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**Differential plasticity of size and mass to environmental change in a hibernating
mammal**

Running head: Differential plasticity of size and mass

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Abstract

Morphological changes following changes in species' distribution and phenology have been suggested to be the third universal response to global environmental change. Although structural size and body mass result from different genetic, physiological and ecological mechanisms, they are used interchangeably in studies evaluating population responses to environmental change. Using a 22-year (1991-2013) dataset including 1768 individuals, we investigated the coupled dynamics of size and mass in a hibernating mammal, the Alpine marmot (*Marmota marmota*), in response to local environmental conditions. We (i) quantified temporal trends in both traits, (ii) determined the environmental drivers of trait dynamics, and (iii) identified the life-history processes underlying the observed changes. Both phenotypic traits were followed through life: we focused on the initial trait value (juvenile size and mass) and later-life development (annual change in size [Δ size] and mass [Δ mass]). First, we demonstrated contrasting dynamics between size and mass over the study period. Juvenile size and subsequent Δ size showed significant declines, whereas juvenile mass and subsequent Δ mass remained constant. As a consequence of smaller size associated with a similar mass, individuals were in better condition in recent years. Second, size and mass showed different sensitivities to environmental variables. Both traits benefited from early access to resources in spring, whereas Δ mass, particularly in early life, also responded to summer and winter conditions. Our study supports the importance of considering the differences between size and mass responses to the environment when evaluating the mechanisms underlying population dynamics. The current practice of focusing on only one trait in population modelling can lead to misleading conclusions when evaluating species' resilience to contemporary climate change.

Introduction

Climate change is affecting population dynamics of numerous species, but the intrinsic mechanisms by which these responses arise remain under-studied (Parmesan, 2006; Somero, 2012). An understanding of the mechanistic relationships between environmental variables and species' demographic responses is needed to reliably predict organisms' vulnerability to climate change (Seebacher *et al.*, 2012). Fitness-related phenotypic traits, acting as state variables, could provide such a mechanistic link (Huey *et al.*, 2012, Ozgul *et al.* 2014). These traits are strongly related to an individual's reproductive success and survival; thus, phenotypic distributions are expected to change and influence population dynamics in response to environmental change (Kearney *et al.*, 2009; McMahon *et al.*, 2011). Phenotypic traits such as structural size and body mass play a pivotal role. First, changes in animal body size have recently been claimed to be the third universal response to contemporary climate change in addition to changes in distribution and phenology (Gardner *et al.*, 2011; Sheridan *et al.*, 2011). Second, their responses to climate change can occur on a short time scale (Gienapp *et al.*, 2008; Boutin *et al.*, 2014). Third, structural size and body mass affect population performances of vertebrates through their direct impact on individual life-histories (Schmidt-Nielsen, 1984; Blackburn *et al.*, 1994; Smith *et al.*, 2013).

Despite evidence of climate-driven changes in endotherms' body traits that has accumulated over the last decades, their environmental drivers remain hotly debated (McNab, 2010; Gardner *et al.*, 2011; Yom-Tov *et al.*, 2011). However, modifications in nutritional and/or thermal environment can be seen as the two major drivers (Millien *et al.*, 2006; McNab, 2010). On one hand, climate related changes in the availability or quality of food can have a direct impact on trait changes through modulation of the energy input (McNab, 2010). For instance, positive trends in size have been associated with earlier vegetation onset and longer growing season (Yom-Tov *et al.*, 2004; Yom-Tov *et al.*, 2005; Ozgul *et al.*, 2010;

Yom-Tov *et al.*, 2010c; Eastman *et al.*, 2012), whereas negative ones have been associated with lower primary productivity (Hersteinsson *et al.*, 2009; Sheridan *et al.*, 2011). On the other hand, a rise in ambient temperature over a critical thermal limit can have a direct consequence on body traits through increasing energy expenditure. Negative size trends have been suggested to be a response to these new thermoregulatory constraints, assuming that heat dissipation is more efficient in smaller bodied species as surface area to volume ratio is reduced (Post *et al.*, 1997; Smith *et al.*, 1998; Yom-Tov *et al.*, 2010a), in line with Bergmann's rule (Bergman, 1847). Despite the various environmental drivers involved, previous studies clearly demonstrate that a disruption of the energy balance can be a common feature of trait shifts, and the variation in responses observed in terms of direction and magnitude could result from differences in exposure and sensitivities (Ashton *et al.*, 2000; Millien *et al.*, 2006; Meiri, 2011; Teplitsky *et al.*, 2014).

Structural size and body mass are often used interchangeably to evaluate organisms' responses to environmental change, especially in trait-based demographic models, although they result from energy allocation to different functions (Piersma *et al.*, 1991). In most endotherms, skeletal size is a reserve-independent structural measure resulting from the allocation of resources to growth during development (Calder, 1984; Hou *et al.*, 2008). From birth, individual size increases follow a logistic curve function of the environmental conditions until a maximum is reached at adulthood (Monaghan, 2008). However, some exceptions concerning peculiar skeletal structures exist, such as a seasonal shrinkage of the braincase observed in soricine shrews and arvicoline rodents living in cold temperate areas (Dehnel phenomenon; Dehnel, 1949; Pucek 1963; McNab, 1999). On the other side, body mass, which is a composite of structural mass including bones, organs, skin, blood, skeletal muscle, and storage mass (Wang *et al.*, 1992; Hume *et al.*, 2002; Fosbøl *et al.*, 2015), is a crude but widely used estimate of nutrient energy reserve. It is a dynamic trait that can change

repeatedly throughout life to maximize survival and/or subsequent reproductive output (Heldmaier, 1989). These distinctions between structural size and body mass may lead to different interpretations of population responses to environmental conditions at different life stages. Unfortunately, most studies are still focusing only on one trait and on particular life stages (Allainé *et al.*, 1998; Pettoirelli *et al.*, 2002, but see Cooch *et al.*, 1991; Guillemain *et al.*, 2005; Rode *et al.*, 2010; Nielsen *et al.*, 2013).

Despite the recent interest in investigating climate-related morphological changes in wild populations, underlying ecological and evolutionary mechanisms remain rarely investigated (Boutin *et al.*, 2014; Teplitsky *et al.*, 2014). Observed body size shifts can be mediated through phenotypic plasticity and/or through selection if the trait is heritable (Coulson & Tuljapurkar, 2008; Boutin *et al.*, 2014; Kopp *et al.*, 2014). The former is the ability of the same genotype to express different phenotypes under different environmental conditions within a lifespan, whereas the latter involves directional genetic changes with survival or reproductive selection acting on the phenotype over generations (Merilä *et al.*, 2014). Plasticity can also evolve if present reaction norms have a genetic basis (Dejong, 1995). Recent studies focusing on body mass have shown that phenotypic plasticity plays an important role in observed changes in body mass distributions (Teplitsky *et al.*, 2008; Ozgul *et al.*, 2009; Husby *et al.*, 2011). Conflicting selection pressures are expected on skeletal growth and body mass fluctuations, as a specific set of genes is associated with adult stature and mass, and another independent set of genes is regulating the rate of growth in body size (Janz, 2004; Marroig *et al.*, 2010). Given the small number of mammal species studied and the limited time frame of these studies, our understanding of whether species will be able to tolerate the speed and magnitude of ongoing environmental change is limited (Williams *et al.*, 2008; Hoffmann *et al.*, 2011).

Alpine species, subject to extreme environmental change over the last decades, are expected to represent excellent indicator species that could help anticipate organisms' vulnerability to climate change and thus forecast likely future impacts on biodiversity (Theurillat *et al.*, 2001; Yoccoz *et al.*, 2010; Büntgen *et al.*, 2014). During the last century, the Alps have shown a 2°C increase in minimal temperature while summer precipitation and winter snowfall have decreased drastically (Keller *et al.*, 2005; Beniston, 2006). Due to their adaptation to extreme and very specific conditions, endemic alpine species are particularly vulnerable to climate change (Davis, 2005; Maiorano *et al.*, 2013), and dramatic consequences have already been detected in vegetation community compositions (Engler *et al.*, 2011). In this context, the Alpine marmot (*Marmota marmota*), an endemic hibernating mammal of the Alps, provides a unique opportunity to study the joint dynamics of structural size and body mass in response to climate change. Using a 22-year dataset (1991-2013) of individual structural size and body mass measurements, we quantified temporal trends in both traits, determined environmental drivers of trait dynamics, and identified the life-history processes underlying the observed changes.

Materials and methods

Model species

The Alpine marmot is a hibernating ground-dwelling squirrel; it lives in family groups from 2 to 20 individuals, composed of a dominant pair (≥ 3 years old), sexually mature adults (≥ 3 years old), subadults (age 2 to 3) and yearlings (age 1 to 2) subordinates, and juveniles (age 0 to 1) (Allainé, 2000). A family group occupies a territory (2.5 ± 0.53 ha, Perrin *et al.*, 1993) including a main burrow and side burrows. It is socially monogamous, and within family groups reproduction is monopolized by the dominant pair (Arnold, 1990a,b; Cohas *et al.*,

2008; Lardy *et al.*, 2012). Dominants inhibit reproduction of same-sex subordinates through aggressive behaviour (Arnold *et al.*, 1997; Hackländer *et al.*, 2003).

