

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

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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. Third, the interannual variation in both traits was caused by changes in early life development. 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 modeling can lead to misleading conclusions when evaluating species' resilience to contemporary climate change.

Keywords: Alpine marmot, body size, climate change, food availability, French Alps, normalized difference vegetation index, phenotypic plasticity, reaction norm

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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 & Franklin, 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 & Porter, 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 & Bickford, 2011). Second, their responses to climate change can occur on a short-time scale (Gienapp *et al.*, 2008; Boutin & Lane, 2014). Third, structural size and body mass affect population performances of vertebrates through their direct impact on individual life-histories (Schmidt-Nielsen, 1984; Blackburn & Gaston, 1994; Smith & Lyons, 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 & Geffen, 2011). However, modifications in nutritional and/or thermal environment can be seen as the two major drivers (Millien *et al.*, 2006; McNab, 2010). On

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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 & Yom-Tov, 2004; Yom-Tov & Yom-Tov, 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 & Bickford, 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 (Bergmann, 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 & Millien, 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 & Davidson, 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 & Zerahn, 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 differ-

ent 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 & Lane, 2014; Teplitsky & Millien, 2014). Observed body size shifts can be mediated through phenotypic plasticity and/or through selection if the trait is heritable (Coulson & Tuljapurkar, 2008; Boutin & Lane, 2014; Kopp & Matuszewski, 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 & Hendry, 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 & Cheverud, 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 & Sgro, 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 & Guisan, 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 snow fall 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 2–3) and yearlings (age 1–2) subordinates, and juveniles (age 0–1) (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 behavior (Arnold & Dittami, 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 (Tafari *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 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; Hemberck, 1958). Then, dominant females are pregnant for 30 days and give birth to a litter of 1–7 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 Sassièrre 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 × 25 × 25 cm, Tomahawk Live Trap, Hazelhurst, WI, USA), baited with dande-

lions (*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 anesthetized 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 colored 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 3 years). Immigrants were assigned to the adult age class as they are known to disperse after 2 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 3 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.*, in press) and reproductive output (Tafari *et al.*, 2013) in this species.

Three seasons with differential impacts on Alpine marmots' size were considered: (i) summer (July–August), when marmots build fat reserves, (ii) winter (December–March), when marmots hibernate, and (iii) early spring (last 2 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 5 km from the field site, respectively Val d'Isère (1840 m), Tignes Brevières (1560 m) and Tignes (2080 m). NDVI provided by the National Oceanic and Atmospheric Administration was obtained from the AVHRR data set (1990–2000) within an 8 × 8 km pixel area and the MODIS data set (2001–2013) with a resolution of 1 × 1 km pixel centered on the study site. Summer variables included a summer condition index measured as the July to August Bagnouls-Gausson aridity index (BGI, total daily rainfall (mm) minus twice the mean ambient temperature (°C). High aridity is represented by low BGI value; Dajoz, 1973). 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; Loison *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 yr⁻¹, $P = 0.012$).

Size and mass dynamics

We omitted the first 2 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 ($\Delta\text{size} = \text{size}_{t+1} - \text{size}_t$) and mass ($\Delta\text{mass} = \text{mass}_{t+1} - \text{mass}_t$) defined as the difference in trait value from 1 year to the next. We modeled Δsize and Δmass conditional on initial size and mass respectively (*i.e.* $\Delta\text{size} \sim \text{size}$, and $\Delta\text{mass} \sim \text{mass}_i$; 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 & Zerahn, 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 3 years old (see Fig. A1 in Appendix S1), subadult Δsize was measured as the difference in size between age two and their first capture as adults ($\geq \text{age } 3$). Subadult Δmass remained as the difference in mass between ages two and three. Fitted values obtained from these models will be referred to as Δsize and Δmass 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).

