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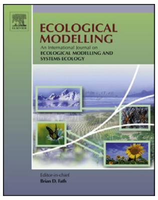

Can individual variation in phenotypic plasticity enhance population viability?

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ABSTRACT

In response to climatic and other sources of environmental 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 to seasonality, as well as variation in climatic factors, may affect body mass growth rates. To cope with the consequences of a harsh period, individuals may, for example, compensate for lost body mass by accelerating their growth rate in the following period. Phenotypically plastic responses like this can, therefore, directly affect body mass, which may affect individual fitness and, ultimately, population dynamics. Here, we use a well-studied population of yellow-bellied marmots, *Marmota flaviventris*, in Colorado to parametrize and develop an individual-based model (IBM) to investigate how phenotypically plastic responses in body mass growth rate may compensate for an individual's bad start after a harsh period (compensatory growth), and to explore whether individual variation in compensatory growth favors population persistence under less favorable climatic scenarios. A simulation model that allowed marmots with a body mass less than the population's average body mass to compensate their growth provided the best match with observed population sizes, suggesting the importance of trade-offs in population dynamics. We also found that compensatory growth plays an important role in decreasing the probability of extinction under both less favorable colder and random climate scenarios. Our results lead to a deeper understanding of the mechanisms that govern population fluctuations and highlight the importance of quantifying the fitness cost of phenotypically plastic responses.

1. Introduction

Individuals within a population may adjust behavioral, morphological or physiological responses to varying environmental conditions 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 being experienced (Bradshaw, 1965; Pigliucci, 2001), is a widely documented phenomenon in natural populations (Gotthard and Nylin, 1995). Plasticity can influence vital rates, and thereby population dynamics and extinction risk. As a result, 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 important to explore the population-level consequences of individual phenotypic plasticity since change in environmental conditions can affect the availability of resources, with consequences for the energy available to an organism and thereby its fitness.

Seasonal environments create challenges for organisms with regard to annual biological events, such as the timing of reproduction, especially when environmental factors vary from one year to the next (Reed et al., 2010). Organisms may undergo behavioral, physiological and morphological responses as a way to cope with seasonal variation in food resource. During winter, organisms may undergo a period of reduced energy intake that results in a depletion of energy reserves and body mass, whereas during the summer

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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 following season (Harrison et al., 2011). Body mass dynamics are, therefore, a key element that can affect life-history processes of a species, including survival and reproduction (Blanckenhorn, 2000). Thus, we might expect natural selection to favor response mechanisms that permit individuals to compensate for an environmentally induced period of slow growth (Metcalfe and Monaghan, 2003).

In seasonal environments, individuals can cope with the consequences of a harsh period such as winter through compensatory growth (Nicieza and Metcalfe, 1997; De Block et al., 2007). Compensatory growth is a form of phenotypic plasticity (Ab Ghani and Merilä, 2014) by which individuals respond to environmental cues indicating that an individual is relatively small at a given point in time with regard to future energy needs (Metcalfe and Monaghan, 2001). Compensatory growth allows individuals to compensate by accelerating growth rates to reduce the risk of having a sub-optimal size during a future stressful period (Ali et al., 2003; Metcalfe and Monaghan, 2001). Compensation may occur in structural components as well as body mass (Abrams et al., 1996; Metcalfe and Monaghan, 2001; Nicieza and Metcalfe, 1997) and, in both cases, influence an individual's fitness (Blanckenhorn, 2000; Stearns, 1992). The fact that growth rates vary among individuals within a population (Kvist and Lindström, 2001), suggests that there may be plasticity in growth rates among individuals due to differences in body mass since growth rates respond to the individual's current body condition or state (Hornick et al., 2000; Metcalfe and Monaghan, 2001). Compensatory growth may, however, be costly (reviewed in Dmitriew, 2011; Hector and Nakagawa, 2012). Depending on whether accelerated growth affects energy allocation, individuals that accelerate their growth rate through increased foraging may pay an immediate cost in the form of delays in structural development (Arendt and Wilson, 2000), individual performance (e.g. swimming sprinting speed; Killen et al., 2014)reduced investment in tissue maintenance (Morgan et al., 2000) or reproduction (Auer et al., 2010; Lee et al., 2012, 2016), increased risk of predation while foraging (Gotthard, 2000). Rapid growth may lead to longer-term costs when it results in damage at the physiological or cellular level (Jennings et al., 1999; and reviewed in Metcalfe and Monaghan, 2001, 2003) and on a decreased lifespan (Lee et al., 2013). Furthermore, other costs, such as reduced quality and fitness of offspring, can also be expected, but these have been less well explored (Ab Ghani and Merilä, 2014).

Here, we develop a non-spatially explicit individual-based model (IBM) to study the effects of phenotypically plastic responses of seasonal growth rate (herein compensatory growth) on the probability of population extinction. In our model, individuals can respond, in general, to the changes in environmental conditions through phenotypic plasticity, paying an immediate cost when they do so. The cost paid by individuals was assumed to be less than the benefits gained through plasticity. Additionally, we assumed that individuals may differ in their degree of plastic response to environmental conditions. Thus, we hypothesize that if individuals start the foraging season in poor conditions (i.e., they are below the average June body mass), then they can compensate by gaining mass faster than would occur absent a plastic response, whereas individuals in good condition will put on mass without responding plastically. This compensatory response can reduce the probability of extinction of a population under more extreme climate scenarios.

Our model focuses on the population dynamics of a well-studied population of yellow-bellied marmots, *Marmota flaviventris*; obligately hibernating, ground dwelling, sciurid rodents, in Colorado (Armitage, 2014; Blumstein, 2013). 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 reduced over-winter mortality (Ozgul et al., 2010). Ozgul et al. (2010) suggested that the increase in body mass is an environmentally driven effect, thus changes in body mass can be due to phenotypically plastic responses, in this case a population level response that affects all individuals. However, individuals differ in their genotypes, their ability to express a trait, and their ability to respond to environmental conditions. Furthermore, individuals can differ in their ability to compensate. Thus, within a population, individuals intrinsically vary in their June body mass, and some such individuals have relatively low weight compared to others in the same cohort. For these individuals, compensatory responses can be an important mechanism to catch up after a bad start following hibernation by growing faster than others. Thus, this compensatory response may have important, direct fitness consequences at the individual level, as well as indirect fitness consequences at the population level.

