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

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Summary

1. In the context of global change, an increasing challenge is to understand the interaction between weather variables and life histories. Species-specific life histories should condition the way climate influences population dynamics, particularly those that are associated with environmental constraints, such as lifestyles like hibernation and sociality. However, the influence of lifestyle in the response of organisms to climate change remains poorly understood.

2. Based on a 23-year longitudinal study on Alpine marmots, we investigated how their lifestyle, characterized by a long hibernation and a high degree of sociality, interacts with the ongoing climate change to shape temporal variation in age-specific survival.

3. As generally reported in other hibernating species, we expected survival of Alpine marmots to be affected by the continuous lengthening of the growing season of plants more than by changes in winter conditions. We found, however, that Alpine marmots displayed lower juvenile survival over time. Colder winters associated with a thinner snow layer lowered juvenile survival, which in turn was associated with a decrease in the relative number of helpers in groups the following years, and therefore lowered the chances of over-winter survival of juveniles born in the most recent years.

4. Our results provide evidence that constraints on life-history traits associated with hibernation and sociality caused juvenile survival to decrease over time, which might prevent Alpine marmots coping successfully with climate change.

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

Introduction

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

Among-species differences in lifestyle should potentially influence both demography and life-history trait responses to climate change. Indeed, species having a lifestyle (*sensu* Harvey & Purvis 1991) that buffers individuals' life-history traits against harsh environmental conditions generally benefit from a longer life span than expected based on their body mass (Healy *et al.* 2014). For instance, aerial, arboreal, or fossorial lifestyles, that allow individuals to escape from predation, are associated with increased longevity in birds and mammals (Shattuck & Williams 2010; Healy *et al.* 2014). Likewise, hibernation directly affects energy allocation, the central process of life-history strategies (Cody 1966; Stearns 1992), by allowing individuals to save energy during seasons of food shortage and to protect themselves from predators. This results in an increase in survival for hibernating species, compared to similar-sized but non-hibernating species (Wilkinson & South 2002; Turbill, Bieber & Ruf 2011). Similarly, sociality

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may be selected in strongly limiting environments for providing higher access to food resources, reducing predation risk, or lowering the costs of thermoregulation during hibernation (Alexander 1974; Arnold 1990b; Boyles, Storm & Brack 2008). Overall, these lifestyles confer advantages to individuals that increase longevity and improve survival (see Keller & Genoud 1997 for an example on social insects, Wasser & Sherman 2010 on social birds, and Williams & Shattuck 2015 on a social mammal).

Lifestyles that evolved in response to climatic constraints should shape the way species are influenced by climate change. In temperate areas, climate change can impact animal populations in two ways: (i) directly *via* changes in the weather conditions during winter, acting on the energy demands of animals, or (ii) indirectly *via* changes in weather conditions in spring and summer (vegetation growth), acting on the availability and quality of food resources, which ultimately determine the amount of fat reserves needed to sustain winter conditions. Those direct and indirect effects may act together or against one another on life histories. For hibernating species, which are sheltered from adverse winter conditions and mostly rely on fat reserves accumulated during their active period to survive hibernation (Lyman *et al.* 1982; Humphries, Umbanhowar & McCann 2004), climate change should mainly influence demographic rates indirectly through changes during the growing season. An overview of studies investigating the responses of hibernating species to climate change suggests that the indirect effects through variation in resource availability and quality, whether positive or negative, are generally observed (Table 1a,b). However, the population dynamics of some hibernating species depend on winter harshness, as shown by the decreased litter size with decreasing snow cover reported in Alpine marmots (*Marmota marmota*) (Tafani *et al.* 2013; Table 1b), suggesting heterogeneous responses of hibernating species to climate change.

The effect of sociality on species life histories is mainly mediated by the size or the composition of the social group (see Emlen & Wrege 1991 and Paquet *et al.* 2015; for example on social birds; Hodge *et al.* 2008 and Lardy *et al.* 2015 on mammals). For instance, in the cooperatively breeding meerkats (*Suricata suricatta*), female reproductive success increases with group size (Hodge *et al.* 2008) and juvenile survival is higher in the presence of helpers which participate in feeding pups (Clutton-Brock *et al.* 2001). The responses of social species to climate change could, hence, depend in part on the influence of climate on the social group structure. Generally, climate change affects reproductive parameters and therefore population recruitment (Table 1b,c). Environmental variability may change the size and/or the composition of social groups with some delay because newly recruited individuals will be helpers in the following years (see Bateman *et al.* 2013). Hence, environmental variability may impact the composition of social groups and could influence the

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

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

Using a 23 year-long monitoring of an Alpine marmot population in the French Alps, we aimed to assess how the species' lifestyle (hibernation and sociality) interacted with weather variation in shaping age-specific survival patterns by testing the three following expectations. (i) Being a long-lived species (Cohas *et al.* 2007), annual survival rates of Alpine marmots should be strongly structured by individual age and social status. We thus expected juveniles to be more sensitive to fluctuations in weather conditions than older individuals because the population growth rate of long-lived species is less sensitive to juvenile than to adult survival (Gaillard *et al.* 2000; Gaillard & Yoccoz 2003). (ii) We expected survival of the Alpine marmot to be influenced both by spring and summer conditions and by winter conditions because weather variation can affect the survival of individuals directly, through changes in the energy requirement during winter, and indirectly, through the availability and quality of resources (Table 1). While yellow-bellied marmots (*Marmota flaviventris*) benefit from earlier springs to achieve improved body condition before hibernation (Ozgul *et al.* 2010), Alpine marmots suffer from harsh winter conditions by