Within a family group, marmots hibernate together from mid-October to early April (Arnold, 1990b). Hibernation plays a central role in their life history. Accumulation of fat during the active period and loss of it during hibernation (Körtner & Heldmaier, 1995) determines winter survival and subsequent reproductive success (Tafani *et al.*, 2013). Subordinate males are called helpers as they increase pup survival during hibernation through thermal benefits of synchronized arousals and active warming (Arnold, 1993; Ruf & Arnold, 2000; Allainé & Theuriau, 2004). Minimal energy expenditure during hibernation has been defined over a burrow temperature range from 5°C to 15°C (Arnold *et al.*, 1991; Ortmann & Heldmaier, 2000). Below the critical threshold of 5°C, energy expenditure increases linearly; for instance, at a burrow temperature of 0°C, minimal metabolic rate during torpor is already four times higher than the torpid metabolic rate (Arnold *et al.*, 1991). Mating occurs in mid-April shortly after the hibernation period (Müller-Using, 1957; Psenner, 1957; Hembeck, 1958). Then, dominant females are pregnant for 30 days and give birth to a litter of 1 to 7 juveniles (median = 4) and nurse them for another 40 days underground in the natal burrow. Juveniles first emerge above ground at weaning (Psenner, 1957), which in our study population occurs between late June and mid-July (Allainé *et al.*, 1998).

Field procedures

We monitored a wild population of Alpine marmots located in a typical alpine meadow of the Grande Sassièrè nature reserve (2340 m a.s.l., French Alps, 45°29'N, 6°59'E), from 1990 to 2013. Marmots belonging to 26 family groups (*i.e* territories) have been captured every year from mid-April to mid-July using two-door live traps (100 x 25 x 25 cm, Tomahawk Live Trap, Hazelhurst, WI, U.S.A), baited with dandelions (*Taraxacum officinale*) and placed near

the entrances of the main burrows in order to assign each captured individual to its family group. Once captured, individuals were anaesthetised with Zolétil 100 (0.1 ml.kg⁻¹). At first capture (as pup or immigrant), all marmots were individually marked using a transponder and a numbered metal ear-tag placed on the right ear of females and on the left ear of males. An additional coloured plastic ear tag was placed on the opposite ear of dominant individuals. Animal identity, sex, age, reproductive status, social status and body measurements (see below) were recorded at each capture. Age class was determined according to known birth date or to body shape (up to three years). Immigrants were assigned to the adult age class as they are known to disperse after two years old (Arnold, 1990a). Social status was determined according to scrotal development for males and teat development for females and then confirmed by behavioral observations as dominant pairs predominantly initiate aggressive interactions (Arnold & Dittami, 1997) and scent-mark their territories by regular cheek rubbing behavior (Bel et al. 1999). In addition, both hair samples and skin biopsies were collected on all trapped individuals for genetic analysis.

Helper presence or absence and identity of the dominant pair were obtained by intensive observations of each family group (see Cohas *et al.* 2008 for details on observations protocol). As weaning occurs when pups first emerge from their natal burrow, the date of weaning and litter size at weaning (hereafter, litter size) in each family was determined from daily observations. Virtually all emerged offspring were either trapped with smaller two-door live traps or caught by hand within three days of emergence. Data collection was consistent across the 24 years as the project was consistently supervised by two of us (DA, AC).

Annual structural size and body mass determination

Structural size was the measure of body length (hereafter, size) from snout to the base of the tail (± 0.5 cm with a measuring tape). Body mass (hereafter, mass) was obtained by weighing

all captured individuals (± 5 g for juveniles, ± 25 g for older individuals) with a Pesola spring balance. Marmot measurements showed strong intra-annual change that varied substantially between sex, age class, reproductive and social status (Körtner & Heldmaier, 1995; and see figures in Appendix S1 for the present study). To account for the pronounced intra-annual size and mass variations within each age, sex, social and reproductive status, we estimated both traits for each individual for a fixed day-of-year. We predicted juvenile size and mass according to the age they had on July 14 (195th day-of-year), which is the latest weaning date observed during the study period. For older age classes, we used the fitted models to predict size and mass on July 1 (182nd day-of-year). July represents the end of the reproductive period and the majority of the data were collected around this date, providing a better estimate for both size and mass (see Appendix S1 for further details on the estimation). For the rest of the analyses, we used estimated values of log-transformed size and mass for each individual and year.

Environmental variables

In mammals, structural size and mass are key phenotypic traits influencing survival and reproductive success. Thus, we focused on environmental variables known to affect survival (Farand *et al.*, 2002; Rézouki *et al.*, unpublished data) and reproductive output (Tafari *et al.*, 2013) in this species.

Three seasons with differential impacts on Alpine marmots' size were considered: (1) summer (July-August), when marmots build fat reserves, (2) winter (December-March), when marmots hibernate, and (3) early spring (last two weeks of April), when marmots emerge from hibernation in our study area. For climatic factors, we used both local weather and Normalized Differential Vegetation Index (NDVI, Pettorelli *et al.*, 2005). Daily ambient temperature, precipitation, and snow depth were recorded from Météo France weather stations

situated within 5km from the field site, respectively Val d'Isère (1840m), Tignes Brevières (1560 m) and Tignes (2080m). NDVI provided by the National Oceanic and Atmospheric Administration was obtained from the AVHRR data set (1990-2000) within an 8x8 km pixel area and the MODIS data set (2001-2013) with a resolution of 1x1 km pixel centered on the study site. Summer variables included a summer condition index measured as the July to August Bagnouls-Gaussen aridity index (BGI, total daily rainfall (mm) minus twice the mean ambient temperature (°C) (Dajoz, 1973; high aridity is represented by low BGI value). This summer condition index is a measure of the conditions for vegetation growth and thus a good proxy of the quality of green forage (Basso *et al.*, 2012). It has been repeatedly related to herbivore performance (Gaillard *et al.*, 1997; Garel *et al.*, 2004; Toïgo *et al.*, 2006). Winter variables included mean snow depth (*i.e.* average of daily accumulated snow depth between December and March) as a proxy for burrow insulation and mean winter temperature (*i.e.* average of daily mean temperature). Spring variables included the NDVI value recorded during April 15 to May 1, which measures plant productivity (Pettorelli *et al.*, 2007). NDVI was used as a proxy of the onset of vegetation (Hamel *et al.*, 2009) and thus of food availability at the time of hibernation emergence, when food availability is crucial. High April NDVI values represent early vegetation onset, whereas low April NDVI values represent late vegetation onset. Note that the effects of spring and summer air temperature were not considered, as buffered burrows represent a way-out to thermoregulatory constraints.

We used linear models to search for temporal trends in climatic variables. Indeed, correlation between the trait and environmental variables may arise because both are changing through time but without a causal link between them. When a trend was detected, we used the residuals from the regression between the climate variable over year as a “de-trended variable” (a measure of the deviation of the variable from its temporal trend). Using the “de-trended” instead of the raw variable reduces the chances of spurious correlations (Grosbois *et*

al., 2008). Only the winter temperature variable showed a significant linear temporal trend during the study period (-0.089 ± 0.032 °C.year⁻¹, $p=0.012$).

Size and mass dynamics

We omitted the first two years owing to lower sampling effort. From 1992 to 2013, we recorded 1829 measures of size and 2276 measures of mass on 1768 individuals.

Base models. We performed age-specific analyses using linear mixed models. For juveniles, we modeled size and mass, which provided the initial trait values. For later age-classes, we modeled the annual changes in size ($\Delta size = size_{t+1} - size_t$) and mass ($\Delta mass = mass_{t+1} - mass_t$) defined as the difference in trait value from one year to the next. We modeled $\Delta size$ and $\Delta mass$ conditional on initial size and mass, respectively (*i.e.* $\Delta size \sim size_t$ and $\Delta mass \sim mass_t$; see Fig. S1 and Table S1 for details). It is important to note that change in body mass is a composite measure and includes changes in bones, organs, skin, blood, skeletal muscle, and storage mass (Wang *et al.*, 1992; Hume *et al.*, 2002; Fosbøl *et al.*, 2015). Note that we chose not to use a body condition index as their use remains hotly debated (Green, 2001; Peig & Green, 2010). Body mass alone provides a better indicator of nutrient reserves than an unverified size-adjusted index (Schamber *et al.*, 2009). Because adult skeletal size is reached at three years old (see Fig. A1 in Appendix S1), subadult $\Delta size$ was measured as the difference in size between age two and their first capture as adults (\geq age 3). Subadult $\Delta mass$ remained as the difference in mass between ages two and three. Fitted values obtained from these models will be referred to as $\Delta size$ and $\Delta mass$ respectively.