2. 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).

Marmot population biology is greatly influenced by a variety of environmental conditions, including 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).

2.1.1. Life history data

Our marmot population is located in the East Valley of Gunnison County, Colorado, USA, with the marmots patchily distributed between elevations of 2700–3100 m.a.s.l. (Armitage, 2014). The study began in 1962, but for this model, we used data collected since 1976 because we have more detailed weather data after that date. Each year, marmots are live-trapped, individually identified with a unique combination of numbered ear tags, weighed, and sexed. In addition, we record each female's reproductive status (for details see Armitage and Wynne-Edwards, 2002) and age category: Juveniles (<1 year old), yearlings (1 year old) and adults (>1 year old). We compared our simulation results with data collected from female marmots at the RMBL.

2.1.2. Body mass estimation

For each 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 were fitted as random effects (details in Appendix A).

2.2. Yellow bellied marmot model description

Trait-based demographic analyses have typically used integral projection models (Easterling et al., 2000; Ellner and Rees, 2006) or physiologically structured population models (González-Suárez et al., 2011; Van Kooten et al., 2007) that allow for 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 simulation 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 5.3.1 (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., 2010, 2006).

2.2.1. Purpose

The purpose of our model is to understand how seasonal compensatory growth affects the population dynamics in yellow-bellied marmots. We specifically ask whether individual variation in compensatory growth can act as a mechanism that buffers the effect of environmental variation thus reducing the probability of extinction in the study area over a period of 50 years.

2.2.2. Entities, state variables, and scales

Our single-species model is non-spatial and has two hierarchical levels: individuals and populations, and one type of entity: female marmots. Each marmot is characterized by the following state variables: individual identity (ID), age (in years) and seasonal body mass. For modeling purposes, we use the marmot's age to categorize each individual into one of two life-history stages: juveniles (<1 year old) and non-juveniles ($\geq$1 year old), where, it should be noted, "non-juveniles" refers to both yearling and adult marmots. Body mass of each individual was cube root transformed to stabilize the variance and improve the normality of the residuals in the statistical models used for parameterizing the submodels. The population is made up by all the individuals, and is characterized by a single state variable: total number of individuals.

The behavior of the model is affected by the annual weather conditions that marmots experience during the winter and spring seasons. The environmental factors describing seasonal fluctuations are winter mean temperature (°C), spring mean temperature (°C) and date of bare ground. Winter and spring mean temperatures correspond to the average daily mean temperature in °C 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 is the first day of the year when no snow remained on the ground at the RMBL weather station (see also Section 2.2.6.). The time horizon of the model is 37 years, except for the climate variation scenarios for which the time horizon is 50 years.

2.2.3. Process overview and scheduling

The model uses annual time steps that simulate the hibernating and active seasons of the marmot's annual cycle. Each year, an individual follows the following events (Fig. 1; sub-model names are given in italics and explained in the seventh ODD element below): (i) *Survival*: marmots survive over winter with a probability based on their body mass before hibernation (estimated as August body mass), and the winter and spring conditions (i.e., temperature and the snow; see Section 2.2.7.1); (ii) *Ageing*: if an individual survives, it increases in age by one year; (iii) *Reproduction*: beginning at age two, an individual reproduces and weans a litter with probability based on its August body mass, and the winter and spring conditions (i.e.,temperature and snow cover; see Section 2.2.7.3); juvenile individuals are born with a body mass based on their mothers' August body mass; (v) *Update body mass*: all non-juvenile individuals update their body mass. This last event occurs in two steps. The first step represents the loss of mass over winter; here, individuals update their June body mass based on their previous 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. Individuals can either follow the baseline seasonal growth or they can use compensatory growth rules. To keep the model biologically realistic, a control rule stopped the simulation when the population size reached 600 marmots.

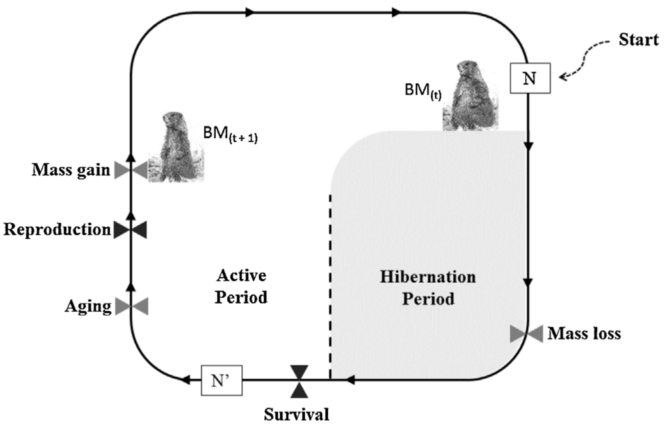

Fig. 1. Life cycle diagram of yellow-bellied marmots and census points. The diagram illustrates the total number of individuals of size z at time t and at time $t+1$. The ontogenetic growth transition was split into two parts. The first part corresponds to the ontogenetic growth from August in year t 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, newly born individuals are censused at time t before any mortality occurs, but they 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, contribute new recruits to the population, and thereby to affect population growth in the next year.

2.2.4. Design concepts

2.2.4.1. 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 individuals in a cohort. The individual-based model links individual-level traits and population dynamics, as well as the environmental dependencies for these associations. The trait, in this case body mass, is flexible and can be considered to be a state variable that reflects an individual's past experience and how this 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. In this case, plasticity is modelled as the amount of August body mass that an individual can gain above and beyond their expected August body mass without plasticity.

2.2.4.2. Emergence. In the simulation model, population dynamics emerge as a result of individual rates, 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. The phenotypically plastic responses in growth rates are imposed via rules operating on individuals

2.2.4.3. Adaptation. The rules indirectly represent adaptation. Non-juveniles can compensate for a bad start through seasonal compensatory growth (i.e., plasticity in body mass growth rate).

