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Population-level consequences of phenotypic plasticity in yellow-bellied marmots (Marmota flaviventris)

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Population-level consequences of phenotypic plasticity in yellow-bellied marmots (*Marmota flaviventris*)

A dissertation submitted in partial satisfaction of

the requirements for the degree

Doctor of Philosophy in Biology

by

Adriana Alexandra Maldonado Chaparro

2015

ABSTRACT OF THE DISSERTATION

Population-level consequences of phenotypic plasticity in yellow-bellied marmots (*Marmota flaviventris*)

by

Adriana Alexandra Maldonado Chaparro

Doctor of Philosophy in Biology

University of California, Los Angeles, 2015

Professor Daniel T. Blumstein, Chair

Individuals vary phenotypically. Phenotypic variation can emerge because of bet-hedging, micro-evolutionary responses, and because of phenotypic plasticity, an important mechanism by which individuals can cope with environmental change. Phenotypic plasticity, the ability of an individual to respond to environmental variation, can influence demographic parameters (e.g., birth and death rates) that influence population dynamics. I used a population of yellow-bellied marmots (*Marmota flaviventris*) as a study system to explore the effect of individual variation due to phenotypically plastic responses on population dynamics. First, I used linear mixed effects models to examine and quantify the plastic responses in a set of morphological, life-history and social traits in response to climatic and social variation. Results showed that individuals have the ability to respond to environmental variation by expressing different phenotypes, and that individuals differ in the nature of their plastic responses. Second, I developed an Integral Projection Model to evaluate the trait-mediated response to environmental variation. Results indicated that variation in survival and reproduction are the main drivers of fluctuation in the population growth rate, and that winter temperature, but not spring temperature and bare ground date, are important environmental drivers of population fluctuations. Furthermore, although variation in a key morphological trait, body mass, does not explain significant variation in population growth rate, it plays an important role in mediating the individuals' response to the environment. Finally, I developed an Individual Based Model, to incorporate individual differences in the rate at which animals gained mass seasonally, and evaluated the effect of such individual heterogeneity for population persistence. Results indicated that the proportion of individuals in the population that engaged in compensatory growth influenced population dynamics, and the cost of expressing such compensatory responses affect population dynamics. If growth rate plasticity varies among-individuals, the population can afford the cost of plasticity; otherwise, plasticity increases the time to population extinction. These findings emphasize the importance of phenotypic plasticity as a mechanism shaping individual variation in a population, and as an important response of a species' adaptation to environmental change.

The dissertation of Adriana Alexandra Maldonado Chaparro is approved.

Dwight Read

Jamie Lloyd-Smith

Daniel T. Blumstein, Committee Chair

University of California, Los Angeles

2015

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CHAPTER 1

Environmentally induced phenotypic variation: from individuals to populations

Individuals may vary because they differ genetically, and/or in response to variation in external conditions, such as climate, food availability or habitat quality (McNamara and Houston, 1996). From an individual's perspective, the environment can be either uniform or variable. Theory predicts that in a uniform environment a fixed phenotype will be favored (Berrigan and Scheiner, 2004), and phenotypic variation can be maintained via several mechanisms--mutation-selection balance, heterozygous advantage, antagonistic pleiotropy and frequency-dependent selection (Roff, 2005). Alternatively, environments can vary in several ways; they can vary among sites (i.e., spatial heterogeneity), or through time (i.e., temporal heterogeneity). Temporal variation can be characterized by periodic or stochastic fluctuations (Doughty and Reznick, 2004). In stochastic environments, individuals cannot anticipate future conditions, whereas in predictably periodic environments individuals can rely on environmental cues that allow them to predict the future conditions. In such predictable environments the expressed phenotype depends on how individuals respond to environmental cues; therefore, phenotypic plasticity—multiple phenotypic patterns from a single genotype —is more likely to occur (Moran, 1992).

Environmental temporal variation, by anthropogenic or natural means, is ubiquitous in natural systems, and has strong effects on population dynamics (Coulson et al., 2001; Sæther et al., 2000). However, over the past 100 years, systematic warming has affected the range of diurnal temperatures; a trend most pronounced in mid-high latitude regions where warming has led to a decrease in snow cover and an extended frost-free period (Walther et al. 2002). This warming has altered the historical patterns of temporal environmental variation and has created novel environments. To cope with changing environments, individuals within a population can respond through genetically based mechanisms either across generations (i.e., a micro-evolutionary response) or through phenotypic plasticity (Charmantier et al. 2008). Phenotypic plasticity, allows individuals to adjust their phenology, or phenotypic traits to novel environmental conditions. By doing so, phenotypic plasticity is an important factor that may explain persistence and later adaptation of populations to novel environments (Ghalambor et al., 2007), and an important short term response of animal populations to global climate change (Chevin et al., 2010; Visser, 2008).

What is phenotypic plasticity and why is it important?

Phenotypic plasticity is the ability of an organism (i.e., genotype) to express different phenotypes depending on the biotic or abiotic environment (Agrawal, 2001). Phenotypic plasticity is a source of phenotypic variation (Sultan, 2000). Plasticity can alter the mean or the variance of the trait value (Reed et al., 2011), hence it provides raw material for natural selection. Moreover, a phenotypically plastic response can be adaptive when the individual's response to environmental cues enhances its fitness (Gotthard and Nylin, 1995), and when plasticity heritable (Pigliucci, 2005). Because plasticity can vary among individuals within a population, natural selection may act both on variation in the mean trait value, and on variation in levels of plasticity. This means that plasticity itself may evolve in response to changes in environmental variability (Gavrilets and Scheiner, 1993). Because morphological, physiological and behavioral traits respond to climatic variation and can affect an individual's life history and therefore population growth (Bradshaw and Holzapfel, 2008; Chevin et al., 2010; Gienapp et al., 2008; Visser, 2008), it is important to ask if phenotypic variation in a population across environments is the result of phenotypically plastic responses (i.e., environmentally induced variation), and its ecological consequences at the population level. This is important because whether populations can persist depends on the degree of plasticity or ability of populations to respond to climate change.

Measuring phenotypic plastic responses in wild populations

To better understand the causes of environmentally-induced phenotypic variation within natural environments, I first studied the phenotypically plastic response of labile traits in a free-ranging animal populations in response to multiple environmental factors and whether individuals differ in their plastic responses to environmental variation (i.e., among-individual variation in plasticity—Brommer *et al.* 2005; Nussey *et al.* 2005a; b). To do this, I used a reaction norm analysis (Pigliucci, 2001). The 'reaction norm' is a function that relates the phenotype expressed by a particular genotype across an environmental gradient (Pigliucci, 2001; Stearns, 1992). In its simplest form, the relation between the environment and a trait value is a straight line; more complex relations can be explained though non-linear reaction norms (Koons et al., 2009). The linear reaction norm is characterized by an elevation (expected trait value in the average environment) and the slope (degree of phenotypic change as a function of changes in the environment). Four basic patterns of linear reaction norms can be defined based on the average plastic response and the differences among the individual's plastic responses to the environment (Fig. 1). The first occurs when phenotypes are characterized by different flat reaction norms, which means that they differ in their mean phenotypic value across-environment or elevation. In this case, individuals do not express plasticity (traits are identical across an environmental gradient), but there is genetic variation within the population (elevations are different) (Fig. 1a). The second occurs when there is an average plastic response to the environment and individuals show a plastic response. The reaction norms differ in their elevation but they have the same slope, which means that there is plasticity but there is no genetic variability for this plasticity (Fig. 1b). The last two patters occur when the reactions norms differ in elevation and slope. In this case, there is genetic variation within the population, plasticity and genetic variation for plasticity. The pattern changes whether there is no average response to the environment (Fig. 1c) or there is an effect of the environment on the average response (Fig. 1d).

To characterize the reaction norm that allows us to determine the pattern of the plastic response exhibited by the population, I used Generalized Linear Mixed Models (Brommer et al.,

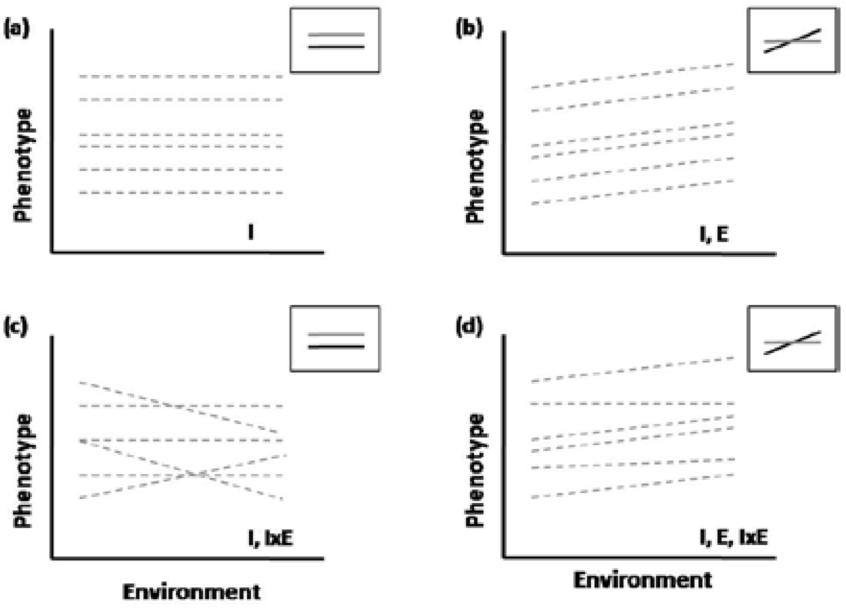

Figure 1.1. Four basic patterns of linear reaction norms. The grey dotted lines represent the individual response to the environment. The inset graphs show the population average response to the environment (black lines) and the change in phenotypic variance across the environment (grey line). a) no response to changes in the environmental conditions (variation in elevation, I) ; b) individuals exhibit different phenotypes as a function of the environment, but the degree of plasticity does not varies (variation in elevation, I, E); c) individuals differ in their plastic response but there is no average population plastic response (variation in slope, I, E, I x E); and d) individuals differ in their plastic response and there is an average population plastic response (variation in slope, I, I x E). Adapted from Pigliucci (2001) and Nussey, Wilson & Brommer (2007).

2005; Daniel H. Nussey et al., 2005; Nussey et al., 2007), although more general models such as Generalized Additive Mixed Models (GAMM) can be used to describe nonlinear patterns. GLMM allowed us to estimate four basic parameters that determine the plastic response, its model can be describe as (van de Pol, 2012):

$$Y_{ij} = \beta_0 + u_{0i} + (\beta_1 + u_{1i})X_{ij} + e_{0ij}$$

Where, Y_{ij} corresponds to the value of the dependent variable and X_{ij} to the value of the environment for measurement *j* from individual *i*. β_0 corresponds to the intercept of the regression equation, and can be interpreted as the population mean in the average environment (i.e., when the environmental variable is mean-centered), and β_1 corresponds to the population slope (i.e. plasticity). Finally, e_{0ij} corresponds to the error term, and u_{0i} the random intercept and u_{1i} the random slope. These terms are assumed to follow a normal distribution and a (co)variance matrix such that:

$$e_{0ij} \sim \text{Normal}(0, \sigma^2_{e0ij}), \text{ and}$$

$$\begin{bmatrix} u_{0i} \\ u_{1i} \end{bmatrix}\begin{bmatrix} u_{0i} \\ u_{1i} \end{bmatrix} \sim \text{MVNormal}(0, \Omega_u) : \Omega_u = \begin{bmatrix} \sigma^2_{u_{0i}} & \\ \sigma_{u_{0i},u_{1i}} & \sigma^2_{u_{1i}} \end{bmatrix}\begin{bmatrix} \sigma^2_{u_{0i}} & \\ \sigma_{u_{0i},u_{1i}} & \sigma^2_{u_{1i}} \end{bmatrix}$$

Where, the terms σ^2_{e0ij}, $\sigma^2_{u_{0i}}\sigma^2_{u_{0i}}$, $\sigma^2_{u_{1i}}\sigma^2_{u_{1i}}$ and the covariance term $\sigma_{u_{0i},u_{1i}}\sigma_{u_{0i},u_{1i}}$ are estimates of the within-individual residual variance (V_R), the among-individual variance in elevation (V_E), the among-individual variance in slopes (V_S), and the correlation between the intercepts and slopes of individuals ($r_{E,S}$), respectively.

In chapter 2, we used 36-years of data, from 1975 to 2011, on a population of yellow-bellied marmots, *Marmota flaviventris*, living in and around the Rocky Mountain Biological Laboratory in western Colorado, USA, to explore the patterns of plasticity in six traits: 1) June mass, 2) August mass, 3) pup mass at emergence; 4) number of weaned pups per litter, 5) reproductive success); and 6) sociality (measured by quantifying embeddedness) in response to ecologically meaningful climatic and social environmental gradients. Additionally, we evaluated the extent of individual differences in plasticity.

We showed that individuals within a population can adjust their phenotypes to changing environmental conditions, and furthermore, that phenotypic plasticity contributes to the maintenance of individual phenotypic variation in our population. Overall, we identified two patterns of phenotypic plasticity: 1) population level plastic response with no difference in the plastic response among individuals (Fig. 2-A in Chapter 2), and 2) population-level plastic response with differences in the plastic response among individuals (Fig. 2-B in Chapter 2). Moreover, our population varied in several of the parameters that define the plastic response, thus: 1) exhibited significant population-level phenotypic plasticity in their life history and social traits across environments (i.e. population intercept, β_0); 2) varied in their individual average response (V_E) (i.e. individual intercept, $\sigma^2_{u_{ni}} \sigma^2_{u_{ni}}$); and 3) varied in the degree of individual plasticity (V_S) (i.e. individual slope, $\sigma^2_{u_{1i}} \sigma^2_{u_{1i}}$). Particularly, June mass showed a correlation between the intercepts and slopes of individuals ($r_{E,S,}$ $\sigma_{u_{ni},u_{1i}} \sigma_{u_{ni},u_{1i}}$). These results demonstrate that climatic fluctuations have led to important phenotypic changes. Therefore, plasticity may be one of the main responses of animal populations to global change in the short term, and such plasticity can play an important role in the persistence of populations in novel environments.

Individuals within our population assess environmental conditions to anticipate favourable conditions to adjust their life-history events. To adjust their phenotypes during the active season, individuals can assess environmental conditions during the early season. Here, we identified several environmental factors that may work as an environmental signal. Interestingly, most of these factors are related to early season environmental conditions. For instance, spring temperatures seem to play an important role in allowing individuals to anticipate future environmental conditions. Warmer spring temperatures may indicate favourable food conditions that aid female's weight gain and reproduction. June mass and female's reproductive successes were favoured by increases in spring temperatures. Similarly, smaller snowpack may indicate an earlier beginning of the plant-growing season; and June and August masses were favoured by such conditions. In addition to early season conditions, other factors related to seasonal fluctuations such as the length of the growing season can also affect traits such as August mass (Armitage, 1994; Ozgul et al., 2010; Vuren and Armitage, 1991). Altogether, these responses reveal that individuals can respond to multiple environmental cues and multiple environmental factors can influence the phenotypic expression of a trait.

Furthermore, within our population, individuals lived in one of two different portions of the valley that have different phenologies (Blumstein, 2009; Schwartz et al., 1998; Vuren and Armitage, 1991) resulting in differences in their circannual cycle (Ward and Armitage, 1981) and therefore in their plastic response to environmental variation. For example, marmots down valley were on average heavier in June than up-valley marmots, but, interestingly, up-valley marmots were slightly heavier in August than down-valley marmots. In addition, pups born up valley were heavier than those born down valley, after controlling for variation explained by litter size and other variables. However, up-valley females weaned smaller litters than down valley females. This suggests adaptive phenotypic plasticity in response to variation in micro-climatic conditions and suggests that a mechanism that enables adult marmots to compensate for a bad start. Moreover, significant differences in the average plastic response among spatially differentiated populations indicates that, in our population, plasticity might vary spatially. The observed differences between the populations up and down valley are mostly driven by local environmental conditions and not to genetic differences, given that gene flow between colonies in our population (Schwartz and Armitage, 1980) prevents gene fixation.

At the individual level, the average plastic response (i.e. elevation) differed among females over all the evaluated traits. Although this variation can also arise as a result of biological differences such as reproductive status and ages, since we controlled for this factors in our analysis, we can suggest that there might be genetic differences between individuals, or, in the case of embeddedness, that there might be behavioural phenotypes (Dingemanse and Dochtermann, 2013). Moreover, we found among-individual variation in the slope (i.e., I x E) of June mass. Thus, females in our population differed in their pattern of plasticity of June mass to spring temperature. For example, for a given spring temperature, some females were larger in June than others. This pattern has implications for selection analysis (Stearns, 1989), and this I x E interaction allows individuals to respond in different ways to changes in the environmental conditions, which can maintain phenotypic variation at the population level. Furthermore, individual differences in plasticity (i.e., slope) could protect poorly adapted genotypes from the actions of directional selection, therefore favouring the maintenance of genetic variation in the population. On the other hand, the lack of among-individual differences in plasticity (non-significant I x E) in August mass, weaning success, litter size, pup mass and embeddedness, suggests that there could be physiological or genetic limitations or that there is directional selection on plasticity that might shape the reaction norm. When considering plasticity as a trait, natural selection can favour an optimal phenotype, therefore reducing the inter-individual variation in the plastic response (i.e., slope). This is especially likely in traits that allow individuals to maximize their individual fitness. For example, reproductive traits are directly related with fitness, therefore females may express a reduced variety of reproductive strategies (i.e., exhibit less variation in plasticity), while still producing pups with diverse phenotypes (Armitage, 1986) to increase their direct fitness.

We showed that individual yellow-bellied marmots exhibit plasticity to multiple environmental factors. Although our results are correlative, they suggest that plasticity in life-history and social traits were largely induced by environmental temporal heterogeneity. We also showed that plasticity is a mechanism by which marmots can respond to temporal environmental variation, especially gradual increases in spring temperatures and early timing of snowmelt that emerges as a result of anthropogenic climate warming. Moreover, our results identified individual differences in the plasticity among female marmots. This provides the basis to further explore the relative importance of genetic or permanent environmental effects in accounting for these patterns. While we did not evaluate the adaptive value of plasticity, anthropogenic climate change will place individuals in a different selective regime, with potential consequences to individual fitness, population genetics, and population dynamics.

How can we incorporate these plastic responses in population models?

Recently, ecologists have been increasingly interested in understanding the importance of individual phenotypic variation in population and community dynamics (Bolnick et al., 2011). Diverse modeling approaches (unstructured, structured, and individual based models) that allow the inclusion of different forms of individual variation have been used to understand how individual variation in morphological traits (e.g., size), fitness related traits (e.g., fecundity and survival), cohort effects, and other forms of individual variation (e.g., in growth rates or in competitive ability) have important consequences on population's dynamics, stability and persistence (de Roos et al., 2002; Filin and Ovadia, 2007; González-Suárez et al., 2011; Grimm and Uchmański, 2002; Lindstrom et al., 2002; van Kooten et al., 2007). However, there is not a consensus of how among individual variation influences population dynamics. It has been suggested that variation can have either a stabilizing or destabilizing effect on populations, and may increase, decrease, or have no effect on a population's extinction risk (Vindenes et al., 2008). Thus, to understand how individual variation in morphological traits (e.g., size), fitness related traits (e.g., fecundity and survival), and other forms of individual variation (e.g., in growth rates or in competitive ability) affect population's dynamics, I developed two different modeling approaches.

First, I used an integral projection model (IPM), a type of matrix projection model, in which individuals can be cross-classified during their life cycle, in regards to different discrete or continuous attributes (Ellner and Rees, 2006). This allows the description of the way in which a continuous individual-level trait varies over time (Easterling et al., 2000), rather than in its age or life cycle stage. IPMs permit the quantification of between-individual variability, in continuous individual-level traits such as body size, age or mass, that reflects differences in external and internal conditions, such as the local competitive environment, the abiotic environment, as well as genetic differences (Ellner and Rees, 2006), and may interact with environmental conditions and influence population vital rates (Vindenes et al., 2011). In this sense, continuous traits are useful when there is differential reproductive contribution of individuals within a particular stage of their life cycle. Therefore, IPMs allow the study of populations with complex structures (e.g., demography, life cycles, and individual attributes) (Ellner and Rees, 2006) that can arise due to the influence of environmental fluctuations as well as the species' life history (Coulson et al., 2001).

From our previous work, we learnt that multiple environmental factors affect the phenotypic response of individuals in our population. However, temporal environmental variation can influence population growth directly, through their immediate impact on survival and fecundity, and indirectly, via changes in population age structure or plasticity-induced shifts in the development of a cohort. The population dynamics consequences of these latter effects can be difficult to quantify because their impacts play out in future years and may involve more than one pathway (Beckerman et al., 2003; Monaghan, 2008; Van De Pol et al., 2006). Therefore, the particular aim of our modeling exercise was to understand how these environmentally-induced phenotypes affected the population dynamics, and to quantify the effect of environmental drivers on the long-term population growth rate. The impact of these different sources of variation on population growth rate can be quantified using an appropriate life table response experiment (LTRE). An LTRE analysis compares a set of vital rates under two or more conditions to determine their impact on a demographic summary statistic such as λ. The specific goal of a random life table response experiment (RLTRE) analysis is to decompose the temporal variance in λ into contributions from the (co)variances of model parameters (Brault and Caswell, 1993; Caswell, 2001). In its simplest form, RLTRE uses a first order approximation of the variance of λ; this method is exact only if the functional dependence of population growth rate on each time-varying parameter is linear with respect to each time-varying parameter. Mark & Ellner (2009) introduced a Monte Carlo approach to RLTRE analysis that uses an additive model to partition contributions to the variance of λ. Their methodology introduces greater flexibility by allowing non-linear relationships to be accommodated, and allows the adequacy of a candidate RLTRE to be assessed using regression diagnostics. However, the original analysis did not consider the effect of delayed effects driven by trait variation or fluctuations in age structure, nor did they consider the contributions of environmental drivers, therefore we constructed an extended version of this method that allowed the quantification of the impact of these two sources of variation.

In chapter 3, we capitalised on 37 years (1976-2012) of individual-based data from a population of yellow-bellied marmots (*Marmota flaviventris*), located at the Rocky Mountain Biological Laboratory (RMBL) in the Upper East Valley, Colorado, USA (38°57’ N, 106°59’ W), to examine the mechanisms influencing variation in population growth rate. To do this, we first parameterized an environmentally driven, stochastic Integral Projection Model with body mass- and stage-dependent demographic rates. We used winter temperature, spring temperature, and bare ground date as environmental drivers, and body mass as the continuous variable trait. Then we developed a simple extension of the Monte Carlo life table response experiment (LTRE) introduced by Mark and Ellner (2009) to partition the contribution of direct and indirect (trait/demographic structure) drivers of population growth rate variation. Finally, we used the resulting RLTRE to understand how different sources of vital rate variation contribute to the variance of population growth rate and then partition the contributions of different environmental factors to this variance.

Our results indicated that in yellow-bellied marmots, the demographic parameters of survival, followed by reproduction, had the largest contributions to observed annual changes in the stochastic population growth. Larger contribution of survival is common in several species (Pfister, 1998; Sæther and Bakke, 2000) such as Columbian ground squirrels (*Spermophilus columbianus*) (Dobson, 1995), golden-mantled ground squirrels (*Callospermophilus lateralis*) (Kneip *et al.* 2011), killer whales (*Orcinus Orca*) (Brault and Caswell, 1993), and polar bears (*Ursus maritimus*) (Hunter et al., 2010). However, differences in the relative contribution of vital rates can vary among (Wisdom et al., 2000) and within species. For example, in collared pikas (*Ochotona collaris*), another alpine species, fecundity is the main driver of population growth (Morrison and Hik, 2007). In yellow-bellied marmots, previous LTRE analysis indicated that changes in fertility, age of first reproduction and juvenile survival made the largest contributions to observed annual changes in population growth rate (Oli and Armitage, 2004). The period analyzed by Oli & Armitage (2004) included a period of relatively stable population size (1962 to 2001), whereas our study period (1975 to 2012) included of a phase of steep population growth during which the population tripled in size. Thus, life-history characteristics, and spatiotemporal variation in factors such as weather, can influence the pattern of the contribution of vital rates to the variation on population growth rate.