Table 1. Effects of weather variables on the life-history traits of medium-sized mammals according to three different lifestyles: mammals that (a) hibernate and are solitary, (b) hibernate and live socially and (c) live socially without hibernating

Species	Weather variables	Life-history traits	Effect	References
(a) Hibernating species				
Rodentia				
Arctic ground squirrel (*Urocitellus parryii*)	Early springs (advanced snowmelt)	Emergence date, breeding date	+	Sheriff *et al.* (2010)
Golden-mantled ground squirrel (*Callospermophilus lateralis*)	Prolonged summer rainfall (reduced food access)	Juvenile survival, reproductive rates	–	Kneip *et al.* (2011)
Edible dormouse (*Glis glis*)	Early springs (increased temperature, seed productivity)	Emergence date, population abundance	+	Adamik & Kral (2008) Kager & Fietz (2009)
Common hamster (*Cricetus cricetus*)	Late springs (delayed snowmelt)	Reproductive output	–	Hufnagl, Franceschini-Zink & Millesi (2011)
Carnivora				
Raccoon dog (*Nyctereutes procyonoides*)	Mild springs (high temperatures, low snow-depth)	Fat deposition	+	Melis *et al.* (2010)
(b) Social hibernating species				
Rodentia				
Columbian ground squirrel (*Urocitellus columbianus*)	Late springs (delayed snowmelt)	Emergence date, individual annual fitness	–	Lane *et al.* (2012)
Yellow-bellied marmot (*Marmota flaviventris*)	Warmer spring temperatures (advanced snowmelt and food availability)	Emergence date, body mass, adult survival rate	+	Schwartz & Armitage (2005) Ozgul *et al.* (2010)
		Reproductive success	+	Maldonado-Chaparro *et al.* (2015)
Alpine marmot (*Marmota marmota*)	Winter severity (thinner snow layer)	Litter size	–	Tafani *et al.* (2013)
Hoary marmot (*Marmota caligata*)	Thin snowpack in winter	Overwinter survival	–	Patil *et al.* (2013)
		Average fecundity	–	Patil, Karels & Hik (2015)
Chiroptera				
Little brown myotis (*Myotis lucifugus*)	Summer dryness	Breeding and survival probability	–	Frick, Reynolds & Kunz (2010)
	Winter temperatures	Over-winter survival	–	Humphries, Thomas & Speakman (2002)
Nothern bat species (×6)	Summer dryness	Reproductive success	–	Adams (2010)
(c) Social species				
Chiroptera				
Flying foxes (*Pteropus spp.*)	High temperature extremes	Survival rates	–	Welbergen *et al.* (2008)
Carnivora				
Meerkat (*Suricata suricatta*)	Dryness of current and previous years	Reproductive success, recruitment, group size	–	Russell *et al.* (2002) Bateman *et al.* (2013)
Eurasian badger (*Meles meles*)	Mild winter	Population abundance	+	MacDonald & Newman (2002)
Lagomorpha				
European rabbit (*Oryctolagus cuniculus*)	High spring precipitation	Population abundance	–	Rödel & Dekker (2012)
	Low winter temperature	Body mass loss, delayed onset of reproduction	–	Rödel *et al.* (2005)
European hare (*Lepus europaeus*)	High summer/autumn precipitation	Population abundance	–	Rödel & Dekker (2012)

showing decreased litter size in response to colder winters with thinner snowpack (Tafani *et al.* 2013). Hence, we expected opposing direct and indirect effects of weather variation on Alpine marmot survival, with marmots of all age-classes benefiting from earlier springs and longer access to food resources, but with a negative impact of colder winters. As generally observed for hibernating species (Table 1), we expected the influence of indirect effects

to be stronger than that of direct effects and the consequences of climate change on demographic rates of Alpine marmots to be positive overall. (iii) Finally, we expected climate change to have a delayed 'socially mediated' effect on juvenile survival by modifying the social structure of groups. We recently reported that climate change is currently inducing a decrease in litter size in our study population (Tafani *et al.* 2013), which could reduce the number

of helpers present in the groups during hibernation 2 years later. Being a cooperative breeder, juvenile survival of Alpine marmots increases with the number of helpers in the family group during hibernation (Allainé *et al.* 2000; Allainé & Theuriau 2004). Consequently, this long-term decrease in litter size (Tafani *et al.* 2013) could contribute to a further decrease in juvenile survival.

Materials and methods

STUDY SPECIES AND POPULATION

Alpine marmots are cooperative breeders, territorial and socially monogamous (Allainé 2000). They live in family groups of up to 20 individuals (Arnold 1990b), composed of a dominant breeding pair, sexually mature subordinates of at least 2-years of age, immature yearlings and juveniles (Arnold 1990b; Perrin, Allainé & Le Berre 1993). Dominant individuals monopolize reproduction by inhibiting reproduction of subordinates through aggressive behaviour (Arnold & Dittami 1997; Hackländer, Mostl & Arnold 2003). Mating occurs shortly after the end of hibernation in mid-April. Gestation lasts 30 days followed by 40 days of lactation inside a natal burrow, and pups emerge and are weaned between mid-June and mid-July. Members of a family group hibernate in the same burrow from mid-October to mid-April (Arnold 1988). Subordinate males are involved in social thermoregulation during hibernation (Arnold 1993b) and act as helpers by improving juvenile overwinter survival (Arnold 1988, 1993a; Allainé *et al.* 2000; Allainé & Theuriau 2004). Subordinates of both sexes start to disperse once they reach the age of 2 years (Arnold 1990a; Magnolon 1999) and themselves become dominant in due course.