Compensatory growth is implemented by a rule stating that a non-juvenile individual whose body mass is below the average population body mass in June increases its growth rate, thereby growing larger than its expected August body mass without compensatory growth. Though the rule applies to all individuals, only those with a below average body mass in June will implement the rule and express a plastic response. Furthermore, whether an individual implements the response rule can vary annually. Thus, individual plasticity is not fixed across generations. However, although the capacity to have a plastic response may be a heritable trait (Scheiner and Lyman, 1989), the occurrence of the plastic response is triggered by the state of a marmot and it is not heritable.

2.2.4.4. Objectives. In our model, behavioral rules do not explicitly increase the reproductive success of marmots

2.2.4.5. Learning. Marmots in our model are not affected by their previous experience (i.e., they do not have the ability to learn)

2.2.4.6. Prediction. Marmots in our model are not able to estimate future consequences of their decisions. Their response to the environment is based on their current environment

2.2.4.7. Sensing. Marmots are able to sense their environment throughout the year and each marmot can relate this to its body mass condition. An individual's fate is determined by the current values of temperature, the bare ground date, and its current body mass.

2.2.4.8. Interaction. We assumed that there is no interaction among individuals in the population, for example no density dependence of growth and survival

2.2.4.9. Stochasticity. We included stochastic processes in several steps of the model. The probability of survival and of reproduction was estimated for each individual at every time step (each probability was calculated as defined in Sections 2.2.7.1, and 2.2.7.3). Additionally, when compensatory growth was activated we selected the magnitude of the plastic response from a probability distribution.

2.2.4.10. Collectives. We did not consider collectives

2.2.4.11. Observations. At each time step, we recorded the total number of individuals in the population

2.2.5. Initialization

Each simulation began with the same initial population conditions. The population size and age distribution at the beginning of the simulations corresponds to the female age distribution extracted from the female population in 1975. We choose to start with this year because it was the year before the first year with the complete environmental series covering all the weather variables used in the model. Each marmot was initialized with an August body mass that was randomly drawn from a normal distribution with mean and standard deviation determined from the life-history data. Because juveniles and non-juveniles differ in their body mass, we created a separated body mass distribution for each of the age-categories. 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.

2.2.6. Input data

The model requires demographic and trait-transition rates to describe the life-history processes: survival, reproduction and body-mass transition. The demographic and trait-transition rates used in the simulation model were extracted from fitted relationships among body mass, climate and survival and reproduction, the number of weaned offspring, the body mass of the offspring, and the body mass transitions between August to June and June to August. We used the individual-based outcome from generalized linear mixed models (GLMMs) from a previous analysis done by Maldonado et al. (*in prep*). As follows, the probabilities of survival and successful reproduction were estimated by fitting a binomial distribution (logit link) and the weaned litter size was estimated by fitting a Poisson distribution (log link). The seasonal mass gain (i.e., ontogenetic growth) and offspring mass were estimated by fitting a normal distribution (identity link). Each of the fitted models included body mass, the previous winter's temperature, spring temperature and the first day of bare ground as fixed effects and year as a random effect.

The model uses an external input that provides the yearly weather conditions of the system. The weather is exogenous to the model. The data used to estimate the average winter temperatures, average spring temperatures and bare ground dates were obtained from the RMBL weather station (106°59.588′N, 38°773′W at 2900 m) from 1976 to 2012.

2.2.7. Sub-models

Our model is composed of sub-models representing life-history processes and trait transitions. These processes were modelled as a function of the weather conditions (i.e., external factors) and an individual's body mass (i.e., internal factors). The average values of the parameter estimates and their names for each function, are presented in Table 1.

2.2.7.1. Survival. Each female marmot in our simulation survives the hibernation period with a probability of survival based on its August body mass (i.e., body mass before hibernation) and the environmental conditions experienced during hibernation (winter and spring). In our model, as is the case for the yellow-bellied marmots, mortality is due to predation or failing to survive the winter. Hibernating environmental conditions are summarized by the winter temperature (winT) and the spring temperature (sprT), and the bare ground date (BrGd). We did not differentiate between these two sources. The survival process represents apparent survival and is governed by a function that describes the probability that an individual of mass z survives:

$$
\begin{aligned}
surv = {} & 1/(1 + (\exp(-(\mathrm{surv_I} + (\mathrm{surv_{aug\text{-}mass}} * z) \\
& + (\mathrm{surv_{sprT}} * \mathrm{sprT}) + (\mathrm{surv_{winT}} * \mathrm{winT}) \\
& + (\mathrm{surv_{BrGd}} * \mathrm{BrGd}))))) \qquad (1)
\end{aligned}
$$

Because compensatory growth is costly, we included a cost of plasticity by penalizing survival ($s\,c$) and reproduction (rc; see Section 2.2.7.3). A reduction in survival can result from an increase in the risk of predation associated with elevated levels of foraging activity (Jönsson et al., 1996; Gotthard, 2000). The default value of sc was 0.009 and, for simplicity, was estimated as the difference in survival probability between non-juvenile female marmots that showed compensatory growth during the active season and the ones that did not (i.e., were below the population average June mass and did not grow larger than the population average August mass), as described in Section 2.3. The cost reduced the survival probability of an individual, thus the survival function was adjusted in the following way:

$$surv' = surv * (1 - sc) \qquad (2)$$

Table 1
Average parameter estimates used in the equations that describe the association between August mass (z) (cube root transformed) and demographic and trait-transition rates (presented in Section 2.2.7). 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. All functions included body mass and the climatic variables winter temperature, spring temperature and bare ground date as fixed effects and year as a random effect. Generalised linear mixed effect models 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	Name	Fitted function	Parameter	Parameter name	Value
Survival	surv	Logit	surv_{I}	Survival intercept	−2.229
			$\text{surv}_{\text{aug-mass}}$	August mass coefficient	0.162
			$\text{surv}_{\text{SprT}}$	Spring temperature coefficient	0.0002
			$\text{surv}_{\text{WinT}}$	Winter temperature coefficient	−0.068
			$\text{surv}_{\text{BrGd}}$	Bare ground coefficient	−0.0001
Reproduction	repr	Logit	repr_{I}	Reproduction intercept	−2.605
			$\text{repr}_{\text{aug-mass}}$	August mass coefficient	0.225
			$\text{repr}_{\text{sprT}}$	Spring temperature coefficient	0.033
			$\text{repr}_{\text{winT}}$	Winter temperature coefficient	0.162
			$\text{repr}_{\text{BrGd}}$	Bare ground coefficient	0.001
Weaned litter size	offs	Log	offs_{I}	Offspring number intercept	−0.557
			$\text{offs}_{\text{aug-mass}}$	August mass coefficient	0.096
			$\text{offs}_{\text{SprT}}$	Spring temperature coefficient	−0.004
			$\text{offs}_{\text{WinT}}$	Winter temperature coefficient	0.002
			$\text{offs}_{\text{BrGd}}$	Bare ground coefficient	−0.0005
Offspring size	offsize	Gaussian	$\text{offsize}_{\text{I}}$	Offspring size intercept	7.788
			$\text{offsize}_{\text{mom-mass}}$	Mom August mass coefficient	0.237
			$\text{offsize}_{\text{sprT}}$	Spring temperature coefficient	0.107
			$\text{offssize}_{\text{winT}}$	Winter temperature coefficient	0.002
			$\text{offsize}_{\text{BrGd}}$	Bare ground coefficient	−0.003
			$\text{Offsize}_{\text{var}}$	Variance	0.771
Ontogenetic growth-Winter	GrowAJ	Gaussian	aj_{I}	August mass intercept	1.975
			aj_{Idiff}	Age difference intercept	0. 074
			aj_{mass}	August mass coefficient	0.651
			aj_{SprT}	Spring temperature coefficient	0.021
			aj_{WinT}	Winter temperature coefficient	0.056
			aj_{BrGd}	Bare ground coefficient	0.013
			$\text{aj}_{\text{ge:massDif}}$	Interaction age and mass coefficient	0.064
			aj_{var}	Variance	0.572

Table 1 (*Continued*)

Process	Name	Fitted function	Parameter	Parameter name	Value
Ontogenetic growth-Summer	GrowJA	Gaussian	ja_{I}	June mass intercept	10.946
			$\mathrm{ja}_{\mathrm{Idiff}}$	Age difference intercept	−0.612
			$\mathrm{ja}_{\mathrm{mass}}$	June mass coefficient	0.360
			$\mathrm{ja}_{\mathrm{SprT}}$	Spring temperature coefficient	0.024
			$\mathrm{ja}_{\mathrm{WinT}}$	Winter temperature coefficient	0.065
			$\mathrm{ja}_{\mathrm{BrGd}}$	Bare ground coefficient	0.0005
			$\mathrm{ja}_{\mathrm{age:massDif}}$	Interaction age and mass coefficient	0.041
			$\mathrm{ja}_{\mathrm{var}}$	Variance	0.611

2.2.7.2. Aging. At each time step in the simulation, the age of each individual is increased by one. The age is used to determine when an individual is sexually mature, and the maximum age to which an individual can survive. Female maximum age in our data set is 14 years old.

2.2.7.3. 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 and the environmental conditions experienced during hibernation (winter and spring). Environmental conditions during hibernation are summarized by the winter (winT) and spring (sprT) temperature, and the bare ground date (BrGd). This process is governed by a function that describes the probability of a non-juvenile individual of mass *z* reproducing the following year:

$$\begin{aligned} \mathit{repr} = {} & 1/(1 + (\exp(-(\mathrm{repr}_{\mathrm{I}} + (\mathrm{repr}_{\mathrm{aug\text{-}mass}} * z) \\ & + (\mathrm{repr}_{\mathrm{sprT}} * \mathrm{sprT}) + \mathrm{repr}_{\mathrm{winT}} * \mathrm{winT}) \\ & + (\mathrm{repr}_{\mathrm{BrGd}} * \mathrm{BrGd}))))) \end{aligned} \tag{3}$$

We included the reproductive cost of plasticity (*rc*) by a penalty expressed through reducing the probability of reproduction. A reduction in the probability of reproduction can result from a trade-off in energy allocation (Stearns, 1992). The default value of *rc* was 0.017 and was estimated, for simplicity, as the difference between the reproduction probability among female individuals that did compensate and those that did not compensate (i.e., were below the population average June mass and did not grow larger than the population average August mass), as described in Section 2.3. The cost reduced the reproductive probability of an individual; hence the reproduction function was adjusted in the following way:

$$\mathit{repr}' = \mathit{repr} * (1 - \mathit{rc}) \tag{4}$$

Each female that reproduced can wean a specific number of female offspring (i.e., weaned litter size) based on her body mass in August and the environmental conditions she experienced during hibernation (winter and spring). Environmental conditions during hibernation are summarized by the winter (winT) and spring (sprT) temperature, and the bare ground date (BrGd). The number of weaned offspring is defined by a function that describes the number of females that a non-juvenile female of mass *z* can wean:

$$\begin{aligned} \mathit{offs} = {} & \exp(\mathrm{offs}_{\mathrm{I}} + (\mathrm{offs}_{\mathrm{aug\text{-}mass}} * z) + (\mathrm{offs}_{\mathrm{sprT}} * \mathrm{sprT}) \\ & + (\mathrm{offs}_{\mathrm{winT}} * \mathrm{winT}) + (\mathrm{offs}_{\mathrm{BrGd}} * \mathrm{BrGd})) \end{aligned} \tag{5}$$

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 and the environmental conditions that her mother experienced during hibernation (winter and spring). Environmental conditions during hibernation are summarized by the winter (winT) and spring (sprT) temperature, and the bare ground date (BrGd).

