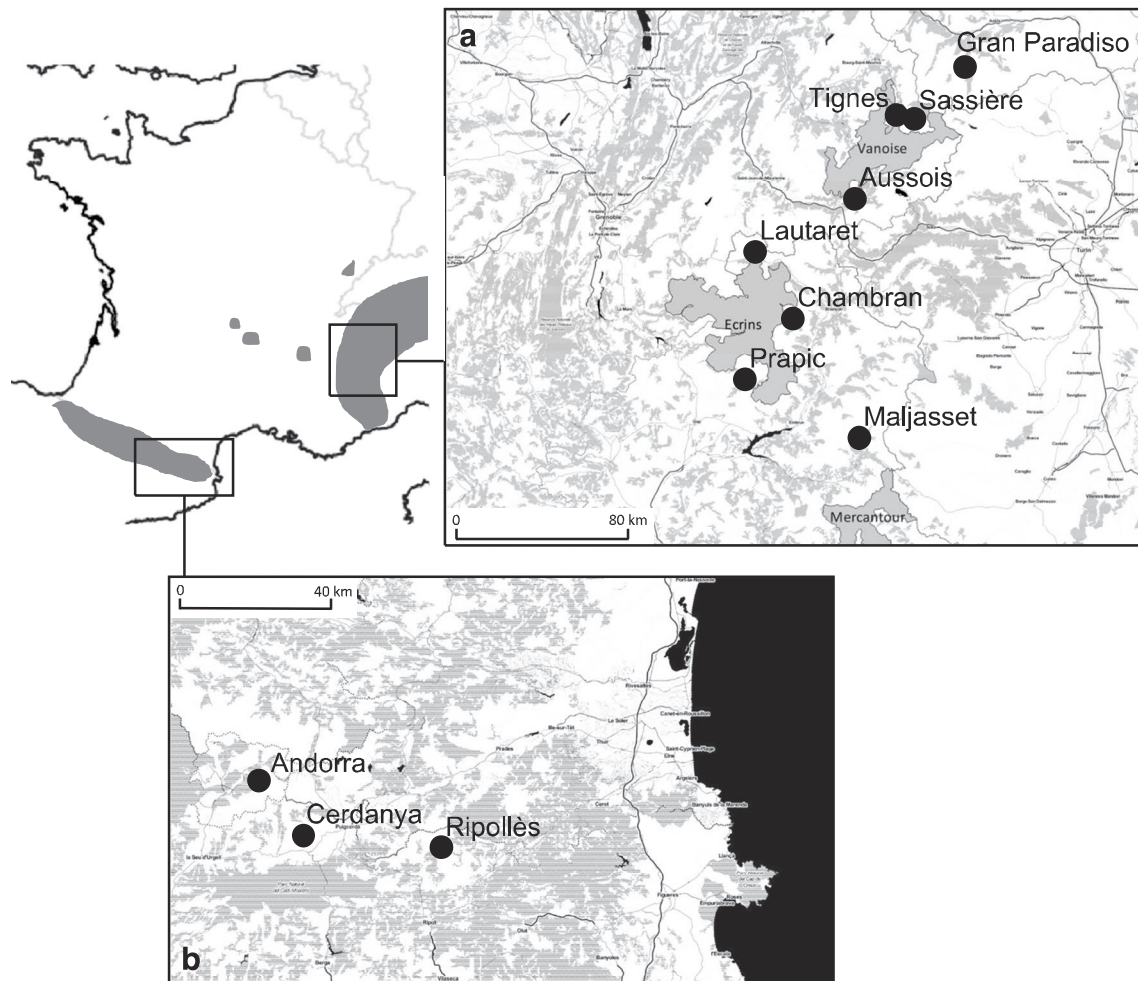
## Materials and methods

### 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 ( $2.5 \pm 0.53$  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, Sassièrre, 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 mounds 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<sup>-1</sup>), 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<sup>3</sup>) 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 $\pm$ SE	Allelic richness $\pm$ SE
Aussois	Alps	Native	45°16'2.98"N	6°43'13.22"E	30 (28)	0.58	0.57 $\pm$ 0.03	3.54 $\pm$ 0.19
Chambran	Alps	Native	44°54'14.64"N	6°29'37.22"E	23 (20)	0.59	0.60 $\pm$ 0.04	3.68 $\pm$ 0.21
Gran Paradiso	Alps	Native	45°34'44.94"N	7°11'27.74"E	28 (27)	0.56	0.51 $\pm$ 0.04	3.79 $\pm$ 0.25
Lautaret	Alps	Native	45°2'14.54"N	6°26'2.87"E	29 (28)	0.65	0.59 $\pm$ 0.03	4.29 $\pm$ 0.22
Maljasset	Alps	Native	44°35'39.55"N	6°50'53.71"E	29 (29)	0.55	0.53 $\pm$ 0.05	4.09 $\pm$ 0.35
Prapic	Alps	Native	44°41'5.51"N	6°22'43.41"E	33 (28)	0.54	0.53 $\pm$ 0.04	3.70 $\pm$ 0.22
Sassièrè	Alps	Native	45°29'28.86"N	6°59'21.27"E	56 (32)	0.57	0.54 $\pm$ 0.02	3.78 $\pm$ 0.18
Tignes	Alps	Native	45°27'44.13"N	6°53'59.88"E	29 (21)	0.63	0.59 $\pm$ 0.03	4.18 $\pm$ 0.27
Andorra	Pyrenees	Reintroduced	42°32'22.15"N	1°38'14.92"E	15 (15)	0.44	0.42 $\pm$ 0.07	2.71 $\pm$ 0.31