The study population is located in La Grande Sassière Nature Reserve (French Alps, 45°29′N, 6°59E) at 2300 m a.s.l. From 1990 to 2013, individuals were monitored by a capture-mark-recapture protocol. Marmots were trapped each year from mid-April to mid-July. Once captured, individuals were tranquillized and individually marked for permanent identification. All captured individuals were sexed and aged, and classified into three categories on the basis of their body size: juveniles (i.e., young of the year), yearlings (i.e., born in the previous year) and adults (i.e., from 2 years of age). Social status was assessed by scrotal and teat development for males and females respectively. We included data collected on 1172 individuals captured between 1990 and 2013 in our analyses (see Appendix S1, Supporting information for additional information about the study design and protocols).

CLIMATE AND WEATHER COVARIATES

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

Given the timing of captures in the field, we defined annual survival of the Alpine marmot as the proportion of individuals that survive between spring at year t and the following spring at year $t+1$. We focused on four weather variables with potential impact on marmot annual survival based on three key periods of the Alpine marmot's annual life cycle when environmental conditions are critical (see Appendix S2 for details about the choice and description of the weather variables): (i) during the active season, at year t, when marmots are storing fat reserves to survive the next hibernation; (ii) during hibernation, between years t and $t+1$, when marmots have to maintain sufficiently high body temperatures while the burrow temperature decreases (Arnold *et al.* 1991); and (iii) at emergence from hibernation the next spring of year $t+1$, when marmots rely exclusively on their remaining body fat to cope with adverse environmental conditions.

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

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

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

We searched for a signature of climate change by testing for temporal trends in the weather variables using linear models and quantified the correlation among our predictive variables using Pearson correlations (Appendix S3).

SOCIAL STRUCTURE OF GROUPS

To investigate the effect of climate change on juvenile survival, through yearly changes in the number of subordinate males

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

MODELLING ANNUAL SURVIVAL OF MARMOTS

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

$$\begin{bmatrix} \Psi^{SS} & 1-\Psi^{SS} \\ 1-\Psi^{DD} & \Psi^{DD} \end{bmatrix}_t \begin{bmatrix} \Phi^S \\ \Phi^D \end{bmatrix}_t \begin{bmatrix} p^S \\ p^D \end{bmatrix}_t \qquad \text{eqn 1}$$

where p_t^a is the probability for an individual of status a to be captured at year t; Φ_t^a is the probability that an individual of status a in year t survives to year $t+1$ and does not permanently emigrate from the study area (apparent survival); and Ψ_t^{ab} is the probability that an individual of status a in year t is of status b in year $t+1$, after it survived or did not permanently emigrate between t and $t+1$. As dominant individuals never return to subordinate status (Arnold 1993a), we fixed the probability of remaining dominant (Ψ^{DD}) to 1. Hence, the probability of staying subordinate (Ψ^{SS}) was the only estimated transition parameter. Moreover, marmots cannot access dominant status before reaching sexual maturity, which generally occurs from age three onwards (Farand, Allainé & Coulon 2002; Cohas *et al.* 2007), although, a few individuals became dominant at the age of two ($N = 34$). We therefore fixed the probability of becoming dominant to 0 for individuals younger than 2 years.

We considered social status, sex, age-class and time effects and their interactions on all capture, survival and state transition probabilities. Hence, the most general model was: $p(status*sex*ageclass*time)$ $\Phi(status*sex*ageclass*time)$ $\Psi(sex*ageclass*time)$, with age-classes corresponding to juvenile *[from 0 to 1 year-old]*, yearling *[from 1 to 2 years-old]*, and adult *[from 2 years-old]* classes. We first tested whether the full time-dependent model fitted adequately our data with respect to the three hypotheses listed by Burnham *et al.* (1987). There are several assumptions for MS-CR models to be valid such as the equal probability for individuals to be recaptured at a given year, or all individuals having the same probability of surviving to time $t+1$, immediately after being marked. We could test whether our data complied with these assumptions with goodness-of-fit tests (GOF tests, Pradel, Wintrebert & Gimenez 2003) implemented in the program U-CARE (Choquet *et al.* 2005). Then, starting from the general model, we reduced the number of parameters by consid-

ering only biological hypotheses based on our field experience and previous studies (Arnold 1993a; Farand, Allainé & Coulon 2002; Allainé & Theuriau 2004) and selected the most parsimonious nested model as the baseline model, from which subsequent survival analyses were performed. This selection was done successively for capture, survival, and then state transition probabilities using the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002).

DIRECT AND INDIRECT EFFECTS OF CLIMATE ON SURVIVAL

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

We also performed these analyses using 'de-trended' covariates for age or social classes exhibiting temporal trends by adding year as a continuous covariate to account for the trend in survival (Appendix S4) because spurious correlations may occur when both survival and climatic covariates show temporal trends (Grosbois *et al.* 2008).

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

SOCIALLY MEDIATED EFFECT OF CLIMATE ON JUVENILE SURVIVAL

We hypothesized that climate change can influence juvenile survival by modifying the social composition of groups during hibernation. We expected the decrease in litter size reported in the population in response to a thinner snow cover (Tafani *et al.* 2013) at year t to result in a lower number of helpers present in the population 2 years later, and thus to a decrease in juvenile survival in those subsequent years. To test this hypothesis, we performed a path analysis (Shipley 2009) where the effect of the winter index (WIN) at $t-2$ on juvenile survival at year t was mediated through a lagged effect on the number of helpers at year t (Fig. 1). We estimated the path coefficients in two steps. We first used a binomial GLM to test for the delayed effect of the winter index at year $t-2$ on the proportion of groups with helpers in the population during hibernation at year t. We then used MS-CR models to test for the immediate effect of the proportion of groups with helpers on juvenile survival. Finally,

path coefficients of the direct effect of the winter weather index at $t−2$ on juvenile survival at t were calculated with MS-CR models, after accounting for the effect of the social factor. The significance of the path coefficients was assessed by investigating whether the confidence interval at 95% of the estimated coefficients included zero or not (Shipley 2009). We also tested for first-order interaction between the proportion of groups with helpers at time t and the weather covariates at time t within juvenile survival analyses.