Our analyses needed to account for the possibility that several variables would confound trait responses to the environment. Thus, we included as fixed effects variables known to affect Alpine marmots' size and mass, namely sex (in all age class models), litter

size and date of weaning (in the juveniles models only), and social status (subordinate or dominant in the adults models only). For juveniles, we also accounted for the helper presence since they have a direct impact on juveniles' energy expenditure during hibernation (Arnold, 1993). For older individuals, we accounted for an interactive effect between the presence of juveniles and sex. Indeed, during the hibernation period, males arouse more often and earlier than females, thus paying a heavier energetic cost (Arnold, 1990b). Territory aspect was also considered since, in Alpine habitats, south-facing slopes receive more direct sunlight than north-facing ones, leading to faster snow melt with direct consequences on vegetation growth.

We further included marmot territories as a random effect on the intercept of each age-specific model and marmot identity in adult models, to account for spatial and individual heterogeneity generated by repeated measurements on the same territories and on the same animals (*i.e.* repeated sampling on the same adult individual in consecutive years).

Inter-annual variation and long-term temporal trends. First, we assessed inter-annual variation using a global χ^2 test comparing a general model accounting for temporal variation in both traits by including year as a discrete factor, and a constant model with no fixed effect of year, both accounting for the confounding variables described above (Table S1). We calculated the percentage of inter-annual variation explained by the factor 'year' as the ratio of the difference in deviance between the general and the constant model to the deviance of the constant model multiplied by 100. Our second analysis was designed to describe the long term temporal trend by including year as a continuous variable and accounting for the confounding variables described above in a linear regression analyses (Table S1). We used an analysis of deviance (ANODEV; Skalski, 1996) to quantify the percentage of inter-annual variation in mean trait value that was explained by long-term temporal trends. We calculated this proportion as $R^2_{\text{dev}} = [\text{Dev}_{\text{constant}} - \text{DEV}_{\text{cova}}] / [(\text{Dev}_{\text{constant}} - \text{Dev}_{\text{FACyear}})]$, where 'constant'

indicates the reduced model built under the hypothesis of no temporal variation, ‘cova’ indicates the covariate model where the temporal variation is accounted for by year as a continuous variable and ‘FACyear’ the model with year as a factor (*i.e.* full time-dependent). The percentage of variance explained was obtained by multiplying R^2_{dev} by 100.

Environmental effects. In juveniles, we tested for the effects of vegetation onset (April NDVI) during their birth year (year t) on their size and mass. In older age classes, we tested summer condition index (BGI) at year t and both the effects of winter severity (snow depth and temperature) and vegetation onset (April NDVI) at year $t+1$ on their Δ size and Δ mass. All of the environmental variables were mean-centered and standardized to allow for a comparison of their relative effects. In all models including the “de-trended” winter temperature, year was added to account for the trend (Grosbois *et al.*, 2008). Only additive effects were considered, except from interactive effects of vegetation onset and the date of weaning, and of vegetation onset and litter size of juveniles. Indeed, there are two main constraints on juvenile size and mass. When pups endure higher energetic constraints either due to late weaning or larger litter size we expected food availability to have a stronger impact. In the adult model, we tested for the interaction of social status and all environmental variables to estimate differential impact between dominant and subordinate adults (Table S2).

We checked for multicollinearity and found no correlation among environmental variables (Table S3, S4). For each age class, we generated a set of models with all possible combinations of model terms of interest (*i.e.* summer condition index, winter temperature, winter snow depth, vegetation onset) taking into account the stage-specific confounding variables (defined above in the base model) (Table S5). We selected models based on the Akaike information criterion corrected for small sample size (AICc)(Burnham *et al.*, 2002).

When alternative models were indistinguishable ($\Delta AIC_c < 2$), the model with fewer parameters was retained (Burnham *et al.*, 2002).

Next, an ANODEV was used to quantify how much of the temporal variation in mean trait value was accounted for by each environmental variable. The percentage of variance explained was calculated similarly as above: $R^2_{dev} = [Dev_{constant} - DEV_{cova}] / [(Dev_{constant} - Dev_{FAC_{year}})] * 100$. To evaluate the proportion of the variance explained by a specific environmental variable, the covariate model (subscripted 'cova') included the focal climatic covariate as a continuous variable.

Life-history processes underlying trait changes

To understand the processes underlying the observed phenotypic change, we decomposed the change in mean trait value into contributions from selection and other processes using the age-structured Price equation (ASPE, Coulson & Tuljapurkar, 2008). We applied the ASPE to a sample that includes 1090 females with known weaning date and mother identity. Mother identity was determined by field observations confirmed by genetic parentage analysis conducted on 16 microsatellite loci (methods and microsatellite characteristics details are provided in Cohas *et al.*, 2008). The exact change in mean value of a trait over a time step is decomposed into seven contributions. The mathematical details are provided in Coulson & Tuljapurkar (2008) and Ozgul *et al.* (2009). Here, we provide further details on the interpretation of terms. The *DCs* term describes change resulting from changes in demographic composition due to ageing, whereas the *DCr* term describes the change resulting from the addition of new individuals due to birth. The *VS* term is the viability selection differential on the trait; it describes how selective removal of individuals through mortality alters the mean trait value. The contribution of age-specific trait development (i.e., growth or reversion) among individuals that survive is captured in the *GR* term. The *FS* term is the

reproductive selection differential; it describes how selective reproduction of individuals alters the mean trait value. The *OMD* term represents the contribution of differences between offspring and parental trait values to observed change plus the contribution from any covariance between *OMD* and number of offspring produced by each individual. Each of these terms is weighted by demographic sensitivities, which describes how survival or reproduction in an age class contributes to population growth. We applied the ASPE to annual fluctuations observed in size and mass separately.

All analyses were conducted in R 3.1.0 (R Core Team, 2014). Linear mixed models were fitted using the package ‘lme4’ (Bates *et al.*, 2012). We used the function dredge in the package ‘MuMin’ to generate a set of models with all possible terms combinations (Barton *et al.*, 2015) and the package ‘Effects’ to obtain fitted values, partial residuals and standard error estimates of mixed models on the predictor of interest (Fox, 2003; Fox *et al.*, 2009).

Results

Inter-annual variations and long-term temporal trends

Size, mass, Δ size and Δ mass strongly varied between years ($df=21$, all $\chi^2 < 0.001$). Inter-annual variations were lower for size and Δ size than for mass and Δ mass, particularly for younger age classes. Year as a discrete factor explained 11% and 58% (*i.e.* variance explained) of the inter-annual variations of juvenile size and mass, respectively. Inter-annual variations remained constant for Δ size (juvenile: 8.7%, yearling: 9.7%, subadult: 9.4%) whereas they decreased with age for Δ mass (juvenile: 44.2%, yearling: 34.4%, subadult: 17.4%, adult: 20.9%).

For each age class, there was a significant negative trend over the 22 years in size and Δ size, while controlling for confounding variables (Table S6). Juvenile size as well as

yearling and subadult Δ size declined approximately by 3.9%, 4.4% and 3.8%, respectively. Juvenile size decreased from 26.23 ± 0.01 (mean \pm SE) cm in 1992 to 25.20 ± 0.01 cm in 2012 (Fig. 1a). Despite a constant juvenile Δ size of 1.63 ± 0.01 , it decreased from 1.14 ± 0.01 to 1.09 ± 0.01 for yearlings and from 1.04 ± 0.01 to 1.00 ± 0.01 for subadults over the study period (Fig. 1c). Our results from ANODEV supported an increased effect of long-term temporal trend over age-classes. Long-term temporal trends explained 7.8% of the inter-annual variations in juvenile size, and 2.4%, 24.9%, 36.4% for juvenile, yearling and subadult Δ size, respectively. On the contrary, mass and Δ mass stayed constant between 1992 and 2012 (Table S6). Juvenile mass remained around 598.46 ± 1.02 g over the study period (Fig. 1b). Except for an increase in subadult Δ mass from 1.05 ± 0.02 in 1992 to 1.11 ± 0.02 in 2012 (+5.7%), Δ mass was constant over time for all the other age classes (Fig. 1d). Long-term temporal trends explained little of the inter-annual variation in juvenile mass (0.2%) and of the inter-annual variation in Δ mass in all classes ($3.8 \pm 2.5\%$).

Effects of environmental variables on size and Δ size

Juvenile size (Fig. 2a) and both juvenile and yearling Δ size (Fig. 3a) were affected solely by vegetation onset (Table 1). Juveniles became larger when vegetation onset was late and when weaned early (mean size: 28.0 cm), but late vegetation onset was detrimental when juveniles were weaned late (mean size: 22.4 cm, Fig. 2a). However, in years of early vegetation onset, late weaning had less effect (mean size: 27.8 cm for early weaning vs. 25.9cm for late weaning, Fig. 2a). Both juveniles and yearlings grew faster in years with earlier vegetation onset, but this positive effect diminished with age (Fig. 3a, Table 1). While juvenile Δ size increased by 0.031 (i.e., regression slope) for every standard deviation of vegetation onset ($SD_{April\ NDTV} = 0.018$), it only increased by 0.014 for yearlings. Finally, subadult Δ size was not affected by the vegetation onset.