Additionally, we found that time-lagged effects significantly contributed to the variation in population growth rate in two ways. First, there was a one-year lagged effect of reproduction (demographic effect) in the population's response to environmental variation. Delayed effects of reproduction negatively influenced population growth by skewing the composition of the population towards non-reproductive individuals and hence decreasing the year-specific population growth rate. Similar time-lagged responses have also been identified in species such as northern fulmar (*Fulmarus glacialis*) where there is a 5-year lag of reproduction in response to variation in the North Atlantic Oscillation (Thompson & Ollason 2001). These examples suggest that in long-lived species, differences in the time to respond to environmental effects depends on the characteristics of a species' life history. Second, there was a one-year lagged effect of ontogenetic growth and offspring size (trait-mediated effects). Thus, in our highly seasonal species, the effects of a good or bad year on body mass are not evident until the next season. These delayed responses can arise because of environmental influences on tradeoffs between current and future vital rates, such as survival and reproduction (Lindström 1999). These tradeoffs are very likely to arise in species experiencing time or resource constrains in growth or other traits associated with survival and reproduction (Boyce et al., 2006). Alternatively, delays can be due to environmental effects on individual's behavior (i.e., foraging time), which in turn, can affect the individual-level variation in performance (Beckerman et al., 2002) and generate more complex dynamics.

Morphological or physiological dynamics in responses to environmental fluctuations are of particular interest because, in many species, body size has been significantly affected by climate change (Gardner et al., 2011). We demonstrated that, despite the evident influence of the environment on body mass dynamics (Ozgul et al., 2010), changes in body size have a small contribution to variation in population growth rate. However, body mass dynamics during the hibernation and summer period indicates that non-juvenile yellow-bellied marmots can exhibit a mechanism of growth compensation by which individuals that emerge from hibernation poor condition can catch up during the summer. Flexible growth rates (Arendt, 1997; Gotthard and

Nylin, 1995) leading to growth compensation could be a mechanism of the phenotypically plastic response previously proposed (Maldonado-Chaparro et al., 2015). Growth compensation may generally be common in species that have a limited time available to grow, such as hibernating species, and may more generally affect these species' population dynamics.

Additionally, our results suggested that year-to-year fluctuations in winter temperatures, followed by spring temperatures, and bare ground date contribute to changes in population growth rate. Winter temperatures made the largest contribution through its negative effects on reproduction and positive effects on survival, whereas spring temperatures had a small contribution through its positive effects on reproduction; bare ground date had a negligible contribution. These results support the idea that population responses to environmental fluctuations depend on the way fluctuations affects the vital rates and the species' life-history traits (Coulson et al., 2001; Sæther, 1997; van de Pol et al., 2010). But why does winter temperature exceed the effect of the other climatic variables? Yellow-bellied marmots are hibernating rodents, thus winter conditions are expected to strongly influence their energy expenditure (Armitage and Woods, 2003). Therefore, winter temperatures that favour a deep snow pack may insulate marmot burrows and ensure that individuals are within their thermo-neutral zone, thus expending the least amount of energy while in deep torpor. While other variables, such as length of growing season have been shown to affect survival and reproduction in our system (Ozgul et al., 2010; Schwartz and Armitage, 2005), the fact that we have identified a new variable suggests that other climatic variables should be scrutinized for their putative effect on demography.

The approach we developed in this study permitted us to identify, in detail, how changes in the population are governed by changes in the environment, which influence population dynamics through their influence on demographic variables (Dobson and Oli, 2001). Compared to previous deterministic IPMs in our studied population, the stochastic version allowed us to incorporate environmental and demographic stochasticity, which plays an important role in life-history evolution (Tuljapurkar et al., 2009). Although in this system body mass is a key life-history trait that influences survival probabilities (Ozgul et al., 2010), we demonstrated that its contribution to population fluctuations was relatively small.

Together, results from chapter 2 and 3, indicated that individuals in our population can adjust their behavioral, morphological and physiological responses to varying environmental conditions through phenotypic plasticity. Moreover, these environmental-mediated shifts in morphological traits can influence vital rates and thereby population dynamics, indicating that phenotypic plastic responses can potentially allow populations to respond to environmental change. However, we also know that there is potential for individuals to vary in their plastic response, and such level of analysis is not captured by the IPM. The difficulty to include individual heterogeneity in the responses to environmental drivers is one of the major shortcomings of IPMs. A second shortcoming of IPMs is the limited ability to incorporate life history traits and population characteristics that may affect the behavior of the state variables (i.e., body size). This may be affected by two circumstances. First, state variables are related to other biological process such as predation risk; therefore, the individuals within a size or demographic category may not behave homogeneously. Second, individual growth can be positively related to size; however, it can also be affected by previous states of the individual (Pfister and Stevens, 2003). This may create methodological issues that influence the predictions of analytical matrix models, since it violates the Markovian process assumption (Caswell, 2001).

An alternative type of demographic model that explicitly models individuals' behavioral responses is the Individual-Based Model (IBM). IBMs work under the assumptions of emergence and fitness (Railsback, 2001). This means that the behavior of the system emerges from the decisions that individuals make based on a fitness-related rule (Grimm and Railsback, 2005) Thus, IBMs can integrate different hierarchical levels of the ecological process such as physiology, behavior, autoecology, as well as population and community characteristics. By doing so, we can understand the interaction of individuals with their biotic and abiotic environment (Huston et al., 1988), and the emergent trophic networks and distribution patterns (Breckling et al., 2006).

Given that climate change can alter the environmental conditions experienced by many organisms, and that environmental conditions can affect the availability of resources, with potential consequences in the allocation of energy in an organism and its fitness, it is important to explore the population-level consequences of phenotypic flexibility. In seasonal environments, environmental factors that may vary across years challenge organisms to time annual biological events, such as reproduction (Reed et al., 2010), creating behavioral, physiological and morphological challenges to cope with environmental variation. During winter, organisms undergo a period of reduced energy intake that results in depletion of energy reserves and body mass lost, whereas during the summer organisms build energy reserves and increase their body mass. Moreover, an individual's body condition at the end of the winter period may influence fitness in the subsequent season (Harrison et al., 2011). The IPM results suggests that the increase in the end-of-season body mass can be a result of compensatory mechanisms that allow individuals to catch up after a bad start, consequently, flexibility in the growth rate can have important consequences for fitness at the individual- and population-levels. In seasonal environments individuals can compensate by accelerating growth rate to catch up to reduce the cost of not being a given size at a given time required (Ali et al., 2003; Metcalfe and Monaghan, 2001). Compensatory growth can directly affect body size (Abrams et al., 1996; Metcalfe and Monaghan, 2001), and, by doing so, influence an individual's fitness (Blanckenhorn, 2000; Roff, 2002; Sogard, 1997; Stearns, 1992). Moreover, growth rates vary among individuals within a population (Kvist and Lindström, 2001). Hence, the ability to alter growth rate may vary among individuals. Furthermore, compensatory growth may, however, be costly (Arendt, 1997), although such costs are not very well documented (Metcalfe and Monaghan, 2003). Individuals that accelerate their growth rate can pay an immediate cost due to an increase their risk of predation associated with increased foraging. Rapid growth may have longer-term costs if there is damage at the physiological or cellular level (Metcalfe and Monaghan, 2001).

In chapter 4, we developed a non-spatially explicit stochastic individual-based model (IBM) where we explicitly modeled individuals' behavioral rules and, hence, determined the effects of phenotypically plastic responses of growth rate to a bad start. Additionally, since climate change can affect population dynamics, we additionally explored if phenotypic plastic responses in growth rate could favor the persistence of the population under less favorable climatic scenarios. The model is based on the population dynamics of a well-studied population of yellow-bellied marmots, *Marmota flaviventris*, in Colorado (Armitage, 2014; Blumstein, 2013). To parameterize the submodels that compriseed the IBM, we used the previously calculated coefficients that described the relationship between the demographic parameters and the developmental growth with body mass in the IPM (chapter 3). The parameters, related to growth rate plasticity, were estimated using individual-based body mass data from individuals monitored between 1976-2012. To evaluate the effects of plasticity we first performed a sensitivity analysis using different phenotypic plasticity scenarios, different proportions of individuals allowed to express the plastic response, and a cost for plasticity (Table 4-1). Then, to evaluate if plasticity favored population persistence, we created three theoretical climatic scenarios that differed in the frequency of warm and cold years.

Our results indicate that plasticity in growth rate, here defined as compensatory growth, may effect population dynamics. First, the proportion of individuals that engaged in compensatory growth influenced population dynamics, and the cost of expressing such compensatory responses had a strong effect on population dynamics. Individuals that were below the average population body mass could benefit from a compensatory response, most likely because the demographic parameters like survival and reproduction rate are size-dependent. Thus, increases in body mass are expected to positively affect marmot population dynamics. Furthermore, if growth rate plasticity varies among-individuals, the population can pay the cost of plasticity. This shows that variation between individuals is dynamically important (Pfister and Stevens, 2003).

Although it is expected that phenotypic plasticity decreases the probability of extinction (Wennersten and Forsman, 2012), it was not the case in all of our scenarios. Compensatory growth can favor population persistence in the long term when future scenarios are highly variable, as shown by our random thermal series. Plasticity in compensatory growth allowed individuals to catch up and reach a body mass closer to the population mean. However, the effects of an increase in body size would not play a role until the next breeding season, and its effect would depend upon individual survival. In scenarios where there is no pattern in the frequency of cold or warm years, individuals can recover from less favorable climate conditions. However, in our warmer future scenarios, individuals were more likely to survive and there is a positive effect of climate on growth. Thus, populations that are less likely to go extinct will increase. By contrast, in our colder future scenarios, survival and growth are negatively affected, and there may be carry-over effects from one season to the next (Harrison et al., 2011). Under this scenario, individuals can gain enough mass to survive hibernation, but not enough to afford the cost of reproduction. Finally, if plasticity is costly, we found that the probability of extinction increased. This may be due to the fact that in our population survival is a major driver of population dynamics (Chapter 3) and in our model the cost of growth rate plasticity was modeled as a decrease in the probability of survival.

Our results highlight the importance of individual heterogeneity in phenotypic plastic responses, and indicate that compensatory response is a mechanism by which individuals can cope with adverse environmental scenarios. Plasticity can mediate the effects of the environment, thus altering the (co)variation between traits through direct or delayed effects (Benton et al., 2006). In our population, compensatory responses resulted in larger end-of-season body sizes, which previous studies determined are related to an increased probability of survival and reproduction (Ozgul et al., 2010; Chapter 3). Larger individuals are more likely to survive (a direct effect) and this may result in a positive effect on fecundity during the subsequent season (a delayed effect), as has been previously identified in this population (Chapter 3). Thus, compensatory growth may be an important mechanism that allows individuals to respond to changes in environmental factors that result in poor body conditions (i.e., individuals have fallen below its expected trajectory).

Synthesis

These findings have important ecological and evolutionary implications. First, the results emphasize the importance of phenotypic plasticity as a mechanism *shaping* individual variation in a population. Second, by integrating individual responses to environmental drivers with higher-level population processes, we gained deeper insights into the interactive effects of environmental variation at both the individual and population level, and contributed to developing a better understanding of the role of phenotypic plasticity as a mechanism of a species' adaptation to environmental change.

What now?

In my dissertation I explored functional and structural relationships to describe mechanisms underlying population fluctuations by integrating the dynamics of individual-level traits that affect age or stage specific vital rates (e.g., fecundity, survival and migration). The next step is to incorporate individual behavior into demographic models because we can consider population dynamics as an emergent property determined by the decision-making process of individuals (Breckling et al., 2006). Thus, individual variation can be considered within the context of emerging population processes such as equilibrium, persistence, resilience or density-dependence (Grimm, 1999). Individual variability (e.g., genotype, age, sex, size, social status) is important since it is feasible that few individuals contribute exceptionally to recruitment and mortality; moreover, individuals may vary its 'allocation' decisions accordingly to the context in which is embedded, thus altering the population-level outcome (Dunham and Overall, 1994). I would like to expand the study of social behavioral mechanisms that affect population dynamics by reducing the strength of environmental fluctuations, by increasing the growth rate, increasing the survival rate of dominant breeders, and by increasing the ability to re-colonize post-winter vacant territories and establish a reproductive unit. Such explorations will help us better understand the role of seemingly important behavioral decisions on population biology.

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Environmentally induced phenotypic variation in wild yellow-bellied marmots

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Phenotypic plasticity, the ability of an individual to modify its phenotype according to the conditions it experiences, is a source of between-individual variation and a mechanism by which individuals can cope with environmental change. Plasticity is expected to evolve in response to environmental heterogeneity, such as seasonality and year-to-year variation. We aimed to characterize patterns of phenotypic change in morphological (body mass), life-history (reproductive success and litter size), and social (embeddedness) traits of female yellow-bellied marmots (*Marmota flaviventris*) in response to climatic and social variation. We used data collected over 36 years on a population of yellow-bellied marmots studied in Colorado. We used mixed effect models to explore phenotypically plastic responses and tested for individual variation in mean trait values (i.e., intercept) and in plasticity (i.e., slope). All examined traits were plastic, and the population's average plastic response often differed between spatially distinct colonies that varied systematically in timing of snowmelt, among age classes, and between females with different previous reproductive experiences. Moreover, we showed individual differences in June mass and pup mass plasticity. We suggest that plasticity plays a key role buffering the effects of continuous changes in environmental conditions.

Key words: environmental change, individual variation, life-history traits, phenotypic plasticity, yellow-bellied marmots

Phenotypic responses to varying environmental conditions can be mediated through genetically based mechanisms across generations (i.e., microevolutionary process) or through phenotypic plasticity (Charmantier et al. 2008). Phenotypic plasticity, the ability of a genotype (i.e., an individual) to express different phenotypes as a function of the environmental conditions experienced (Bradshaw 1965; Pigliucci 2001), is a ubiquitous and widely documented phenomenon in natural populations (Gotthard and Nylin 1995). Plastic responses, such as those entailing changes in an individual's behavioral, morphological, or physiological traits, constitute important sources of variation in natural populations (Sultan 2000; Sultan and Spencer 2002). Moreover, plasticity may be adaptive (Pigliucci 2001), may be altered by natural selection (Gotthard and Nylin 1995), and may have significant effects at different levels of ecological organization (Miner et al. 2005; Vindenes et al. 2008). Due to its evolutionary and ecological importance, there has been increased interest in understanding the types and sources of such environmentally induced phenotypic variation (Gotthard and Nylin 1995).

Phenotypic expression of morphological, physiological, and behavioral traits can be continuously affected by external factors such as climate and other interannual environmental variation (i.e., precipitation, food availability) within the lifetime of an individual. Climatic variation occurs naturally over time; however, present rates of warming temperatures are unprecedented and known to affect many species (Parmesan 2006). Global warming has induced shifts in geographical distributions and has altered the timing of life-history events of species (Parmesan and Yohe 2003). Additionally, warming temperatures have affected both mean body size of many species (Gardner et al. 2011; Sheridan and Bickford 2011), including marine fish (Thresher et al. 2007), lizards (Chamaillé-James et al. 2006), birds (Yom-Tov 2001), and mammals (Yom-Tov et al. 2008), and behavior of organisms (Biro et al. 2010). Given that both morphological and behavioral traits respond to climatic variation and are ecologically important because they affect an individual's life history and therefore population growth (Chevin et al. 2010), it is important to ask if such changes are the result of phenotypically plastic responses (i.e., environmentally induced variation). Additionally, it is important to know whether individuals differ in their responses to environmental variation (i.e., among-individual variation in plasticity—Brommer et al. 2005; Nussey et al. 2005a, 2005b) since such variation is necessary for the evolution of plasticity.

Yellow-bellied marmots (*Marmota flaviventris*) are 3–5 kg diurnal, facultatively social, sciurid rodents that hibernate for 7–8 months (Armitage 1991). During the active season (from mid-April or early May to August or September), individuals must gain sufficient body mass to survive hibernation, retain sufficient fat stores to allow them to survive until food resources become available, and maintain sufficient body condition to reproduce the next year during the mating season that occurs immediately after emergence (Armitage 1998).

We explored how female phenotypes change in response to variation in multiple environmental factors and how this response varies among individuals. For our analyses, we used 36 years (1975–2011) of individual-based data from a population of yellow-bellied marmots living in and around the Rocky Mountain Biological Laboratory (RMBL) in western Colorado, where spring temperatures have increased and summer precipitation has become more variable in recent years (Fig. 1). Specifically, we examined how climatic conditions experienced by individuals during hibernation (i.e., winter), emergence from hibernation (i.e., spring), and active season (i.e., summer) affected morphology, physiology, and behavior. These labile traits vary during the lifetime of the individual and describe the ability of an individual to obtain food resources effectively from the environment, establish social relationships, and reproduce, thus providing essential information on fitness and population dynamics.

We first focused on body mass (in June, in August, and pup mass at emergence), a morphological trait known to be influenced by temperature and precipitation (Sheridan and Bickford 2011) and that affects marmot life history and demography (Armitage et al. 1976; Ozgul et al. 2010). Second, we focused on reproductive traits (reproductive success and weaned litter size) known to be important fitness components and influenced by climate change (Tafani et al. 2013). Finally, we evaluated how social cohesion, which we measured as embeddedness—a trait known to influence dispersal decisions (Blumstein et al. 2009), varied in response to these environmental and social variables.

Environmental conditions at RMBL have varied over time (Fig. 1—Inouye et al. 2000). If environmental conditions potentially affect morphological, reproductive, and behavioral traits, and additionally, morphological variation identified since 2000 in the marmot population is not a result of selection (Ozgul et al. 2010), we hypothesized that phenotypic plasticity can be a mechanism that explains phenotypic variation observed in the last decades. Furthermore, due to the lack of evidence of selective pressures on body mass (Ozgul et al. 2010), we expected to see among-individual variation in the plastic response of this trait. Reproductive traits strongly influence demography and are thus potentially canalized against temporal variation (Stearns and Kawecki 1994); therefore, we expected no individual variation in plasticity (i.e., no significant differences among individuals in the slope of the reaction norm). Because of the trend of increasing body mass over time (Ozgul et al. 2010) and the relationship between body mass and reproductive traits (Stearns 1992), we expected to see an increasing trend in the plastic responses to environmental conditions at both population and individual levels. Finally, since the behavioral responses of an individual are influenced by their past environment and experiences (Dingemanse and Wolf 2013), we expected to see plasticity in social cohesion (i.e., embeddedness) and among-individual variation in the specific form of the plastic response.

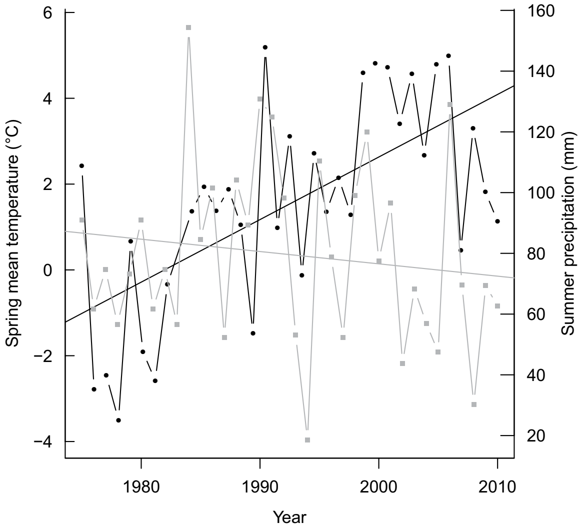

Fig. 1.—Yearly variation (with temporal trend) in mean spring temperature (°C; in black) and in summer precipitation (mm; in gray) at the Rocky Mountain Biological Laboratory (RMBL), Colorado.

Materials and Methods

Monitoring and measurement of biological variables.—Yellow-bellied marmots at the RMBL are patchily distributed between elevations of 2,700–3,100 m a.s.l. (Armitage 2003a), leading to spatially distinct colonies that vary systematically in the timing of snowmelt (up-valley versus down-valley—Van Vuren and Armitage 1991; Schwartz et al. 1998).

Since 1962, marmots were livetrapped multiple times during the active season (between mid-May and early September) each year. Individuals were trapped under permits issued by the Colorado Division of Wildlife, and trapping and handling protocols followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Marmots were ear-tagged the 1st time they were captured and marked with fur dye for identification from afar. Additionally, we weighed, sexed, and recorded reproductive status following Armitage and Wynne-Edwards (2002) as nonreproductive (nipples prominent) or reproductive (nipples swollen or lactating). Animals were classified into pups (< 1 year), yearlings (1 year old), and adults (2 years and older). Pups were caught usually within 1 week after being seen above ground for the 1st time (i.e., emergence date). Behavioral observations were conducted from mid-April to early September, and social interactions were recorded following an all-occurrence sampling scheme (details in Wey and Blumstein 2010). For each individual interaction, we recorded the type (i.e., affiliative or agonistic), the initiator and recipient, and the location.

Body mass estimation.—We used a linear mixed effect model with a restricted maximum likelihood (REML) method to adjust body mass of yearling and adult females to a specific date by fitting mass as a function of a linear and quadratic effect of day of the year (Ozgul et al. 2010; Martin and Pelletier 2011). We included identity (ID, as an intercept), individual mass gain rate (Day × ID), year, and colony as random effects. We then used the predicted values of yearly individual intercepts and slopes (provided by best linear unbiased predictors, BLUPs) to adjust individual mass on 1 June and 15 August for each year. Despite the uncertainty around BLUPs (Hadfield et al. 2010), the mixed model approach provides adjusted body masses that are more accurate than those generated from a linear regression for each individual (Martin and Pelletier 2011). We used 5,599 body mass measurements from 1,448 female-years ($\bar{X}$ = 3.86 mass measurements per individual per year; range: 1–20). For pups (pup mass), we used a similar model to estimate body mass at emergence (the 1st day a pup from a litter was seen above ground during the reproductive season) based on 7,172 body mass measurements from 2,277 pups ($\bar{X}$ = 3.14 mass measurements per individual; range: 1–18).

Reproductive traits.—Every summer, and for each adult female, we noted weaning success (0—failed to wean a litter, 1—weaned a litter) and size of the litter produced (number of pups that emerged from the natal burrow). The prior reproduction of a female is the reproductive status (weaning and number of offspring) of the individual in the previous year.

Sociality.—For each yearling and adult female, we used embeddedness, defined as the degree to which an individual is well integrated in the group (Moody and White 2003), as a measure of social cohesion (details in Blumstein et al. 2009). We used affiliative interactions to construct social networks for each social group in the colony sites each year. Within each social group, we calculated the embeddedness of each individual for each year by converting the social matrix into a symmetric, undirected matrix and then applying the Moody and White (2003) cohesive blocking algorithm, as implemented in the igraph package v. 0.6.5-2 (Csardi and Nepusz 2006) in R software (R Development Core Team 2013).

Quantifying environmental variation.—We used a set of 7 climatic variables and 2 social variables to describe environmental conditions experienced by marmots (see definitions in Supporting Information S1). Winter mean temperature and spring mean temperature (°C) were obtained from the RMBL weather station (38°57′29″N, 106°59′20″W at 2,900 m) from 1975 to 2011. Length of the growing season was calculated as number of days from the 1st day of bare ground to the 1st mean daily temperature below 0°C. Summer (i.e., June and July) precipitation records were obtained from the National Oceanic and Atmospheric Administration weather station in Crested Butte (9.5 km from RMBL at 2,700 m). As a measure of vegetation productivity of the valley, we used a normalized difference vegetation index (NDVI) obtained from satellite images from the Global Inventory Modelling and Mapping Studies–corrected data set for a period spanning from 1981 to 2006 (Tucker et al. 2005). NDVI values for April (ANDVI) and July (JNDVI) for each year were used to reflect seasonal variation in food availability within and among years.

We used 2 different indices of social environment. First, we estimated yearly colony size as number of yearling and adult individuals of both sexes present in a colony in the current year (including individuals that potentially disperse). Second, within each colony, we estimated the yearly yearling and adult group size from 2002 to 2011 using a network approach based on marmots observed at least 5 times within a year. To do so, we first determine the pairwise association indices based on the current space-use overlap (i.e., 2 individuals trapped or seen at the same time and place or observed using the same burrow within a 1-day interval) and the proportion of time that a pair of individuals was seen together (based on livetrapping and observations). Then, we applied a random walk algorithm (Rosvall and Bergstrom 2008) to determine the number and identity of yearling and adult marmots that belonged to a particular group. Group membership and group size were calculated annually (i.e., April–September).

Analysis of phenotypic responses.—To test for phenotypically plastic responses, we used a reaction norm approach, which relates phenotypic expression of an individual to an environmental gradient (Pigliucci 2001). Such a framework allows us to calculate the expected trait value in the mean environment (i.e., intercept or "I"), the phenotypic change per unit of change of the environment (i.e., slope or "E"), individual differences in the plastic response (i.e., individual by environment interaction or "I × E"—Nussey et al. 2007), and correlations among an individual's intercept and slope (r_{ES}). We used repeated measures for an individual across multiple years to fit generalized linear mixed models for each dependent variable: June mass, August mass, pup mass, weaning success, litter size, and embeddedness. We used a Gaussian distribution (identity link function) to fit each model, except for weaning success, for which we used a binomial distribution (logit link function). We scaled variables (by subtracting the mean and dividing the centered value by 2 *SD* following Gelman 2008) to facilitate comparison of model coefficients within and between analyses (Nussey et al. 2007). We constructed and analyzed the mixed effect models in 2 stages.