(6) $\mathit{offsize} = \mathrm{offsize}_{\mathrm{I}} + (\mathrm{offsize}_{\mathrm{momhbox\text{-}mass}} {}^{*} z) + (\mathrm{offsize}_{\mathrm{sprT}} {}^{*} \mathrm{sprT}) + (\mathrm{offsize}_{\mathrm{winT}} {}^{*} \mathrm{winT}) + (\mathrm{offsize}_{\mathrm{BrGd}} {}^{*} \mathrm{BrGd})$

2.2.7.4. 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. During the winter hibernation period, individuals lose body mass. The change in the body mass for an individual between August and June, the following year, is defined by the winter growth equation:

$$\begin{aligned} \mathit{growAJ}_0 = {} & \mathrm{aj}_{\mathrm{I}} + (\mathrm{aj}_{\mathrm{mass}} * z) + (\mathrm{aj}_{\mathrm{sprT}} * \mathrm{sprT}) \\ & + (\mathrm{aj}_{\mathrm{winT}} * \mathrm{winT}) + (\mathrm{aj}_{\mathrm{BrGd}} * \mathrm{BrGd}) \end{aligned} \tag{7a}$$

$$\mathit{growAJ}_1 = \mathrm{growAJ}_0 + \mathrm{aj}_{\mathrm{IDif}} + (\mathrm{aj}_{\mathrm{age:massDif}} * z) \tag{7b}$$

Here the body mass in June is defined by the body mass of the individual in August (*z*) the previous year and the environmental conditions experienced during hibernation. Environmental conditions during hibernation are summarized by the winter (winT) and spring (sprT) temperature, and the bare ground date (BrGd). Because juveniles and non-juveniles grow at different rates, each category has its own growth equation (*growAJ*$_0$ and *growAJ*$_1$, respectively). During the active period (i.e., summer), individuals gain body mass. The relationship between the body mass in June (*z*') and in August (*z*) is defined by the summer growth equations below. Summer growth is also influenced by the environmental conditions experienced during hibernation. Environmental conditions during hibernation are summarized by the winter (winT) and spring (sprT) temperatures, and the bare ground date (BrGd). Because juveniles and non-juveniles grow at different rates, each category has its own growth equation (*growJA*$_0$ and *growJA*$_1$, respectively). For juveniles the summer growth is defined by:

$$\begin{aligned} \mathit{growJA}_0 = {} & \mathrm{ja}_{\mathrm{I}} + (\mathrm{ja}_{\mathrm{mass}} * z') + (\mathrm{ja\text{-}}_{\mathrm{sprT}} * \mathrm{sprT}) \\ & + (\mathrm{ja}_{\mathrm{winT}} * \mathrm{winT}) + (\mathrm{ja}_{\mathrm{BrGd}} * \mathrm{BrGd}) \end{aligned} \tag{8a}$$

Non-juveniles can express *compensatory growth*. In this case, non-juveniles can grow larger than their expected August body mass if their body mass in June is below a threshold estimated from the population average body mass in June. The compensatory growth is included in the summer growth equation as follows: at the end of the season, marmots add to their August body mass, a value *p*, that represents the amount of mass gained over the summer. Thus, the summer growth is described by:

$$\begin{aligned} growJA_1 = {} & \mathrm{ja}_{\mathrm{I}} + (\mathrm{ja}_{\mathrm{mass}} * z') + (\mathrm{ja}\text{-}_{\mathrm{sprT}} * \mathrm{sprT}) + (\mathrm{ja}_{\mathrm{winT}} * \mathrm{winT}) \\ & + (\mathrm{ja}_{\mathrm{BrGd}} * \mathrm{BrGd}) + \mathrm{ja}_{\mathrm{IDif}} + (\mathrm{ja}_{\mathrm{age:massDif}} * z') + p \end{aligned} \tag{8b}$$

The value of *p* is defined at the beginning of the simulations. We used *p* to define two alternative strategies of *compensatory growth*. The first strategy corresponds to *Fixed gain in compensatory growth*. In this strategy, individuals gain the same body mass (*p*). The amount of gain was defined at the beginning of the simulation. We evaluated three levels of *p* corresponding to 1.75, 2.32 and 3.26 (cube root units of body mass in grams) that were determined from the observed population values. The values of *p* correspond to the low, average and high mass gain in the population, and were used to define three sub-scenarios. Thus, in the low gain sub-scenario, all the marmots that compensate would gain 1.75 (cube root units of body mass in grams) at the end of the season. The second strategy corresponds to *Variable gain in compensatory growth*. In this strategy, individuals differed in the amount of body mass (*p*) gained. The value of *p* was chosen randomly from a uniform distribution over the interval [0,3.26], the minimum and maximum amount of mass gained obtained from observed values in the population. This means that at every time step of the simulation, if an individual met the conditions for compensatory growth, the amount of mass it would gain was determined randomly (i.e., each individual would gain a different amount).

Because we were interested in identifying under which body condition individuals expressed compensatory growth, we first included a rule to characterize the body condition of the individual. Thus, individuals were allowed to express compensatory growth if their body mass in June was below a threshold estimated from the population average body mass in June. We created three thresholds: 1) *below average* (SD = 0): all individuals under the average body mass can express compensatory growth, 2) *poor body condition* (SD = 1): individuals whose body mass is one standard deviation below the population average, and 3) *very poor body condition* (SD = 2): individuals whose body mass is two standard deviations below the population average. Each threshold was evaluated separately in different runs of the model.