All statistical analyses were performed using R version 3.1.0 (R Development Core Team 2011) and all MS-CR analyses were conducted using MARK (White & Burnham 1997) and the package RMARK 2.1.7 (Laake & Rexstad 2007). All weather and social covariates were standardized (i.e. with a mean of 0 and SD of 1) for the survival analysis. Parameter estimates are given as mean ± SE and on the logit scale for analyses using MS-CR or GLM models.

Results

TEMPORAL TRENDS IN ENVIRONMENTAL AND SOCIAL VARIABLES

Temporal variation in climatic and weather indices revealed trends in the environmental conditions at La Grande Sassière over the 23 years of study. The winter index decreased by $0·07 ± 0·03$ per year from 1990 to 2013 ($r² = 0·21$, P-value $= 0·02$; Fig. 2a) and correlated with the NAO ($r² = 0·59$, P-value $< 0·01$), which also decreased over time ($β = −0·17 ± 0·06$, $r² = 0·22$, P-value $< 0·01$), pointing out a locally expressed signature of climate change. Hence, the harshness of winters at La Grande Sassière increased over years, with colder temperatures that favoured frost rather than snow. No temporal trends occurred in spring and summer weather indices related to the growing season (NDVI, $β = 0·02 ± 0·03$, $r² = 0·02$; BGI, $β = 0·02 ± 0·03$, $r² = 0·02$, Fig. 2b,c). We also found a negative temporal trend in the proportion of families with helpers during hibernation. Over the past 23 years, the proportion of groups with helpers decreased from 80% in 1990 to 46% in 2013 on average ($β = −0·05 ± 0·02$, $r² = 0·42$, P-value $< 0·01$, $N = 375$;

Fig. 2d). Thus, a marked change in the group structure of marmots occurred at La Grande Sassière over the period, with fewer groups having helpers during hibernation.

SELECTION OF THE REFERENCE MS-CR MODEL

The two components of the GOF tests, testing for trap-dependence and transience, were not statistically significant when accounting for the age structure of the population, suggesting that the full age- and time-dependent model satisfactorily fitted marmot survival data (see Appendix S5 for details). The model with additive effects of age and time was the most parsimonious for capture probabilities (Appendix S6, Table 6a). The probability for an individual to be captured increased throughout the study period from $0·76 ± 0·07$ to $0·92 ± 0·03$, and decreased with age from $0·91 ± 0·02$ at 1 year-old to $0·66 ± 0·02$ for older individuals. The variables selected for survival were the effects of social status, age and time (Appendix S6, Table 6b). We did not find any evidence of between-sex differences in survival ($β = −0·08 ± 0·09$, for the male vs. female difference). As expected, survival increased with age, from $0·59 ± 0·08$ in juveniles to $0·80 ± 0·12$ in yearlings, and was then markedly higher for dominant adult marmots than for subordinates ($0·81 ± 010$ vs. $0·52 ± 0·15$, respectively). Finally, survival varied from year to year for each age and social class (Fig. 3). The selected model for state transition probabilities only included an age-class effect on the probability of becoming dominant (Appendix S6, Table S6c), which markedly increased with age, from $0·07 ± 0·02$ at 2 years of age to an average of $0·45 ± 0·03$ in older individuals.

EFFECTS OF CLIMATE, WEATHER AND SOCIAL FACTORS ON ALPINE MARMOT SURVIVAL

We detected a temporal trend in survival of juveniles only, which decreased from $0·85 ± 0·16$ in 1990 to $0·42 ± 0·07$ in 2013 ($β = −0·06 ± 0·01$, $R² = 0·39$, Fig. 3a). We could not detect any trend over time in
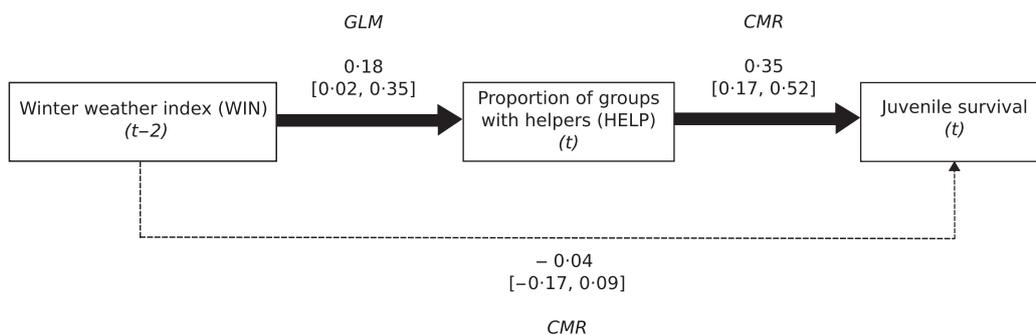