The goal of the 1st stage was to identify, for each model, the significant environmental effects (i.e., I and E). We did not test for variation in individual plasticity during this step to avoid overfitting the model (see Zuur et al. 2009 for model selection approaches). For each dependent variable, we constructed the full model that included all biologically meaningful explanatory variables in the fixed-effect component (Table 1). We included as random effects: female identity, to control for repeated measures on individuals; year, to control for unexplained annual variation in the response variable; and group identity (i.e., the identity of the social group to which a marmot belonged), to control for repeated measures on groups. Then, using a backwards-stepwise approach (Zuur et al. 2009), we excluded the least significant fixed effect and refit the model until we obtained the minimum fitted model in which all explanatory variables were significant at the 5% level. Significance of fixed effects was estimated using Satterthwaite's approximation for degrees of freedom in the lmerTest package v. 2.0-3 in R (Kuznetsova et al. 2013). Random effects were not tested at this stage and only included to correct for the hierarchical structure of the data.

In the 2nd stage, we evaluated, for each variable in the minimum fitted model, patterns of variation in individual plasticity. Specifically, we tested for among-individual variation of the trait value in the mean environment (i.e., I, fitted with individual ID), individual variation in plasticity (i.e., I × E, fitted as environment × ID), and a significant correlation between the trait value in the mean environment and plasticity at the individual level (i.e., r_{ES}, fitted as the correlation between ID and environment × ID). We tested significance of each random effect by performing a likelihood ratio test (Pinheiro and Bates 2000), where we compared models with and without the specific random effect of interest fitted using a REML approach. All analyses were implemented in R v.3.0.2 (R Development Core Team 2013) and the R package lme4 (Bates et al. 2013).

RESULTS

Trends in climate.—In general, over time, our study site was getting warmer, but food availability also increased (Supporting Information S2). From 1975 to 2011, winter mean temperatures increased by 0.105±0.020°C (*SE*) per year ($r^2 = 0.439$, $t_{34} = 5.330$, $P < 0.0001$) and spring mean temperatures increased by 0.150±0.032°C/year ($r^2 = 0.383$, $t_{32} = 4.636$, $P < 0.0001$; Fig. 1). The growing season shortened by 0.734±0.290 days/year ($r^2 = 0.134$, $t_{34} = -2.528$, $P = 0.016$), as a result of an earlier start of permanent snow cover. Growing season ended 1.16±0.163 days earlier per year ($r^2 = 0.587$, $t_{34} = -7.125$, $P < 0.0001$), although it also showed trends of an earlier snowmelt (−0.318±0.218 days/year, $r^2 = 0.030$, $t_{35} = -1.459$, $P = 0.154$). Precipitation during summer did not change significantly over time (−0.406±0.482 mm/year, $r^2 = -0.008$, $t_{34} = -0.841$, $P = 0.406$; Fig. 1). From 1981 to 2005, food availability in April increased slightly, 0.006±0.002 NDVI per year ($r^2 = 0.214$, $t_{23} = 2.748$, $P = 0.011$), whereas food availability in July did not change (0.002±0.002 NDVI per year, $r^2 = -0.02$, $t_{24} = 0.717$, $P = 0.480$).

Table 1.—Fitted fixed effects in the linear mixed models (LMM) for each of 6 evaluated traits. Fixed effects are as follows: winter mean temperature (WMT), spring mean temperature (SMT), April NDVIs (ANDVI), colony size (CS), age category (AC), previous reproductive status (PRS), valley (V), June body mass (JBM), summer precipitation (SP), length of growing season (LGS), July NDVI (JNDVI), litter size (WLS), pup emergence date (PED), pup sex (sex), and group size (GS). Valley indicates differences in the altitudes of the spatial location of a marmot in its natural environment (up- and down-valley). Variables in bold are fixed effects that remained in the final mixed model. NDVI = normalized difference vegetation index.

Response trait	Fixed effects
June mass	WMT + **SMT** + ANDVI + CS + **AC** + **PRS** + **V**
August mass	**JBM** × **CS** + SMT + SP + **LGS** + JNDVI + **AC** × JBM + **V**
Pup mass	ANDVI + WLS + **PED** × CS + **Sex** + V
Weaning success	JBM × CS + WMT + **SMT** + ANDVI + **PRS** + V
Litter size	WMT + SMT + ANDVI + **JBM** × **CS** + PRS + **V**
Embeddedness	ANDVI + **GS** + **AC**+ **PRS** + V

Population-level phenotypic response.—Across the study period, rate and direction of phenotypic changes differed (i.e., value and sign of the slope; Table 2, see Supporting Information S3 for nonsignificant effects). At the population level, we identified positive and negative responses to changes in environmental variables. June mass exhibited a positive response to spring temperature, that is, females were heavier in June when spring temperatures were warmer (Table 2; Fig. 2a). Length of growing season negatively influenced August body mass, thus August mass increased with shorter growing seasons (Table 2). Pup mass was positively correlated with emergence date (Table 2); pups that came out of the burrow earlier in the year were heavier. Weaning success was positively correlated with spring temperatures, whereas the number of weaned pups increased with increases in maternal June mass and when there were fewer individuals in the colony (Table 2). Finally, embeddedness increased as group size increased (Table 2).

In addition to variation in the pattern of plasticity, mean plastic response differed significantly among spatially distinct colonies (up-valley versus down-valley), age category, and reproductive status. Female marmots living up-valley had smaller litters than females living down-valley (Table 2). In addition, up-valley females were smaller during June than down-valley females were; however, at the end of the season (i.e., August), up-valley females were heavier (Table 2). In general, adult females that had reproduced the year before compared to females that did not reproduce were heavier in June, had greater weaning success in the current year, and were more socially cohesive (Table 2). Finally, yearling females appeared to be the most socially cohesive among females of all age categories (Table 2).

Individual-level phenotypic response.—Individuals differed in the mean (i.e., intercept) June mass, August mass, and litter size, as indicated by the significant random effect of female identity (Table 3). We identified significant individual variation in the plasticity (i.e., the slope) of female June mass as a function of spring temperature (Table 3; Fig. 2a) and pup body mass as a function of date of emergence (Table 3; Fig. 2b). Finally, we found a significant positive correlation, at the individual level, between intercept and the effect of spring temperature on female June mass (Table 3; Fig. 2a).

Table 2.—Estimates of significant fixed effects obtained through a linear mixed effect model for female yellow-bellied marmots (*Marmota flaviventris*). The reference categories for the (*) factors are as follows: valley (down-valley); age category (adults); reproduce previous year (no); in the case of pup body mass, sex (female). *Z*-value is reported for binomial models and *t*-values for Gaussian models.

Fixed effects	Estimate	*SE*	*t*[a], *Z*[b]	*P*-value
June mass (*n* = 1,418 observations on 591 females over 34 years)				
Intercept	0.476	0.019		
Spring mean temperature	0.233	0.030	7.79[a]	< 0.001
Age category (adults)*				
2 years old	−0.251	0.012	−20.45[a]	< 0.001
Yearlings	−0.878	0.011	−80.65[a]	< 0.001
Reproduced last year (yes)*	0.041	0.012	3.40[a]	0.001
Valley (up-valley)*	−0.215	0.013	−16.23[a]	< 0.001
August mass (*n* = 1,424 observations on 593 females over 35 years)				
Intercept	0.258	0.031		
June mass	1.185	0.037	31.97[a]	< 0.001
Colony size	0.053	0.016	3.21[a]	0.001
Length of growing season	−0.134	0.043	−3.98[a]	0.004
Colony size × June mass	−0.155	0.028	−5.59	< 0.001
Valley (up-valley)*	0.042	0.017	2.43[a]	0.015
Age category (adults)*				
2 years old	0.179	0.021	8.55[a]	< 0.001
Yearlings	0.482	0.037	13.04[a]	< 0.001
Weaning success (*n* = 751 observations on 233 females over 34 years)				
Intercept	−0.270	0.143		
Spring mean temperature	0.901	0.244	3.70[b]	< 0.001
Reproduced last year (yes)*	0.369	0.166	2.23[b]	0.026
Weaned litter size (*n* = 339 observations on 151 females over 32 years)				
Intercept	0.066	0.048		
June mass	0.240	0.065	3.66[a]	< 0.001
Colony size	−0.154	0.066	−2.61[a]	0.01
Pup body mass at emergence (*n* = 813 observations on 104 females over 11 years)				
Intercept	−0.054	0.044		
Date of emergence	0.337	0.070	4.78[a]	< 0.001
Sex (M)	0.116	0.030	3.88[a]	< 0.001
Embeddedness (*n* = 429 observations on 176 females in 21 groups over 10 years)				
Intercept	−0.278	0.073		
Group size	0.414	0.048	8.53[a]	< 0.001
Age category (adults)*				< 0.001
2 years old	−0.004	0.061	−0.064[a]	0.064
Yearling	0.379	0.053	6.94[a]	< 0.001
Reproduced last year (yes)*	0.119	0.054	2.20[a]	0.028

[a] Indicates *t*-values.
[b] Indicates *Z*-value.

Discussion

All measured phenotypic traits of female yellow-bellied marmots were affected by multiple environmental factors, and the observed variation may be explained by phenotypically plastic responses. In general, female marmots exhibited significant population-level phenotypic plasticity in morphological, life-history, and social traits across environments; they varied in their individual average response (i.e., intercept); and, for June mass and pup mass, females varied in the degree of individual plasticity (i.e., slope). Mean response differed between spatially distinct colonies that varied systematically in the timing of snowmelt (up-valley versus down-valley), age categories, and females with prior reproductive experiences. Our finding is consistent with an expectation that most quantitative traits have some degree of phenotypic plasticity (Pigliucci 2001).

This marmot population showed different phenotypically plastic trends across morphological, reproductive, and behavioral traits that can be attributed to differences in how rapidly each trait responded to environmental changes. Moreover, climatic conditions during hibernation and emergence affected many traits in the population. Warmer winter temperatures were associated with increased weaning success, a reproductive trait that was also positively affected by food availability in April (measured as NDVI index) and warmer spring temperatures. Likewise, June mass and August mass of females were enhanced by warmer springs and shorter growing seasons, respectively, which suggests that body size and fecundity can be affected positively by anthropogenic climate warming (i.e., increases in spring temperatures and early timing of snowmelt). These results showed an opposite trend than that seen in other species where body mass and litter size decreased with warmer temperatures (Gardner et al. 2011; Ohlberger 2013; Tafani et al. 2013, but see Yom-Tov et al. 2008). Thus, we suggest that the observed increase in body mass, and associated reproductive outcomes, is a response to warmer temperatures that may

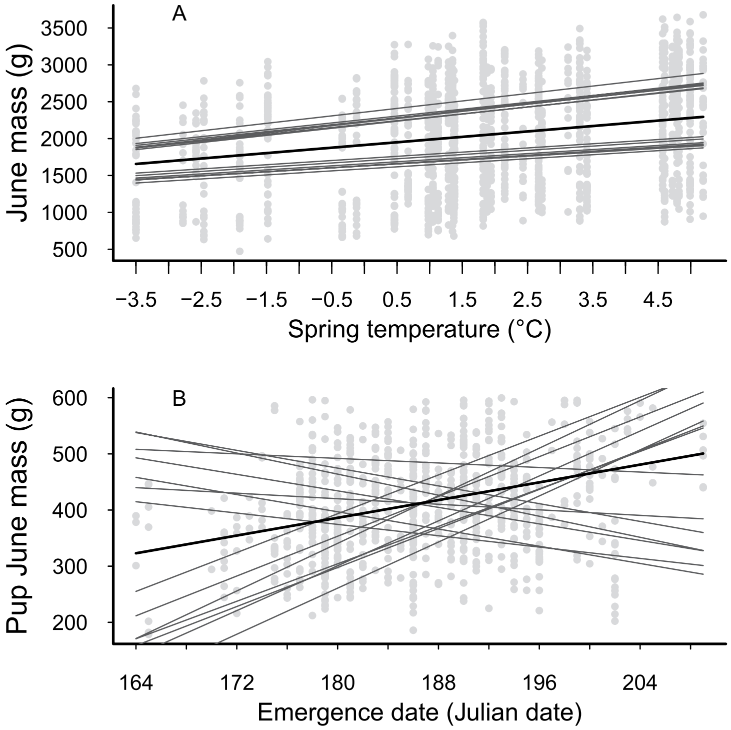

Fig. 2.—Reaction norm patterns of morphological and reproductive traits in yellow-bellied marmots (*Marmota flaviventris*). Black lines represent the mean population plastic response, and gray lines represent individual-level plastic responses. For the sake of clarity, in a) and b), plastic responses for only 14 individuals are illustrated, chosen from females with the highest and lowest slopes and estimated from models in Table 2 using population means for all other parameters.

emerge as a result of changes in physiological responses that affect metabolic rates (Boyles et al. 2011) or changes in foraging strategies (Van Beest and Milner 2013).

Warmer ambient temperatures may affect marmots in 2 ways: they can facilitate energy savings on metabolism, especially during hibernation in winter, and they can induce an earlier snowmelt, thus increasing food availability during spring, which enhances individual body condition and body size. Moreover, our results revealed intraspecific differences in the nature of the body mass response in habitats with different phenologies. Marmots at up-valley sites were, on average, lighter in June than down-valley marmots, but, interestingly, up-valley marmots were slightly heavier in August than down-valley marmots. This finding suggests a mechanism that enables adult marmots to compensate for a bad start. Furthermore, pups born up-valley were heavier than those born down-valley after controlling for variation explained by litter size and other variables, but up-valley females weaned smaller litters than down-valley females. Within-population differences in the plastic response may result from some level of genetic adaptation in response to climate change (Bradshaw et al. 2006; Bradshaw and Holzapfel 2008; Husby et al. 2011), which would be inferred if spatially distinct colonies differed genetically within a population. Although Schwartz and Armitage (1980) did not previously identify genetic differences among colonies in the population, such differences might have appeared in the last decade. Therefore, observed differences are likely to be driven mostly by local environmental conditions. Thus, we suggest that differences in microclimatic conditions can affect life-history traits within populations and can trigger differences in the mean phenotypic response of a population.

Variation in the social environment can trigger phenotypically plastic responses. Colony size, which can be interpreted as a measure of local density, can modify intraspecific competition experienced by an individual, thus affecting reproductive and foraging decisions (Parker and Begon 1986). At low local densities, females can increase litter size through phenotypic plasticity. For instance, female marmots living in small groups can increase their per capita offspring production (Armitage 1986), perhaps as a result of decreased competition within and among matrilines (Armitage 2003b). In general, litter size allocation decisions depend on the predicted competitive environment of adult offspring and on body condition (Mousseau and Fox 1998; Dobson et al. 1999). In our study, females in better body condition in June were more likely to wean larger litters; however, because body size is often correlated with reproductive output (Lindström 1999), we can expect increases in body size to positively affect weaning success. Likewise, body mass is positively associated with increases in colony size. This result may differ from the negative relationship between body size and local abundance expected from intraspecific competition (Begon et al. 1986). However, in populations where food is not

Table 3.—Estimates of random effects obtained through a linear mixed effect model for June and August female body mass. Proportion of variance explained (PVar) was estimated as the ratio of a variance component over sum of the variance components. r_{ES} represents the correlation between identity (ID) and spring temperature × ID. LRT = likelihood ratio test.

Random effects	Estimate	PVar	LRT	*P*-value
June mass (*n* = 1,418 observations on 591 females over 34 years)				
Year	0.007	0.192	224.78	< 0.001
ID (intercept)	0.013	0.336	319.28	< 0.001
Spring mean temperature × ID (slope)	0.002	0.054	8.11	0.018
r_{ES}	0.60		30.91	< 0.001
Residual	0.016			
August mass (*n* = 1,424 observations on 593 females over 35 years)				
Year	0.016	0.218	231.44	< 0.001
ID	0.005	0.078	25.71	< 0.001
Residual	0.051			
Weaning success (binomial, *n* = 751 observations on 233 females over 34 years)				
Year	0.267		15.0	< 0.001
ID	0.202		2.13	0.140
Weaned litter size (*n* = 339 observations on 151 females over 32 years)				
Year	0.004	0.020	0.25	0.620
ID	0.038	0.171	10.01	< 0.001
Residual	0.179			
Pup body mass at emergence (*n* = 813 observations on 104 females over 11 years)				
Year	0.014	0.116	24.83	< 0.001
Emergence date × ID (slope)	0.286	0.534	65.71	< 0.001
Residual	0.163			
Embeddedness (*n* = 429 observations on 176 females from 21 groups over 10 years)				
Year	0.012	0.068	14.01	< 0.001
ID	0.002	0.015	0.14	0.702
Group	0.031	0.185	45.38	< 0.001
Residual	0.119			

a limiting resource, such as the RMBL yellow-bellied marmots (Blumstein 2013), we might expect individuals to increase their mean body size regardless of local population size.

Additionally, social group size within colonies is positively associated with social structure. In species in which group size fluctuates annually, like the marmots we study, the ability of an individual to establish social relationships with other individuals might affect its fitness (Sibly 1983). Therefore, individuals should increase their affiliative interactions with other group members to maintain group cohesion until costs of living in a group outweigh advantages of group living (Sueur et al. 2011). Such plasticity in social behavior varied among age categories and reproductive status. Thus, yearling females may increase their group cohesion as a way to remain philopatric and increase their direct fitness (Blumstein et al. 2009), whereas older females increase their amicable behaviors and cohesiveness as a way to increase their ability to recruit younger individuals (Armitage 2011; Armitage et al. 2011). Furthermore, females that reproduced the year before (i.e., mothers) are more socially cohesive, perhaps because they can play a role as promoters of social cohesiveness (Armitage 2011; Armitage et al. 2011).

Individual females differed in their mean phenotypic response (i.e., intercept) for 3 evaluated traits (June mass, August mass, and litter size). This variation can occur as a result of biological differences, such as reproductive status and age, or as a result of genetic differences between individuals. In addition, such differences could emerge as a result of the specific ecological conditions experienced by each individual (so-called permanent environment effect—Kruuk and Hadfield 2007), or they could emerge from variation in individual quality (Nussey et al. 2007; Dingemanse et al. 2010; Dingemanse and Wolf 2013). Future studies will be required to determine the relative importance of the aforementioned processes in this population.

We found among-individual variation in the slope (i.e., I × E) of June mass as a function of spring temperature, and pup mass as a function of date of emergence, indicating that individuals can respond differently to changes in current environmental conditions. In both cases, differences may emerge as a consequence of differences in the internal state of the individual because of variation in individual-specific habitat use (Dingemanse and Wolf 2013) or because of intraspecific competition for resources (Wolf et al. 2008). Specifically, individual variation in pup mass plasticity may result from the pup's internal state and nongenetic maternal effects, whereby the mother can shape the phenotype of offspring according to the environment in which the pup develops (Mousseau and Fox 1998; Lindström 1999). Assuming existence of some genetic variation, the presence of individual differences in plasticity creates the opportunity for selection and evolution of plasticity in body mass with environmental changes.

Finally, the intercept was positively correlated with slope for June mass plasticity, which means that heavier females in June can express larger plastic responses than lighter females. Thus, we suggest that warmer springs lead to heavier females that can get disproportionally larger than smaller females. Correlations among intercept and slope may also indicate that plasticity is heritable (Nussey et al. 2007) and therefore can be subject to natural selection. In contrast, the lack of among-individual differences in plasticity (shown by the nonsignificant I × E) in August mass, weaning success, litter size, and embeddedness suggests physiological or genetic constraints on plasticity. Even though we did not evaluate underlying genetic differences in the plastic response (i.e., G × E), individual variation in plasticity can maintain phenotypic variation at the population level, therefore fostering population stability and persistence (Dingemanse and Wolf 2013).

In conclusion, long-term, individual-based studies provide unique insights into phenotypic plasticity and may allow us to predict how climate changes can affect the fate of natural populations. Female marmots responded to environmental variation through phenotypically plastic responses, and importantly, plasticity of some traits differed among individuals, which could enhance the potential of the population to adapt to a warming environment. Individual differences in our population suggest that further studies could elucidate the relative importance of genetic and environmental effects in accounting for these patterns. While we did not evaluate the adaptive value of plasticity, anthropogenic climate change will place individuals in a different selective regime, with potential consequences to individual fitness, population genetics, and population dynamics. More importantly, our findings suggest that phenotypic responses have direct conservation implications regarding the importance of environment in the maintenance of natural variation within a population, and they encourage further exploration of interactive effects of plasticity of morphological, life-history, and social traits in population dynamics.

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SUPPORTING INFORMATION

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

Supporting Information S1.—Description of the life history and environmental variables used to evaluate phenotypic plastic responses in a population of yellow-bellied marmots (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory (RMBL), Colorado.

Supporting Information S2.—Descriptive statistics of the environmental variables used to evaluate phenotypic plastic responses in a population of yellow-bellied marmots (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory (RMBL), Colorado, and the period for which they were calculated. Spring mean temperature was not recorded in 1985.

Supporting Information S3.—Estimates of the nonsignificant effects obtained through a linear mixed effect model used to evaluate the phenotypic plastic responses in body mass (June, August, and pup mass at emergence), reproductive traits (weaned success and weaned litter size), and social cohesion (embeddedness), in a population of yellow-bellied marmots (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory (RMBL), Colorado. The reference categories for the (*) factors are: Valley [Down Valley]; Reproduce previous year [No].

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CHAPTER 3

Trait-mediated demographic responses to stochastic environmental variation in yellow-bellied marmots

Summary

1. Temporal variation in environmental conditions affect population dynamics directly through its effects on survival and fecundity, and indirectly by its changes in population age structure or plasticity-induced shifts in cohort development. Despite the recognizable effects of environmental drivers on population growth rates, the interplay between fluctuating environmental conditions, plastic trait variation, and realised vital rates is still relatively understudied.

2. We investigated the mechanisms influencing variation in population growth rate and quantified the contribution of direct and indirect (demographic and trait structure), and climate drivers of population growth rate variation using a stochastic Integral Projection Model (IPM), and a long-term individual-based (1976-2012) data set from a population of yellow-bellied marmots (*Marmota flaviventris*).

3. We developed an extension of the Monte Carlo life table experiment response (LTRE) to understand how different demographic and environmental sources contribute to the variance of the projected stochastic population growth rate (λ_s).

4. We found that direct effects of survival and reproductive probability are the major drivers of population fluctuations, whereas environmentally trait-mediated effects have small direct contributions to variation in growth rate but have larger impacts on the variation in growth rate through time-lagged indirect effects. Among the climatic variables studied, variation in winter temperature is a major factor influencing growth rate. We provide evidence for a direct positive effect of winter temperature on survival and a direct negative effect on reproductive probability.

5. Our results illustrate the importance of properly identifying the relationships between climate variability, demographic and trait-mediated responses, and population dynamics. Our results also provide a deeper understanding of the mechanisms underlying the effects of environmental change on population dynamics. It highlights the need for further analyses to better understand the importance of trait-mediated and time-delayed responses, and the consequences of a changing climate on population growth of environmentally-sensitive species in temporally variable environments.

Key words: environmental stochasticity, integral projection models, population dynamics, yellow-bellied marmots

Introduction

Temporal variation in environmental conditions is a ubiquitous feature of natural systems, with potentially strong effects on vital rates and population dynamics (Sæther *et al.* 2000; Coulson *et al.* 2001). Prevailing environmental conditions influence population growth directly, through their immediate impact on survival and fecundity, and indirectly, via changes in population age structure or plasticity-induced shifts in the development of a cohort. The population dynamic consequences of these latter effects can be difficult to quantify because their impacts play out in future years and may involve more than one pathway (Beckerman *et al.* 2003; Van De Pol *et al.* 2006; Monaghan 2008). For example, unfavourable environmental conditions in one year may reduce the population mean value of a fitness-linked trait such as body size, leading to reduced survival or reproduction of a cohort in future years. These delayed effects occur as a consequence of a change in the performance of individuals with altered trait values, or because trait-linked shifts in the timing of key life history events such as maturation impact age-specific patterns of reproduction and mortality (Benton, Plaistow & Coulson 2006). Despite the role it may play in determining variation in population growth rate, the interplay between fluctuating environmental conditions, plastic trait variation and realised vital rates is still relatively understudied (Dahlgren & Ehrlén 2009).