Effects of environmental variables on mass and Δ mass

Contrary to juvenile size and Δ size, mass and Δ mass were affected not only by vegetation onset during the spring but also by summer and winter conditions. Mass of juveniles (Fig. 2b) and Δ mass of juveniles, yearlings and adults (Fig. 3b) were all affected by vegetation onset (Table 1). As for size, juveniles became heavier when vegetation onset was late and when weaned early (mean mass: 852.4 g), but late vegetation onset was detrimental when juveniles were weaned late (mean mass: 365.2 g, Fig. 2b). However, in years of early vegetation onset, late weaning had less effect (mean mass: 822.6 g for early weaning vs. 574.9 g for late weaning, Fig. 2b). Similar to Δ size, Δ mass was influenced by vegetation onset in older animals less than in juveniles and yearlings (Fig. 3b, Table 1). For every standard deviation increase in vegetation onset ($SD_{April\ NDVI} = 0.018$), Δ mass increased by 0.21, 0.04, 0.02 and -0.01 in juveniles, yearlings, adult subordinates and adult dominants, respectively (Fig. 3b). Subadult Δ mass was not impacted by vegetation onset (Table 1), and, surprisingly, dominant adults gained less mass with earlier vegetation onset compared to subordinate adults (Table 1, Fig 3b).

In addition to vegetation onset, both summer condition index and winter snow depth affected Δ mass of all age classes, except in subadults (Table 1, Fig. 3c,d). Δ mass of juveniles, yearlings and adults increased more when the summer was mild and the winter was characterized by a thin snow layer (Table 1). Subadult Δ mass has increased only in years with thin snow layer (Table 1). Again, Δ mass response to both the summer condition index (Fig. 3c) and the winter snow depth (Fig. 3d) declined with age, although the differences among age classes were stronger for summer than for winter variables. For every standard deviation increase in summer condition index ($SD_{BGI} = 75.51$), Δ mass increased by 0.13, 0.03 and 0.01 in juveniles, yearlings and adults, while for every standard deviation increase in winter snow

depth ($SD_{\text{snow depth}} = 22.84$ cm), it increased by -0.05, -0.02, -0.02 and -0.01 in juveniles, yearlings, subadults and adults, respectively. Δmass was not affected by winter temperature in any of the age classes.

Relative influence of environmental variables

From ANODEV, vegetation onset represented the most influential environmental variable (Fig. 4). Within each age class, the relative amount of annual variation explained by vegetation onset was similar for size and mass, and also for Δsize and Δmass . Summer condition index and winter snow depth only accounted for inter-annual variations in Δmass . Summer condition index explained a higher percentage of annual variation in juvenile and yearling Δmass than winter snow depth with lower evidence when individuals aged. Winter snow depth explained a relatively small amount of these variations except in subadults. Similar annual variations in adult Δmass were explained by summer condition index and winter snow depth.

Components of phenotypic changes

Using an age-structured Price equation, we decomposed the change in mean size and mass into contributions from different life-history processes. Among individuals that survived, the fluctuations observed for both size and mass were predominantly explained by age-specific trait development accounted for by the growth term (GR: 49.3 % and 50% respectively; Fig. 5). Changes in the demographic composition accounted for more of the temporal fluctuations in size than in mass. Demographic change due to aging (DCs) contributed more to the total variation of both traits than the addition of new individuals (DCr). Inheritance-related term (OMD) did not affect size variation and accounted for only a small fraction of the observed

change in mass (4.8%, Fig. 5). Selection terms (FS and VS) did not contribute to the observed fluctuations either in size or in mass (Fig. 5).

Discussion

Our results provide an in-depth evaluation of the dynamics of size and mass in response to environmental change using a hibernating mammal as the study species. Over the 22 years of study, Alpine marmots' size decreased while mass stayed constant in each age class. Moreover, initial size and Δ size responded only to inter-annual variations in spring conditions whereas initial mass and Δ mass were further adjusted to summer and winter conditions. Overall, phenotypic plasticity was the joint main origin of both traits dynamics.

Differential dynamics of size and mass

Over the study period, we found a slight decrease in juvenile size and yearling and subadult Δ size, but not in juvenile Δ size. The absence of a temporal trend observed in juvenile Δ size is possibly due to strong viability selection against smaller juveniles (Fig. S2). In contrast, juvenile mass and subsequent Δ mass during juvenile, yearling and adult stages remained constant. Concerning subadults, the positive trend observed in Δ mass might result from more delayed dispersal in recent years. Indeed, subadult apparent survival increased over the studied period while all other age classes' survival decreased or remained constant (Rézouki *et al.*, unpublished data). Although body mass had no impact on the decision to disperse in another Alpine population (Arnold, 1990a; Arnold, 1993), in our population, body mass was influential on dispersal (Magnolon, 1999). Thus, recent environmental harshness at our study site might have led subadults to stay longer in their natal territory in order to reach a critical mass threshold for successful dispersal.

As a consequence of a smaller structural size associated with similar mass over the study period, individuals were in better condition in recent years. In terms of energetics, smaller structural size has two important consequences. First, it decreases per capita food requirements and increases fasting resistance as individuals metabolize energy storage at a lower size-specific rate, which in our case may be an advantage to overcome predictable winter food shortage during the hibernation period (Millar *et al.*, 1990; Kooijman, 2000). Second, decreasing size changes the sensitivity to the thermal environment, with smaller individuals increasing their heat dissipation surface. Greater body heat loss is expected to be beneficial during their active period to increase feeding time despite high ambient temperature (Türk & Arnold, 1988) but should be detrimental during the hibernation period. An increased cold-exposed body surface area should reduce hibernation efficiency through an increase in energy expenditure to maintain a constant body temperature. But thermoregulatory costs might be buffered by social thermoregulation through huddling (Arnold, 1990b; Arnold *et al.*, 1991; Gilbert *et al.*, 2010), which is beneficial in two ways. It increases thermal conduction between close individuals and reduces the rate of cooling. Indeed, it prevents them against further body temperature decrease during period of deep torpor when costly cyclic heat bursts appear (Ortmann & Heldmaier, 2000; Ruf & Arnold, 2000).

The significant negative trend observed in size and Δ size is in line with the general pattern evidenced by other studies examining size cline as a response to environmental change (review in Sheridan *et al.*, 2011; Boutin *et al.*, 2014). On the contrary, the maintenance of mass and Δ mass over the study period contrasts with this negative cline, but it reinforces the fact that contemporary size responses are quite variable (*i.e* increasing or no change at all, reviewed by Millien *et al.*, 2006; Gardner *et al.*, 2011; Yom-Tov *et al.*, 2011; Teplitsky *et al.*, 2014) and it highlights the contrasted dynamics between both traits. Despite the paucity of long-term studies on wild birds and mammals evaluating the dynamics of both structural size

and mass (see Table 2), opposite cline between traits have also been reported in several other endotherms species (eleven bird species and two mammal species, see details in Table 2). The non-negligible number of studies showing different dynamics between structural size and mass emphasizes the risk of looking at a single trait in trait-based population models evaluating fitness consequences of morphological changes. In fact, among similar-weighted individuals, smaller ones should present a better nutritional state than larger ones, which may have direct consequences on individual life histories and ultimately fitness (Dobson, 1992; Wauters *et al.*, 1995). Thus, studying one or the other trait can lead to ambiguous and misleading conclusions. We should also note that studying their associations, using body condition index, for example, can be inadequate to describe the potentially complex changes in morphology that take place through time and can distort interpretation of the results. For example, in roe deer fawns the synchronous responses of structural size and mass (fawns were both lighter and smaller) led to a lack of response of body condition to a wide range of changes in environmental conditions whereas their phenotypic quality was reduced (Toïgo *et al.*, 2006).

Different environmental drivers: a matter of sensitivity

The phenotypic quality of Alpine marmots was favored by an early growing season resulting from an early snowmelt with a moderately warm and rainy summer. Indeed, all traits benefited from early access to resources in spring and in addition, Δ mass also responded to summer and winter conditions with greater responses observed in early life, as expected both from a theoretical and an empirical point of view (Forchhammer *et al.*, 2001; Gaillard & Yoccoz, 2003). The strong responses of both morphological traits to spring phenology reinforce the key role of nutritional condition during the green-up phase as the main driver of phenotypic quality of mammalian herbivores (Inouye *et al.*, 2000; Pettorelli *et al.*, 2007;

Campbell *et al.*, 2013). To a lower extent than spring, hot and dry summer limited annual Δ mass in juveniles, yearlings and adults probably as a result of lower quantity and quality of food ingested, and restricted foraging time during the hot hours of the day (Türk & Arnold, 1988). Unexpectedly, winter severity plays a minor to no role on morphological variations. Unsurprisingly, winter conditions did not affect Δ size as growth is greatly suppressed during hibernation (Lyman *et al.*, 1956). Only snow depth showed a weak negative impact on Δ mass in all age classes but no effect on weaning size or mass, whereas winter temperature did not influence any traits. These counter-intuitive results might arise from social thermoregulation that could have buffered the effect of winter conditions on individuals or from compensatory effects during spring. Indeed, a catch-up might occur between the end of winter (April 15) and the date of measurement (*i.e* July 14 for the juveniles and July 1 for other age class), hiding the impact of winter severity.