Fig. 1. Path diagram showing the two putative effects of winter weather conditions at year $t−2$, acting on juvenile survival at year t, in the Alpine marmots of La Grande Sassière, France. Path coefficients are given with their associated 95% confidence intervals (95% CI). Solid lines indicate statistically supported effects (95% CI excludes 0), and dashed lines non-statistically supported effects (95% CI include 0).
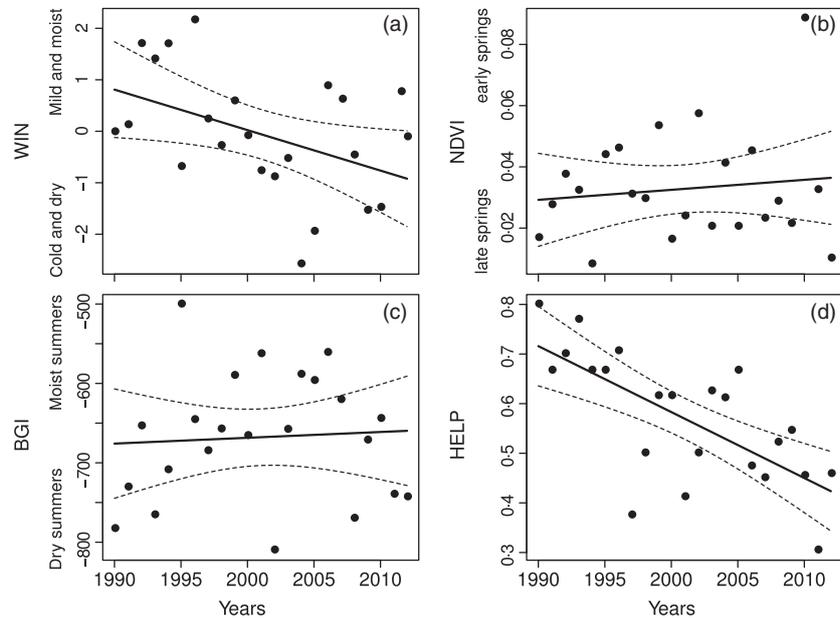
Fig. 2. Yearly variations between 1990 and 2012 in (a) the winter weather index (WIN), (b) the spring weather index (NDVI), (c) the summer drought Bagnouls-Gaussen index (BGI) and in (d) the proportion of family groups with helpers (HELP) in the Alpine marmot population, used as a proxy of the social structure of groups, at La Grande Sassière, France. Solid lines represent the predictions of the linear effect of time and dashed lines their associated confidence intervals (±95% CI).
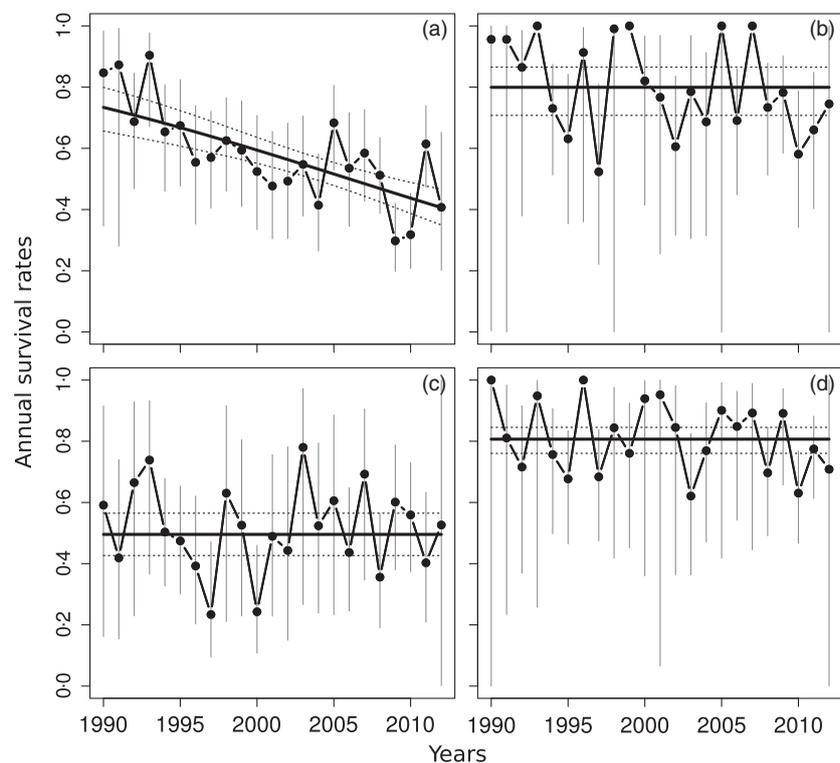

Fig. 3. Annual estimates (±95% CI, vertical segments) of age-specific survival of Alpine marmots in La Grande Sassière (France) from 1990 to 2012, estimated from the full time-dependent capture-mark-recapture model, and the corresponding time trends (±95% CI, dashed lines) for (a) juveniles, (b) yearlings, (c) subordinate adults and (d) dominants.

survival of other age-classes (yearlings: $\beta = -0.04 \pm 0.03$, $R^2 = 0.11$, Fig. 3b; dominant adults: $\beta = -0.02 \pm 0.02$, $R^2 = 0.06$, Fig. 3d; subordinate adults: $\beta = 0.01 \pm 0.02$, $R^2 = 0.002$, Fig. 3c).

In accordance with our first expectation, juvenile survival increased with NAO ($\beta = 0.35 \pm 0.08$, $R^2 = 0.34$), reflecting a strong response of juveniles to climate change, while no effect of the NAO was detected on survival in any other age-class (yearlings: $\beta = 0.10 \pm 0.14$, $R^2 = 0.02$; subordinates: $\beta = -0.01 \pm 0.11$, $R^2 < 0.01$;

dominants: $\beta = 0.04 \pm 0.13$, $R^2 < 0.01$). Among all the combinations of local weather and social variables we analysed to explain the observed yearly variation in juvenile survival, only the interactive effects between the winter index and the proportion of families with helpers during hibernation were statistically significant (Table 2a). The interactive effects accounted for about 60% of the between-year variation observed in juvenile survival (Table 2a). No effect of weather conditions during the active vegetation period was detected on juvenile