Data-driven, structured population models such as Matrix Projection Models (MPM, Caswell 2001) and Integral Projection Models (IPM, Easterling, Ellner & Dixon 2000) offer a useful framework for unpicking these relationships in natural populations (Dahlgren & Ehrlén 2011). These models have been widely adopted to identify mechanisms driving population responses to environmental variation (Boyce & Haridas 2006). For example, MPMs and IPMs have recently been used to explore the influence of environmental variation on population dynamics (Jenouvrier *et al.* 2005; Miller *et al.* 2009; Nicolè *et al.* 2011), species distributions (Dahlgren & Ehrlén 2009) and competition (Adler, Ellner & Levine 2010); to understand the selection pressures imposed by stochastic variation in vital rates (Childs *et al.* 2004; Metcalf *et al.* 2008); and to evaluate population responses to current and future climate conditions (Morris *et al.* 2008;

Molnár *et al.* 2011; Barbraud *et al.* 2011; Adler, Dalgleish & Ellner 2012). Though many such studies have incorporated demographically relevant traits such as body size, few have sought to quantify how environmentally induced variation in a focal trait contributes to population growth rate.

Dissecting the dependence of population growth on environmental conditions and trait / vital rate variation creates a number of challenges. Sufficient individual-based data collected across many sets of environmental conditions are needed to reliably identify appropriate covariates and characterise key functional relationships (Morris *et al.* 2008; Frederiksen *et al.* 2008). Estimating these relationships is challenging if many vital rates or trait-transitions are temporally variable, or if multiple environmental drivers are operating. Limiting the number of time-varying parameters in a model may partially negate these challenges. This is most easily achieved using an IPM framework, where it is natural to adopt a regression-based approach to model parameterisation (Merow *et al.* 2014; Rees, Childs & Ellner 2014), though the same tactic can be adopted for many MPMs. Information about the trait dynamics and the relationship between traits and vital rates – including the environmental dependence of these associations – is completely described by the resulting set of (time-varying) regression parameters.

The impact of these different sources of variation on population growth rate (λ) can be quantified using an appropriate life table response experiment (LTRE). An LTRE analysis compares a set of vital rates under two or more conditions to determine their impact on a demographic summary statistic such as λ. The specific goal of a random life table response experiment (RLTRE) analysis is to decompose the temporal variance in λ into contributions from the (co)variances of model parameters (Brault & Caswell 1993; Caswell 2001). In its simplest form, RLTRE uses a first order approximation of the variance of λ; this method is exact only if the functional dependence of population growth rate on each time-varying parameter is linear with respect to each time-varying parameter. Mark and Ellner (2009) introduced a Monte Carlo approach to RLTRE analysis that uses an additive model to partition contributions to the variance of λ. Their methodology introduces greater flexibility by allowing non-linear relationships to be accommodated, and allows the adequacy of a candidate RLTRE to be assessed using regression diagnostics. However, the original analysis did not consider the effect of delayed effects driven by trait variation or fluctuations in age structure, nor did they consider the contributions of environmental drivers.

Here, we capitalise on 37 years (1976-2012) of individual-based data from a population of yellow-bellied marmots (*Marmota flaviventris*), located at the Rocky Mountain Biological Laboratory (RMBL) in the Upper East Valley, Colorado, USA (38°57’ N, 106°59’ W), to examine the mechanisms influencing variation in population growth rate. Individual vital rates and body mass in yellow-bellied marmots are strongly influenced by environmental conditions (Van Vuren & Armitage 1991; Ozgul *et al.* 2010; Maldonado-Chaparro *et al.* 2015), although the impact of this variation on population growth has not yet been quantified. We first parameterise an environmentally driven, stochastic Integral Projection Model with body mass- and stage-dependent demographic rates. We then develop a simple extension of the Monte Carlo RLTRE introduced by Mark and Ellner (2009) to enable us to partition the contribution of direct and indirect (trait/demographic structure) drivers of population growth rate variation. We use the resulting RLTRE to understand how different sources of vital rate variation contribute to the variance of population growth rate and then partition the contributions of different environmental factors to this variance.

Materials and Methods

The study system

Yellow-bellied marmots are hibernating, diurnal, facultatively social sciurid rodents that are greatly influenced by the environment, particularly by winter duration and summer rainfall (Armitage 1994, 2014), which vary from year to year. Marmots hibernate from 7-8 months annually (Armitage 1991). During their relatively brief active season, they must gain sufficient body mass to survive hibernation. Additionally, marmots must reproduce with young being weaned in early July (Armitage 1998).

Our population of yellow-bellied marmots at the RMBL (elevation 2,700 to 3,100 m.a.s.l.) has been studied since 1962 (Armitage 2014). Marmots in each site were live-trapped each year during the active season (between mid-May and early September). Individuals received a numbered ear tag the first time they were captured. Each time captured, individuals were weighed (to the nearest 10 g), sexed, and their reproductive status scored following Armitage & Wynne-Edwards (2002) categories. Each individual was classified into the following age categories: juveniles (< 1 year), yearlings (one-year old), and adults (≥ two years). We used demographic data and body masses collected from all trapped females between 1976 and 2012 because this time period had detailed weather data available that was collected at the RMBL. Female reproductive success was calculated based on the reproductive status of the female each year (0 – failed to wean a litter, 1 – weaned a litter). The number of female juveniles weaned was estimated as the number pups that emerged from the natal burrow and were assigned to a female as her offspring either observationally (1976 to 2000—Armitage 2014) or using a molecular genealogy (2001-2012; details on the molecular genealogy in Blumstein, Wey & Tang 2009). Body masses were adjusted to June 1 and August 31 by fitting mass as a function of date and age using a generalized mixed model (for details see Supporting Information Appendix S1).

Environmental variation

Data to estimate the environmental variation were obtained from the RMBL weather station (106º59.588'N, 38º773'W at 2,900 m) from 1976 to 2012. We used a set of 3 climatic variables. Winter and spring mean temperatures correspond to the average daily mean temperature in ºC calculated from November 1 of the previous year to March 31 of the current year, and from April 1 to May 31 of the current year, respectively. Bare ground, represents the day of the year when no snow remained on the ground at the weather station.

Describing population demography

We used a post-reproductive census to describe marmot life cycles (Supporting Information Fig. 3-S1). Consequently, the census point occurs before the main mortality period (i.e., winter), and individuals must survive to reproduce and add new recruits to the population. For simplification we: 1) only considered the dynamics of females of known age; 2) assumed that the mass-distribution of new born individuals is captured immediately after they are weaned; 3) assumed that birth and death rates in our population is density-independent (Oli & Armitage 2003; Armitage 2014); 4) assumed that all individuals the population expressed the same amount of plasticity in response to environmental change; and 5) the size distribution of the population was well captured by two age categories, juveniles (age = 0) and non-juveniles (age > 0).

We constructed a series of functions that described size-dependent demography (Supporting Information Fig. 3-S1). First we specified how body mass distribution varied with mortality and reproductive probability, and second we specified how body mass was transformed across development (i.e. the trait-transformation rate). The demographic functions were: 1) annual probability of survival ($s(z, t)$), which describes the probability of an individual of age a and mass z survives to the next time step $t + 1$; 2) annual probability of reproduction ($p_b(z, t)$), which describes the probability of a non-juvenile individual of mass z reproduces the following year given that the individual has survived, and 3) recruitment ($b(z, t)$), which describes the number of individuals that a non-juvenile individual of mass z weans in time $t + 1$ (i.e. weaned litter size). The trait transition rates included two components. First, it included ontogenetic growth, which describes the probability of an individual of age a, grows from mass z in August in year t to mass z' in August in year $t + 1$. We divided the ontogenetic growth function in two steps in order to resemble the two main developmental seasons of yellow-bellied marmot life cycles. The first step modelled the winter growth ($G^*(z^*, z, t)$), the body mass loss from August (z) in year t to June (z^*) in year $t + 1$. The second step modelled the summer growth ($G(z', z^*, t)$), after individuals emerged from hibernation. It describes the body mass gain from June (z^*) to August (z') in the year $t + 1$. Second, it included offspring body mass distribution ($C_0(z', z, t)$), which describes the body mass probability distribution of the number of juveniles weaned observed at time $t + 1$, conditioned on the mother's August body mass z in the previous year, t.

We used a model selection and information-theoretic model-averaging approach (Burnham & Anderson 2002) to identify the important variables that describe each demographic and trait transition rate function. We build a set of generalised mixed effect models (GLMMs) for each of the demographic and transition rates as a function of body mass and climatic variables (i.e. spring temperature, winter temperature, and bare ground date) as fixed effects, and year as a random effect to account for temporal environmental variation. In case of the ontogenetic growth functions we also included age category and the interaction between age and body mass. We started with a full model that contained all independent variables and the corresponding random effects model (i.e. the global model). Then, we created a set of candidate models that included nested combinations of the terms contained in the global model. All the model combinations in the full set of candidate models contained body mass in the fixed effects and year in the random effects. We assumed a binomial error distribution (logit link function) for the probability of survival (s) and reproduction (p_b) functions, a Poisson error distribution (log link function) for the recruitment function (b), and a Gaussian error distribution (identity link) for the remaining functions. We ranked all the models in the full set of candidate models based on their Δ_i values (i.e. the difference between the model's AIC value and the minimum AIC value in the full set) and then we scaled each model by their Akaike weight (w_i) relative to the identified best model. We computed mode-averaged parameters based on the full set of candidate models. All models were fitted using the glmer function from the lme4 package in R ver. 1.1-7 (Bates *et al.* 2014) in the R statistical environment ver. 3.1.1(R Core Team 2014). The fitted mixed effect-demographic and trait transition models used to parameterize the IPM are summarized in Supporting Information Table 3-S1.

Model structure and parameterisation

Using the mixed-effects demographic and trait transition functions, we constructed and parameterised, from field data, a density-independent, discrete, stochastic IPM following Rees & Ellner (2009) and Rees, Childs & Ellner (2014). The model describes the temporal dynamics of the bivariate distribution of body mass (z) and age-stage (a), and tracks the body mass distribution in juvenile ($a = 0$) and non-juvenile ($a = 1$) stages. The number of individuals of a given age-stage in the mass range $[z, z + dz]$ at time t is described by a density function $n_a(z, t)$. The general structure of the stochastic age and mass-structured IPM that describes the net result of survival and reproduction of the population, for the total population, is:

$$n_0(z', t+1) = \int_\Omega F^{(t)}(z', z)\, n_a(z, t)dz \quad (for\ a = 1)$$

$$n_a(z^*, t+\tau) = \int_\Omega P_a^{(t)}(z^*, z')\, n_a(z, t)dz$$

$$n_a(z', t+1) = n_a(z^*, t+\tau),$$

where, $F_a^{(t)}(z', z)$ corresponds to the fecundity kernel component that describes the production of size z' offspring by females of size z. This is the contribution of juveniles by adults to the next generation. Thus, this function applies to individuals in the age stage a = 1 (i.e. one year and older). The integration occurs over the entire range of possible sizes z in the population.

$P_a^{(t)}(z', z)$ is the survival-growth kernel component that describes how individuals of size z at time t, survive to reach size z^* at time $t + \tau$, and how individuals of size z^* at time $t + \tau$, grow to reach size z' at time $t + 1$. This is the transition of individuals among age classes. The term (t) corresponds to a random year-specific kernel that describes the environment at each time-step from year 1 to t.

The survival-growth kernel for individuals of age *a*, can be written as:

$$P_a(z', z) = s_a(z) G_a(z', z) \qquad \textit{for } a = 0, 1$$

This function specifies that, in order to grow, an individual in the population must survive from one year to the next with a time varying and size dependent probability, $s_a(z)$. The second term models ontogenetic grow, where:

$$G_a(z', z) = \int G^*_a(z^*, z)\, G_a(z', z^*)\, dz^*$$

winter growth, $G^*_a(z^*, z)$ describes the conditional probability of size z* (size in June) given the current size *z* of the individual in August, and summer growth, $G_a(z', z)$ describes the conditional probability density of size *z'* (size in August) given the current size *z**, of the individual in June. The fecundity kernel is given by:

$$F_a(z', z) = s_a(z) p_{b_a}(z) b_a(z) C_0(z', z) \qquad \textit{for } a = 1$$

where, $F_a(z', z)$, defines the number of juveniles of size *z'* that individuals of size *z* can contribute to the population the following summer (i.e., individuals 1 year old in the current year can contribute to the population as 2 years old, in year t + 1). Notice that individuals must first survive, $S_a(z)$, and then reproduce with a probability, $p_{b_a}(z)$. The number, $b_a(z)$, and size, $C_0(z', z)$, of the contributed offspring is defined by the size *z* of the mother in the August of the previous year. Since the model only accounts for females, $b_a(z)$ corresponds to the number of female offspring per litter.

Once the model kernel was constructed, the final step was to define the integration parameters

(m, L and U) used to iterate the model by numerical integration. To define the upper, U, and lower, L, limits of the body mass (square root transformed) we made slightly larger the largest observed size, and slightly smaller the observed smallest size, thus the total size range was 13 units of mass (i.e. L = 7 and U = 20). We set the number of mesh points, m to 100 because the accuracy of the method increases as the number of mesh points increases. We divided the size interval [20, 7] into 100 size classes of equal length and set z_i as the midpoint of the ith class (a detailed explanation and implementation of the method can be found in Ellner & Rees (2006) and Rees *et al.* (2014)).

Finally, we used the matrix approximation of the model to estimate the stable distribution of the body mass and the stochastic population growth rate. To do this, we first draw a random sample with replacement from the 37 year-specific parameter set to generate a set of 2,000 year-specific parameters. Then we projected the population and calculated the corresponding body mass distribution and values of λ for each year-specific model. The stable mass distribution, $\omega(z)$, was calculated as the relative abundance of the body masses (Caswell 2001). To calculate $\omega(z)$ we added the year-specific body mass distribution from time 0 to 2,000, and then we normalized it to a discrete density function $\omega/\mathrm{sum}(\omega)$. The stochastic population growth rate, $\log(\lambda_s)$, corresponds to the time-averaged growth rate from time 0 to 2,000 (Caswell 2001).

Retrospective demographic analysis

To quantify the contributions from each time-varying model parameter (i.e. fecundity, recruitment, survival, and growth) to the observed temporal variation in $\log \lambda_s$ in our population, we performed a random life table response experiment (RLTRE). We implemented Mark and Ellner's (2009) Monte Carlo approach to LTRE analysis that capitalise on the mixed-model regression framework to partition the contribution on the variation of λ_s. First, we draw a random sample with replacement from the 37 year-specific parameter set to generate a set of 100,000 year-specific parameters. Then we computed the corresponding values of λ for each year-specific model. Finally, we used regression analysis to estimate the contribution of each parameter to the variance for λ_s. Under this approach, the fitted slopes are analogous to sensitivities (Mark & Ellner 2009).

We ran four different RLTRE analyses, the first three estimated the contribution of each model parameter to λ_s, and the last one estimated the contribution of each environmental variable (i.e. winter temperature, spring temperature and bare ground date) in the population model to λ_s. We first modelled λ_s as a function of each time-varying parameters in the model using a multiple linear regression analysis. The second RLTRE was identical to the first, but we added one-year time lags for each parameter estimate. The third LTRE accounted for non-linear relationships. To do so we modified the second analysis by fitting a generalized additive regression model (GAM). To compare the relative contribution of each parameter to λ_s, we normalized the variance contribution of each model parameter, by dividing each contribution by the sum of all contributions.

Finally, our fourth RLTRE analysed the contribution of the environmental drivers. To do so, we first separated the year effects (i.e. unexplained variation from the random effects) from the model's demographic parameter effects (i.e. variation explained by the fixed effects) in the set of 100,000 year-specific parameters. Then, based on the contributions calculated in our third RLTRE, we reduced the data set by eliminating those demographic parameters that had zero contribution to λ. We used this data set to compute the corresponding values of λ for each year-specific model using the basic structure of the previously analysed (GAM). Finally, we fitted a generalised additive model (GAM) to estimate the impact of each climate variable on λ_s. We calculated the contribution of each climatic variable for each demographic process. In each of these cases, we normalised the variance contribution of each model parameter, by dividing each contribution by the sum of all contributions.

Results

Model parameterisation

The logistic regression models describing the relationships between body mass in August and the vital rates demonstrated that the probability of survival and reproduction, and recruitment (i.e., weaned litter size) significantly increased with increases in body mass (Supporting Information Fig. 3-S2). Similarly, there was a significant positive correlation between offspring body mass and mother's body mass in August (Supporting Information Fig. 3-S2). The regression models describing the ontogenetic growth showed a negative relationship between body mass in August the previous year and body mass in June, whereas body mass in June against body mass in August were positively related (Supporting Information Fig. 3-S3). These results describe the loss of body mass during the hibernation period and the gain of body mass during the summer period. Overall, the models predicted that larger juvenile and non-juvenile females were more likely to survive, reproduce, recruit more juveniles, produce bigger offspring, lose less weight during the winter period, and gain more weight during the summer period. Parameter values and functions fitted are described in Table 3-1.

The model selection approach suggested differences in the importance of the environmental factors on each of the vital rates (Supporting Information Table 3-S1). Changes in winter temperature were significantly associated with changes in both survival and reproductive probability, but recruitment did not show a particular trend in the environmental response. Ontogenetic mass changes during the winter and summer were mainly associated with bare ground date and winter temperature, respectively. Finally, offspring mass in August was mainly influenced by spring temperature.

The annual asymptotic population growth rate (λ) of the population for the period from 1976-2012 was 1.017. The values of population size predicted by the model match those calculated from the observed data (Supporting Information Fig. 3-S4). The stable mass distribution predicted by the IPM model captured the bimodal distribution of body masses for juveniles and non-juvenile marmots, although the predicted values for smaller sizes slightly differ from the observed pattern (Supporting Information Fig. 3-S5).

Results of the life table response experiments

In all of the RLTRE analyses presented, the interaction effects had a negligible contribution to variability in log(λ_s). In the case of the liner regression approaches, the interaction terms explained less than 10% of the model residual variation, and none of the interaction terms contributed significantly. In the case of the additive regression approach, the bivariate smooth functions, explained less than 10% of the model residual variation, and the interaction between reproductive probability and lagged reproductive probability in the GAM-based approach, contributed 15.2 % to the model residual variation. These results indicate that the temporal covariances are not important in this analysis. Therefore, we decided not to include them in the final models and to focus on the main effect terms.

The first RLTRE analysis, which included only the current estimated parameters, explained 91% of the variance in log(λ_s). This model suggested that the observed variation in population growth rate was due to the variation in survival and reproductive probability (each accounting for ~53% and ~34% of the variation in log(λ_s), respectively), and that the variation in growth from June to August accounted for a further ~3%. All the other terms contributed less than 1%. The second RLTRE analysis, which included the current and time lagged vital parameters, improved the amount of variance explained (97.5 %). This model yielded essentially the same results as the first RLTRE analysis. Survival and reproductive probability, each explained ~51% and ~33% of the variation in log(λ_s). However, this model indicated the importance of the time lagged reproductive probability term, which explained ~7%. This result indicates that indirect, delayed effects, due to demographic structure fluctuations or trait-mediated effects play a significant role in population growth. Finally, our third RLTRE, which assumed non-linear relationships, and included both the current and lagged vital rates, accounted for 99.5% of the variation in log(λ_s). This model produced similar results to the previous linear RLTRE analyses, yearly variation in survival, reproductive probability and lagged reproductive probability accounted for ~57%, ~33% and ~8% of the variation, respectively. Together, the results of this comprehensive analysis suggests that although the linear-regression-based LTRE analysis may be sufficient to describe the contributions of the demographic parameters to the population growth rate, the GAM-based LTREs allow as to capture non-linearities that describe more complex relationships between vital parameters and stochastic population growth rate log(λ_s).

Our LTRE analyses indicated that the direct effects of survival and reproductive probability accounted for most of the variation in population growth rate (Fig. 3-1). The contribution of survival is particularly high in the GAM-based RLTRE (Fig. 3-1), indicating that variation in survival is more important than suggested by the linear analysis. The direct effect of recruitment to the variation in λ_s was negligible mostly because this process did not show year-to-year variation. Among the time-lagged effects, the direct effect of the time-lagged reproductive probability showed the highest contribution. This suggests that fluctuations in the demographic structure of the population plays a relatively important role in population growth variation.

The trait-mediated effects had a considerable smaller contribution to the variation in λ_s compared to the contribution of the direct effects, and showed a less consistent trend across the RLTRE analyses. In the linear-regression-based RLTREs the ontogenetic growth had a non-zero contribution (Fig. 3-1). However, this trend disappeared in the GAM-based RLTRE. The immediate effects of winter and summer growth had a zero contribution, whereas the time-lagged effects contributed 1.5 % to the variation in λ_s. Since changes in ontogenetic growth cannot affect the population dynamics the same year, our results indicate that the contributions of growth captured by the linear-regression-based RLTRE are inaccurate.

The GAM-based RLTRE analysis explained most of the variation in λ and captured some nonlinearities (Fig. 3-2). In this model, the immediate effect of survival is larger than the immediate effect of reproductive probability, because it is associated with a larger sensitivity, which is indicated by a more positive slope. Moreover, the increase in the contribution of survival with respect to contribution estimated using the linear-regression-based approach is due to the nonlinear response of λ (Fig. 3-2). As previously noted, the immediate effects of recruitment has a negligible contribution to the variation of lambda, although it exhibits a large sensitivity (i.e., steeper slope; Fig. 3-2), and the immediate contribution from growth is zero, even though the different terms are variable, because the slopes are zero (i.e. it does not matter how much body size changes this year).

The time-lagged effects in the GAM-based LTRE showed that the delayed effect of survival has a negligible contribution to lambda and that such parameter is mostly non-sensitive (i.e. slope is close to zero, Fig. 3-3). The vital rates reproductive probability and recruitment exhibited a negative slope (Fig. 3-3), indicating that the large contribution of reproductive probability and recruitment from the previous year leads to an increase in the proportion of non-reproductive individuals in the current year, thus, decreasing the population growth rate. The delayed effects attributed to the trait-mediated effects are positive (Fig. 3-3), suggesting that body size responses to the current environment will not affect the population dynamic until the next year. Changes in the juveniles and non-juveniles winter growth have a smaller contribution to population variation than summer growth (Fig. 3-1), although summer growth showed larger variation ((Fig. 3-3). Moreover, changes in the ontogenetic growth of non-juvenile individuals is more important than that of juveniles because they represent a larger proportion of the population (~60 % of the population) and because non-juveniles, older than 1 year old, reproduce.

Finally, the GAM-based environmental RLTRE indicated that from the set of climatic variables analysed, fluctuations in winter temperature explained the most variation (18.4 %), followed by spring temperature (1.2 %) and bare ground date (0.2%). However, there is a still a large proportion of unexplained variation (80.1%). Each environmental variable has a different effect on each of the vital rates, thus contributing differently to the variation in λ (Fig. 3-4). Winter temperature noticeably contributed through the variation in reproductive probability, survival, time-lagged reproductive probability and time-lagged summer growth in non-juveniles and juveniles. Most of the contribution of spring temperature was via reproduction and time-lagged reproduction. Finally, the small contribution of bare ground was via reproduction and time-lagged winter growth in non-juveniles.

Discussion

Quantifying the contribution of direct and trait-mediated effects of climate variation on population growth rate requires characterizing the key functional relationships between demographic parameters and environmental variables (Morris *et al.* 2008; Frederiksen *et al.* 2008). Using a long-term individual data set, a stochastic integral projection model, and an extended version of the LTRE developed by Mark & Ellner (2009) we identified the relationships between winter temperature, spring temperature, and bare ground date and direct and indirect population responses in a wild population of yellow-bellied marmots. Our results show that the direct effects of survival and reproductive probability and the indirect time-lagged effects, associated with reproduction and ontogenetic growth, have the biggest impact on population growth rate. Moreover, variation in winter temperature was the most important driver of variation in population growth rate, both through its direct influence on reproduction and survival and its indirect delayed effects on reproduction. Finally, we demonstrated that the Monte Carlo LTRE approach is a suitable tool to capture more complex responses (but see Caswell 2010) that are generally considered as biologically more relevant (Mysterud *et al.* 2001), such as non-linear relationships between the (co)variances of model parameters and the temporal variance in λ, and previously undetected lagged effects on population dynamics. Although this is a species-specific population model, our approach to explore how time-lagged effects and trait-mediated responses to environmental fluctuations affect population dynamics can be broadly used in other systems.