Size-related traits showed weaker inter-annual variations than mass-related traits. At the intra-annual scale, Δ size responded only to spring conditions whereas Δ mass was constantly adjusted to environmental conditions throughout the year. The extreme variability of mass compared to size indicates distinct sensitivity to environmental variables arising from the different underlying physiological mechanisms driving energy allocation to these functions. The longitudinal skeletal growth is driven by energy allocation to development from birth to adulthood and mainly controlled by the growth hormone, the insulin-like growth factor-1, glucocorticoids, and thyroid hormones interacting at the level of the hypothalamopituitary axes (Robson *et al.*, 2002). Despite some exceptions of seasonal reduction in braincase in small mammals (Dehnel, 1949; Pucek 1963), structural size remains fixed at the adult stage in most endotherms, and its constituents cannot be utilized for energy even under extreme starvation (Rizzoli, 2008). On the contrary, body mass is a composite of structural mass, including bones, organs, skin, blood, skeletal muscle, and storage mass

(Wang et al., 1992; Fosbøl et al., 2015). It results from the fluctuations in energy intake and expenditure (*i.e* energy homeostasis) that is down regulated by complex nutrient, cytokines and hormonal processes controlled by the whole central nervous system (Morton *et al.*, 2006). If energy intake exceeds expenditure, the surplus is stored as fat, which can then fuel energy demanding processes (*i.e.*, maintenance, growth or reproduction) during food shortage periods (Piersma *et al.*, 1991). However, during a long fasting period, Δ mass might also result from reduction in energy expensive tissues such as seasonal shrinkage of gastrointestinal tract in alpine marmots during hibernation (Hume *et al.*, 2002) or garden warblers (*Sylvia borin*) during migration (Hume & Biebach, 1996). Thus, it is not surprising that the energy allocation trade-off between size and mass varied over season, life and environmental conditions. In spring, energy is allocated to both constituents. However, later in the season, the irresponsive growth to bad environmental conditions indicates priority of energy allocation to ensure skeletal development, body fat probably being mobilized for it to compensate nutritional deficiency as already observed in deer (Klein, 1964). However, in the case of favorable summer environmental conditions, surplus nutrient are instead allocated to fattening, as storage is crucial in marmots to overcome the fasting hibernation period.

In accordance with our study, other studies have shown different sensitivity to environmental drivers between structural size and mass (Table 2). However, mass appears to be sensitive to a larger number of environmental variables than size in only three other species, namely great tits, river warblers and grizzly bears. In birds, similar environmental drivers between both traits might not be surprising as they cannot store excess fat because increased wing loading may decrease their flight performance and thus may increase their susceptibility to predation (*i.e* starvation-predation risk trade-off; Macleod *et al.*, 2005). However, these results might be different when looking at migratory birds that can double their mass due to different fuel loads and body composition (Lindström *et al.*, 1993).

Unfortunately, the studies reported in Table 2 were only on sedentary or pre-migratory birds (except Kanuscack et al. 2004 that studied them on their migratory route). Concerning mammals, we cannot draw any conclusion from only six studies among which four examined at most two environmental drivers (Table 2). Moreover, given that the environmental drivers chosen were mostly global change index processing both nutritional and thermal conditions (Post *et al.*, 1997: North Atlantic Oscillation index; Toïgo *et al.*, 2006: spring and summer Gaussen Index; Rode *et al.*, 2010: availability of sea ice habitat; Yom-Tov *et al.*, 2010b: mean annual temperature and number of days of ice coverage), distinct dynamics resulting from different energetic pressure on size and mass cannot be disentangled.

Phenotypic change: a plastic response

The annual variation in both traits observed in this study was mainly triggered by their development in early life stage. Although the ‘growth term’ from the age-structured Price equation can include genetic components (Coulson *et al.*, 2008), the strong response we observed to environmental conditions indicates mostly phenotypic plasticity that an animal model type of approach should confirm. Our results add a sixth wild vertebrate species, in addition to yellow-bellied marmots (Ozgul *et al.*, 2010), Soay sheep (Ozgul *et al.*, 2009), red-billed gull (Teplitsky *et al.*, 2008), great tits (Husby *et al.*, 2011) and Siberian jays (Gienapp *et al.*, 2014), that quantitatively demonstrates mostly ecological responses of morphological traits to environmental variations. Mass variations of the Alpine marmot were subject to similar relative contributions of plasticity and selection as the yellow-bellied marmots (Ozgul *et al.*, 2010) despite harsher environmental conditions (*i.e* colder, prolonged winter with extensive snow cover) reducing favorable foraging period in the Rocky Mountains (Armitage, 2014). Selection terms accounted for even less variation in our study population (0.96 % vs. 3% in yellow-bellied marmots). However, the paucity of evidence for genetic responses to

climate-mediated selection might arise from both methodological difficulties and/or biological issues such as evolutionary time lags (Merilä, 2012). Our 22-year study period may have been too short to detect a genetic response, as the rate of climate change might be too fast for genetic adaptation to occur in species with long life spans as already observed in an emperor penguin population (Forcada *et al.*, 2009; Jenouvrier *et al.*, 2009). It has also recently been advocated that new phenotypes can first be induced by environmental conditions and then be genetically assimilated, leading to genetic adaptation; as a result phenotypic plasticity is not only a product but also a driver of genetic evolution (Kopp *et al.*, 2014).

The phenotypic plasticity observed in Alpine marmots does not appear adaptive despite their wide ranged reaction norms (*i.e.*, phenotype as a function of an environmental variable) showing their ability to withstand extreme environmental conditions. Indeed, recent studies on this population showed a decline of individual performances over the past decades with observed decreasing litter size, juvenile survival and family group size (Tafari *et al.*, 2013; Rézouki *et al.*, unpublished data). These results contrast with the abrupt increase in population size of yellow-bellied marmots triggered by their mass shift (Ozgul *et al.*, 2010). Although the structural size changes of yellow-bellied marmots remain unknown, the different strategy between these species to maintain or increase their body condition by decreasing structural size in Alpine marmots or increasing mass in yellow-bellied marmots leads to drastic differences on their survival and reproductive rate. While both species are closely related and respond plastically to environmental change, the strikingly different fitness consequences highlight their different adaptive ability to face environmental change.

Future directions and general implications

Our research provides new insight for population modeling by drawing attention to consideration of the differences between size and mass in response to the environment. We

612 provide further incentives to now disentangle causes and effects with environmental
613 manipulation to assess the underlying mechanisms of the different dynamics, and to quantify
614 the consequences of our measured changes on energy balance (Porter *et al.*, 2009; Gardner *et*
615 *al.*, 2011). To achieve further insight into the mechanisms driving population dynamics, the
616 challenge ahead will be to model the link between these traits and demographic performances.
617 The range of resilience conferred by plastic phenotypic compensations remains poorly
618 understood in wild species (Ghalambor *et al.*, 2007; Canale *et al.*, 2010) and might
619 dramatically differ between even closely related species as suggested for Alpine and yellow-
620 bellied marmots. The evaluation of the complex dynamics between traits and their distinct
621 sensitivity to environmental change will enhance our ability to assess whether or not
622 phenotypic plasticity could provide an adaptive response to environmental change.

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References

- Allain  D (2000) Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behavioural Processes*, **51**, 21-34.
- Allain  D, Graziani L, Coulon J (1998) Postweaning mass gain in juvenile alpine marmots *Marmota marmota*. *Oecologia*, **113**, 370-376.
- Allain  D, Theuriau F (2004) Is there an optimal number of helpers in Alpine marmot family groups? *Behavioral Ecology*, **15**, 916-924.
- Armitage KB (2014) Marmots habitats in *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*, Cambridge University Press, 43-56.

647 Arnold W (1990a) The evolution of marmot sociality: I. Why disperse late? Behavioral
 648 Ecology and Sociobiology, **27**, 229-237.
 649 Arnold W (1990b) The evolution of marmot sociality: II. Costs and benefits of joint
 650 hibernation. Behavioral Ecology and Sociobiology, **27**, 239-246.
 651 Arnold W (1993) Energetics of social hibernation. Life in the Cold: Ecological, Physiological
 652 and Molecular Mechanisms, 65-80.
 653 Arnold W, Dittami J (1997) Reproductive suppression in male alpine marmots. Animal
 654 Behaviour, **53**, 53-66.
 655 Arnold W, Heldmaier G, Ortmann S, Pohl H, Ruf T, Steinlechner S (1991) Ambient
 656 temperatures in hibernacula and their energetic consequences for alpine marmots
 657 (*Marmota marmota*). Journal of Thermal Biology, **16**, 223-226.
 658 Ashton KG, Tracy MC, De Queiroz A (2000) Is Bergmann's rule valid for mammals? The
 659 American Naturalist, **156**, 390-415.
 660 Barton K, Barton MK (2015) Package 'MuMIn'. R package version, **1**, 18.
 661 Basso B, De Simone L, Cammarano D et al. (2012) Evaluating responses to land degradation
 662 mitigation measures in Southern Italy. International Journal of Environmental
 663 Research, **6**, 367-380.
 664 Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes.
 665 Bel MC, Coulon J, Sreng L, Allaine D, Bagneres AG, Clement JL (1999) Social signals
 666 involved in scent-marking behavior by cheek-rubbing in Alpine marmots (*Marmota*
 667 *marmota*). Journal of Chemical Ecology, **25**, 2267-2283.
 668 Beniston M (2006) Mountain weather and climate: a general overview and a focus on climatic
 669 change in the Alps. Hydrobiologia, **562**, 3-16.
 670 Bergmann C (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.
 671 Gottinger Studien, **3**, 595-708.