Table 2. Model selection based on AICc of the five best weather models of the Alpine marmots survival, at La Grande Sassière, France: (a) juveniles, (b) yearlings, (c) subordinate adults, (d) dominant adults

	CST	T	$NDVI_t$	BGI_t	WIN_t	$NDVI_{t+1}$	$HELP_t$	k	Deviance	AICc	Delta AICc	R^2
	+	.	.	.	.	.	.	*31*	*2782·13*	*4748·29*	–	–
(a) Juveniles	.	+	.	.	.	.	.	*53*	*2718·13*	*4729·98*	–	–
	.	.	.	.	*	.	*	**34**	**2744·27**	**4716·60**	**0·00**	**0·59**
	.	.	.	+	*	.	*	35	2743·49	4717·88	1·28	0·60
	.	.	.	.	*	+	*	35	2743·78	4718·17	1·57	0·60
	.	.	+	.	*	.	*	35	2744·24	4718·64	2·04	0·59
	.	.	.	+	*	+	*	36	2743·34	4719·80	3·20	0·61
(b) Yearlings	.	+	.	.	.	.	.	*50*	*2760·53*	*4766·09*	–	–
	.	.	.	.	.	+	.	**32**	**2779·02**	**4747·23**	**0·00**	**0·14**
	.	.	.	.	*	*	.	34	2777·30	4747·42	0·19	0·22
	.	.	.	+	.	+	.	33	2778·03	4748·30	1·07	0·19
	.	.	.	.	+	+	.	33	2778·37	4748·64	1·41	0·17
	.	.	+	.	.	+	.	33	2778·97	4749·24	2·01	0·15
(c) Subordinates	.	+	.	.	.	.	.	*53*	*2764·01*	*4775·86*	–	–
	.	.	.	+	.	.	.	**32**	**2778·21**	**4746·42**	**0·00**	**0·22**
	.	.	+	+	.	.	.	33	2777·41	4747·68	1·26	0·26
	.	.	.	+	.	+	.	33	2777·80	4748·08	1·66	0·24
	.	.	.	+	+	.	.	33	2778·03	4748·30	1·88	0·23
	.	.	+	.	.	.	.	32	2780·50	4748·71	2·29	0·09
(d) Dominants	.	+	.	.	.	.	.	*51*	*2755·32*	*4762·98*	–	–
	.	.	.	+	.	+	.	**33**	**2771·71**	**4741·98**	**0·00**	**0·39**
	.	.	.	*	.	*	.	34	2770·80	4743·13	1·15	0·42
	.	.	.	.	.	+	.	32	2777·62	4745·83	3·85	0·17
	.	.	.	+	.	.	.	32	2777·85	4746·07	4·09	0·16
	.	.	.	*	*	.	.	34	2774·11	4746·44	4·46	0·30

The constant (CST) and the full time-dependent (T) models for each age-class are presented in italic. Four local climatic variables were tested on each age-class: the NDVI in April, before ($NDVI_t$) and after hibernation ($NDVI_{t+1}$), the BGI_t in summer before hibernation and the seasonal winter index WIN_t. One social covariate, the proportion of families having helpers during hibernation ($HELP_t$) was tested on juvenile survival. Covariates included in each model are marked with a '+' for additive effects and with the '*' for interactive effects between the two concerned covariates. k = number of parameters, AICc = Akaike's Information Criterion corrected for sample size, R^2 = proportion of annual survival variation accounted for by the entered covariates, computed with an analysis of deviance. Selected models are in bold.

survival after controlling for this interactive effect, which runs counter to our expectations. The negative effects of harsh winters on juvenile survival appeared to be buffered by a high proportion of groups having helpers during hibernation (WIN_t, $\beta = 0.33 \pm 0.07$; $HELP_t$, $\beta = 0.35 \pm 0.09$; Interaction, $\beta = -0.29 \pm 0.09$, Fig. 4a, b). Hence, through time, the detrimental effect of harsher winters on juvenile survival was reinforced by the simultaneous decrease in the proportion of groups with helpers.

The selected model for yearling survival only included the effect of the NDVI in April the year after hibernation ($NDVI_{t+1}$) (Table 2b), which accounted for 14% of the total observed variation in annual survival (Table 2b). Earlier snowmelt at emergence ($NDVI_{t+1}$) was detrimental for yearling survival ($\beta = -0.26 \pm 0.14$, Fig. 4c).

Survival of subordinate adults was related to summer weather conditions before hibernation (Table 2c) with the best model including the index of summer drought (BGI_t), accounting for 22% of the observed between-year variation (Table 2c). However, subordinate adult survival tended to be positively influenced by hot and dry summers ($\beta = -0.21 \pm 0.11$, Fig. 4d).

For dominant adults, the selected model included the BGI_t index, together with the additive effect of the $NDVI_{t+1}$ at the end of hibernation (Table 2d). These effects accounted for 39% of the observed variation in adult survival of dominant marmots (Table 2d). Unlike subordinates, dominant marmots suffered from dry summers ($\beta = 0.34 \pm 0.14$, Fig. 4f) and, given the negative correlation between their survival and NDVI values ($\beta = -0.27 \pm 0.10$, Fig. 4e), earlier springs were detrimental for dominant adults at the time of their emergence from burrows.