Interannual variation and long-term temporal trends. First, we assessed interannual 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 interannual 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 interannual variation in mean trait value that was explained by long-term temporal trends. We calculated this proportion as $R_{\text{dev}}^2 = (\text{Dev}_{\text{constant}} - \text{DEV}_{\text{cova}}) / (\text{Dev}_{\text{constant}} - \text{Dev}_{\text{FACyear}})$, 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_{dev}^2 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 (Tables S3 and 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 & Anderson, 2002). When alternative models were indistinguishable ($\Delta\text{AICc} < 2$), the model with fewer parameters was retained (Burnham & Anderson, 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: $R_{\text{dev}}^2 = [(\text{Dev}_{\text{constant}} - \text{DEV}_{\text{cova}}) / (\text{Dev}_{\text{constant}} - \text{Dev}_{\text{FACyear}})] * 100$. 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 aging, 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 & Barton, 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 & Hong, 2009).

Results

Interannual variations and long-term temporal trends

Size, mass, Δ size and Δ mass strongly varied between years ($\text{df} = 21$, all $\chi^2 < 0.001$). Interannual 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 interannual variations of juvenile size and mass

respectively. Interannual 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 interannual 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 interannual variation in juvenile mass (0.2%) and of the interannual 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. 25.9 cm 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 ($SD_{\text{April NDVI}} = 0.018$), 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 ($SD_{\text{April NDVI}} = 0.018$), 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 ($SD_{\text{BGI}} = 75.51$), 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. Δ mass 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 Δ size and Δ mass. Summer condition index and winter snow depth only accounted for interannual variations in Δ mass. Summer condition index explained a higher percentage of annual variation in juvenile and yearling Δ mass than winter snow depth with lower evidence when individuals aged. Winter

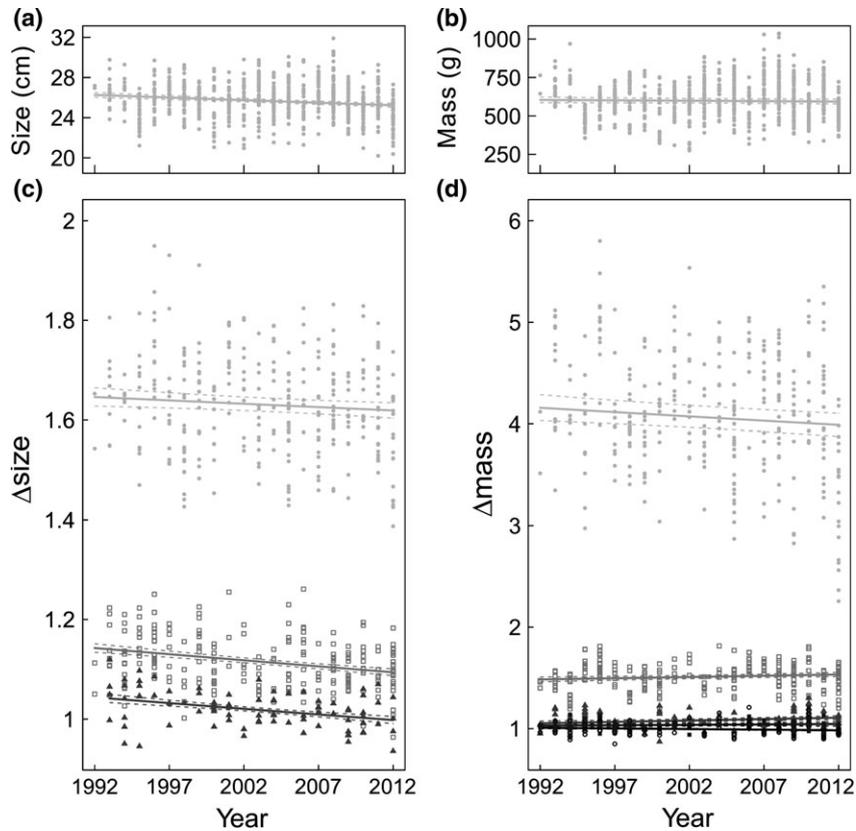


Fig. 1 Temporal changes in stage specific size, mass, Δ size and Δ mass. Yearly variation in (a) size, (b) mass, (c) Δ size, and (d) Δ mass of juvenile (●), yearling (□), subadult (▲), subordinate adult (◊), and dominant adult (■) Alpine marmots at La Grande Sassièrre (French Alps) from 1992 to 2012. 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).