672 Blackburn TM, Gaston KJ (1994) Animal body size distributions: patterns, mechanisms and
673 implications. *Trends in Ecology & Evolution*, **9**, 471-474.

674 Boutin S, Lane JE (2014) Climate change and mammals: evolutionary versus plastic
675 responses. *Evolutionary Applications*, **7**, 29-41.

676 Büntgen U, Liebhold A, Jenny H *et al.* (2014) European springtime temperature synchronises
677 ibex horn growth across the eastern Swiss Alps. *Ecology Letters*, **17**, 303-313.

678 Burnham KP, Anderson DR (2002) *Model selection and multi-model inference: a practical*
679 *information-theoretic approach*, Berlin, Germany, Springer.

680 Calder WA (1984) *Size, function, and life history*, Courier Corporation.

681 Campbell RD, Newman C, Macdonald DW, Rosell F (2013) Proximate weather patterns and
682 spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and
683 reproductive success: the implications of climate change and topography. *Global*
684 *Change Biology*, **19**, 1311-1324.

685 Canale CI, Henry PY (2010) Adaptive phenotypic plasticity and resilience of vertebrates to
686 increasing climatic unpredictability. *Climate Research*, **43**, 135-147.

687 Cohas A, Yoccoz NG, Bonenfant C *et al.* (2008) The genetic similarity between pair members
688 influences the frequency of extrapair paternity in alpine marmots. *Animal Behaviour*,
689 **76**, 87-95.

690 Cooch E, Lank D, Rockwell R, Cooke F (1991) Long-term decline in body size in a snow
691 goose population: evidence of environmental degradation? *The Journal of Animal*
692 *Ecology*, 483-496.

693 Coulson T, Tuljapurkar S (2008) The Dynamics of a Quantitative Trait in an Age-Structured
694 Population Living in a Variable Environment. *The American Naturalist*, **172**, 599-612.

695 Dajoz R (1973) *Précis d'écologie*, Gauthier Villars.

696 Davis EB (2005) Comparison of climate space and phylogeny of *Marmota* (Mammalia :
 697 Rodentia) indicates a connection between evolutionary history and climate preference.
 698 Proceedings of the Royal Society B-Biological Sciences, **272**, 519-526.
 699 Dehnel A (1949) Studies on the genus *Sorex* L. Annales of the university of M. Curie-
 700 Sklodowska, Section C, **4**, 17-102.
 701 Dejong G (1995) Phenotypic plasticity as a product of selection in a variable environment
 702 American Naturalist, **145**, 493-512.
 703 Dickey M, Gauthier G, Cadieux M-C (2008) Climatic effects on the breeding phenology and
 704 reproductive success of an arctic-nesting goose species. Global Change Biology, **14**,
 705 1973-1985.
 706 Dobson FS (1992) Body mass, structural size, and life-history patterns of the Columbian
 707 ground squirrel. American Naturalist, 109-125.
 708 Eastman LM, Morelli TL, Rowe KC, Conroy CJ, Moritz C (2012) Size increase in high
 709 elevation ground squirrels over the last century. Global Change Biology, **18**, 1499-
 710 1508.
 711 Engler R, Randin CF, Thuiller W *et al.* (2011) 21st century climate change threatens
 712 mountain flora unequally across Europe. Global Change Biology, **17**, 2330-2341.
 713 Farand E, Allainé D, Coulon J (2002) Variation in survival rates for the alpine marmot
 714 (*Marmota marmota*): effects of sex, age, year, and climatic factors. Canadian Journal
 715 of Zoology-Revue Canadienne De Zoologie, **80**, 342-349.
 716 Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean.
 717 Global Change Biology, **15**, 1618-1630.
 718 Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD (2001) Climate and population
 719 density induce long-term cohort variation in a northern ungulate. Journal of Animal
 720 Ecology, **70**, 721-729.

721 Fosbøl MØ, Zerah B (2015) Contemporary methods of body composition measurement.
722 Clinical Physiology and Functional Imaging, **35**, 81-97.

723 Fox J (2003) Effect displays in R for generalised linear models. Journal of Statistical
724 Software, **8**, 1-27.

725 Fox J, Hong J (2009) Effect displays in R for multinomial and proportional-odds logit
726 models: Extensions to the effects package. Journal of Statistical Software, **32**, 1-24.

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

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

731 Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third
732 universal response to warming? Trends in Ecology & Evolution, **26**, 285-291.

733 Garel, M. et al. (2004) The effects of a severe drought on mouflon lamb survival. -
734 Proceedings of the Royal Society of London. Series B: Biological Sciences, **271**, 471-
735 473.

736 Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive
737 phenotypic plasticity and the potential for contemporary adaptation in new
738 environments. Functional Ecology, **21**, 394-407.

739 Gienapp P, Merilä J (2014) Disentangling plastic and genetic changes in body mass of
740 Siberian jays. Journal of Evolutionary Biology, **27**, 1849-1858.

741 Gienapp P, Teplitsky C, Alho JS, Mills JA, Merila J (2008) Climate change and evolution:
742 disentangling environmental and genetic responses. Molecular Ecology, **17**, 167-178.

743 Gilbert C, Mccafferty D, Le Maho Y, Martrette JM, Giroud S, Blanc S, Ancel A (2010) One
744 for all and all for one: the energetic benefits of huddling in endotherms. Biological
745 Reviews, **85**, 545-569.

746 Green AJ (2001) Mass/length residuals: Measures of body condition or generators of spurious
747 results? Ecology, **82**, 1473-1483.

748 Grosbois V, Gimenez O, Gaillard JM *et al.* (2008) Assessing the impact of climate variation
749 on survival in vertebrate populations. Biological Reviews, **83**, 357-399.

750 Guillemain M, Mondain-Monval J-Y, Johnson AR, Simon G (2005) Long-term climatic trend
751 and body size variation in teal *Anas crecca*. Wildlife Biology, **11**, 81-88.

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

754 Hamel S, Garel M, Festa-Bianchet M, Gaillard JM, Côté SD (2009) Spring Normalized
755 Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal
756 crude protein in mountain ungulates. Journal of Applied Ecology, **46**, 582-589.

757 Heldmaier G (1989) Seasonal acclimatization of energy requirements in mammals: functional
758 significance of body weight control, hypothermia, torpor and hibernation. Energy
759 transformations in cells and organisms. Thieme, Stuttgart, 130-139.

760 Hembeck H (1958) Zum Paarungsverhalten der Murmeltiere. Z Jagdwiss, **4**, 40-41.

761 Hersteinsson P, Yom-Tov Y, Geffen E (2009) Effect of Sub-Polar Gyre, North Atlantic
762 Oscillation and ambient temperature on size and abundance in the Icelandic Arctic
763 fox. Global Change Biology, **15**, 1423-1433.

764 Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature, **470**,
765 479-485.

766 Hou C, Zuo W, Moses ME, Woodruff WH, Brown JH, West GB (2008) Energy uptake and
767 allocation during ontogeny. Science, **322**, 736-739.

768 Huey RB, Kearney MR, Krockenberger A, Holtum JaM, Jess M, Williams SE (2012)
769 Predicting organismal vulnerability to climate warming: roles of behaviour,

770 physiology and adaptation. Philosophical Transactions of the Royal Society B-
 771 Biological Sciences, **367**, 1665-1679.

772 Hume I, Biebach H (1996) Digestive tract function in the long-distance migratory garden
 773 warbler, *Sylvia borin*. Journal of Comparative Physiology B, **166**, 388-395.

774 Hume I, Beiglböck C, Ruf T, Frey-Roos F, Bruns U, Arnold W (2002) Seasonal changes in
 775 morphology and function of the gastrointestinal tract of free-living alpine marmots
 776 (*Marmota marmota*). Journal of Comparative Physiology B: Biochemical, Systemic,
 777 and Environmental Physiology, **172**, 197-207.

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

781 Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal
 782 migrants and hibernating species. Proceedings of the National Academy of Sciences of
 783 the United States of America, **97**, 1630-1633.

784 Janz KF (2004) *Growth, maturation, and physical activity, 2nd edition*. American Journal of
 785 Human Biology: The Official Journal of the Human Biology Council.