CLIMATE CHANGE EFFECT ON JUVENILE SURVIVAL THROUGH SOCIAL COMPOSITION OF GROUPS

We found little evidence for any effect of winter weather conditions at year $t-2$ on juvenile survival at year t, after accounting for the effect of the proportion of groups with helpers during hibernation ($\beta = -0.04 \pm 0.07$; Fig. 1). However, as expected, past winter conditions influenced juvenile survival through effects on social factors. The winter weather conditions at year $t-2$ was associated with the proportion of
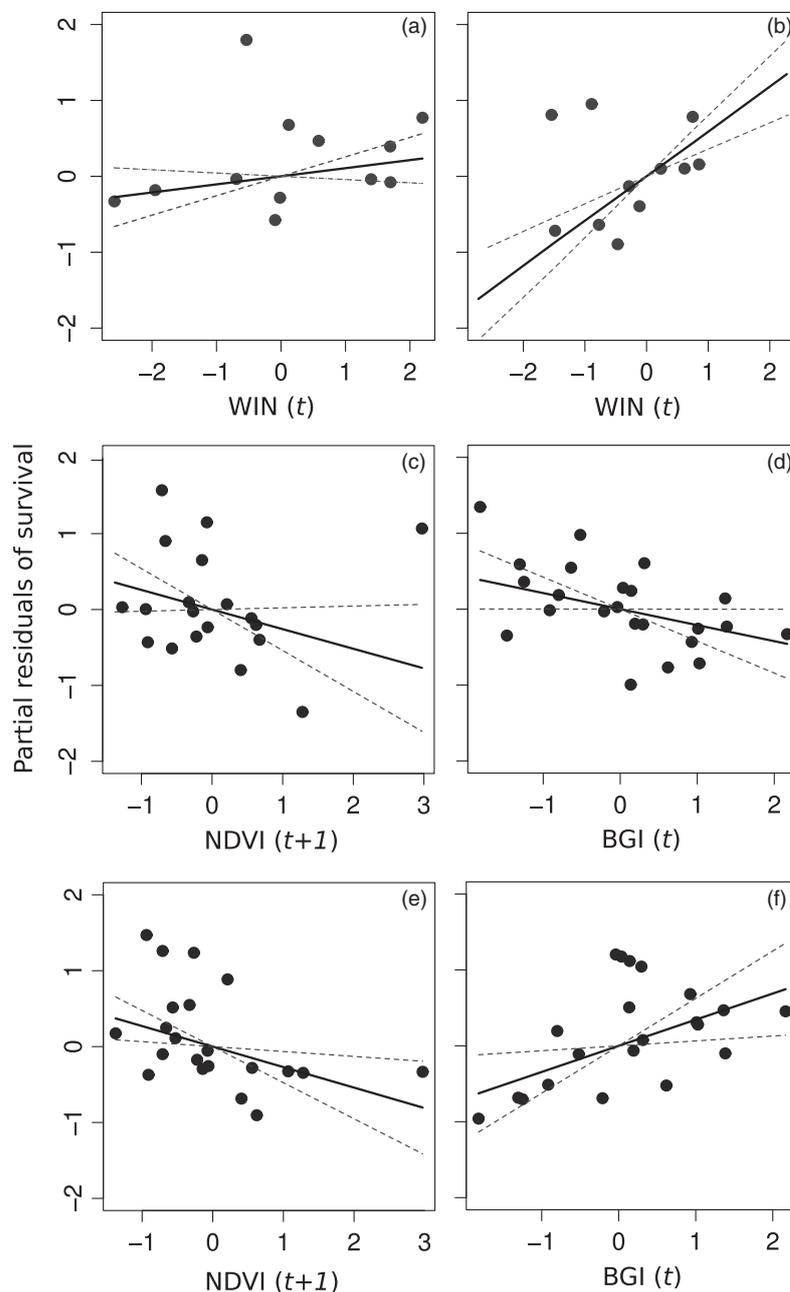
Fig. 4. Variation in age-specific survival as a function of environmental covariates between 1990 and 2012 for the Alpine marmots of La Grande Sassière, France. Dots represent partial annual residuals of juvenile survival in relation to the standardized winter harshness index (WIN) at year t (a) when a high proportion (more than 60%) and (b) when a low proportion (less than 60%) of groups have helpers in the population, (c) residuals of annual survival of yearlings in relation to the Normalized Difference Vegetation Index (NDVI), a proxy of the timing of snowmelt, in April at year $t+1$ (d) residuals of annual survival of subordinate adults in relation to the Bagnouls-Gaussen Index (BGI), a proxy of the summer drought, in summer at year t, and partial annual residuals of dominant adults in relation (e) to the NDVI in April at year $t+1$ after accounting for the effect of the BGI index, and (f) to the BGI index at year t after accounting for the effect of the NDVI in April at year $t+1$. Solid lines represent the model predictions and dashed lines their associated confidence intervals (±95% CI).

groups with helpers during hibernation at year t ($\beta = 0·18 \pm 0·08$; Fig. 1), accounting for 27% of the observed variation between years in the proportion of groups with helpers. Harsher winters induced a decrease in the proportion of groups with helpers two years later, which in turn decreased juvenile survival ($\beta = 0·35 \pm 0·08$; Fig. 1).

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

Discussion

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

SOCIALITY MATTERS

The two different effects of climate change we report on juvenile survival through the social composition of groups (Fig. 1) provide new evidence for socially mediated effects of weather conditions on demographic rates in a social species. Winters are known to be a major cause of mortality in juvenile marmots because of their lower body condition at the entrance in hibernation and their lower ability to thermoregulate (French 1990). Until now, there were evidences to show that social thermoregulation (Barash 1974; Armitage 1999) and the low energetic balance characterizing marmot species (Armitage, Blumstein & Woods 2003) limited juvenile overwinter mortality. Juveniles might benefit from having helpers in their family group since subordinate males may warm them during hibernation by producing heat during periodic arousal (Allainé *et al.* 2000; Allainé & Theuriau 2004). Our results agreed with this assumption as the helper's presence during hibernation buffered the effect of winter weather conditions on juvenile survival. Furthermore, we showed that the observed decrease in the proportion of groups with helpers has amplified the negative effect of winters on juvenile survival. Colder winters with thinner snowpack reduced the insulation effect of snow and may have increased the energetic costs of hibernation when temperatures in burrows are very low (Tafani *et al.* 2013). Those energetic costs have been strengthened by a decrease in the presence of helpers and this has probably contributed to the decrease in juvenile survival during hibernation.