In many species, survival strongly influences population growth rate, and thus population dynamics (Pfister 1998; Sæther & Bakke 2000). Our results indicate that in yellow-bellied marmot, the demographic parameters of survival, followed by reproductive probability, had the largest contributions to observed annual changes in the stochastic population growth ($\log(\lambda_s)$). Survival is a key demographic parameter in species such as Columbian ground squirrels (*Spermophilus columbianus*) (Dobson 1995), golden-mantled ground squirrels (*Callospermophilus lateralis*) (Kneip *et al.* 2011), killer whales (*Orcinus Orca*) (Brault & Caswell 1993), and polar bears (*Ursus maritimus*) (Hunter *et al.* 2010). However, differences in the relative contribution of vital rates can vary among species (Wisdom, Mills & Doak 2000). For example, in collared pikas (*Ochotona collaris*), another alpine species, fecundity is the main driver of population growth (Morrison & Hik 2007). Moreover, previous LTRE analysis in yellow-bellied marmots indicated that changes in fertility, age of first reproduction and juvenile survival made the largest contributions to observed annual changes in population growth rate (λ) (Oli & Armitage 2004). Such differences suggest that relative importance of the different demographic parameters can vary temporally (Oli & Dobson 2003; Coulson, Gaillard & Festa-Bianchet 2005). The period analyzed by Oli & Armitage (2004) included a period of relatively stable population size (1962 to 2001), whereas our study period (1975 – 2012) included of a phase of steep population growth during which the population tripled in size. Thus, life-history characteristics, and spatiotemporal variation in factors such as weather, can influence the pattern of the contribution of vital rates to the variation on population growth rate.

Populations can also have delayed effects in response to environmental fluctuations and these can significantly influence population dynamics (Beckerman *et al.* 2002). We found that time-lagged effects significantly contributed to the variation in population growth rate in two ways.

First, there was a one-year lag effect of reproduction (demographic effect) in the population's response to environmental variation. Delayed effects of reproduction negatively influence population growth by skewing the composition of the population towards non-reproductive individuals (i.e., age-structure effect) and hence decreasing the year-specific population growth rate. Similar time-lagged responses have also been identified in species such as northern fulmar (*Fulmarus glacialis*) where there is a 5-year lag of reproduction in response to variation in the North Atlantic Oscillation (Thompson & Ollason 2001). These examples suggest that in long-lived species, differences in the time to respond to environmental effects depend on the characteristics of a species' life history.

Second, there was a one-year lag effect of ontogenetic growth and offspring size (trait-mediated effects). Thus, in our highly seasonal species, the effects of a good or bad year on body mass are not evident until the next season. These delayed responses can arise because of environmental influences on tradeoffs between current and future vital rates, such as survival and reproduction (Lindström 1999). These tradeoffs are very likely to arise in species experiencing time or resource constrains in growth or other traits associated with survival and reproduction (Boyce *et al.* 2006). Alternatively, delays can be due to environmental effects on individual's behaviour (i.e. foraging time), which in turn, can affect the individual-level variation in performance (Beckerman *et al.* 2002) and generate more complex dynamics.

Morphological or physiological dynamics in responses to environmental fluctuations are of particular interest because, in many species, body size has been significantly affected by climate change (Gardner *et al.* 2011). We demonstrated that, despite the evident influence of the environment on body mass dynamics (Ozgul *et al.* 2010), changes in body size have a small contribution to variation in population growth rate. However, body mass dynamics during the hibernation and summer period indicates that non-juvenile yellow-bellied marmots can exhibit a mechanism of growth compensation by which individuals that emerge from hibernation in poor condition can catch up during the summer. Flexible growth rates (Arendt 1997; Nylin & Gotthard 1998) leading to growth compensation could be a mechanism of the phenotypically plastic response. Growth compensation may generally be common in species that have a limited time available to grow, such as hibernating species, and may more generally affect these species' population dynamics.

Co-variation between demographic rates can significantly contribute to the variation in population growth rate (Coulson *et al.* 2005). Yellow-bellied marmots vary in their life-history, thus, we could expect temporal co-variation among demographic parameters (Beckerman *et al.* 2003) and stronger effects on the contribution to the population growth rate. Rather, we found negligible effects of demographic rate co-variation on population growth rate. This result could reflect either limited variation or low sensitivities in the vital rates (Brault & Caswell 1993).

Alternatively, they may indicate that our first order approximation LTRE failed to explain some variation and it is more likely to be misleading when delayed, trait-mediated effects are operating. Thus, our results illustrate an advantage of using the Monte Carlo LTRE approach.

Inter-annual fluctuations in climate are likely to generate changes in the long-term population growth rate (Jongejans *et al.* 2010). Our results suggest that year-to-year fluctuations in winter temperatures, followed by spring temperatures, and bare ground date contribute to changes in population growth rate. Winter temperatures made the largest contribution through its negative effects on reproduction and positive effects on survival, whereas spring temperatures had a small contribution through its positive effects on reproduction; bare ground date had a negligible contribution. These results support the idea that population responses to environmental fluctuations depend on the way fluctuations affects the vital rates and the species' life-history traits (Sæther 1997; Coulson *et al.* 2001; van de Pol *et al.* 2010). But why does winter temperature exceed the effect of the other climatic variables? Yellow-bellied marmots are hibernating rodents, thus winter conditions are expected to strongly influence their energy expenditure (Armitage, Blumstein & Woods 2003). Therefore, winter temperatures that favour a deep snow pack may insulate marmot burrows and ensure that individuals are within their thermo-neutral zone, thus expending the least amount of energy while in deep torpor. While other variables, such as length of growing season have been shown to affect survival and reproduction in our system (Schwartz & Armitage 2005; Ozgul *et al.* 2006), the fact that we have identified a new variable suggests that other climatic variables should be scrutinised for their putative effect on demography.

The approach we developed in this study permitted us to identify, in detail, how changes in the population are governed by changes in the environment, which influence population dynamics through their influence on demographic variables (Dobson & Oli 2001). Compared to previous deterministic IPMs in our studied population, the stochastic version allowed us to incorporate environmental and demographic stochasticity, which plays an important role in life-history evolution (Tuljapurkar, Gaillard & Coulson 2009). Although in this system body mass is a key life-history trait that influences survival probabilities (Ozgul *et al.* 2010), we demonstrated that its contribution to population fluctuations was relatively small. Future studies in this and other systems should seek to identify the conditions under which we expect substantial trait-mediated effects. Due to the known effects of climate warming on body size (Gardner *et al.* 2011; Sheridan & Bickford 2011), future work should focus understating the importance of trait-mediated and time delayed responses, and the underlying mechanisms that facilitate these responses.

Acknowledgments

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Data accessibility

Data are archived at www.eeb.ucla.edu/Faculty/Blumstein/MarmotsOfRMBL/data.html

Figures

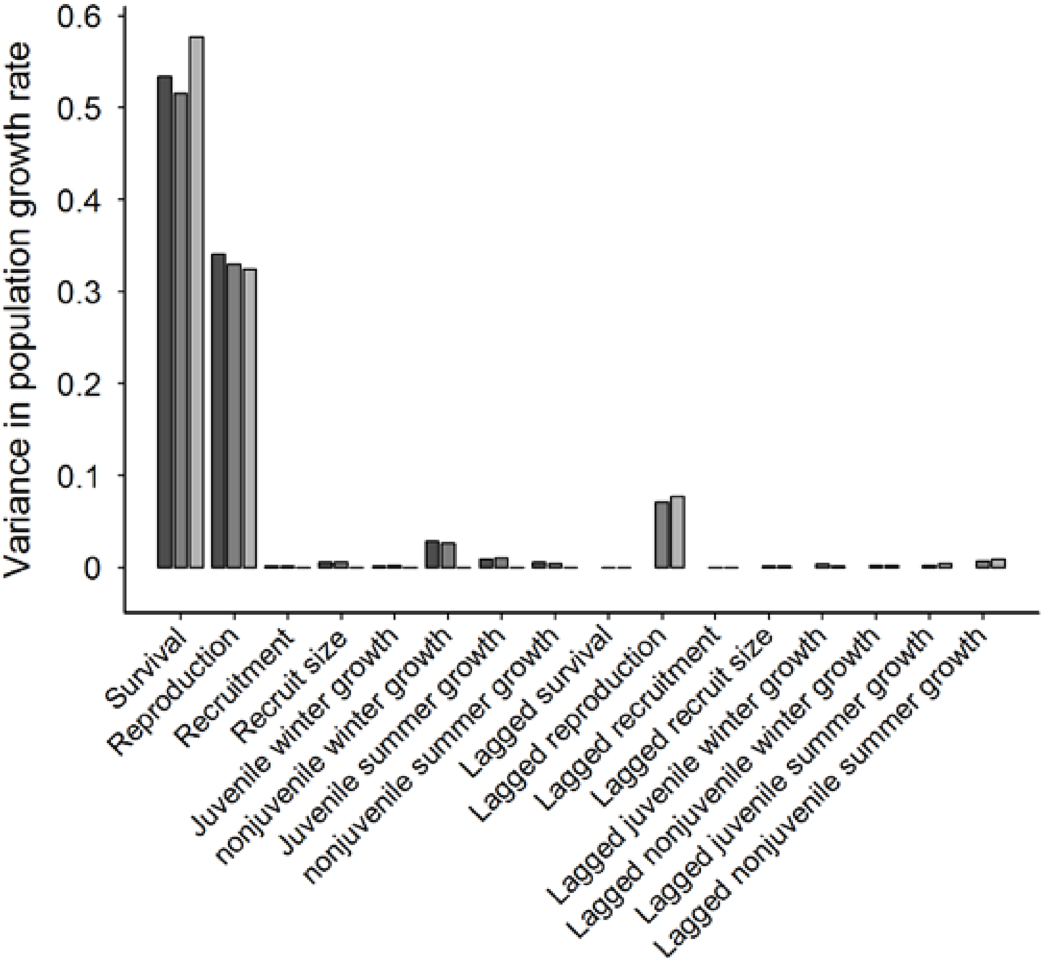

Figure 3-1. Relative contribution of vital rates and lagged vital rates to the variation in the stochastic population growth rate (log(λ_s)), given by three different random life table response experiments (RLTRE) analysis: linear-regression-based (dark grey bars), linear-regression-based that includes lagged vital rates (medium grey bars), and generalized additive model (GAM)-based that included lagged vital rates (light grey bars).

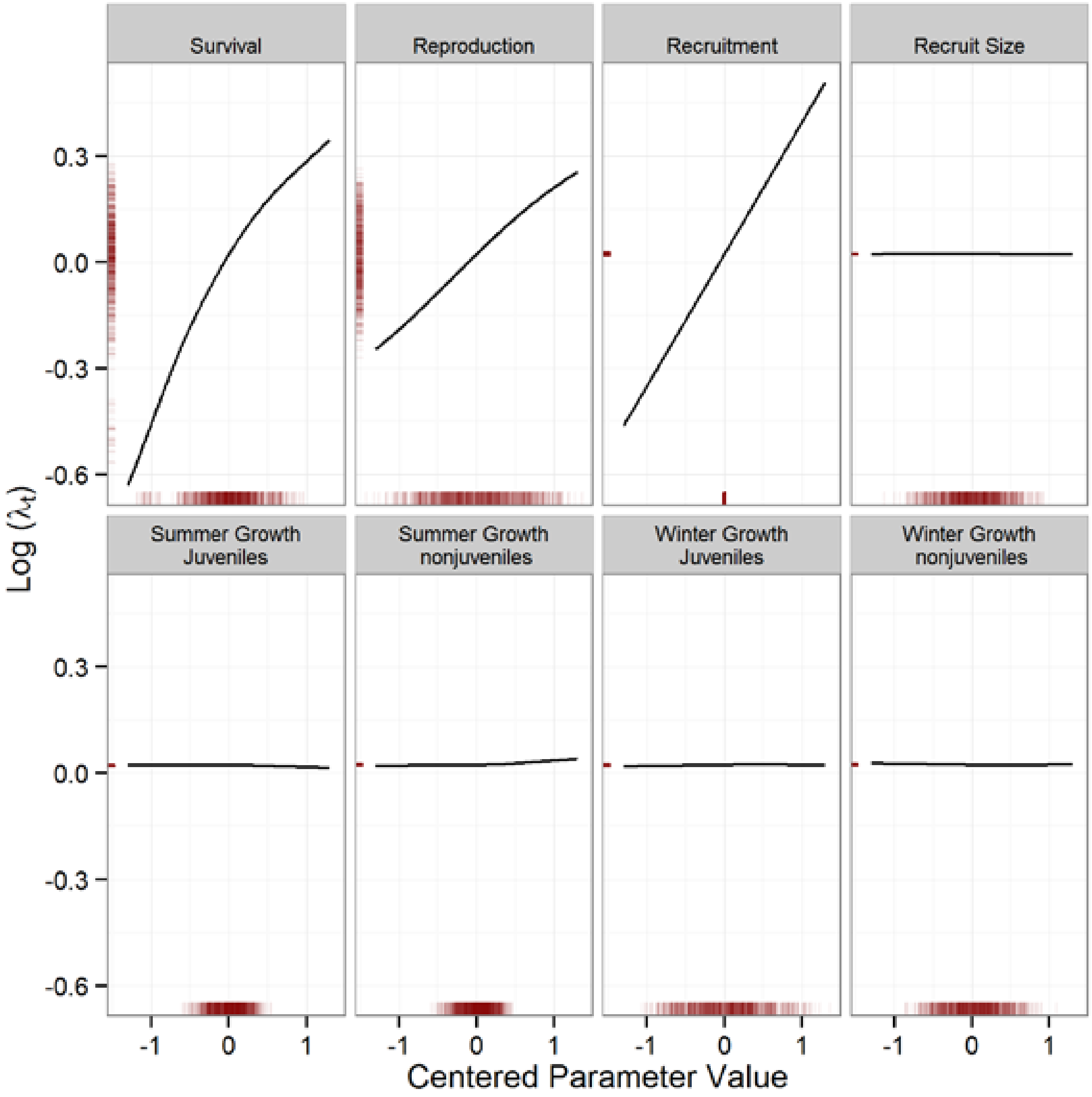

Figure 3-2. Random life table response experiment (RLTRE) analysis using the generalised additive model (GAM)-based analysis for the vital rates. Smoothed terms illustrate the relationship between each of the vital rates and the long-term stochastic population growth rate ($\log(\lambda_s)$) (Black continous line). Variation in $\log(\lambda_s)$ (y-axis) and vital rate parameters (x-axis) were scaled to facilitate comparisons. Rugs on the x-axis and y-axis of the graph represent the distribution of the vital rate data and the distribution of the long-term stochastic population growth rate, respectively.

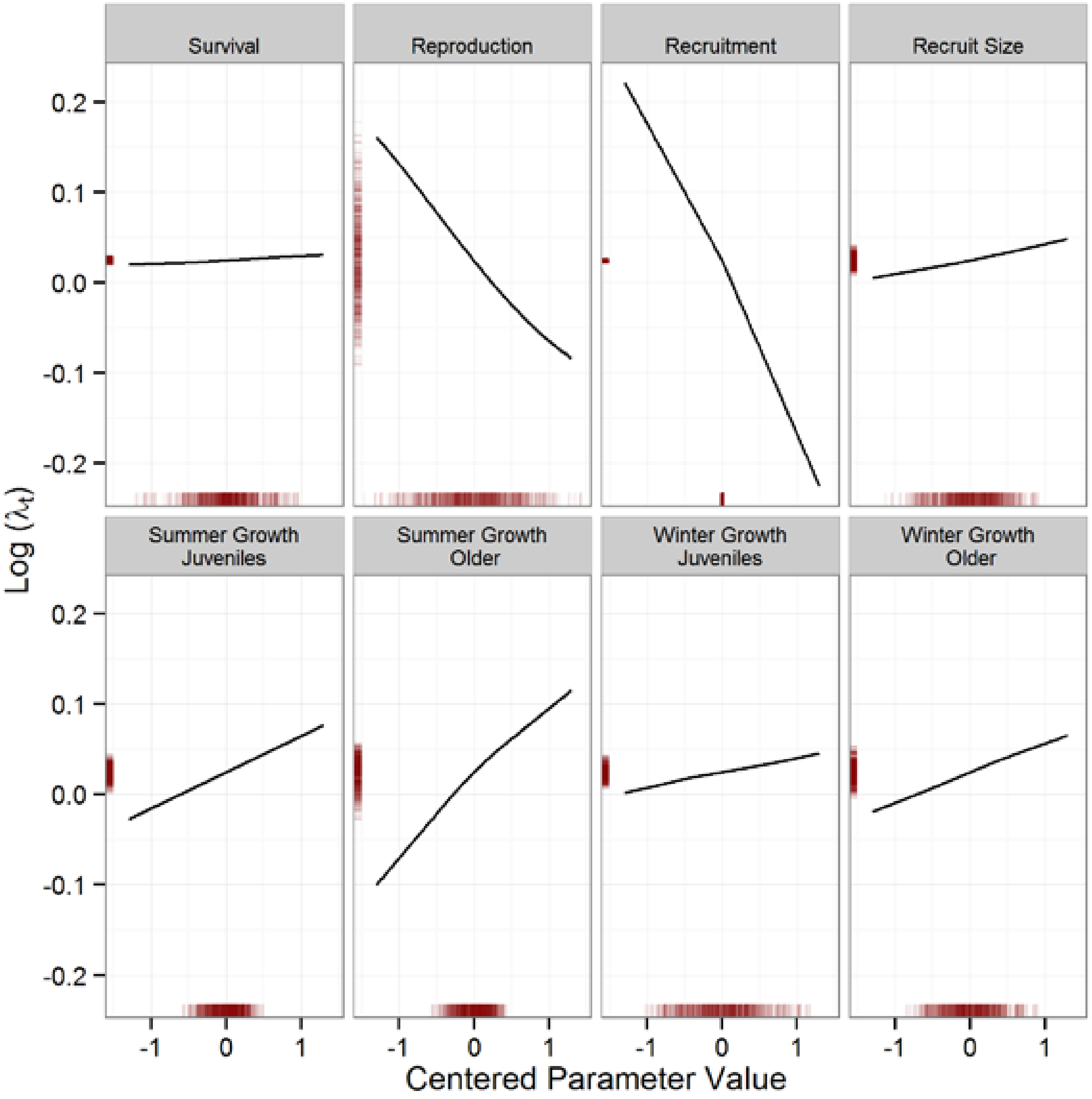

Figure 3-3. Random life table response experiment (RLTRE) analysis using the generalised additive model (GAM)-based analysis for the time-lagged vital rates. Smoothed terms illustrate the relationship between each of the time-lagged vital rates and the long-term stochastic population growth rate (log(λ_s)). Variation in log(λ_s) (y-axis) and lagged vital rate parameters (x-axis) were scaled to facilitate comparisons. Rugs on the x-axis and y-axis of the graph represent the distribution of the vital rate data and the distribution of the long-term stochastic population growth rate, respectively.

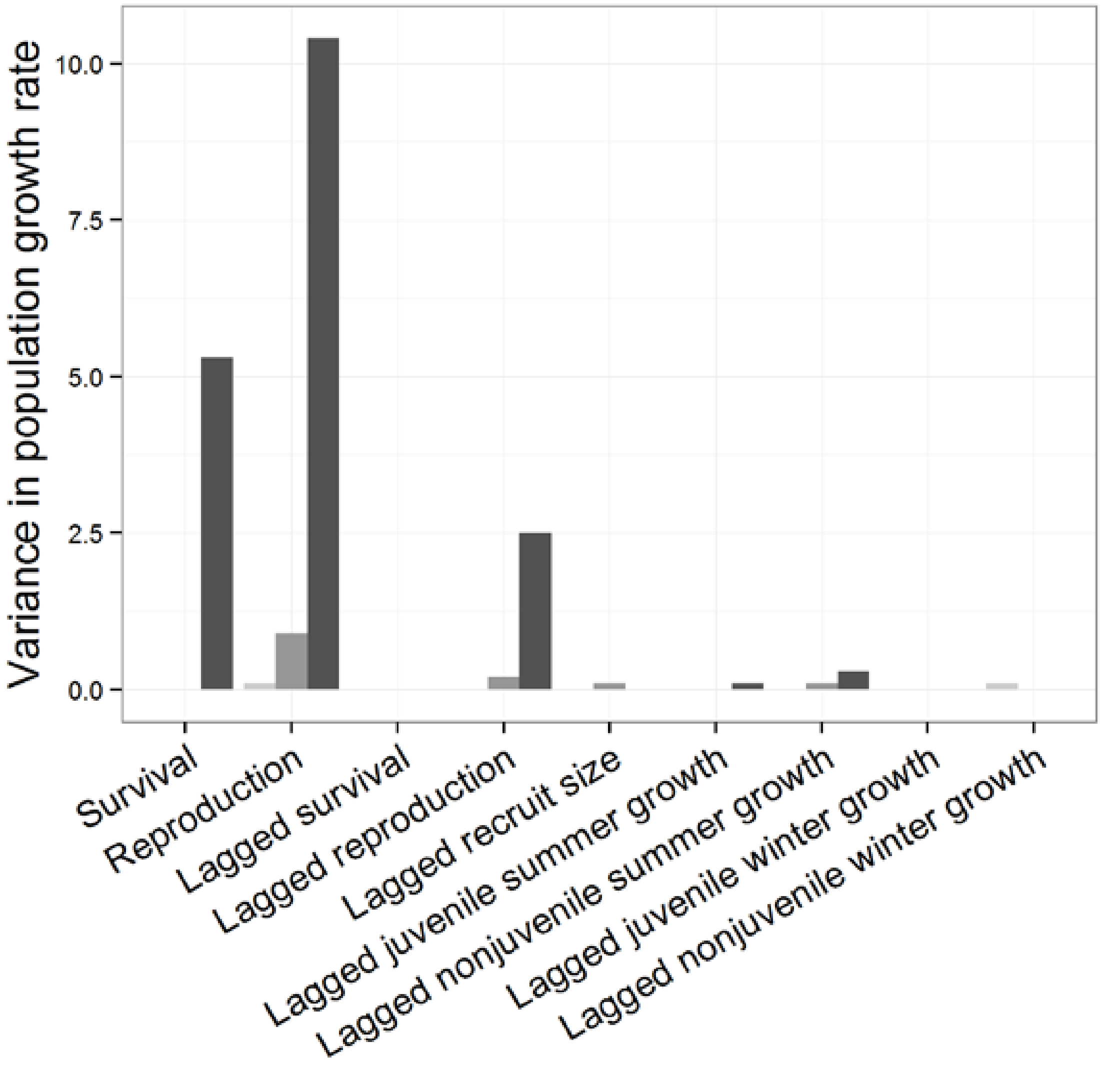

Figure 3-4. Relative contribution of climate variables to the variation in the stochastic population growth rate ($\log(\lambda_s)$) estimated by the random generalized additive model (GAM)-based life table response experiment. The contribution of each climatic variable was differentiated by its influence on the vital rates (x axis). Winter temperature (dark grey bars), spring temperature (medium grey bars), and bare ground date (light grey bars).

Supporting Information

Appendix 3-S1. Estimation of June and August body mass. For every individual in the population we estimated its body mass conditional on the full set of observed body masses for any individual female marmot, at two census points in the growing season June 1st and August 31st. To do this, we fitted a generalized additive mixed model (GAMM) of the form:

$$E\left[z_i\right] = a_{V(i)} + b_{BY(i)} + g_{YR(i)} + f\left(a_i, d_i\right) \qquad (1)$$

$$Z \sim Norm\left(z, R\right) \qquad (2)$$

Where, $E[z_i]$ is the expected body mass of an observation. The first three terms in this expression (1) correspond to the valley location-specific intercept, the birth year effect, and the observation year effect, respectively. The birth year and observation year effects are random effects. The last term is a bivariate smooth function of the age and Julian day. We assume that the vector of observed body masses, **Z**, are normally distributed with expectation **z** (the vector of z_i) and covariance matrix **R**. We used the gamm4 package in R. However, the challenge of the approach is to find a structure for **R** that allows the correlation between the observations belonging to a particular individual to decay within and among years in a way that accurately reflects the data. That is, pairs of observations that are close together in time are more correlated than those that are further apart. Therefore, we empirically model the correlations structure of the residuals from a model that assumes observations are *iid.*

To achieve our goal, we used a three-step procedure based on the data collected throughout the active season. First, we used model selection approach to determine the power transformation of the body mass using Generalized Additive Model (GAM). The best model was the one that stabilized the variance and improved the normality of the residuals. Then we refitted the model using the square root transformation of the response variable, body mass. Second, we extracted the residuals from the final model fitted in step 1 and constructed an empirical model with the following correlation structures: a) within-year correlation structure among the residuals, and b) among-year correlation structure among the residuals. In both cases, for every individual, in each year where two or more observations of body mass were recorded, we recorded every possible pairwise combination of residuals that correspond to that year. We also recorded the time elapsed (in days) between each pair of observations. We then used the resulting dataset to calculate the empirical correlation between pairs of observations at every possible time difference. Finally, we used these empirical models to predict the distribution of the residuals at two census points in the growing season, for every age between birth and the end of the study, conditioning predictions on the observed residuals for that individual. The joint distribution of the observed and unobserved residuals is multivariate normal with mean of $\mathbf{0}$ and correlation matrix defined by the models fitted in the second step.