2.3. Model analysis

We used individual-based data from 1294 females monitored between 1976 and 2012 to parameterize our model. In our dataset, female's age ranged between 0 and 14 years old, and their body mass between 6.64–17.36 (cube root transformed grams) in June, and 7.46–18.92 (cube root transformed grams) in August. We recorded on average two reproductive events per female. Females produced on average four juveniles per litter. For the parameters in the sub-models (e.g., survival, reproduction) we used the individual-based outcome from generalized linear mixed models (GLMMs) that were used in a previous analysis done by Maldonado et al. (*in prep*) (Table 1). The compensatory growth values and the cost parameters were estimated using female individual-based body mass data (Table 2). To do this, we estimated the average body mass of the population at the beginning and at the end of the growing season (i.e., June and August body mass). Then, we divided the population into two groups: 1) individuals that were below the average June body mass and below the average body mass in August the same year (i.e., no compensatory growth), and 2) individuals that were below the average body mass in June and above the August body mass (i.e., compensatory growth). The gain in growth attributed to compensatory growth was calculated as the difference between the August mass of groups one and two. Similarly, the costs for survival and reproduction were calculated using the same reasoning. Thus, our model was calibrated at the individual-level, and therefore, we do not expect that the simulation trajectories from the model to accurately match the historical trajectory of the observed population. However, we predict a better fit of the model when including compensatory growth.

To assess the degree of concordance between a simulation model, such as the baseline model where the population is composed of individuals without compensatory growth or the compensatory growth model, with the observed data, we ran each model 500 times. For each run, we tracked the population annual rate of change, λ_t, predicted by the model, and computed the Pearson's product moment correlation coefficient (*r*) between the predicted λ_t and λ_{obs} calculated from the observed data. The best fitting model is taken to be the model with the combination of parameters that maximizes the correlation between the predicted and the observed λ. Correlations were estimated for each run using the cor.test function in R 3.3.1 (R Core Team, 2016), implemented in NetLogo using the R extension (Thiele and Grimm, 2010). Based on the results of the 500 runs, we calculated the mean correlation coefficient (*r*) and its 95% confidence interval. We identified significant differences between the baseline and the compensatory growth models by determining whether the confidence intervals of the models overlapped. We used the best fitting model in further analysis.

Once we identified the scenario (i.e., the set of parameter values) whose corresponding models best agreed with the observed population annual rate of change, λ_{obs}, we proceeded to evaluate the sensitivity of the model. To identify the extent to which change in the survival and reproductive cost parameters affected the population annual rate of growth, we used 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 evaluated the effect of survival and reproductive cost over a range from 0.004–0.022 and 0.008–0.027, respectively, with a constant increment of 10% for each run. We ran each scenario 100 times in order to account for stochasticity in the corresponding model. At each time step of the simulation, we recorded the population size, and calculated the population annual rate of change, λ_t for quantitative comparisons.

2.4. Simulation experiments

To investigate the effects of plasticity in growth rate on population dynamics under different climatic conditions, we created three *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. In contrast, for 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 years where the winter temperature was one standard deviation above its historical mean and/or the spring temperature was one standard deviation above its historical mean. Cold years were defined as years where the winter temperature was

Table 2
Parameters used in the model. The baseline model includes no plasticity in growth rate.

Parameter	Analyzed range	Description
Compensatory growth (growth rate plasticity)	Fixed gain in compensatory growth: 1.75, 2.32, 3.26	The range represents expected values of population-specific distributions. The values correspond to the minimum, mean and maximum of the distribution.
	Variable gain in compensatory growth	Individuals within the population can differ in the amount of plasticity. The value of plasticity each individual can express depends on a uniform distribution.
Survival cost to plasticity	0.004–0.022	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, with a default of 0.009
Reproductive cost to plasticity	0.008, 0.027	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, with a default of 0.017
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 each individual is from the population mean. Values represent the number of standard variation below the mean.

one standard deviation below its historical mean and/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 a cost to plasticity. We ran each scenario 500 times over a period of 50 years. To determine whether plasticity facilitated population persistence, we calculated and compared the population's probability of extinction under each scenario. The probability of extinction was defined as the proportion of the 500 simulations where the population went extinct. We used a multiple proportions test to determine statistical differences among simulations within each climate scenario. The test was performed using the prop.test function in R statistical environment ver. 3.3.1 (R Core Team, 2016).

3. Results

3.1. Baseline non-plasticity model

The Pearson's correlation test between the predicted and the observed λ shows that the parameters used in the baseline non-plasticity model provide a reasonably good match between predicted and observed lambda values ($r = 0.573$; 95% CI = 0.542–0.604) However, this result suggests that the baseline non-plasticity model has not captured all of the factors that affect the actual marmot population dynamics, and can be improved upon. Therefore, we would expect that if plasticity in growth rate were a mechanism compensating for a bad start in the actual marmot population, its inclusion in the model would improve the accuracy of the predicted population annual rate of change, λ. When compensatory growth was considered, the Pearson's correlation coefficients tended to stay the same or to increase in comparison to the Pearson's correlation for the baseline non-compensatory growth model (Table 3). The best fitting model was the compensatory growth model where individuals in poor body conditions (i.e., individual's June body mass was below 1 SD of the average population body mass) were allowed to compensate their growth, and it was significantly different from the baseline model. Thus, we used this model in further analyses. Three sub-scenarios of this model showed better agreement with the observed data than the baseline model: *Fixed gain in compensatory growth* with plasticity levels of 1.75 and 2.32, and *Variable gain in compensatory growth*. The alternative models where either (1) all individuals below average June body mass were allowed to compensate or (2) individuals in very poor conditions (i.e., June body mass below 2 SD) were allowed to express a plastic response performed worse than, or similar to the baseline model. These results suggest that only individuals in poor body conditions benefitted from plasticity.

We then explored the effects of co-varying survival cost and reproductive cost of plasticity with compensatory growth expressed by individuals in poor body conditions as this maximized the correlation between the predicted and the observed population growth rate (Fig. 2). For each scenario, we calculated the average population growth rate with the default values to facilitate the interpretation of the results. For *fixed gain in compensatory growth* scenario with low gain ($p = 1.75$) the average population growth was 1.031 (SD = 0.018), whereas in the average gain ($p = 2.32$) scenario was 1.029 (SD = 0.024), and in the *fixed gain in compensatory growth* scenario was 1.028 (SD = 0.020). When survival and reproductive cost were set to low values, population growth was higher than average values in all scenarios (Fig. 2). When survival and reproductive cost were set to high values, population growth was lower than average values for the default cost settings in all scenarios (Fig. 2). When survival cost was low but reproductive cost was high, population growth was higher; however, when the opposite settings were used, survival cost was high, the population growth was lower than average scenarios. These results suggest that our model is more sensitive to changes in survival cost, lower values lead to larger values of population growth whereas higher values lead to low values of population growth.