Cerdanya	Pyrenees	Reintroduced	42°25'25.87"N	1°44'16.24"E	54 (30)	0.46	0.46 $\pm$ 0.03	2.91 $\pm$ 0.12
Ripollès	Pyrenees	Reintroduced	42°21'51.58"N	2°14'48.03"E	12 (12)	0.53	0.55 $\pm$ 0.08	3.44 $\pm$ 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  $F_{ST} = F_{ST}/(1-F_{ST})$ ) 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  $\Delta K$ , 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  $\Delta K$  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  $\Delta K$ ) 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  $\pm$  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, Sassièrè 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.

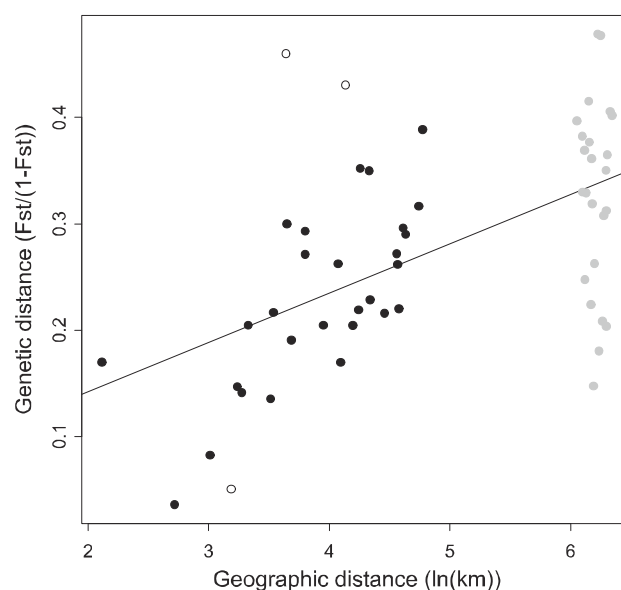
### Assessment of the genetic structure using pairwise $F_{ST}$

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  $0.18 \pm 0.01$  and  $0.22 \pm 0.09$  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).

### 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  $\Delta K$  criterion at  $K = 3$  (Supplementary material 2). The first cluster was composed by four native populations including the three Vanoise populations (Aussois, Sassièrè and Tignes), and the Gran Paradiso population, as well as one reintroduced Pyrenean