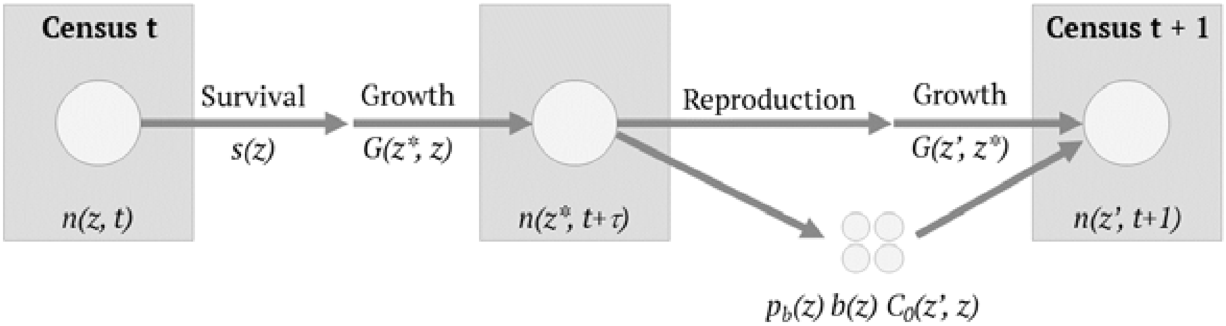

Figure 3-S1. Life cycle diagram of yellow-bellied marmots and census points. The diagram represent the total number of individuals of size z at time t and at time t + 1. The ontogenetic growth transition was split into two parts. The first part corresponds to the ontogenetic growth from August in year t to June the next year t + 1 (i.e. winter growth), whereas the second part represents the ontogenetic growth from June to August in the year t + 1 (i.e. summer growth). In this case, reproduction occurs before the census period therefore, new born individuals are censused at the time t before any mortality occurs but they do suffer mortality before their next census at time t+1 at age 1. Individuals must survive with a size-dependent probability (s(z)) in order to be able to reproduce (p_b(z) b(z)) and contribute with new recruits to the population (C_0(z', z)), and to growth to the next year (G(z*, z), G(z', z*)).

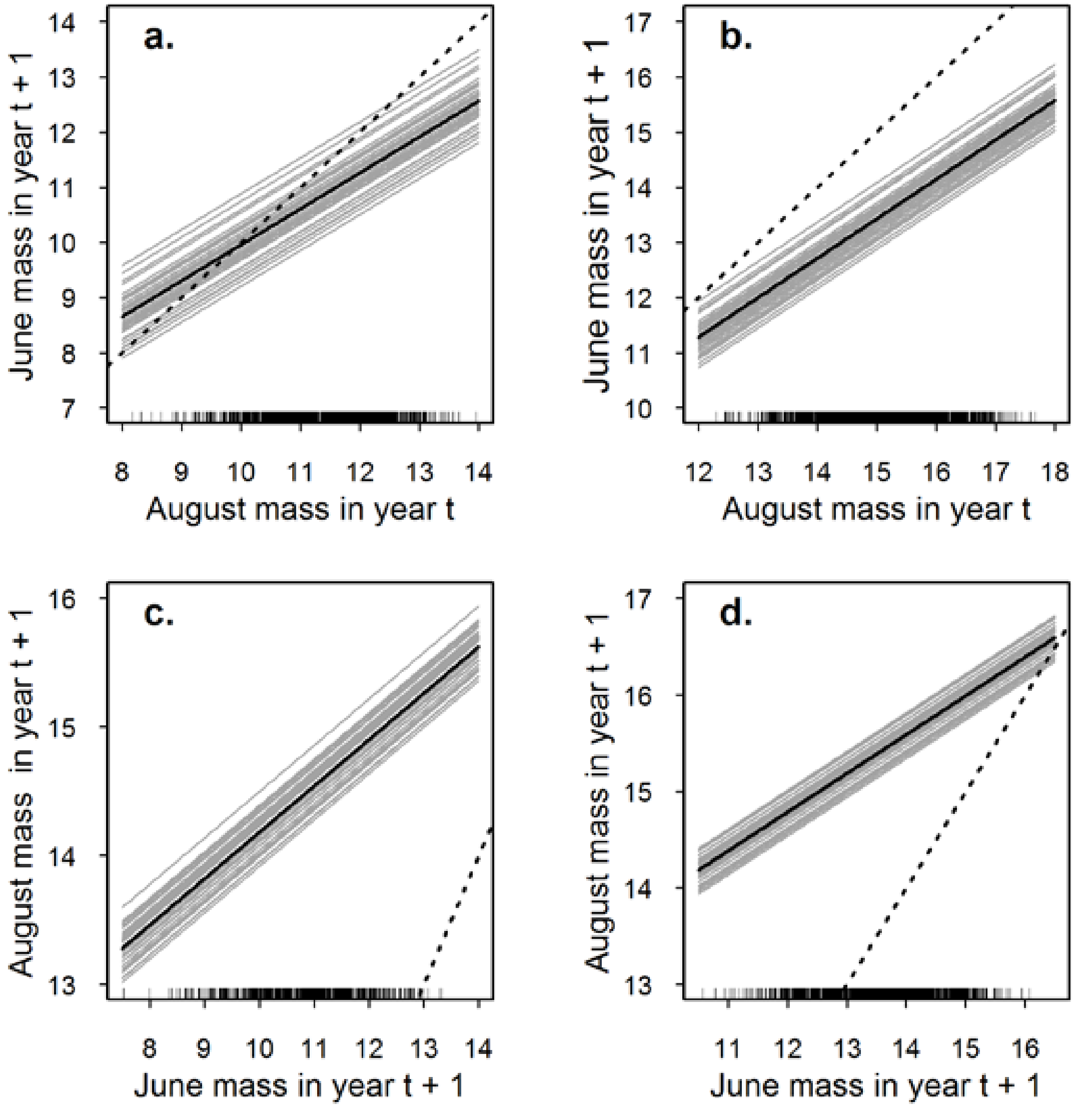

Figure 3-S2. Statistical functions describing the relationship between body mass (square root) and juvenile (a, c) and non-juveniles (b, d) individual's growth. Upper panel illustrates winter growth, and lower panel corresponds to summer growth. Grey lines illustrate the mean response for each year in the study (from 1976 – 2012). Grey dotted lines illustrate the function y = x. Black continuous lines illustrate the mean population response, and rugs below the graph represent the distribution of the body mass data for the corresponding age class.

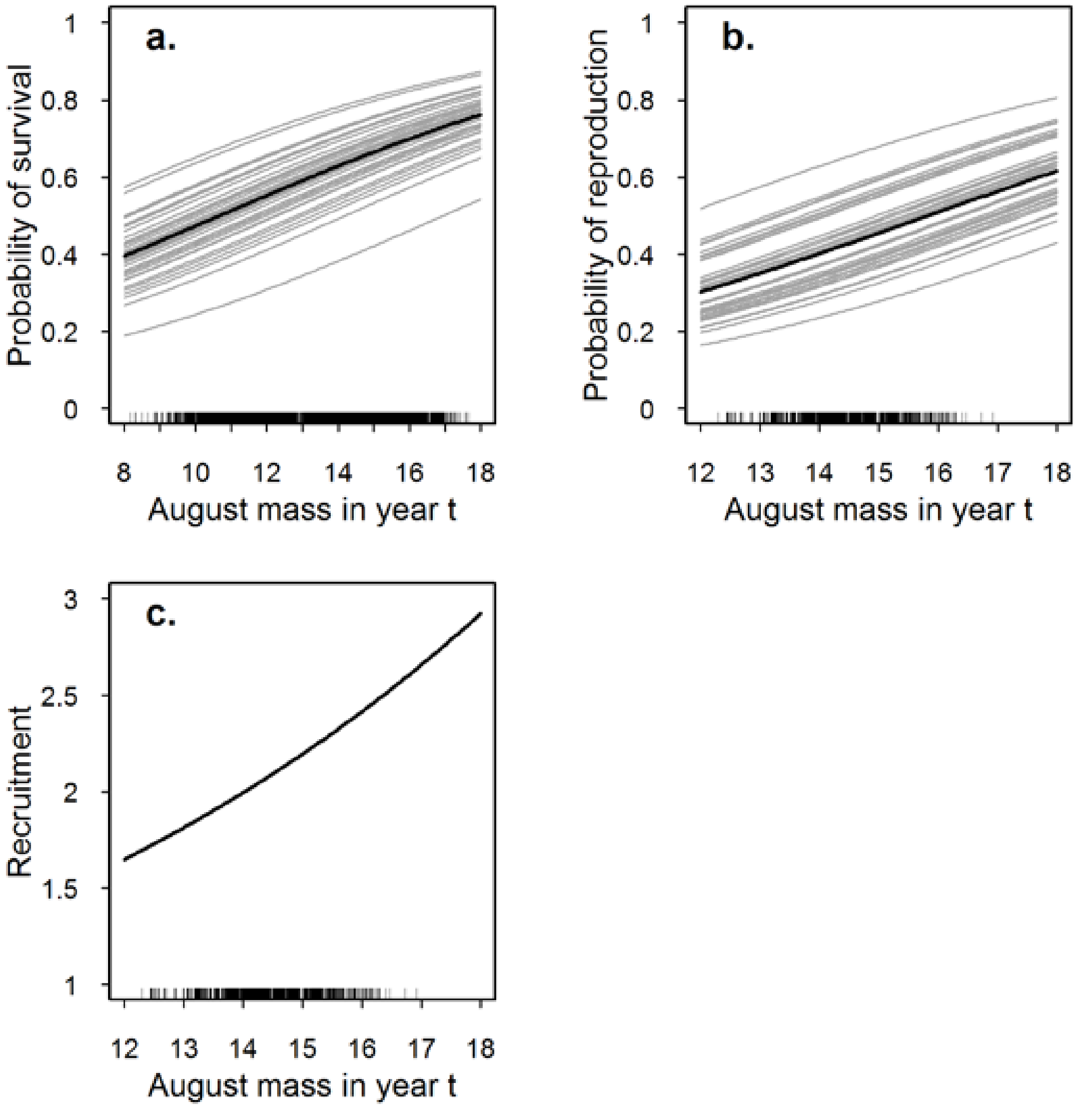

Figure 3-S3. Statistical functions describing the relationship between August 31st body mass (square root) and probability of survival (a), probability of reproduction (b), and recruitment (c). Grey lines illustrate the mean response for each year in the study (from 1976 – 2012). Black continuous lines illustrate the mean population response, and rugs below the graph plot the distribution of the body mass data for non-juveniles.

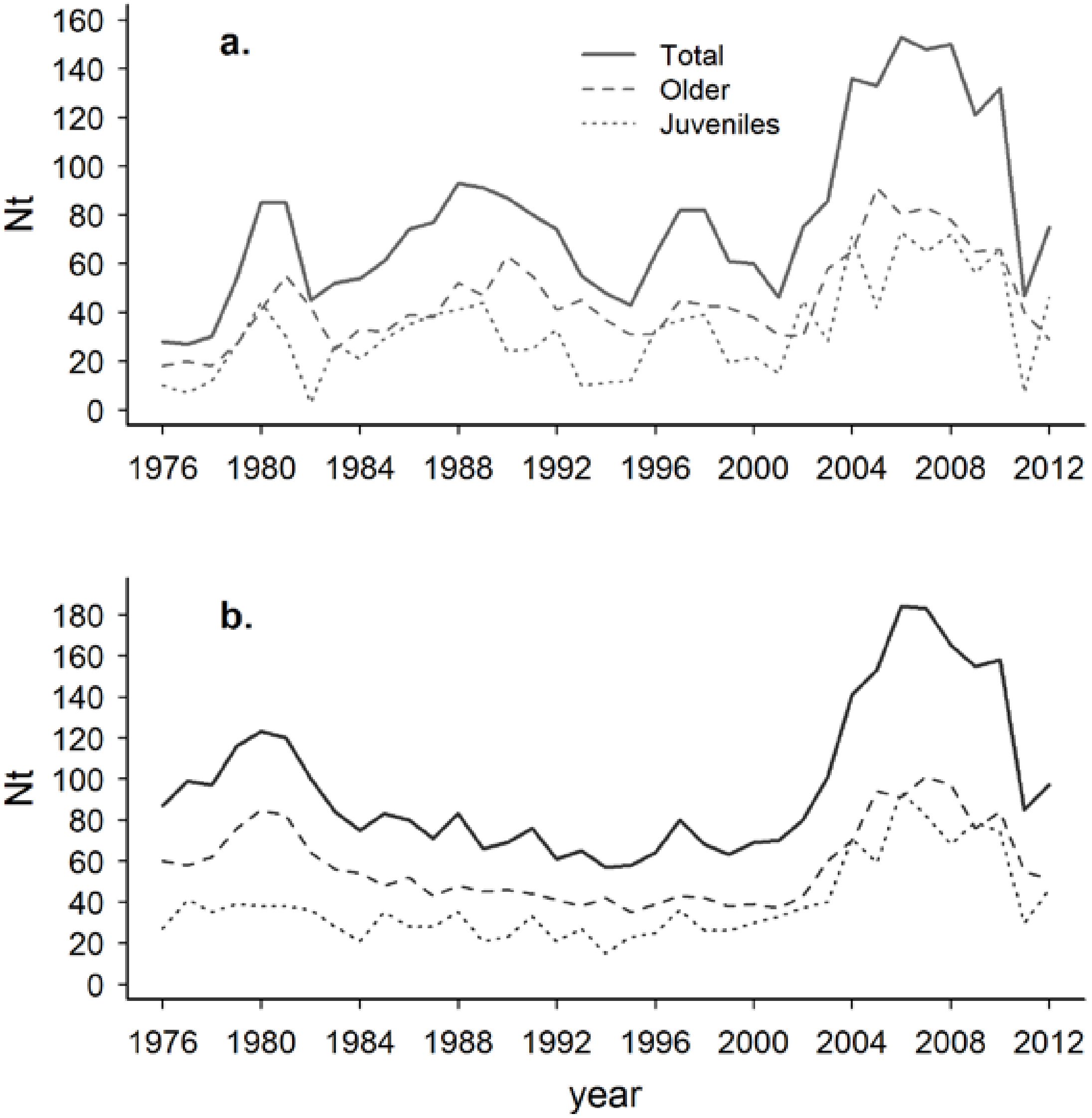

Figure 3-S4. Examination of model fit – comparison of (a) observed and (b) simulated population growth of yellow-bellied marmot (*Marmota flaviventris*) over 37 years of study.

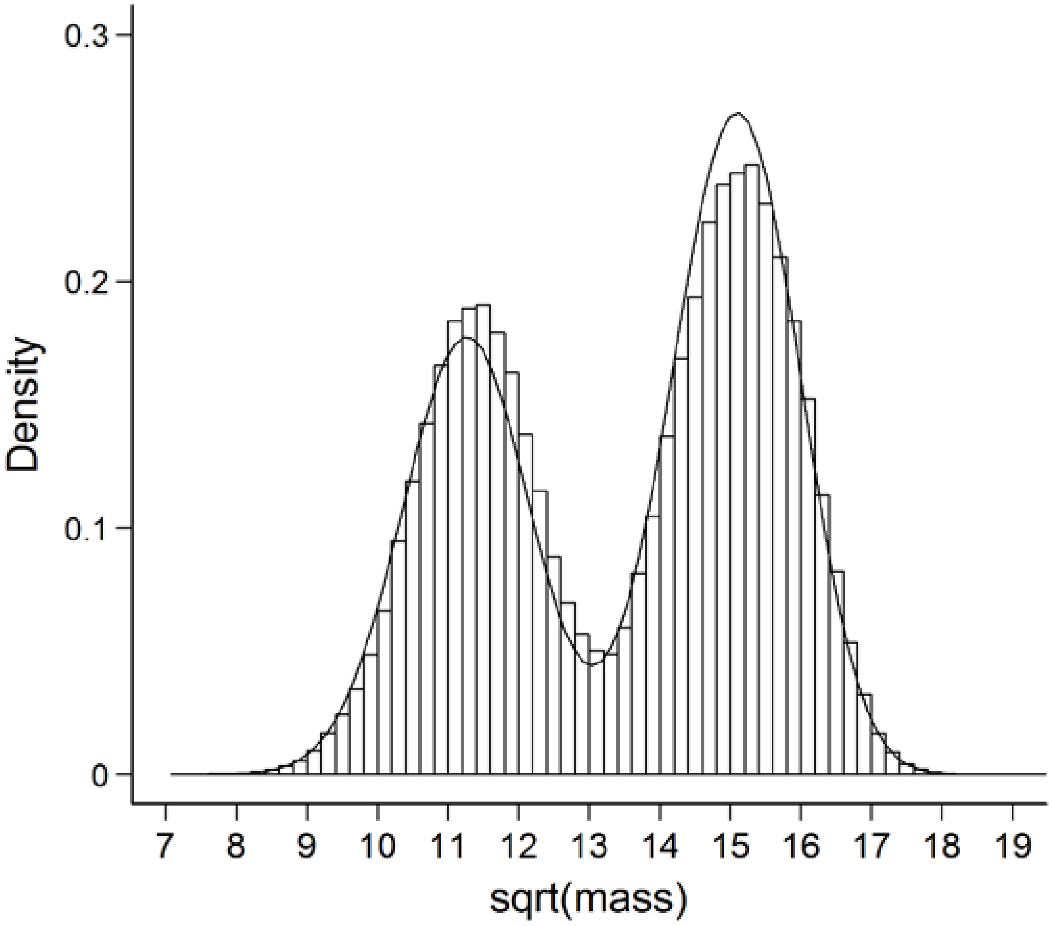

Figure 3-S5. Estimated stable state distribution for body mass. Continuous line: estimated distribution of the integral projection model. Histogram: observed size distribution.

Table 3-S1. Average parameter estimates describing the association between August 31st mass (z) (square root transformed) and demographic and trait transition rates. All functions included square root body mass and the climatic variables winter temperature, spring temperature and bare ground date as fixed effects and year as a random effect. The functions ontogenetic growth in winter, ontogenetic growth in summer additionally included age and the interaction between age and body mass in the fixed effects. All functions were modelled using generalized linear mixed models using the specified error structure. Data on female yellow-bellied marmots of all ages from a population in and around the Rocky Mountain Biological Laboratory (RMBL) from 1976 to 2012.

Function	**Model**	**Fitted GLM**
Survival	logit(s)	$-2.229 + 0.163z - 0.068\,T_{winter} + 0.0002T_{spring} - 0.0001BG$
Reproduction	logit(p_b)	$-2.605 + 0.225z + 0.162T_{winter} + 0.033T_{spring} + 0.001BG$
Recruitment	log(b)	$-0.557 + 0.096z + 0.002T_{winter} - 0.004T_{spring} - 0.0005\mathrm{BG}$
Ontogenetic growth$_w$	G_0 G_1	$\mu_0 = 1.975 + 0.651z + 0.056T_{winter} + 0.021T_{spring} + 0.013\mathrm{BG}$ $\mu_1 = \mu_0 - 0.742 + 0.064z$ $\sigma^2 = 0.572$
Ontogenetic growth$_s$	G'_0 G'_1	$\mu_0 = 10.946 + 0.360z{*} + 0.065T_{winter} + 0.024T_{spring} + 0.0005BG$ $\mu_1 = \mu_0 – 0.612 + 0.041z$ $\sigma^2 = 0.611$
Recruitment size	C_0	$7.788 + 0.237z + 0.002T_{winter} + 0.107T_{spring} - 0.003BG$ $\sigma^2 = 0.771$

Table 3-S2. Summary of the environmental variables that appear in the set of a priori models that best describes each of the demographic process and trait-transitions. The models were selected from the set of candidate models using Akaike information criterion (ΔAIC < 2).

	Number of models in the *a priori* set	**Winter Temperature**	**Spring Temperature**	**Bare ground**
Survival	4	3	1	1
Reproduction	3	3	1	1
Recruitment	4	1	1	1
Winter growth	3	2	1	3
Summer growth	3	3	2	1
Recruit size	3	1	3	1

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CHAPTER 4

Can individual heterogeneity in phenotypic plasticity enhance population viability?

Abstract

In response to climatic variation, individuals within a population may adjust their behavioral, morphological or physiological responses to varying environmental conditions through phenotypic plasticity. In seasonal environments, time constraints related with seasonality and variation in climate factors can affect the developmental growth of individuals. To cope with the consequences of a harsh period, individuals can compensate their growth by accelerating growth rate to catch up. This phenotypic plastic response can directly affect body size, therefore is expected to affect an individual's fitness and the population dynamics. Here, we used a well-studied population of yellow-bellied marmots, *Marmota flaviventris*, in Colorado to parametrize and developed an individual-based model (IBM) to investigate the effects of phenotypically plastic responses of growth rate to a bad start, and to explore if phenotypic plastic responses in growth rate could favor the persistence of the population under less favorable climatic scenarios. We found that among-individual variation in the plastic response of growth rate allowed us to match better the observed population sizes, hence suggesting the importance of individual heterogeneity for population dynamics. Moreover, we found that growth rate plasticity plays an important role in decreasing the probability of extinction under colder and random climate scenarios, but not under warmer climate scenarios. Our results allowed us to gain a deeper understanding of the mechanisms that govern population fluctuations, and highlight the importance of quantifying the fitness cost of phenotypically plastic responses.

Keywords: growth-rate plasticity, individual heterogeneity, individual-based model, population persistence, yellow-bellied marmots

1. Introduction

Individuals within a population may adjust their behavioral, morphological or physiological responses to varying environmental conditions through phenotypic plasticity (Charmantier et al., 2008). Phenotypic plasticity, is a widely documented phenomenon in natural populations (Gotthard and Nylin, 1995). Phenotypic plasticity, can be defined as the ability of a genotype (i.e., individual) to express different phenotypes as a function of the environmental conditions experienced (Bradshaw, 1965; Pigliucci, 2001), and can influence vital rates and thereby population dynamics and extinction risk (Vindenes et al., 2008). In this way, phenotypic plasticity is potentially a key element that allows populations to respond non-genetically to environmental change and variability (Chevin et al., 2010; Reed et al., 2010; Stearns, 1989; Visser, 2008). Given that climate change can alter the environmental conditions experienced by many organisms, it is fundamentally important to explore the population-level consequences of phenotypic flexibility because environmental conditions can affect the availability of resources, with potential consequences in the allocation of energy in an organism and its fitness.

Seasonal environments challenge organisms to annual biological events, such as reproduction and to environmental factors that may vary across years (Reed et al., 2010), thus creating behavioral, physiological and morphological challenges for coping with environmental variation. During winter, organisms undergo a period of reduced energy intake that results in a depletion of energy reserves and body mass, whereas during the summer organisms build energy reserves and increase their body mass. Moreover, an individual's body condition at the end of the winter period may influence fitness in the subsequent season (Harrison et al., 2011). Body mass dynamics are, therefore, a key element that may affect life-history processes of a species such as survival and reproduction (Blanckenhorn, 2000). Thus, we might expect that natural selection favors mechanisms allowing individuals to compensate for an environmentally induced period of slow growth (Metcalfe and Monaghan, 2003). Indeed, compensatory growth is a widespread mechanism for coping with the consequences of a harsh period (Nicieza and Metcalfe, 1997).

In seasonal environments, individuals compensate by accelerating growth rates to reduce the cost of having a sub-optimal size at the required time period (Ali et al., 2003; Metcalfe and Monaghan, 2001). Compensation may occur for both body mass and structure (Nicieza and Metcalfe, 1997). Thus, compensatory growth can directly affect body mass (Abrams et al., 1996; Metcalfe and Monaghan, 2001), and, by doing so, influence an individual's fitness (Blanckenhorn, 2000; Roff, 2002; Sogard, 1997; Stearns, 1992). The ability of an individual to compensate by increasing its growth rate demonstrates that growth rates are flexible (Abrams et al., 1996), and that they may respond to environmental cues. Compensation can be triggered by environmental cues indicating that an individual is small for the time of the year in question (Metcalfe and Monaghan, 2001). Moreover, growth rates vary among individuals within a population (Kvist and Lindström, 2001). Hence, the ability to alter growth rates may also vary among individuals. However, compensatory growth may be costly (Arendt, 1997), although this has not been documented very well (Metcalfe and Monaghan, 2001). Individuals that accelerate their growth rate may pay an immediate cost due to an increased risk of predation associated with increased foraging. Rapid growth may also have longer-term costs when there is damage at the physiological or cellular level (Metcalfe and Monaghan, 2001).