786 Jenouvrier S, Caswell H, Barbraud C, Holland M, Ströve J, Weimerskirch H (2009)
 787 Demographic models and IPCC climate projections predict the decline of an emperor
 788 penguin population. Proceedings of the National Academy of Sciences, **106**, 1844-
 789 1847.

790 Kaňuščák P, Hromada M, Tryjanowski P, Sparks T (2004) Does climate at different scales
 791 influence the phenology and phenotype of the River Warbler *Locustella fluviatilis*?
 792 Oecologia, **141**, 158-163.

793 Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and
 794 spatial data to predict species' ranges. Ecology Letters, **12**, 334-350.

795 Keller F, Goyette S, Beniston M (2005) Sensitivity analysis of snow cover to climate change
796 scenarios and their impact on plant habitats in alpine terrain. *Climatic Change*, **72**,
797 299-319.

798 Klein DR (1964) Range-related differences in growth of deer reflected in skeletal ratios.
799 *Journal of Mammalogy*, 226-235.

800 Kooijman SaLM (2000) *Dynamic energy and mass budgets in biological systems*, Cambridge
801 University Press.

802 Kopp M, Matuszewski S (2014) Rapid evolution of quantitative traits: theoretical
803 perspectives. *Evolutionary Applications*, **7**, 169-191.

804 Körtner G, Heldmaier G (1995) Body weight cycles and energy balance in the alpine marmot
805 (*Marmota marmota*). *Physiological Zoology*, 149-163.

806 Lardy S, Cohas A, Desouhant E, Tafani M, Allaine D (2012) Paternity and dominance loss in
807 male breeders: the cost of helpers in a cooperatively breeding mammal. *Plos One*, **7**,
808 e29508.

809 Lenihan C, Van Vuren D (1996) Growth and survival of juvenile yellow-bellied marmots
810 (*Marmota flaviventris*). *Canadian Journal of Zoology*, **74**, 297-302.

811 Lindström A, Piersma T (1993) Mass changes in migrating birds: the evidence for fat and
812 protein storage re-examined. *Ibis*, **135**, 70-78.

813 Lyman CP, Chatfield PO (1956) Physiology of hibernation in mammals. *The Physiology of*
814 *Induced Hypothermia*, **1**, 80-122.

815 Macleod R, Barnett P, Clark J, Cresswell W (2005) Body mass change strategies in blackbirds
816 *Turdus merula*: the starvation–predation risk trade-off. *Journal of Animal Ecology*, **74**,
817 292-302.

818 Magnolon S (1999) La dispersion natale chez la marmotte alpine (*Marmota marmota*).
819 Modalités et effets de quelques facteurs proximaux. Thèse de Doctorat. Université
820 Francois Rabelais, Tours.

821 McNab BK (1999) On the comparative ecological and evolutionary significance of total and
822 mass-specific rates of metabolism. *Physiological and Biochemical Zoology*, **72**, 642-
823 644.

824 Maiorano L, Amori G, Capula M *et al.* (2013) Threats from climate change to terrestrial
825 vertebrate hotspots in Europe. *Plos One*, **8**, e74989.

826 Marroig G, Cheverud J (2010) Size as a line of least resistance II: Direct selection on size or
827 correlated response due to constraints? *Evolution*, **64**, 1470-1488.

828 McMahon SM, Harrison SP, Armbruster WS *et al.* (2011) Improving assessment and
829 modelling of climate change impacts on global terrestrial biodiversity. *Trends in*
830 *Ecology & Evolution*, **26**, 249-259.

831 McNab BK (2010) Geographic and temporal correlations of mammalian size reconsidered: a
832 resource rule. *Oecologia*, **164**, 13-23.

833 Meiri S (2011) Bergmann's Rule—what's in a name? *Global Ecology and Biogeography*, **20**,
834 203-207.

835 Merilä J (2012) Evolution in response to climate change: in pursuit of the missing evidence.
836 *Bioessays*, **34**, 811-818.

837 Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the
838 problem and the evidence. *Evolutionary Applications*, **7**, 1-14.

839 Michener DR (1974) Annual cycle of activity and weight changes in Richardson's ground
840 squirrel, *Spermophilus richardsonii*. *Canadian Field-Naturalist*, **88**, 409-413.

841 Millar J, Hickling G (1990) Fasting endurance and the evolution of mammalian body size.
842 *Functional Ecology*, 5-12.

843 Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom-Tov Y (2006) Ecotypic variation
844 in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**, 853-
845 869.

846 Monaghan P (2008) Early growth conditions, phenotypic development and environmental
847 change. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**,
848 1635-1645.

849 Moreno-Rueda G, Rivas JM (2007) Recent changes in allometric relationships among
850 morphological traits in the dipper (*Cinclus cinclus*). *Journal of Ornithology*, **148**, 489-
851 494.

852 Morton G, Cummings D, Baskin D, Barsh G, Schwartz M (2006) Central nervous system
853 control of food intake and body weight. *Nature*, **443**, 289-295.

854 Müller-Using D (1957) Die Paarungsbiologie des Murmeltieres. *Z Jagdwiss*, **3**, 24-28.

855 Nielsen SE, Cattet MR, Boulanger J, Cranston J, Mcdermid GJ, Shafer AB, Stenhouse GB
856 (2013) Environmental, biological and anthropogenic effects on grizzly bear body size:
857 temporal and spatial considerations. *BMC Ecology*, **13**, 31.

858 Ortmann S, Heldmaier G (2000) Regulation of body temperature and energy requirements of
859 hibernating Alpine marmots (*Marmota marmota*). *American Journal of Physiology-*
860 *Regulatory, Integrative and Comparative Physiology*, **278**, R698-R704.

861 Ozgul A, Bateman AW, English S, Coulson T, Clutton-Brock TH (2014) Linking body mass
862 and group dynamics in an obligate cooperative breeder. *Journal of Animal Ecology*,
863 **83**, 1357-1366.

864 Ozgul A, Childs DZ, Oli MK *et al.* (2010) Coupled dynamics of body mass and population
865 growth in response to environmental change. *Nature*, **466**, 482-485.

866 Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T (2009)
867 The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda. *Science*,
868 **325**, 464-467.

869 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual*
870 *Review of Ecology Evolution and Systematics*, **37**, 637-669.

871 Peig J, Green AJ (2010) The paradigm of body condition: a critical reappraisal of current
872 methods based on mass and length. *Functional Ecology*, **24**, 1323-1332.

873 Perrin C, Allainé D, Leberre M (1993) Socio-spatial organization and activity distribution of
874 the Alpine marmot (*Marmota marmota*) - preliminary results. *Ethology*, **93**, 21-30.

875 Pettorelli N, Gaillard J-M, Van Laere G *et al.* (2002) Variations in adult body mass in roe
876 deer: the effects of population density at birth and of habitat quality. *Proceedings of*
877 *the Royal Society of London. Series B: Biological Sciences*, **269**, 747-753.

878 Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the
879 satellite-derived NDVI to assess ecological responses to environmental change.
880 *Trends in Ecology & Evolution*, **20**, 503-510.

881 Pettorelli N, Pelletier F, Hardenberg AV, Festa-Bianchet M, Côté SD (2007) Early onset of
882 vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates.
883 *Ecology*, **88**, 381-390.

884 Piersma T, Davidson NC (1991) Confusions of mass and size. *The Auk*, 441-443.

885 Porter WP, Kearney M (2009) Size, shape, and the thermal niche of endotherms. *Proceedings*
886 *of the National Academy of Sciences*, **106**, 19666-19672.

887 Post E, Stenseth NC, Langvatn R, Fromentin J-M (1997) Global climate change and
888 phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of*
889 *London. Series B: Biological Sciences*, **264**, 1317-1324.

890 Psenner H (1957) Neues vom Murmeltier, *Marmota m. marmota* (Linne, 1758). Säugetierk
 891 Mitt, **5**, 4-10.

892 Pucek Z (1963) Seasonal changes in the braincase of some representatives of the genus *Sorex*
 893 from the Palearctic. *Journal of Mammalogy*, **44**, 523-536.

894 R Core Team (2014). R: A language and environment for statistical computing. R Foundation
 895 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

896 Rioux Paquette S, Pelletier F, Garant D, Bélisle M (2014) Severe recent decrease of adult
 897 body mass in a declining insectivorous bird population. *Proceedings of the Royal*
 898 *Society B: Biological Sciences*, **281**, 20140649.

899 Rizzoli R (2008) Nutrition: its role in bone health. *Best Practice & Research Clinical*
 900 *Endocrinology & Metabolism*, **22**, 813-829.

901 Robson H, Siebler T, Shalet SM, Williams GR (2002) Interactions between GH, IGF-I,
 902 glucocorticoids, and thyroid hormones during skeletal growth. *Pediatric research*, **52**,
 903 137-147.

904 Roche EA, Brown MB, Brown CR (2014) The Effect of Weather on Morphometric Traits of
 905 Juvenile Cliff Swallows. *Prairie Naturalist*, **46**, 2.

906 Rode KD, Amstrup SC, Regehr EV (2010) Reduced body size and cub recruitment in polar
 907 bears associated with sea ice decline. *Ecological Applications*, **20**, 768-782.