3.2. Climate variability scenarios

Our exploration of climate variation illustrates the relative importance of plastic responses under different future climatic scenarios. Compared to the baseline non-plasticity model, where the extinction probabilities were 0.028, 0.166, and 0.492 for the warmer, cooler, and random scenario, respectively; plastic responses in growth rate were important for population persistence (i.e., under plasticity the extinction rates are lower). Moreover, when comparing the three climate scenarios, plasticity played a larger role under the random and colder scenarios than under the warmer scenario, as it reduced the probability of extinction of the population by 55%, 24% and 7%, respectively. Under the warmer scenario, the probability of extinction was equally low for all explored growth strategies (Table 4), and there were no significant differences among them ($\chi^2 = 0$, df = 2, $P = 1$). Under the colder scenario, the probability of extinction was lower than in the baseline or random scenarios, suggesting a significant effect of plasticity on population responses to climate variation. Moreover when individuals expressed an average fixed amount of compensatory growth ($p = 2.32$, Table 4), the probability of extinction was significantly lower compared to the other growth strategies ($\chi^2 = 6.98$, df = 2, $P = 0.0305$). Finally, under random climate variation, the probability of extinction was reduced by 50% compared

Table 3
Calibration results. The numbers correspond to the Pearson's product moment correlation coefficient (r) between the predicted λ and the calculated from the observed data, λ_{obs} (out of 37 years). In square brackets the lower and upper limits of the 95% confidence interval of the Pearson's coefficient.

Compensatory growth		Proportion of individuals expressing plasticity		
		0	1	2
Fixed gain in compensatory growth	1.75	0.532[0.500–0.565]	0.693[0.668–0.718]	0.491[0.457–0.525]
	2.32	0.268[0.236–0.300]	0.686[0.660–0.711]	0.482[0.449–0.515]
	3.26	0.047[0.031–0.063]	0.551[0.518–0.583]	0.535[0.502–0.567]
Variable gain in compensatory growth	[0,3.26]	0.598[0.525–0.627]	0.683[0.657–0.708]	0.492[0.459–0.526]

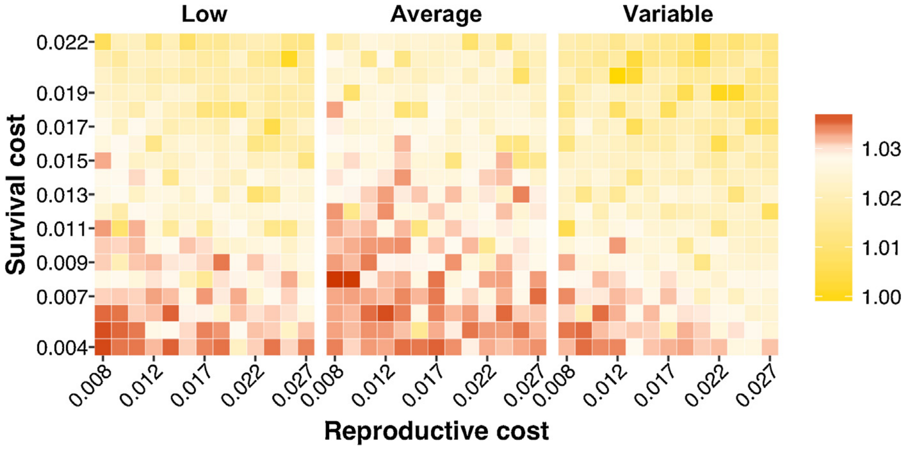

Fig. 2. The effect of survival and reproductive cost on population growth rate. The effect of co-varying survival cost and reproductive cost on the average geometric population growth rate (500 realizations) over a period of 37 years, when individuals expressed compensatory growth. Three scenarios are represented: 1) Fixed gain in compensatory growth with low levels of plasticity (1.75), 2) Fixed gain in compensatory growth with average levels of plasticity (2.32), and 3) Variable gain compensatory growth. The intensity of the color gradient indicates increases in the population growth values. All other parameters except the ones in the x and y axes were fixed at the values given in Tables 1 and 2. The reference values for survival and reproductive cost are 0.009 and 0.017, respectively.

to the baseline non-plastic model. This effect can arise because individuals can adjust better their behavioral responses to sudden changes in the environmental conditions, yet is only possible if the correct cues are still in place (as it is assumed in this model). Moreover, models where individuals expressed an average fixed level of compensatory growth ($p = 2.32$) had a lower probability of extinction than models where individuals expressed a low fixed level of compensatory growth ($p = 1.75$) or where plasticity varied among individuals (Table 4). These differences in the extinction probability among the growth strategies were significant ($\chi^2 = 20.73$, df = 2, $P = 3.152\text{e-}5$). This finding reinforces the importance of plasticity for individuals in poor body mass condition.

Table 4
Probability of extinction of the population under three theoretical *climate variability scenarios* (warmer, colder and random). The experimental simulations included two types of compensatory growth: non-among individual variation ($p = 1.75$, 2.32) and among-individual variation, considered a survival and reproductive cost ($sc = 0.006$ and $rc = 0.022$), and allowed some individuals below the average body mass in June to express plasticity (SD = 1). The probability of extinction corresponds to the proportion of the 500 simulations where the population went extinct, after removing the simulations where the population reached 600 marmots.