In this study, we developed a non-spatially explicit individual-based model (IBM) to investigate the effects of phenotypically plastic responses of growth rate when an individual experiences a bad start after the winter season. Our model is based on the population dynamics of a well-studied population of yellow-bellied marmots, *Marmota flaviventris*, in Colorado (Blumstein, 2013; Armitage, 2014). Marmots are an obligately hibernating, ground dwelling, sciurid rodent. Marmots at this location have increased their end-of-season body mass over the past 12 years, which means that they now enter hibernation in better body condition and have lower over-winter mortality (Ozgul et al., 2010). Previous studies suggest that the increase in the end-of-season body mass can be a result of compensatory mechanisms allowing individuals to catch up after a bad start after hibernation (Maldonado et al. *in prep*), so flexibility in the growth rate may have important consequences for fitness at both the individual- and population-levels. Moreover, since climate change can affect population dynamics, we additionally explored whether phenotypic plastic responses in growth rate could favor the persistence of the population under less favorable climatic scenarios.

2. Materials and Methods

2.1 Study species

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL). Yellow-bellied marmots hibernate for 7-8 months annually (Armitage, 1991). Thus, they must gain sufficient body mass during their relatively short active season to survive hibernation. Reproduction, gestation and lactation take place during the active period (Armitage, 1991). Mating occurs in the spring, after emergence. Females do not start to reproduce until age two and, once they breed, they are able to produce at most a single litter per year. Juveniles are born after about 32 days of gestation and are weaned in early July when first emerging from the natal burrow after about four weeks of lactation (Armitage, 1998). Litter sizes vary between 1 and 8, with a 1:1 sex ratio (Schwartz et al., 1998).

Marmots are greatly influenced by environmental conditions such as summer precipitation, snowfall (Armitage, 1994) and winter temperatures (Maldonado et al., *in prep*). Thus, overwinter survival and reproductive success depends on the ability of an individual to store enough energy for hibernation during its active season (Armitage, 1998).

2.2 Life history data

We used data collected from female yellow-bellied marmots at RMBL to compare them to our simulation data. Our population is located in the East Valley of Gunnison County, Colorado, USA, where marmots are patchily distributed between elevations of 2700 to 3100 m.a.s.l. (Armitage 1991; Armitage 2003). The study began in 1962, but we focus on data collected since 1976 because we have more detailed weather data after that date. Marmots are live-trapped, individually identified with a unique combination of numbered ear tags, weighed, and sexed at each trapping event. In addition, we record its age and reproductive status (for details see Armitage & Wynne-Edwards 2002).

2.3 Body mass estimation

For every individual in the population we estimated its body mass at two census points in the growing season June 1st and August 31st. To do this, we fitted a generalized additive mixed model (GAMM) that included the valley location, the year of birth of each individual, the year of observation, and a bivariate smooth function of the age and Julian day. The birth year and observation year correspond to the random effects. (for details see Maldonado-Chaparro et al. *in prep*).

2.4 Estimation of life-history processes

The demographic and trait-transition rates used in the simulation model were extracted from a previously fitted population model developed by Maldonado et al. (*in prep*). In their model, the authors characterized the relationships between body mass in August and the probability of survival and reproduction, the number of weaned offspring, body mass of the offspring, and the body mass transitions between August to June and June to August using generalized linear mixed models (GLMMs). They assumed a binomial distribution (logit link) for modeling probabilities of survival and successful reproduction, a Poisson distribution (log link) for modeling the weaned litter size, and a normal distribution (identity link) for modeling ontogenetic growth and offspring mass. Each of the fitted models included body mass, previous winter temperature, spring temperature and first day of bare ground as fixed effects and year as a random effect.

2.5 Model description

Trait-based demographic analyses have typically used approaches such as integral projection models (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006) or physiologically structured population models (de Roos, Diekmann & Metz 1992; de Roos 1997), which allow analytical tractability similar to commonly used population models. Due to the plasticity mechanisms and demographic stochasticity in this population, however, we used an individual-based model tailored specifically to yellow-bellied marmot life history so that we do not have to assume all individuals act in the same way. The model was developed in NetLogo 5.2 (Wilensky, 1999). The description of our model follows the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm *et al.* 2006; Grimm *et al.* 2010).

2.5.1 Purpose

The purpose of the model is to understand how individual heterogeneity in phenotypic plasticity in growth rate affects the population dynamics and probability of extinction in yellow-bellied marmots in the study area over the next 50 years.

2.5.2 Entities, State variables, and scales

Our single-species model is a non-spatially explicit population model with two hierarchical levels: individuals (female marmots) and population. Each marmot is characterized by the following state variables: individual identity (ID), age (in years) and seasonal mass (square root of body mass in grams), and one of two life-history stages: juveniles (< 1 year old) and non-juveniles (> 1 year old). Age is updated every time step during the individual's lifetime, and is used to determine the age at sexual maturity and the maximum age an individual can survive.

Temporally, the model uses annual time steps that simulate the hibernating and active season characteristic of the annual cycle. To do so, it includes processes and schedules (see next section) driven by environmental factors. The environmental factors describing the seasonal fluctuations are winter mean temperature (°C), spring mean temperature (°C) and bare ground (Julian date). The time horizon of the model is 37 years, except for the climate variation scenarios, for which the time horizon is 50 years.

2.5.3. Process overview and scheduling

The model covers the entire life cycle of yellow-bellied marmots and follows the body mass of each individual. The life cycle compromises two life-history stages: (1) juvenile individuals -- newborns that have not yet emerged from their first winter, (2) non-juvenile individuals – individuals that have survived at least one winter. Individuals are reproductively mature at age two, after surviving at least two winters. Every year, each individual follows the following processes (Figure 4-1): (i) marmots survive over winter with a probability based on their body mass before hibernation (i.e., August body mass); (ii) if an individual survives, it increases its age by one year; (iii) beginning at age two, an individual reproduces and weans a litter with probability based on its August body mass; (iv) newborn individuals are born with a body mass based on their mothers' August body mass; and (v) all non-newborn individuals update their body mass. This last process occurs in two steps. The first step represents the loss of mass over winter; here, individuals update their June body mass based on their August body mass. The second step represents the gain of mass during the summer; therefore, they update their August body mass based on their June body mass. When growth rate flexibility is allowed in the model, individuals whose body mass is below the average population body mass in June are permitted to catch up and grow more than predicted by the mass gain equation without plasticity.

2.5.4. Design concepts

2.5.4.1. Basic principles. Environmental conditions can influence population dynamics directly, through their immediate impact on survival and fecundity, and indirectly, via changes in population age structure or plasticity-induced shifts in the development of a cohort.

The individual-based model links individual-level traits and population dynamics, and the environmental dependence of these associations. The trait, in this case body mass, which is a labile, flexible trait, can be considered to be a state variable that reflects an individual's past experience and affects its future performance (Ozgul et al., 2014). The model also considers phenotypically plastic responses. In our model, individuals can adjust their state variable, body mass, in response to changes in their environment through plasticity in their growth rate.

2.5.4.2. Emergence. In the simulation model, population dynamics emerge as a result of individual fates, which are imposed stochastically from empirically observed relationships between stage-specific life-history processes and individual traits. All life-history processes are driven by changes in environmental factors. Additionally, the phenotypic plastic responses in growth rates emerge solely from the rules operating at the level of individuals.

2.4.4.3. Adaptation. Non-juveniles individuals can compensate for a bad start. We modeled plasticity in growth rate as the response of body mass to the body condition of the individual at the beginning of the active season (i.e., June) in comparison to the population distribution of body mass (i.e., internal environment). Plasticity is implemented by allowing an individual that has a bad start to increase its growth rate, thereby growing larger than their expected August body under non-plasticity conditions. Although body mass is directly related to an individual's fitness, plasticity in our model does not explicitly increase a measurement of an individual's fitness. In addition, we assumed that all individuals can potentially express a plastic response, that such response can vary from year to year and from individual to individual (i.e., plasticity is not fixed), and that it is not heritable.***2.5.4.4. Sensing.*** Marmots are able to sense their environment throughout the year and each marmot can relate this to its body mass condition. An individuals' fate is determined by the current values of temperature and bare ground date, and its current body mass.

2.5.4.5. Stochasticity. We included stochastic processes in several steps in the model. Individuals have a unique probability of survival and reproduction every time step. Additionally, the variability in the plastic response among individuals where plasticity was activated was introduced by selecting the magnitude of the plastic response from a uniform distribution over the interval [0, 3.2], chosen from observed values in the population.

2.5.4.6. Collectives. We consider the population to be a collective. The population and its size corresponds to the set of individuals at the end of an annual cycle. Within the population, individuals in each stage are governed by the same life-history functions of body mass, excluding the effects of plasticity on body mass, winter temperature, spring temperature and bare ground date.

2.5.4.7. Observations. To examine the performance of the model, we compare the observed population trajectory recorded from the field with the population trajectory emergent from the model. At each time step of the simulations, we recorded and analyzed the total number of individuals in the population for the baseline, non-plasticity model and for the experimental scenarios.

2.5.5. Initialization

The initial stage-size distribution at the beginning of the simulations corresponds to the female age distribution extracted from the estimated size of the female population in 1975 (i.e., a year before the first year of the environmental series). Each marmot was initialized with an August body mass randomly drawn from a normal distribution with mean and standard deviation determined by the life-history stage probability distribution. The initial weather conditions correspond to the values of winter temperature, spring temperature and bare ground in 1976. The model begins in August, just before the hibernation period.

2.5.6. Input Data

The model uses an external input that determines the yearly weather conditions of the system and the weather is not affected by the internal dynamics of the model. The data used to estimate the winter temperatures, spring temperatures and bare ground dates were obtained from the RMBL weather station (106º59.588'N, 38º773'W at 2,900 m) from 1976 to 2012. Winter and spring mean temperatures correspond to the average daily mean temperature in ºC calculated from November of the previous year to March of the current year, and to March to May of the current year, respectively. Bare ground represents the day of the year when no snow remained on the ground at the weather station.

2.5.7. Submodels

In our model, the submodels represent demographic processes and trait transitions. These life-history processes were modelled as a function of the weather conditions (i.e., external factors) and the individual's body mass (i.e., internal factors). We used previously parametrized equations (Maldonado et al. *in prep*) to describe the relationship between the life-history processes, the individual's body mass and the climatic factors. We used these equations to calculate the values for each life-history process for each individual at each time step. Here we provide a description of the process model by the submodel, and the statistical relationships describing each of the life-history processes (i.e., GLMs). The definitions of the variables are presented in Table 4-S1.

***2.5.7.1. Survival*:** At the beginning of the simulation, each female calculates her probability of survival based on her body mass in August. In our model, as is the case for the yellow-bellied marmots, mortality is due to predation or failing to survive the winter. The survival process is governed by a function that describes the probability that an individual of size *z* survives:

$$surv = 1 / (1 + (\exp (- (\mathrm{surv}_{\mathrm{I}} + (\mathrm{surv}_{\text{aug-mass}} * z) + (\mathrm{surv}_{\mathrm{sprT}} * \mathrm{sprT}) + (\mathrm{surv}_{\mathrm{winT}} * \mathrm{winT}) + (\mathrm{surv}_{\mathrm{BrGd}} * \mathrm{BrGd})))))$$

***2.5.7.2. Aging*:** At each time step in the simulation, the age of each individual is increased by one.

2.5.7.3. Reproduction: Each non-juvenile female two years or more in age that survived the hibernation period can reproduce with a probability based on her body mass in August. This process is governed by a function that describes the probability of a non-juvenile individual of size *z* reproducing the following year:

$$repr = 1 / (1 + (\exp (- (\mathrm{repr}_{\mathrm{I}} + (\mathrm{repr}_{\text{aug-mass}} * z) + (\mathrm{repr}_{\mathrm{sprT}} * \mathrm{sprT}) + (\mathrm{repr}_{\mathrm{winT}} * \mathrm{winT}) + (\mathrm{repr}_{\mathrm{BrGd}} * \mathrm{BrGd})))))$$

Each female that reproduced can wean a specific number of female offspring (i.e., weaned litter size) based on her body mass in August. The number of weaned offspring is defined by a function that describes the number of individuals that a non-juvenile individual of size *z* can wean:

$$\begin{aligned} \mathit{offs} = \exp\,(&\text{offs}_{\text{I}} + (\text{offs}_{\text{aug-mass}} * z) + (\text{offs}_{\text{sprT}} * \text{sprT}) + (\text{offs}_{\text{winT}} * \text{winT}) + \\ &(\text{offs}_{\text{BrGd}} * \text{BrGd})) \end{aligned}$$

Each female in the litter has a characteristic weaned body mass (i.e., offspring body mass). Her body mass is a function of her mother's body mass in August:

$$\begin{aligned} \mathit{offsize} = {} & \text{offsize}_{\text{I}} + (\text{offsize}_{\text{mom-mass}} * z) + (\text{offsize}_{\text{sprT}} * \text{sprT}) + (\text{offsize}_{\text{winT}} * \text{winT}) + \\ &(\text{offsize}_{\text{BrGd}} * \text{BrGd}) \end{aligned}$$

***2.5.7.5. Body mass update*:** Body mass is updated twice throughout the year. Individuals in the model can grow or shrink depending on the period of the year (i.e., ontogenetic growth). During winter (i.e., hibernation period), individuals lose body mass. The change in the body mass for an individual between August and June, the next year, is defined by the winter growth equation:

$$\begin{aligned} \mathit{growAJ}_0 &= \text{aj}_{\text{I}} + (\text{aj}_{\text{mass}} * z) + (\text{aj}_{\text{sprT}} * \text{sprT}) + (\text{aj}_{\text{winT}} * \text{winT}) + (\text{aj}_{\text{BrGd}} * \text{BrGd}) \\ \mathit{growAJ}_1 &= \text{growAJ}_0 + \text{aj}_{\text{IDif}} + (\text{aj}_{\text{age:massDif}} * z) \end{aligned}$$

During summer, (i.e., active period), individuals gain body mass. The relationship between the body mass in June (*z'*) and in August (*z*) is defined by the summer growth equation:

$$\begin{aligned} \mathit{growJA}_0 &= \text{ja}_{\text{I}} + (\text{ja}_{\text{mass}} * z') + (\text{ja-}_{\text{sprT}} * \text{sprT}) + (\text{ja}_{\text{winT}} * \text{winT}) + (\text{ja}_{\text{BrGd}} * \text{BrGd}) \\ \mathit{growJA}_1 &= \text{growJA}_0 + \text{ja}_{\text{IDif}} + (\text{ja}_{\text{age:massDif}} * z') \end{aligned}$$

2.6. Model parameterization and calibration

We used the outcome from a previous analysis done by Maldonado et al. (*in prep*) to parameterize the submodels (Supplementary Material Table 4-S1). Parameters related to growth rate plasticity were estimated using individual-based body mass data from individuals monitored between 1976-2012 at the RMBL.

To calibrate the baseline non-plasticity model where the population was comprised of individuals that had a fixed growth rate, we compared the population size trajectory predicted by the model with the field estimated female-population sizes trajectories. To examine the departures of the predicted population sizes from the empirical time series, we compared the observed population size to the calculated the 95% confidence interval for the predicted population size. If the observed size fell within the confidence interval we consider the model to be in agreement with the observed data.

2.7. Model comparison

To identify the effect of each parameter on the output of the model, we used both a one-factor-at-a-time (OAT) approach (Morris, 1991) and sensitivity experiments (Railsback and Grimm, 2012). We set up the experiments using the BehaviorSpace feature in NetLogo (Shargel and Wilensky, 2002). BehaviorSpace creates different scenarios by changing a single parameter per simulation, while keeping the others constant, and generates replicates of each scenario evaluated, allowing us to observe the variation in the output across different simulation runs. We simulated each scenario with 100 repetitions in order to account for stochasticity in the model, and recorded the population size at each time step of the simulation. We then calculated the mean and standard error of the population size at each time step for quantitative comparisons.

We performed the following simulations using different phenotypic plasticity scenarios, proportion of individuals allowed to express the plastic response and cost to plasticity (Table 4-S1).

a. No growth rate plasticity: This corresponds to the baseline non-plasticity model, where none of the individuals were allowed to express the phenotypically plastic response. Therefore, the system was governed simply by the equations that determined the fate and body mass transition in each time step (described in section 2.5.7.5). This model was used as the default for the sensitivity analysis.

b. Growth rate plasticity: In this scenario, non-juveniles individuals that were in bad body mass condition in June were allowed to express the phenotypic plastic response (*p*). We examined two sub-scenarios. Within each of the sub-scenarios examined, the proportion of individuals (*i*) allowed to express the plastic response varied between zero, one and two standard deviations below the average body mass in June in each time step, and the cost of plasticity (*c*) varied between zero and 0.0125. Therefore the body mass gain equation in section 2.5.7.5 was modified by *p* in the following way:

$$growJA_1 = \text{ja}_{\text{I}} + (\text{ja}_{\text{mass}} * z') + (\text{ja-}_{\text{sprT}} * \text{sprT}) + (\text{ja}_{\text{winT}} * \text{winT}) + (\text{ja}_{\text{BrGd}} * \text{BrGd}) + \text{ja}_{\text{IDif}} + (\text{ja}_{\text{age:massDif}} * z') + p$$

The cost of plasticity, *c* was included by penalizing survival. Therefore, the survival probability defined in equation in section 2.5.7.1 was modified by *c* in the following way:

$$surv - (surv * c)$$

b.1. No among-individual variation in plasticity: In this case, the individuals that were in bad conditions in June expressed the same amount of plasticity (*p*). We examined three sub-scenarios, each of them defined by a value of *p*. The plastic response in each sub-scenario corresponded to 1.74, 2.3 and 3.2 (square root units of body mass in grams). These values were selected from the observed values in the population, and correspond to the minimum, average and maximum growth rates.

b.2. Among-individual variation in growth rate plasticity: In this scenario, the individuals that were in bad conditions in June expressed a plastic response (*p*), but individuals differed in the amount of plasticity expressed. Plasticity values were chosen randomly from a uniform distribution over the interval [0, 3.26], chosen from observed values in the population (square root units of body mass in grams).

2.8. Simulation experiments

Once we identified the scenarios where the model prediction best agreed with the observed population size, we proceed to investigate the effects of plasticity in growth rate on population dynamics. To do this, we created three theoretical *climate variability scenarios* (warmer, colder and random) by sampling from the historical weather data. The *climate variability scenarios* were implemented by changing the occurrence probabilities of the weather types with respect to the historical probabilities. In the warmer scenario, warmer years had three times the probability of being selected compared to any other year type. By contrast, in the colder scenario, colder years had three times the probability of being selected compared to any other year type. In the random scenario, all year types had the same probability of being selected. We defined warm years as a year where the winter temperature was one standard deviation above its historical mean or the spring temperature was one standard deviation above its historical mean. A cold year was defined as a year where the winter temperature was one standard deviation below its historical mean or the spring temperature was one standard deviation below its historical mean. Both scenarios were evaluated under two different conditions of phenotypic plasticity (no-among individual variation and among individual variation) and two values of cost to plasticity (no-cost and cost). We ran each scenario 100 times over a period of 50 years. To evaluate if plasticity facilitates population persistence, we calculated and compared the population's probability of extinction under each scenario. The probability of extinction was defined as proportion of the 100 simulations where the population went extinct. We used a multiple proportions test to determine statistical differences among simulation within each climate scenario. The test was run using the prop.test function in R statistical environment ver. 3.1.1(R Core Team 2014).

3. Results

3.1. Baseline non-plasticity model

The population sizes predicted by the baseline non-plasticity model were consistently smaller than the observed population sizes (on average, there were 23 fewer animals). Nonetheless, particularly in the later years, the baseline non-plasticity model better tracked population size changes and overall, in 6 out of the 37 year-comparisons the observed population size was within the 95% confidence intervals of the predicted population size. Furthermore, the fact that the predicted population size was smaller than the observed population size (Figure 4-2) suggests that the baseline non-plasticity model has not captured all the factors that affect marmot population dynamics. Therefore, we would expect that if plasticity in growth rate were a mechanism compensating for a bad start, its inclusion in the model would improve the accuracy of the predicted population size.

3.2 Sensitivity analysis

The OAT-results are described separately for cost-related scenarios, and are presented in Table 4-S2 and supplementary material Figures 4-S1, and 4-S2.

3.2.1 No-cost of plasticity. All the models where individuals expressed a plastic response and there was no cost of plasticity, predicted the same or smaller population sizes than the baseline non-plasticity model (Figure 4-S1). When comparing the number of years that the observed population size fell within the confidence interval of the predicted population size, only one model performed better than the baseline non-plasticity model (Table 4-2). This model considered all individuals below the average population mass expressing a fixed value of plasticity of 2.3.

3.2.2 Cost of plasticity. When considering a cost of plasticity, the models where individuals did not differ in the amount of plasticity expressed, predicted the same or smaller population sizes than the baseline non-plasticity model (Supplementary material Fig. 4-S2). However, the models where there was individual heterogeneity in the amount of plasticity, predicted population sizes closer to the observed population sizes (bottom row in Supplementary material Fig. 4-S2). When comparing the number of years that the observed population size fell within the confidence interval of the predicted population size, only one model performed better than the baseline non-plasticity model (Table 4-2). This model considered all individuals below average population mass expressing plasticity and individual heterogeneity in the plastic response. This suggests that being able to vary growth rate plasticity is the best strategy for those individuals whose body mass is below the population average.

3.3. Climate variability scenarios

Our theoretical exploration of climate variation illustrated the relative importance of plastic responses under different future climatic scenarios. Compared to the baseline non-plasticity model, plastic responses in growth rate were more important under the colder scenario than under the warmer scenario. When the frequency of warmer years increased, the probability of extinction was very low for all of the scenarios explored (Table 4-3). There was no significant differences among the probabilities of extinction under warmer climates (χ^2 = 2.362, df = 4, p-value = 0.670). However, when the frequency of colder years increased, the probability of extinction depended on whether or not we assume a cost of plasticity. Indeed, without a cost, the probability of extinction was about the same as the baseline scenario when plasticity did not differ among individuals, but it was higher when it differed (Table 4-3). However, when costs were added, the probability of extinction increased when plasticity did not differ among individuals, but it was decreased when it differed. The differences among the probabilities of extinction were significant (χ^2 = 10.319, df = 4, p-value = 0.035). Finally, under random climate variation, when no cost was considered the population with fixed plasticity had a decrease in the probability of extinction, whereas when the cost was included, the simulations with differences in plasticity among individuals showed a smaller probability of extinction (Table 4-3). The differences among the probabilities of extinction were significant ($\chi^2 = 12.246$, df = 4, p-value = 0.016).

4. Discussion

We developed a stochastic, environmentally driven, individual based demographic model for yellow-bellied marmots. This model allowed us to evaluate the effect of individual phenotypic plasticity in growth rates on population dynamics and persistence where we varied the proportion of individuals that expressed plasticity and included a cost for plasticity. Our model showed that plasticity in growth rate, here defined as compensatory growth, affects population dynamics. Simulations where individuals could compensate for a bad start, with no cost to plasticity, had different population size trajectories than simulations without compensation or simulations with compensation and a cost to plasticity. Specifically, we found that when a large proportion of individuals in the population were allowed to compensate, and when the individuals expressed an average plasticity in growth rate, the population trajectory of the model better matched the observed population trajectory. We also found that if we assumed costs to plasticity, predicted population sizes were overall smaller than the estimated with the baseline non-plasticity model. However, this cost of plasticity was modulated by individual variation in plasticity: a population with all individuals expressing costly plasticity did better than a population where only a proportion of the individuals expressed costly compensatory growth. Together, this suggests that the population dynamics of yellow-bellied marmots is influenced by the ability of individual marmots to compensate their growth during the active period. However, the cost of plasticity we simulated may not be the cost that the marmots may experience. Finally, we demonstrated that compensatory growth could reduce the probability of extinction under colder and random climatic scenarios when there is individual heterogeneity and a cost to plasticity.

Because this is a mechanistic model that links environmental variation to population dynamics, these results provide novel insights into the rules by which organisms make decisions that trade-off current and future states. Moreover, our model incorporates variation among individuals in survival and reproduction that should be more biologically realistic (Vindenes et al., 2008). The fact that the baseline non-plasticity simulations did not perfectly capture the historical population fluctuations indicates that there are other mechanisms not considered in this model that are likely to influence marmot population dynamics. First, we do not know the fate of dispersers, and emigration makes it likely that these simulations overestimate mortality, which in turn may lead to a decrease in estimated population size. Second, we did not consider immigration. Although immigration is rare (Armitage, 2014), it ultimately plays an important role in the replacement of individuals in a population (Armitage, 1991). For example, in 1995, a prolonged snowfall caused a substantial population crash (Armitage, 2014), and our baseline non-plasticity model failed to capture the full recovery. This may reflect the absence, in the simulation, of female immigrants that contributed to reproduction. Additionally, marmots can respond to environmental fluctuations through phenotypic plasticity. Here we demonstrated that when growth rate plasticity was considered, the simulated models captured better the dynamics of the population.