908 Ruf T, Arnold W (2000) Mechanisms of social thermoregulation in hibernating alpine
 909 marmots (*Marmota marmota*). *Life in the Cold*. Berlin: Springer, 81-94.

910 Salewski V, Hochachka WM, Fiedler W (2010) Global warming and Bergmann's rule: do
 911 central European passerines adjust their body size to rising temperatures? *Oecologia*,
 912 **162**, 247-260.

913 Schamber JL, Esler D, Flint PL (2009) Evaluating the validity of using unverified indices of
 914 body condition. *Journal of Avian Biology*, **40**, 49-56.

915 Schmidt-Nielsen K (1984) *Scaling: why is animal size so important?*, Cambridge University
916 Press.

917 Seebacher F, Franklin CE (2012) Determining environmental causes of biological effects: the
918 need for a mechanistic physiological dimension in conservation biology. *Philosophical*
919 *Transactions of the Royal Society B-Biological Sciences*, **367**, 1607-1614.

920 Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate
921 change. *Nature Climate Change*, **1**, 401-406.

922 Skalski JR (1996) Regression of abundance estimates from mark recapture surveys against
923 environmental covariates. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**,
924 196-204.

925 Smith FA, Browning H, Shepherd UL (1998) The influence of climate change on the body
926 mass of woodrats *Neotoma* in an arid region of New Mexico, USA. *Ecography*, **21**,
927 140-148.

928 Smith FA, Lyons SK (2013) *Animal body size: linking pattern and process across space,*
929 *time, and taxonomic group*, University of Chicago Press.

930 Somero GN (2012) The Physiology of Global Change: Linking Patterns to Mechanisms.
931 *Annual Review of Marine Science*, **4**, 39-61.

932 Tafani M, Cohas A, Bonenfant C, Gaillard JM, Allainé D (2013) Decreasing litter size of
933 marmots over time: a life history response to climate change? *Ecology*, **94**, 580-586.

934 Teplitsky C, Millien V (2014) Climate warming and Bergmann's rule through time: is there
935 any evidence? *Evolutionary Applications*, **7**, 156-168.

936 Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merila J (2008) Bergmann's rule and climate
937 change revisited: Disentangling environmental and genetic responses in a wild bird
938 population. *Proceedings of the National Academy of Sciences of the United States of*
939 *America*, **105**, 13492-13496.

940 Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the
 941 European Alps: A review. *Climatic Change*, **50**, 77-109.

942 Toïgo C, Gaillard JM, Van Laere G, Hewison M, Morellet N (2006) How does environmental
 943 variation influence body mass, body size, and body condition? Roe deer as a case
 944 study. *Ecography*, **29**, 301-308.

945 Türk A, Arnold W (1988) Thermoregulation as a limit to habitat use in alpine marmots
 946 (*Marmota marmota*). *Oecologia*, **76**, 544-548.

947 Wang Z-M, Pierson R, Heymsfield SB (1992) The five-level model: a new approach to
 948 organizing body-composition research. *The American Journal of Clinical Nutrition*,
 949 **56**, 19-28.

950 Wauters L, Dhondt AA (1995) Lifetime reproductive success and its correlates in female
 951 Eurasian red squirrels. *Oikos*, 402-410.

952 Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an Integrated
 953 Framework for Assessing the Vulnerability of Species to Climate Change. *PLoS*
 954 *Biology*, **6**, 2621-2626.

955 Yoccoz NG, Delestrade A, Loison A (2010) Impact of climatic change on alpine ecosystems:
 956 inference and prediction. *Journal of Alpine Research-Revue de géographie alpine*, no
 957 98-4.

958 Yom-Tov Y (2001) Global warming and body mass decline in Israeli passerine birds.
 959 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 947-
 960 952.

961 Yom-Tov Y, Geffen E (2011) Recent spatial and temporal changes in body size of terrestrial
 962 vertebrates: probable causes and pitfalls. *Biological Reviews*, **86**, 531-541.

Yom-Tov Y, Leader N, Yom-Tov S, Baagøe HJ (2010a) Temperature trends and recent decline in body size of the stone marten *Martes foina* in Denmark. Mammalian Biology-Zeitschrift fur Saugetierkunde, **75**, 146-150.

Yom-Tov Y, Roos A, Mortensen P, Wiig Ø, Yom-Tov S, Heggberget TM (2010b) Recent changes in body size of the Eurasian otter *Lutra lutra* in Sweden. Ambio, **39**, 496-503.

Yom-Tov Y, Yom-Tov J (2005) Global warming, Bergmann's rule and body size in the masked shrew *Sorex cinereus* Kerr in Alaska. Journal of Animal Ecology, **74**, 803-808.

Yom-Tov Y, Yom-Tov S (2004) Climatic change and body size in two species of Japanese rodents. Biological Journal of the Linnean Society, **82**, 263-267.

Yom-Tov Y, Yom-Tov S, Angerbjorn A (2010c) Body size of the weasel *Mustela nivalis* and the stoat *M. erminea* in Sweden. Mammalian Biology-Zeitschrift fur Saugetierkunde, **75**, 420-426.

Supporting Information

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

Appendix S1. Intra-annual variation in size and mass.

Fig. S1. Timeline of size and mass estimates shown on the life cycle of alpine marmots.

Table S1. Age-specific linear mixed models describing inter-annual variations and long-term temporal trends.

Table S2. Age-specific linear mixed models describing the effect of environmental variables.

Table S3. Correlation matrix among environmental variables.

Table S4. Variance inflation-factors among environmental variables.

Table S5. Model selection of the full set of models for all alternatives concerning environmental variables.

988 **Table S6.** Age-specific linear mixed models testing for long-term linear temporal trend.
989 **Table S7.** Age-specific linear mixed models testing for environmental effects.
990 **Fig S2.** Age-specific viability selection contributions to changes in the mean value of size.
991

FIGURES AND TABLES CAPTION

Fig. 1 Temporal changes in stage specific size, mass, Δ size and Δ mass. Yearly variation in (a) size, (b) mass, (c) Δ size and (d) Δ mass of juvenile (), yearling (), subadult (), subordinate adult () and dominant adult () Alpine marmots at La Grande Sassi re (French Alps) from 1992 to 2012. Solid lines represent model predictions and dashed lines their associated standard error. Symbols represent model residuals after controlling for confounding variables (for details see the Materials and methods section).

Fig. 2 Vegetation onset and date of weaning effects on (a) size and (b) mass of juveniles. The grey surface represents model predictions. Dots represent model residuals after controlling for confounding variables (for details see the Materials and methods section). Black dots are above the predicted values and white dots below the predicted values.

Fig. 3 Environmental factors driving stage specific Δ size and Δ mass. Effects of (a) vegetation onset on Δ size, and of (b) vegetation onset, (c) summer condition index, (d) winter snow depth on Δ mass of juvenile (), yearling (), subadult (), adult subordinate (), adult dominant () or both subordinate adult and dominant adult () Alpine marmots at La Grande Sassi re (French Alps) from 1992 to 2012. Solid lines represent model predictions and dashed lines represent their associated standard error. Symbols represent the residuals after controlling for confounding variables (for details see the Materials and methods section). Environmental variables were mean-centered and standardized.

Fig. 4 Relative influence of environmental variables. Proportion of the variance in size, mass, Δ size and Δ mass explained by significant environmental variables.

Fig. 5 Components of phenotypic changes. Percentage contribution of the different terms to the observed total variation in size and mass. The change in the mean value of both traits were decomposed into contributions from age-specific trait development (Gr), changes in demographic structure caused by age-specific survival rates (DCs) or caused by age-specific reproduction (DCr), offspring-mother difference (OMD), age-specific viability selection (VS) and age-specific fertility selection (FS).

Table 1 Environmental effects in size, mass and Δ size and Δ mass. Statistically significant environmental effects in (a) size and mass in juvenile and on Δ size and Δ mass in (b) juvenile, (c) yearling, (d) subadult and (e) adult Alpine marmots at La Grande Sassi re (French Alps) from 1992 to 2012. We modeled Δ size and Δ mass conditional on initial size and mass, respectively. All size and mass measurements in the response variables and model terms were log-transformed. We controlled for confounding variables (not shown here, see Table S7 for details) and we included as additive random effects on the intercept, territory in all models and marmot identity in the adult models. Parameter estimates and their associated standard errors (SE) were obtained from the best model based on the Akaike Information Criterion for small sample size (AICc) (see Table S5). Baseline intercepts are established for dominants in the adult model.

Table 2 A synopsis of long-term studies looking at both size and mass dynamics in wild birds and mammals. We excluded studies reporting changes from museums specimens. Temporal

1037 trends in bold indicates opposite trends between size and mass. For environmental drivers, we
1038 show the number of environmental factors that had a significant impact on size and mass over
1039 how many have been tested. Bold numbers show studies demonstrating that mass and size
1040 were driven by a different number of environmental variables. * indicates studies where mass
1041 was adjusted to a larger number of environmental variables than size.