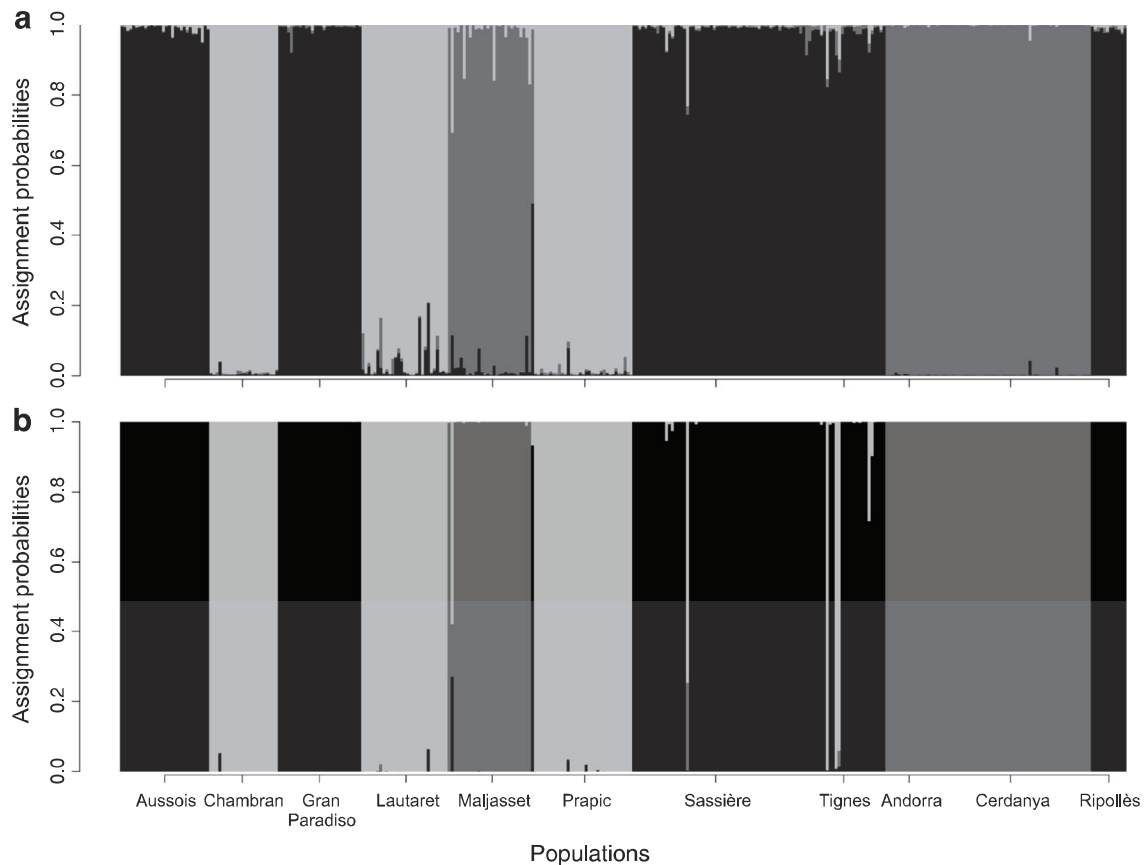
**Fig. 2** Correlation between the genetic and the spatial structure of the eight native populations of Alpine marmots of the Alps and the three reintroduced populations of the Pyrenees studied. *Black dots* symbolized Alpine pairs, *white dots* symbolized Pyrenean pairs, and *grey dots* Alpine–Pyrenean pairs

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	Sassièrè	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	–					
Sassièrè	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, Sassièrre, 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 Sassièrre 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 (Sassièrre 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*

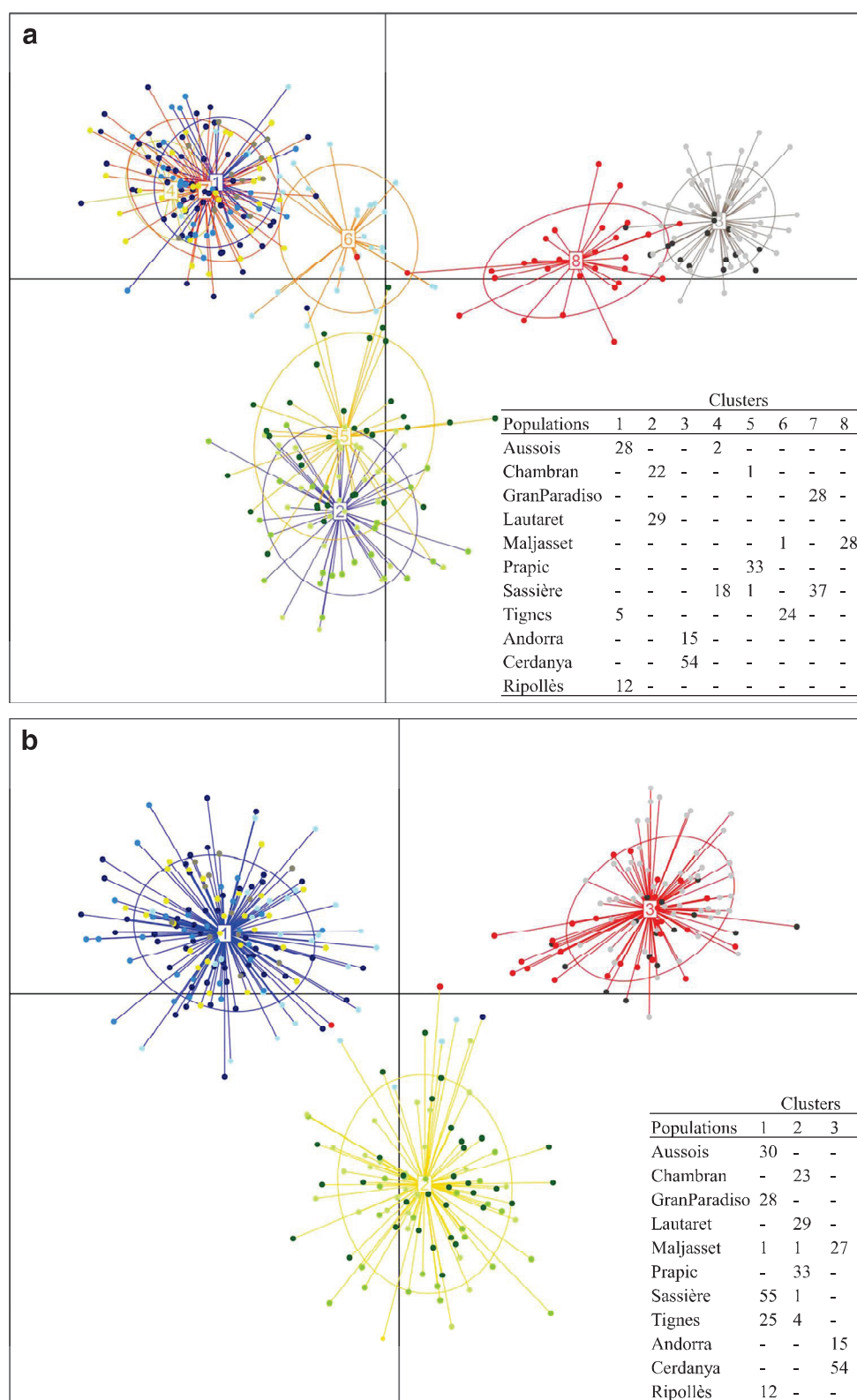
We identified eight genetic clusters (Supplementary material 2). After the cross-validation procedure (Supplementary