The temporal changes we report in the demographic structure of the Alpine marmot population have their origin in past winter weather conditions, thus revealing delayed effects of climate change on survival through social factors. This decrease over time in the presence of subordinate males in families has to be linked with the decrease in litter size observed in the studied population (Tafani *et al.* 2013), but also with the lower survival of juveniles from previous years, resulting later in a smaller number of 2-year-old subordinate individuals. Hence, a negative looping effect of climate change on juvenile survival of marmots may currently be at work, in which a decrease in juvenile survival at a given year leads to a decrease in the survival of juveniles born in the subsequent years.

THERMAL AND RESOURCE-MEDIATED EFFECTS OF WEATHER ON ALPINE MARMOT SURVIVAL

That spring conditions negatively influenced the survival of older marmots more than winter harshness contradicted our expectations. In mountains, NDVI measures the timing of the onset of vegetation and is directly related to the timing of spring snowmelt (Pettorelli *et al.* 2007). Our results indicate a negative influence of earlier snowmelt on survival of both yearling and dominant adults. For Alpine marmots, an earlier snowmelt means a thinner snowpack

at the end of winter when animals are in their poorest condition and strongly sensitive to cold. A similar pattern also occurs in *Marmota caligata* (Patil *et al.* 2013).

The survival of dominant Alpine marmots was negatively affected by warm and dry summers, whereas the survival of subordinate marmots was positively influenced by summer drought, a conflicting and surprising result. Results on dominant adult marmots were in agreement with previous studies on other mammalian herbivores (Van Horne *et al.* 1997; Garel *et al.* 2004). By constraining the ability of Alpine marmots to thermoregulate efficiently, high temperatures reduce the time window in which they can forage in summer (Türk & Arnold 1988). In addition, high summer temperatures lead to an earlier senescence of the vegetation, and thus forage of poor nutritional quality (Pettorelli *et al.* 2007), perhaps limiting fat storage.

For subordinate individuals, the positive effect of warm and dry summer conditions on survival could reflect a change in dispersal. We measured apparent survival, which cannot distinguish between death and permanent dispersal in open populations. Alpine marmots generally disperse from 2-years-old onwards (Arnold 1990a; Magnolon 1999), between late April to July. Thus, given the condition-dependent dispersal events and the high constraints of drought periods, subordinate marmots might have delayed summer dispersal to increase their chances of surviving winter, resulting in a slight increase in apparent survival when summer conditions are unfavourable.

COMPARISON WITH OTHER HIBERNATING SPECIES

The increasingly critical role of the hibernation period over the years we reported for Alpine marmot survival sharply contrasts with what is generally reported for survival in other hibernating species, which are mainly influenced by weather variation during the growing season (Table 1). Such a discrepancy can be explained by between-site differences in local weather conditions, or by between-species differences in physiology. Indeed, hibernating species may be subjected to opposing environmental changes depending on their location, as illustrated by the comparison between the Arctic ground squirrel (*Urocitellus parryii)* and the Columbian ground squirrel (*U. columbianus)*. The former benefited from earlier springs over time (Sheriff *et al.* 2010; Table 1a) while the latter suffered from delayed springs (Lane *et al.* 2012; Table 1a). In addition, some biological characteristics such as the ability to save energy efficiently during hibernation could shape the response of hibernating species to climate change. For instance, small-sized hibernating species with reduced fat reserve capacity, such as some bat species (Humphries, Thomas & Speakman 2002; Rebelo, Tarroso & Jones 2009), the pygmy-possum (*Burramys parvus*, Geiser & Körtner 2010) or the hazel dormouse (*Muscardinus avellanarius*, Pretzlaff & Dausmann 2012), are expected to suffer from an increase in winter harsh-

ness because of a dramatic increase in energy depletion during hibernation.

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

CONCLUSION

As a whole, the ability of the Alpine marmots to cope successfully with climate change appears to be undermined by constraints associated with hibernation and sociality. Any demographic compensation did not counteract the negative time trends we reported in juvenile survival (Fig. 2) and litter size (Tafani *et al.* 2013) in this population of Alpine marmots. Indeed, the deterministic growth rate decreased from 0·99 during the first period (1990–2000), to 0·96 in recent years (2001–2013, see Appendix S7 for the Leslie matrices analysed), supporting the hypothesis of an overall negative impact of climate change on Alpine marmots. Finally, our results highlight the importance of the species' lifestyle in shaping population response to climate change. We therefore encourage a greater consideration of the species' lifestyle when analysing climate change impact on life-history traits variation.

Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cp1cc (Rézouki *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional information on the study design, monitoring protocol and field data on the Alpine marmot population.

Appendix S2. Additional information about the choice of weather variables.

Appendix S3. Correlation matrix between the different climatic and weather covariates (see the manuscript for more details).

Appendix S4. Complementary analyses on the effect of climate on juvenile survival using "de-trended" weather covariates to avoid spurious correlation when both survival and climatic covariates show a temporal trend.

Appendix S5. General details on the Goodness-of-fit tests realized for MS-CR analysis.

Appendix S6. Selection of the baseline model for MS-CR analysis.

Appendix S7. Leslie matrices used to compute the deterministic growth rates of the Alpine marmot population.