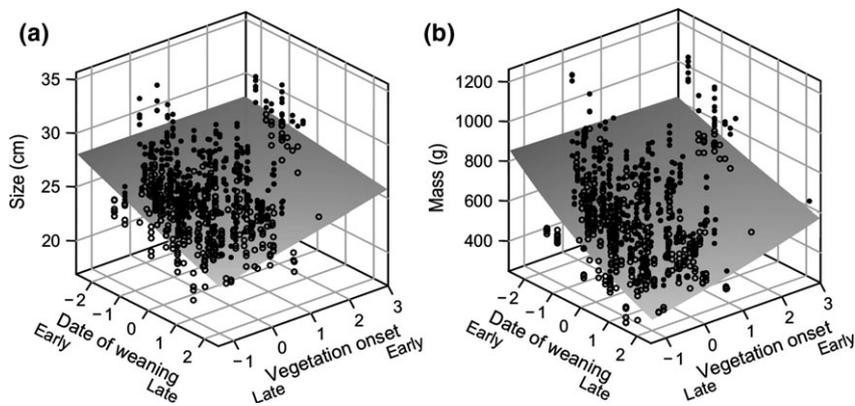


Fig. 2 Vegetation onset and date of weaning effects on (a) size and (b) mass of juveniles. The gray surface represents model predictions. Dots represent model residuals after controlling for confounding variables (for details see the Materials and methods section). Black dots are above the predicted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

snow depth explained a relatively small amount of these variations except in subadults. Similar annual variations in adult Δ mass 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