material 2), the DAPC (Fig. 4) revealed that the native Gran Paradiso and Vanoise (Aussois, Sassièrre, 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*, Sassièrre: *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  $2.71 \pm 0.31$  in Andorra to  $4.18 \pm 0.37$  in Tignes, the eleven populations presented a rather high level of heterozygosity: from  $0.42 \pm 0.10$  in Andorra to  $0.60 \pm 0.15$  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:  $0.56 \pm 0.01$  vs.  $0.47 \pm 0.01$ ,  $F = 27.22$ ,  $df = 1$ ,  $p < 0.001$ ; allelic richness:  $3.81 \pm 0.12$  vs.  $3.00 \pm 0.16$ ,  $F = 13.99$ ,  $df = 1$ ,  $p < 0.001$ ).

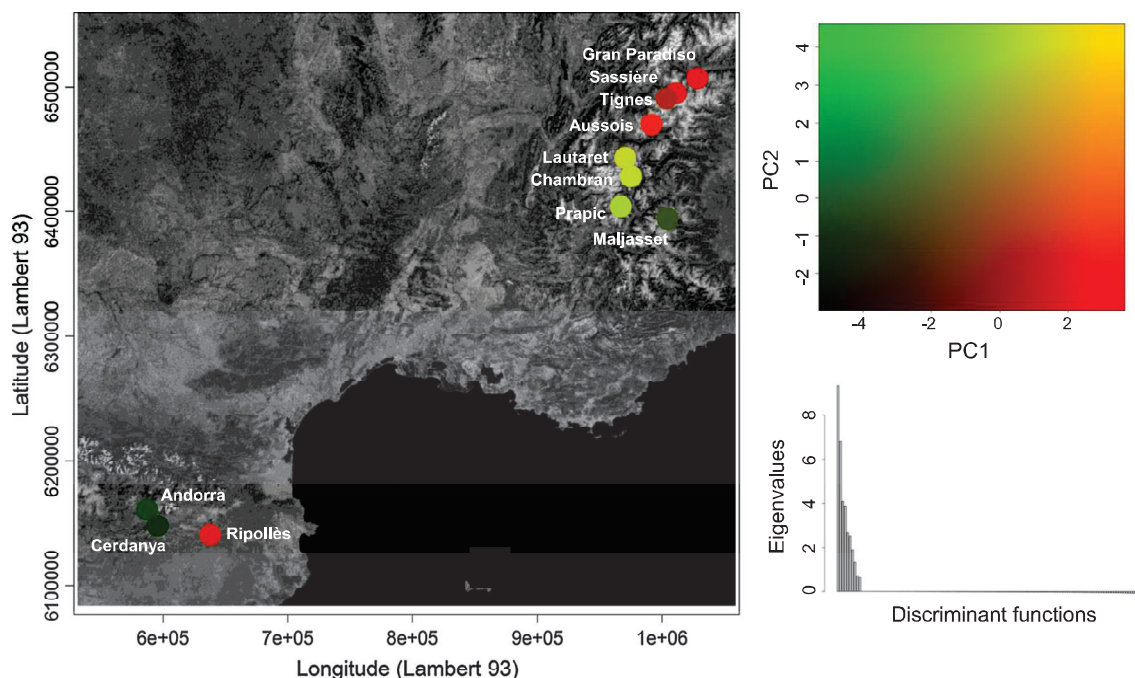
### Discussion

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 Kruckenhauer 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 identify 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* genus. Among the 14 marmot 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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