Compensatory growth		Climate scenario		
		Warmer	Cooler	Random
Fixed gain in compensatory growth	1.75	0.002	0.04	0.27
	2.32	0.002	0.02	0.21
Among-individual variation	[0,3.26]	0.002	0.05	0.34

4. Discussion

We developed a stochastic, environmentally-driven, individually-based, demographic model for yellow-bellied marmots. This model allowed us to evaluate the effect of phenotypic plasticity in growth rates (i.e., compensatory growth) on population dynamics and persistence when we take into account variation in the plastic response among marmots, a cost for plasticity and the body mass conditions under which an individual can express plasticity at a given time. Our model showed that compensatory growth, affects population dynamics. More specifically, the simulation where individuals could compensate for a bad start yet paid a cost for plasticity showed an improvement in the model fit compared to the baseline non-plastic model. These results suggest that, as we hypothesized (but with the added proviso that there is cost to plasticity), the population dynamics of yellow-bellied marmots is influenced positively by the ability of marmots to compensate for a bad start by their growth during the active period, and that there exists two trade-offs between rapid growth and mortality, and reproduction. Moreover, our model incorporates individual variation in survival and reproduction that is biologically more realistic than assuming all individuals respond in the same way, and mechanistically links environmental variation to population dynamics, which allows us to gain insight into the implicit rules by which organisms make decisions affecting trade-offs between current and future states.

The fact that neither the baseline non-plasticity simulations, nor the simulations with plasticity, perfectly fit the observed data, indicates that there are still other mechanisms not considered in the simulations that also influence marmot population dynamics. This was also reflected by the differences between the observed and simulated annual rate of change, λ, in the plasticity scenarios. Two main factors may be driving this effect. 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 take immigration into consideration. Although immigration is rare (Armitage, 2014), it ultimately plays an important role in the replacement of individuals lost to 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 by the population. This may reflect the absence, in the simulation, of female immigrants and their subsequent reproduction.

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 have determined are related to an increased probability of survival (Ozgul et al., 2010). Larger individuals are more likely to survive overwinter (a direct effect) and this may have a positive effect on fecundity during the subsequent season (a delayed effect). 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 population mean body mass).

Compensatory growth influences population dynamics and entails a trade-off between rapid growth and survival plus reproduction. First, the fact that models that included a cost for plasticity had a better fit than the baseline non-plastic model supports empirical evidence found in other systems that showed a trade-off between fast growth and mortality due, for example, to increased predation risk (Gotthard, 2000). However, the immediate cost of compensatory growth is not the only cost that individuals pay for growing faster; other costs, such as a decrease in reproductive output (Ab Ghani and Merilä, 2014) or long term cell damage may also occur (Jennings et al., 1999). These costs are understudied in our system and elsewhere. Second, within the cost-plasticity scenarios we explored, the population dynamics were positively influenced when individuals below the average body mass condition (SD = 0) or in poor conditions (SD = 1) were allowed to express plasticity in the population. This suggests that individuals in poor body conditions at the beginning of the season benefit from a compensatory response since survival and reproduction rates are body size-dependent, However, when body condition is far below the average body mass (i.e., severe under-nutrition), the benefit of expressing a plastic response may not outweigh the cost. Therefore, increases in body mass can positively affect the population dynamics only if individuals can afford the cost of plasticity and gain a net benefit by engaging in compensatory growth.

It has been proposed that phenotypic plasticity decreases the probability of extinction (Wennersten and Forsman, 2012), a trend we saw in all of our scenarios. Because compensatory growth allows individuals to catch up to, and reach, a body mass closer and larger than the population mean, it can favor population persistence in the long term when future scenarios are highly variable, as shown by our random thermal series of simulations. 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 be seen only in the next breeding season, and its effect would depend upon the way individual survival and reproduction relates to factors such as weather. In our scenarios where there was no pattern in the frequency of cold or warm years, individuals could recover from less favorable climate conditions. Alternatively, 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 sub-models). Thus, under these conditions, populations are less likely to go extinct and may increase. In contrast, in our colder future scenarios, survival and growth are negatively affected (see the sign of the coefficients in the equations governing each of the sub-models), and there may be carry-over effects from one season to the next (Harrison et al., 2011). Under these scenarios, individuals can gain sufficient mass through plasticity to survive hibernation, but possibly not enough to be able to reproduce the next year. Furthermore, adding a cost of plasticity did not increase the probability of extinction, which indicates that we correctly captured the two trade-offs between rapid growth and survival and reproduction in our simulated population. Although the cost of growth rate plasticity has a negative effect on the probability of survival and reproduction, the fact that individuals are able to achieve larger body masses than expected under scenarios without plasticity has a positive influence on the population dynamics.

Finally, we expected that variation in the plasticity of the growth rate would decrease the probability of extinction compared to fixed values of plasticity. However, our results showed that variation did not have a large effect under warmer, colder or random climatic scenarios. There are two likely explanations for these results. First, since the cost of plasticity is the same for all individuals regardless of the initial body mass, some individuals may have paid a proportionally larger cost. For example, among individuals with lower body mass in June, the benefit of rapid growth may be reduced by the cost of plasticity in those individuals that were skinnier to begin with. Thus, survival and reproductive costs need to be modelled based on the individual's body mass condition and amount of plasticity expressed by the individual, rather than as a population average cost. Second, the lack of difference between variation and fixed plasticity in the probability of extinction can also indicate that variation in plasticity contributes to the maintenance of individual differences in growth rate trajectories. If individual differences in growth rates can result, for example, from a trade-off between growth and predation risk (Mangel and Stamps, 2001), individuals in the same population can plastically adjust their growth rate trajectory based on their perceived predation risk. These possible explanations support the idea that individuals can strategically evaluate alternative growth trajectories based on the cost and benefits of expected outcomes (Gotthard, 2000), and thereby optimize their degree of compensation.

5. Conclusion

In conclusion, by constructing individual-based models, we gained a deeper understanding of the role 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) that assume uniformity across individuals. Our results highlight the role of compensatory responses as a mechanism by which individuals in poor body condition can cope with adverse environmental scenarios and the importance of better understanding the precise costs of phenotypic plasticity 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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Appendices A. 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:

$$E|Z_i| = \alpha_{V(i)} + \beta_{BY(i)} + \gamma_{YR(i)} + f(a_i, d_i) \quad (1)$$

$$\mathbf{Z} \sim Norm(\mathbf{z}, \mathbf{R}) \quad (2)$$

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 modelled the correlation 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 cube-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 **0** and correlation matrix defined by the models fitted in the second step.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.02.023.

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