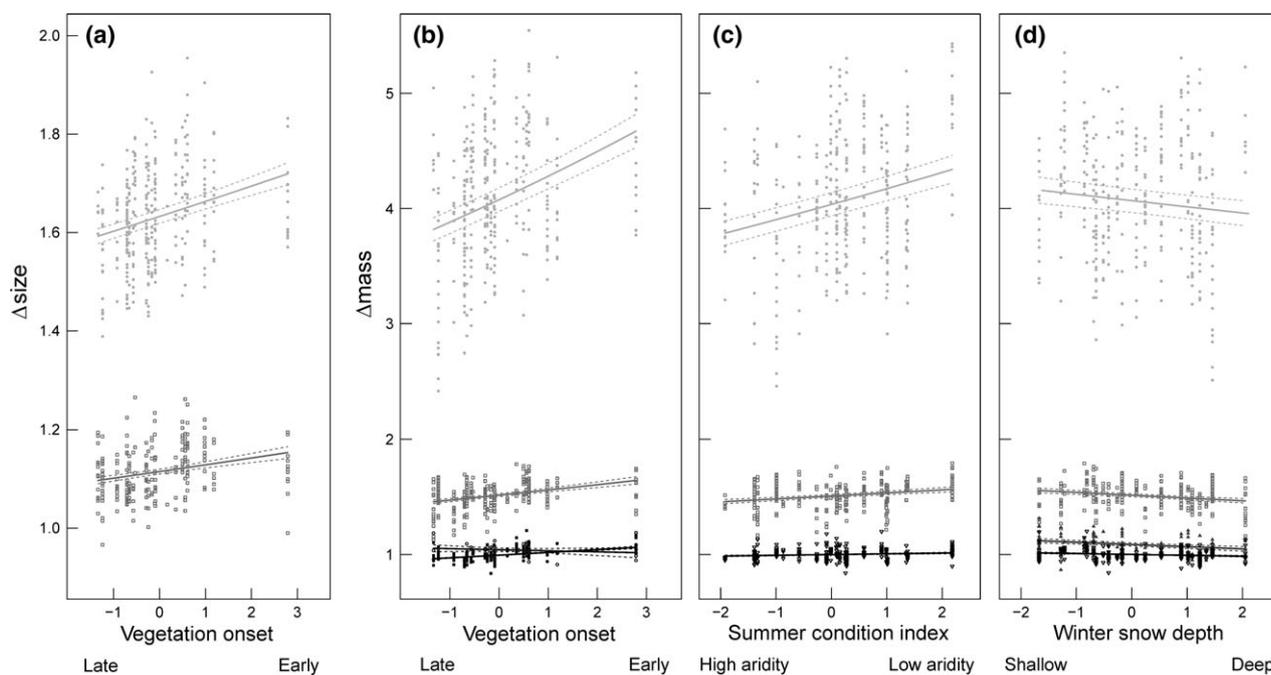


Fig. 3 Environmental factors driving stage specific Δ size and Δ mass. Effects of (a) vegetation onset on Δ size, and of (b) vegetation onset, (c) summer condition index, (d) winter snow depth on Δ mass of juvenile (\circ), yearling (\square), subadult (\triangle), adult subordinate (\diamond), adult dominant (\blacksquare) 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.

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 (R zouki *et al.*, in press). Although body mass had no impact on the decision to disperse in another Alpine population (Arnold, 1990a, 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.

Table 1 Environmental effects in size, mass, 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

	Estimate	SE	P	Estimate	SE	P
(a) Juvenile	Size, $n = 769$			Mass, $n = 778$		
Vegetation onset	0.016	0.003	<0.001	0.048	0.008	<0.001
Date of weaning: Vegetation onset onset	0.007	0.003	<0.01	0.022	0.006	0.001
Litter size: Vegetation onset						
(b) Juvenile	Δ size, $n = 311$			Δ mass, $n = 315$		
Summer condition index				0.033	0.006	<0.001
Winter temperature						
Winter snow depth				-0.013	0.006	0.03
Vegetation onset	0.018	0.003	<0.001	0.049	0.006	<0.001
(c) Yearling	Δ size, $n = 217$			Δ mass, $n = 235$		
Summer condition index				0.017	0.005	<0.001
Winter temperature						
Winter snow depth				-0.016	0.005	0.003
Vegetation onset	0.012	0.003	<0.001	0.029	0.006	<0.001
(d) Subadult	Δ size, $n = 87$			Δ mass, $n = 86$		
Summer condition index						
Winter temperature						
Winter snow depth				-0.018	0.007	0.01
Vegetation onset						
(e) Adult				Δ mass, $n = 292$		
Summer condition index				0.006	0.003	0.05
Winter temperature						
Winter snow depth				-0.008	0.003	0.02
Vegetation onset				0.024	0.004	<0.001
Social status: Summer condition index						
Social status: Winter temperature						
Social status: Winter snow depth						
Social status: Vegetation onset				-0.025	0.007	<0.001

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 & Hickling, 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 (T rk & 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

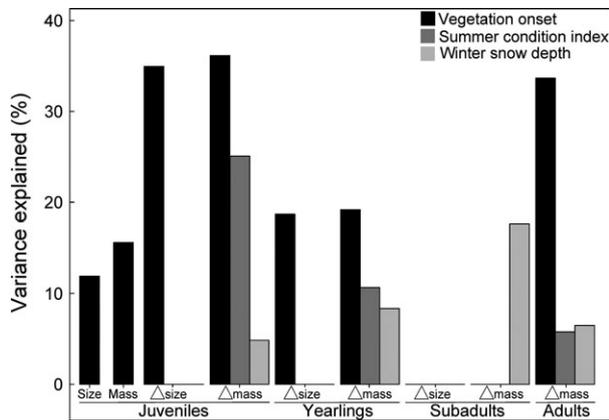


Fig. 4 Relative influence of environmental variables. Proportion of the variance in size, mass, Δ size, and Δ mass explained by significant environmental variables.

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 & Bickford, 2011; Boutin & Lane, 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 & Geffen, 2011; Teplitsky & Millien, 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 & Dhondt, 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

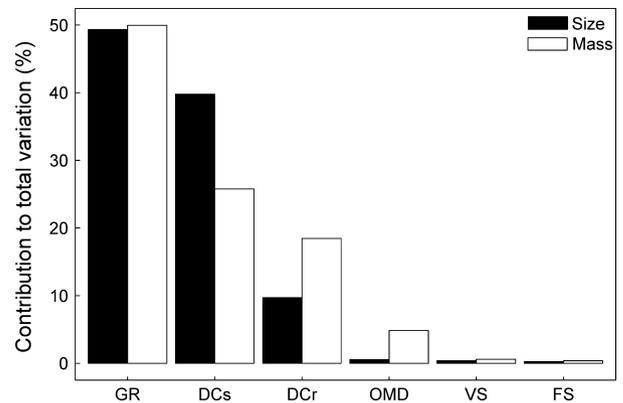


Fig. 5 Components of phenotypic changes. Percentage contribution of the different terms to the observed total variation in size and mass. The change in the mean value of both traits were decomposed into contributions from age-specific trait development (GR), changes in demographic structure caused by 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).

