



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.

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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 (Metcalf and Monaghan, 2003).

In seasonal environments, individuals can cope with the consequences of a harsh period such as winter through compensatory growth (Niecieza 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 (Metcalf 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; Metcalf and Monaghan, 2001). Compensation may occur in structural components as well as body mass (Abrams et al., 1996; Metcalf and Monaghan, 2001; Niecieza 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; Metcalf 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 Metcalf 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).

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