Plasticity can mediate the effects of the environment, thus altering the (co)variation between traits through direct or delayed effects (Benton et al., 2006). In our population, compensatory responses resulted in larger end-of-season body sizes that previous studies determined are related to an increased probability of survival and reproduction (Ozgul et al., 2010; Maldonado et al. *in prep*). Larger individuals are more likely to survive (a direct effect) and this may result in a positive effect on fecundity during the subsequent season (a delayed effect), as has been previously identified in this population (Maldonado et al. *in prep*). Thus, compensatory growth may be an important mechanism that allows individuals to respond to changes in environmental factors that result in poor body conditions (i.e., individuals that are below the average population mean body mass).

The sensitivity analysis indicated, in two ways, that the proportion of individuals engaging in compensatory growth influences population dynamics, and the cost of expressing such compensatory response has an effect on population dynamics. First, we showed that the population sizes predicted by the simulations where all individuals that were below the average population body mass compensated their growth were closer to the observed population size. Thus, individuals in poor body conditions at the beginning of the season could benefit from a compensatory response. This is because the demographic parameters like survival and reproduction rate are size-dependent. Therefore, increases in body mass can positively affect the population dynamics. Second, we showed that the predicted population sizes of the simulated models that included individual heterogeneity in their compensatory growth and a cost of plasticity were closer to the observed population sizes than the baseline model. Therefore, if growth rate plasticity varies among-individuals, the population can pay the cost of plasticity. This shows that variation among individuals is dynamically important (Pfister and Stevens, 2003).

Although it has been proposed that phenotypic plasticity decreases the probability of extinction (Wennersten and Forsman, 2012), this was not the case in all of our scenarios. Compensatory growth can favor population persistence in the long term when future scenarios are highly variable, as shown by our random thermal series. Plasticity in compensatory growth allows individuals to catch up and reach a body mass closer to the population mean. Thus, in our case, plasticity may be shifting the population mean for body mass upwards due to an increase in the number of larger individuals. However, the effects of an increase in body size would not play a role until the next breeding season, and its effect would depend upon the way individual survival relates to factors such as weather conditions. In our scenarios where there is no pattern in the frequency of cold or warm years, individuals can recover from less favorable climate conditions. However, in our warmer future scenarios, individuals are more likely to survive and there is a positive effect of climate on growth (see sign of the coefficients in the equations governing each of the submodels). Thus, populations are less likely to go extinct and can increase in size. In contrast, in our colder future scenarios, survival and growth are negatively affected (see sign of the coefficients in the equations governing each of the submodels), and there may be carry-over effects from one season to the next (Harrison et al., 2011). Under these scenarios, individuals can gain enough mass through plasticity to survive hibernation, but possibly not enough to afford the cost of reproduction. Finally, if plasticity is costly, not surprisingly we found that the probability of extinction increased. This may be due to the fact that in our population fluctuations in survival is a key factor influencing the population dynamics (Maldonado et al. *in prep*) and the cost of growth rate plasticity negatively influenced the probability of survival.

In conclusion, individual-based models allowed us to gain a deeper understanding of individual differences in the mechanisms that govern population fluctuations in comparison to similarly structured population-level models, such as matrix projection models (MPM; Caswell, 2001) or integral projection models (IPM; Easterling et al., 2000) that assume uniformity across individuals. Our results highlight the importance of individual heterogeneity in phenotypic plastic responses and indicate that compensatory response is a mechanism by which marginal individuals can cope with adverse environmental scenarios. The model also highlights the importance of better understanding the precise costs of phenotypic plasticity (i.e., Charmantier et al., 2008b) so as to be able to properly include them in population models. Future modeling exercises could also benefit from understanding how other factors such as the social environment, weather, and food availability, including their spatial variability, affect compensatory responses. While our model is specific to yellow-bellied marmots, the modeling approach we used in this paper can be applied to other systems in which population dynamics are size dependent and can be used to explore other scenarios under which phenotypic plasticity at the individual level may be important, for example spatial variability in food availability driven by environmental conditions.

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Figures

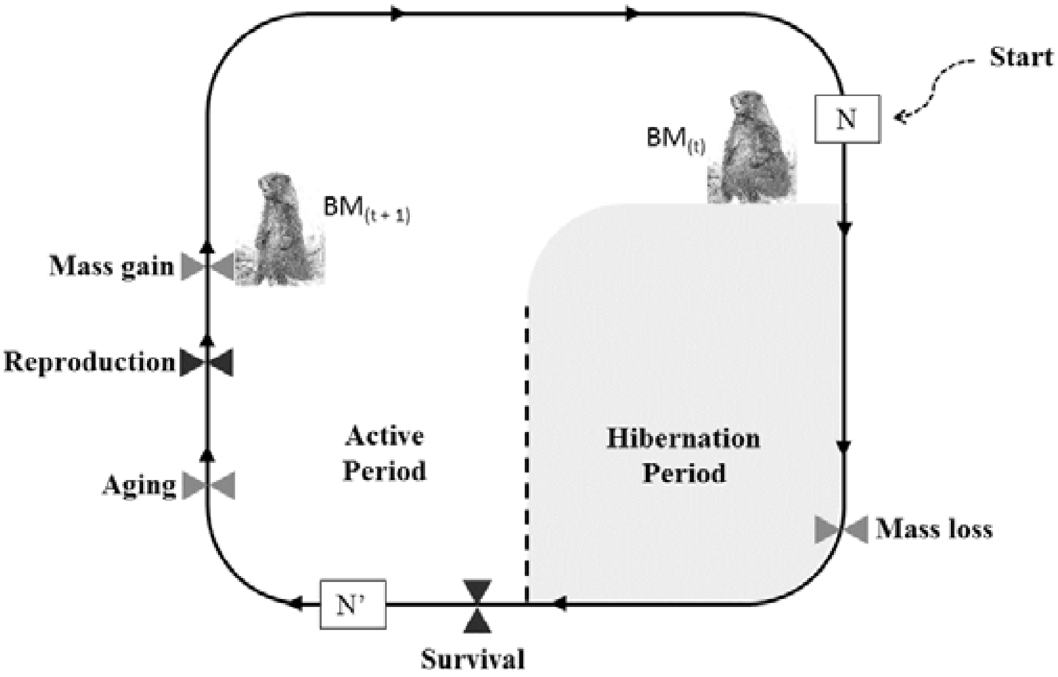

Figure 4-1. Life cycle diagram of yellow-bellied marmots and census points. The diagram illustrates the total number of individuals of size z at time t and at time t + 1. The ontogenetic growth transition was split into two parts. The first part corresponds to the ontogenetic growth from August in year t to June the next year t + 1 (i.e., winter growth), whereas the second part represents the ontogenetic growth from June to August in the year t + 1 (i.e., summer growth). In this case, reproduction occurs before the census period therefore, new born individuals are censused at the time t before any mortality occurs but they do suffer mortality before their next census at time t+1 at age 1. Individuals must survive with a size-dependent probability to be able to reproduce and contribute new recruits to the population, and to population growth in the next year. BM: body mass.

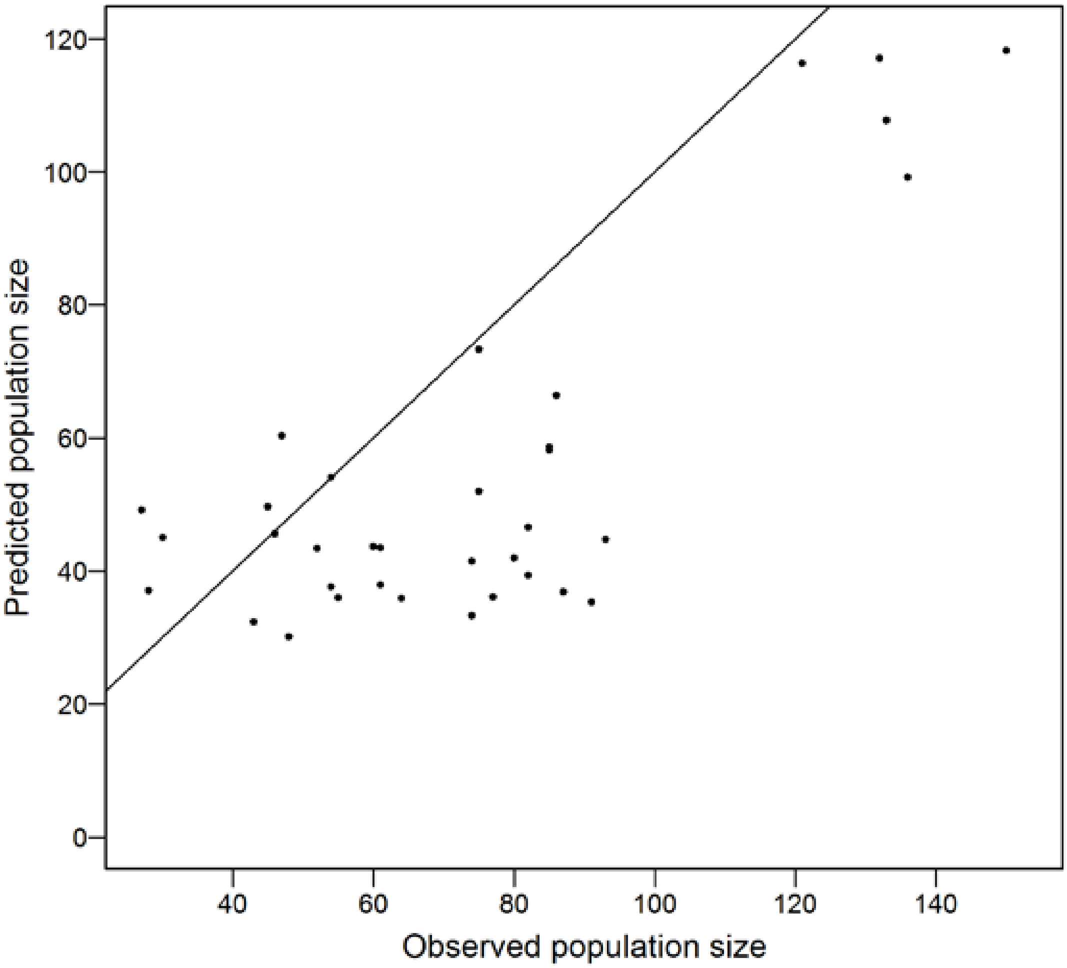

Figure 4-2. Scatterplot representing the observed and predicted population size for the period from 1976 – 2012. The black line corresponds to the 1:1 relationship between observed and predicted population size.

Tables

Table 4-1. Parameters used for OAT-sensitivity analyses. The baseline model includes no plasticity in growth rate. Results of the analysis are described in section 3.2.

Parameter	Analyzed range	Description
Growth rate plasticity	No among-individual variation: 1.74, 2.31, 3.25	The range represents expected values of population-specific distributions. The values correspond to the minimum, mean and maximum of the distribution.
	Among-individual variation	Individuals within the population can differ in the amount of plasticity. The value of plasticity each individual can express depends on a uniform distribution.
Cost to plasticity	0, 0.0125	The expression of a plastic response is assumed to have a cost. There are no previous studies that explore this cost we included an estimated value.
Proportion of individuals expressing plasticity	0, 1, 2	Variations in the body condition of the individuals in the population can be defined by how far is each individual from the population mean.

Table 4-2. Experimental design for the OAT-sensitivity analyses. The numbers indicate the number of years that the observed population size fell within the 95% confidence interval of the predicted population size.

Cost	Proportion of individuals	Plasticity in growth rate			
		No among-individual variation			Among-individual variation
		1.74	2.31	3.25	[0, 3.25]
0	0	6	9[b]	6	6
	1	4[w]	6	4[w]	4[w]
	2	6	3[w]	6	6
0.0125	0	7[b]	3[w]	3[w]	9[b]
	1	2[w]	1[w]	0[w]	6
	2	1[w]	2[w]	3[w]	3[w]

[b] Indicates that the simulation model did better than the baseline non-plasticity model.

[w] Indicates that the simulation model did worse than the baseline non-plasticity model.

Table 4-3. Probability of extinction of the population under three theoretical climate variability scenarios (warmer, colder and random). The experimental simulations included two types of plasticity: non-among individual variation (p = 2.31), and among-individual variation, and considered a cost for plasticity. The probability of extinction corresponds to the proportion of the 100 simulations where the population went extinct.

Type of plasticity in growth rate	Cost	Colder	Warmer	Random
No	**-**	0.11	0.02	0.44
Fixed	**Yes**	0.17	0.01	0.45
	No	0.09	0.01	0.25
Individual variation	**Yes**	0.12	0.0	0.36
	No	0.23	0.02	0.44

Supplementary Material

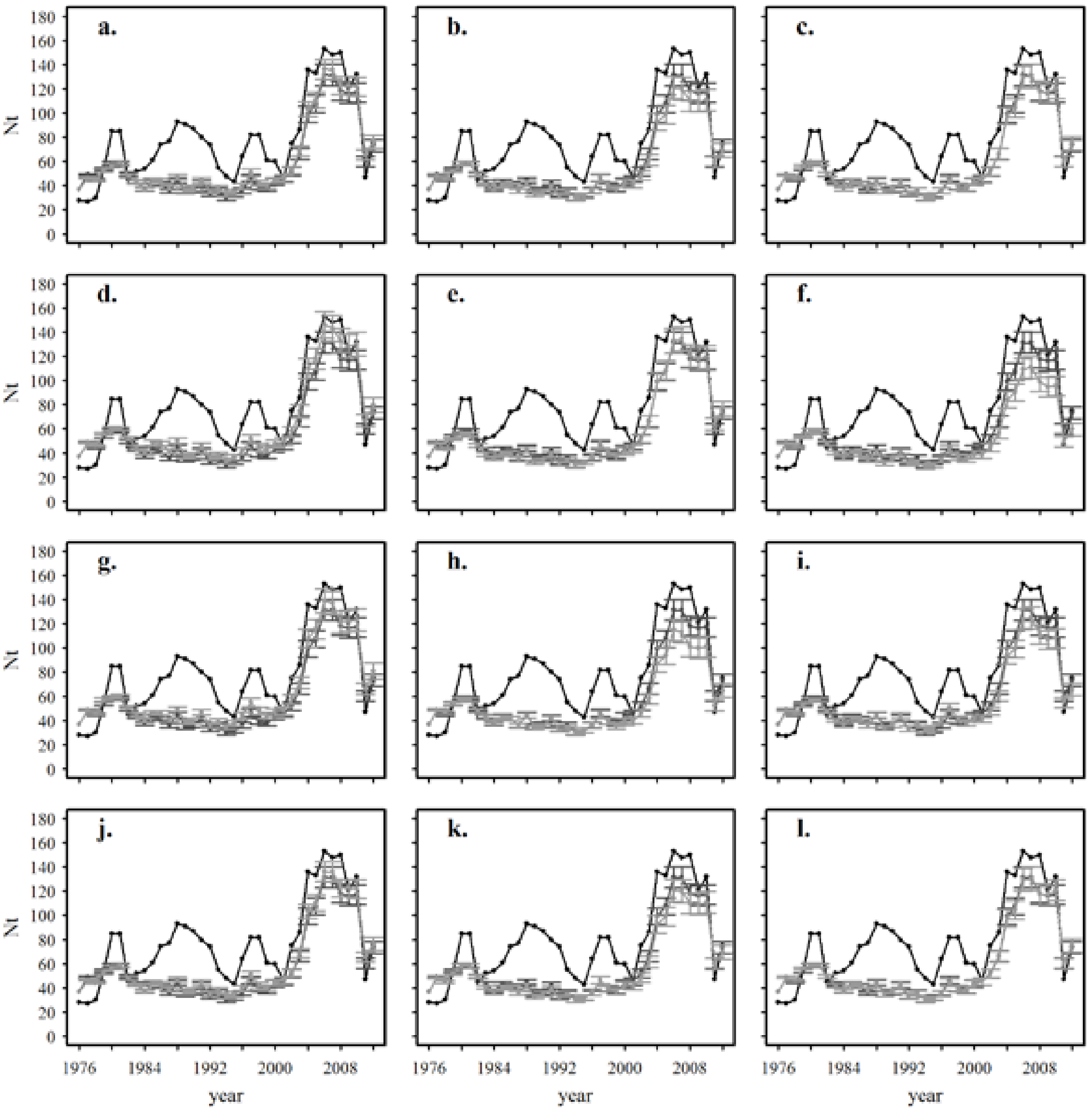

Figure 4-S1. Population size trajectories (1976 – 2012) obtained for the different scenarios with no cost of plasticity defined for OAT-sensitivity analyses. The baseline model has no plasticity in growth rate. Observed population size (black line), baseline prediction (dark gray line), and prediction under varying assumptions about plasticity (light gray line). The rows represent variation in the amount of plasticity express by the individuals in the population. From top to bottom, the first three rows illustrate non-among individual variation, with values 1.74, 2.31, 3.25. The last row illustrates among individual variation in plasticity. The columns represent the proportion of individuals expressing a plastic response. An individual is in poor condition if its body mass is below the average population body mass (± SD). From left to right, the columns correspond to 0, 1, and 2 standard deviations below the population mean.

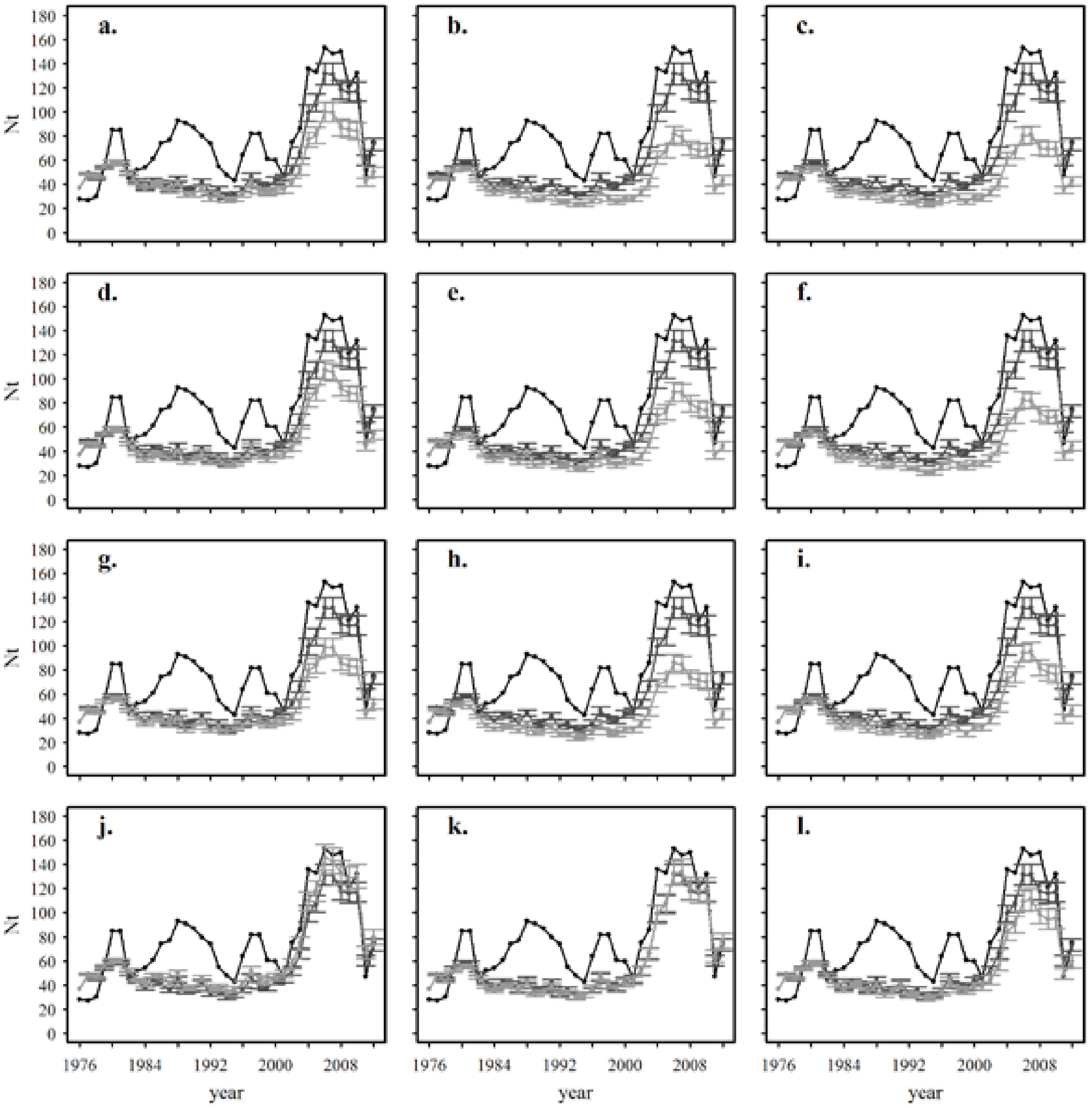

Figure 4-S2. Population size trajectories (1976 – 2012) obtained for the different scenarios with a cost of plasticity defined for OAT-sensitivity analyses. The baseline model has no plasticity in growth rate. Observed population size (black line), baseline prediction (dark gray line), and prediction under varying assumptions about plasticity (light gray line). The rows represent variation in the amount of plasticity express by the individuals in the population. From top to bottom, the first three rows illustrate non-among individual variation, with values 1.74, 2.31, 3.25. The last row illustrates among individual variation in plasticity. The columns represent the proportion of individuals expressing a plastic response. An individual is in poor condition if its body mass is below the average population body mass (± SD). From left to right, the columns correspond to 0, 1, and 2 standard deviations below the population mean.

Table 4-S1. Average parameter estimates used in the equations that describe the association between August mass (z) (square root transformed) and demographic and trait-transition rates. The functions ontogenetic growth in winter, ontogenetic growth in summer additionally included stage category and the interaction between stage category and body mass in the fixed effects. Statistical functions were fitted to data on female yellow-bellied marmots of all ages from a population in and around the Rocky Mountain Biological Laboratory (RMBL) studied between 1976 and 2012.

Process	Parameter	Value
Survival	Surv_{I}	-1.9559
	$\text{Surv}_{\text{aug-mass}}$	0.1623
	$\text{Surv}_{\text{SprT}}$	0.0002
	$\text{Surv}_{\text{WinT}}$	-0.0677
	$\text{Surv}_{\text{BrGd}}$	-0.0001
Reproduction	Repr_{I}	-2.5270
	$\text{Repr}_{\text{aug-mass}}$	0.2250
	$\text{Repr}_{\text{sprT}}$	0.0333
	$\text{Repr}_{\text{winT}}$	0.1624
	$\text{Repr}_{\text{BrGd}}$	0.0014
Weaned litter size	Offs_{I}	-0.5567
	$\text{Offs}_{\text{aug-mass}}$	0.0955
	$\text{Offs}_{\text{SprT}}$	-0.0035
	$\text{Offs}_{\text{WinT}}$	0.0017
	$\text{Offs}_{\text{BrGd}}$	-0.0005
Offspring size	$\text{Offsize}_{\text{I}}$	7.6681
	$\text{Offsize}_{\text{mom-mass}}$	0.2372
	$\text{Offsize}_{\text{sprT}}$	0.1069
	$\text{Offssize}_{\text{winT}}$	0.0015
	$\text{Offsize}_{\text{BrGd}}$	-0.0026
	$\text{Offsize}_{\text{sd}}$	0.7709
Ontogenetic growth-Winter	$\text{GrowAJ}_{\text{WinT}}$	0.0560
	$\text{GrowAJ}_{\text{BrGd}}$	0.0133
	$\text{GrowAJ}_{\text{age:massDif}}$	0.0640
	$\text{GrowAJ}_{\text{sd}}$	0.5724
Ontogenetic growth-Summer	GrowJA_{I}	10.9990
	$\text{GrowJA}_{\text{Idiff}}$	-0.6090
	$\text{GrowJA}_{\text{mass}}$	0.3603
	$\text{GrowJA}_{\text{SprT}}$	0.0243
	$\text{GrowJA}_{\text{WinT}}$	0.0644
	$\text{GrowJA}_{\text{BrGd}}$	0.0005
	$\text{GrowJA}_{\text{age:massDif}}$	0.0413
	$\text{GrowJA}_{\text{sd}}$	0.6112

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