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 snow melt 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; Pettoelli *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 & Chatfield, 1956).

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 museum specimens. Temporal trends in bold indicates opposite trends between size and mass. For environmental drivers, we show the number of environmental factors that had a significant impact on size and mass over how many have been tested

Order	Species	Population	Age class	Sex	Size measurement	Temporal trend		Environmental drivers		References
						Size	Mass	Size	Mass	
Birds										
Anseriformes	Lesser snow goose <i>Anser caerulescens</i>	La Pérouse Bay, Manitoba, 1969–1988	First year Adult	F	Tarsus length	Negative	Negative	1/1 (PCA)	1/1 (PCA)	Cooch <i>et al.</i> (1991)
Anseriformes	Greater snow goose <i>Chen caerulescens atlantica</i>	Bylot Island, Canada, 1989–2004	First year	F,M	PC1 (head, tarsus and culmen lengths)	–	–	3/5	3/5	Dickey <i>et al.</i> (2008)
Anseriformes	Eurasian teal <i>Anas crecca</i>	Tour du Valat, France, 1954–1971	First year First year Adult Adult Adult	F M F M F,M	Wing length Wing length Wing length Wing length Tarsus length	Negative Negative Negative Negative No trend	– – – – Negative	2/4 2/4 1/4 2/4 0/5	0/4 0/4 0/4 0/4 3/5*	Guillemain <i>et al.</i> (2005)
Passeriformes	Great tit <i>Parus major</i>	Hoge Veluwe, Netherlands, 1979–2008	Adult	F,M	Tarsus length	No trend	Negative	0/5	3/5*	Husby <i>et al.</i> (2011)
Passeriformes	River warbler <i>Locustella fluviatilis</i>	Piešťany, Slovakia, 1989–2003	Adult	F,M	Tarsus length	Positive	Negative	0/5	3/5*	
Passeriformes	Dipper <i>Cinclus cinclus</i>	Sierra Nevada, Spain, 1985–2005	Adult Adult	M F	Tarsus length Tarsus length	Positive Negative	Positive No trend	0/5 –	1/5* –	Kaňuščák <i>et al.</i> (2004) Moreno-Rueda & Rivas (2007)
Passeriformes	Tree swallow <i>Tachycineta bicolor</i>	Southern Québec, Canada, 2005–2011	Adult Adult	M F	Tarsus length Tarsus length	Positive Negative	Negative Negative	– –	0/1 0/1	Rioux Paquette <i>et al.</i> (2014)
Passeriformes	Cliff swallow <i>Petrochelidon pyrrhonota</i>	Nebraska, USA, 2001–2006	First year	F,M	Tarsus length	–	–	2/2	2/2	Roche <i>et al.</i> (2014)

Table 2 (continued)

Order	Species	Population	Age class	Sex	Size measurement	Temporal trend		Environmental drivers		References	
						Size	Mass	Size	Mass		
Passeriformes	Duncock	Lake Constance, Germany, 1973–2006	First year	F,M	Flight feather length	No trend	No trend	0/2	0/2	Salewski <i>et al.</i> (2010)	
	<i>Prunella modularis</i>										
	Robin <i>Erithacus rubecula</i>		First year	F,M	Flight feather length	Positive	No trend	1/2	0/2		
	Song thrush <i>Turdus philomelos</i>		First year	F,M	Flight feather length	No trend	No trend	0/2	0/2		
	Blackbird <i>Turdus merula</i>		First year	F,M	Flight feather length	Positive	Negative	2/2	1/2		
	Garden Warbler <i>Sylvia borin</i>		First year	F,M	Flight feather length	No trend	No trend	0/2	0/2		
	Blackcap <i>Sylvia atricapilla</i>		First year	F,M	Flight feather length	Negative	Positive	2/2	1/2		
	Reed warbler <i>Acrocephalus scirpaceus</i>		First year	F,M	Flight feather length	Negative	Positive	2/2	2/2		
	Willow warbler <i>Phylloscopus trochilus</i>		First year	F,M	Flight feather length	Negative	Negative	2/2	1/2		
	Chiffchaff <i>Phylloscopus collybita</i>		First year	F,M	Flight feather length	Negative	Positive	2/2	2/2		
	Great tit <i>Parus major</i>		First year	F,M	Flight feather length	No trend	No trend	0/2	0/2		
	Blue tit <i>Cyanistes caeruleus</i>		First year	F,M	Flight feather length	Negative	Positive	2/2	2/2		
	Reed bunting <i>Emberiza schoeniclus</i>		First year	F,M	Flight feather length	No trend	No trend	0/2	0/2		
	Red-billed gull <i>Larus novaehollandiae</i>		Adult (5 years)	F,M	Tarsus length	Negative	Negative	–	1/1	Teplitsky <i>et al.</i> (2008)	
	Charadriiformes		Kaikoura, New Zealand, 1958–2004								

Table 2 (continued)

Order	Species	Population	Age class	Sex	Size measurement	Temporal trend		Environmental drivers		References
						Size	Mass	Size	Mass	
Mammals										
Rodentia	Alpine marmot <i>marmota marmota</i>	French Alps, France, 1992–2013	Juvenile at weaning Juvenile Yearling Subadult Adult	F,M F,M F,M F,M F,M	Body length Body length Body length Body length Body length	Negative No trend Negative Negative –	No trend No trend No trend Positive No trend	1/1 1/4 1/4 0/4 –	1/1 3/4* 3/4* 1/4* 3/4	Current study
Carnivora	Grizzly bear <i>Ursus arctos</i>	Rocky Mountains, Alberta, Canada, 1999–2008	2–22 years old	F,M	Body length	–	–	4/12	7/12*	Nielsen <i>et al.</i> (2013)
Artiodactyla	Red deer <i>Cervus elaphus</i>	Norway, 1971–1995	Adult Adult	F M	Mandibular skeletal ratio Mandibular skeletal ratio	Positive Positive	Negative Negative	1/1 1/1	1/1 1/1	Post <i>et al.</i> (1997)
Carnivora	Polar bear <i>Ursus maritimus</i>	Alaska to US-Canadian border, 1982–2006	Juvenile and yearling Slow-growing adult (<5–8 years) Slow-growing adult (>8 years)	F,M F F	Body length Body length Body length	– Negative Negative	Negative Positive Negative	– – –	1/1 1/1 0/1	Rode <i>et al.</i> (2010)
		(NB: only spring body mass is reported here)	Slow-growing adult Fast-growing adult Fast-growing adult (<9 years) Fast-growing adult (9–11 years)	M F M M	Body length Body length Body length Body length	Negative Negative Negative Negative	No trend Negative No trend No trend	– – – –	0/1 0/1 1/1 1/1	
Artiodactyla	Roe deer <i>Capreolus capreolus</i>	Chizé, France, 1987–2003	Juvenile	F,M	Hind foot length	–	–	1/2	1/2	Toigo <i>et al.</i> (2006)

Bold numbers show studies demonstrating that size and mass were driven by a different number of environmental variables.

*Indicates studies where mass was adjusted to a larger number of environmental variables than size.

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 interannual 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 & Zerah, 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 & Davidson, 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 alloca-

tion 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 & Piersma, 1993). Unfortunately, the studies reported in Table 2 were only on sedentary or premigratory birds (except Kaňuščák *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 Gausse 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 & Tuljapurkar, 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 & Merilä, 2014), that quantitatively demon-

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

Acknowledgments

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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.

Fig S2. Age-specific viability selection contributions to changes in the mean value of size.

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.

Table S6. Age-specific linear mixed models testing for long-term linear temporal trend.

Table S7. Age-specific linear mixed models testing for environmental effects.