

Is Compensatory Growth Costly?

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Abstract

1. Compensatory growth is well-studied and exhibited across a variety of taxa, including plants, invertebrates, and a variety of vertebrates. Compensatory mechanisms allow individuals to recover from adverse conditions, potentially enhancing survival and fitness. However, to compensate for a low body condition, individuals may allocate energetic resources to a few physiological functions, affecting the ability of other bodily functions to perform efficiently. Such costs associated with compensatory growth are shown in previous studies, and are expected to be strongest at early life stages. The allocation of resources to accelerate body growth may be traded-off against other essential physiological processes, such as bone growth, immunocompetence, and tissue repair.
2. We quantified short and long-term consequences of differential body growth rates in a wild population of yellow-bellied marmots, *Marmota flaviventer*, obligate hibernators with a short active season. We used mass measurements collected from 2002-2014 to calculate individual growth trajectories, and estimated annual survival from 688 females at distinct life stages (142 adults, 239 yearlings, 643 juveniles) distributed along a mild elevational gradient (165 m). We also estimated longevity utilizing 322 longitudinal mass measurements throughout the lifespan of 72 females.
3. We found that increased mass gain rate, coupled with the demands of a harsher higher-elevation environment, reduced annual survival in the young cohort. Older individuals with accelerated mass gain had higher survival, regardless of location in the elevational gradient. Collectively, we found that rapid mass gain had no effect on longevity.

4. Thus, while adults may benefit from accelerated mass gain, it may be that younger individuals pay a price. This cost in the younger cohort varies according to environmental conditions. Developing individuals face conflicting demands of structural vs. fat reserve growth, and one may be prioritized over the other in adverse conditions. Therefore, the benefits and costs of rapid growth are age and site- specific, and the costs are concentrated in young individuals in harsh environments. Furthermore, the costs of accelerated growth in this species may be exerted in the short-term, rather than paid later in life.

Introduction

The phenotypic plasticity found within populations exemplifies how interactions between an individual and its surrounding environment can profoundly impact life history (Pigliucci, 2001). Compensatory mechanisms are well-documented responses to environmental challenges in which individuals compensate for a low body condition by modifying behavior or physiology (Metcalf & Monaghan, 2001). Such compensatory strategies are often observed in the patterns of individual growth, particularly when a critical body size must be attained within a restricted time limit, such as for hibernation or sexual reproduction (Arendt, 1997), and following periods of nutritional deficiency (Metcalf & Monaghan, 2001). Wild brown trout showed complete compensation of body mass within a mere month following food deprivation (Johnsson & Bohlin, 2005), and lab-reared rats demonstrated an 80% increase in growth after the restoration of an essential amino acid in their diet (Ishida et al., 2011). A meta-analysis found that children who experienced malnutrition early in life but then entered adoptive homes had nearly complete recovery in height and weight, but only partial recovery of head circumference (Van IJzendoorn et al., 2007), revealing that early life is a critical period for bone growth development in humans,

and likely many other vertebrates. Thus, compensatory growth is necessary for the immediate survival or reproductive success of individuals exposed to adverse conditions, and therefore may increase individual fitness and improve the likelihood of populations to persist under different scenarios (Maldonado-Chaparro et al. 2017, Ferreri & Taylor, 1996).

Despite potential benefits, compensatory growth may also be costly. Individuals increase their growth rate via increased foraging at the cost of decreased vigilance and shelter, and thus may become more vulnerable to predators (Mangel & Stamps, 2001). Furthermore, individuals exhibiting compensatory growth may also have cellular and physiological costs. Two similar-sized individuals exhibiting different intrinsic growth rates differ in anatomical efficiency; the faster-growing individual will exhibit poorer functional capacity (Morgan et al., 2000). Bone growth and density may also be compromised (Leterrier & Constantin, 1999); this is of primary concern in individuals that have not yet completed structural growth. Dampened immune responses have also been observed (Lochmiller & Deerenberg, 2000), predisposing rapidly growing individuals to illness and infection. Numerous studies in humans over the past few decades concerning the effects of low birth weight have revealed a multitude of sometimes subliminal and other times profound effects on health, including links to breast and testicular cancer, osteoporosis, multiple sclerosis, adult asthma and hearing loss, depression and other mood problems, liver cirrhosis, renal disease, cardiac complications, polycystic ovary syndrome, and ironically, obesity (Negrato & Gomes, 2013). Babies born at a low birth weight may accelerate their growth to compensate for a poor start in development; such rapid growth is associated with higher blood pressure and future hypertension (Eriksson et al., 2000).

While increased growth rate is a well-investigated example of compensatory strategies across a variety of taxa, the majority of studies focus on physiological effects and biomedical

consequences (Metcalf & Monaghan, 2001). Few studies focus on the evolutionary aspect of compensatory growth. In this respect, Maldonado-Chaparro et al. (2017) showed that compensatory growth may play a key role in population dynamics and persistence in seasonal and unpredictable environments, especially in species where body mass is highly correlated with survival. Indeed, disparities in growth rates provide the variation necessary for evolutionary forces to act upon (Arendt, 1997). Here, we investigate the short and long-term ecological consequences of compensatory growth on the individual level, which complements previous findings at the population level in yellow-bellied marmots (Maldonado-Chaparro et al., 2017), and aids to fill the knowledge gap regarding the impact of rapid growth rate on individual fitness, particularly on survival and longevity.

The benefits of a higher body mass are of particular significance to small homoeothermic mammals in seasonal environments that must undergo extended periods of fasting (Lindstedt & Boyce, 1985). Yellow-bellied marmots, *Marmota flaviventris*, are ground-dwelling, diurnal, sciurid rodents that live in social groups consisting of female matrilineal groups that are defended by a locally dominant male (Armitage & Downhower, 1974). During their short active season (~5 months), marmots must accumulate and maintain adequate fat stores in order to prepare for the energetic demands of hibernation (Armitage, 1998). Body mass prior to emergence is a strong predictor of both overwinter survival (Monclús et al., 2014), and of the probability that adult females will successfully wean a litter (Blumstein et al., 2016). Climatic changes have further amplified the benefits of increased body mass on survival and reproduction in our well-studied population (Ozgul et al., 2010). In addition, larger marmots are less affected by predators and have increased energetic efficiency and diet flexibility, enabling them to digest more fibrous plant material (Armitage, 2014). In conclusion, mass gain during the active season is an

important life history trait in marmots, as marmots lose on average half their body mass during hibernation (Armitage et al., 1976). Thus, marmots starting the active season with a low body condition are likely to compensate by increasing their mass gain rate, and the capacity for this plastic response was shown in previous studies (Maldonado-Chaparro et al., 2015). It remains to be determined whether the potential costs of such rapid growth can be observed within an individual's lifetime.

Additionally, the costs associated with rapid growth are likely to be harsher in early life stages. Juveniles and yearlings (one year old) are investing energetic resources in both structural growth and fat accumulation (Armitage, 2014); therefore, the trade-offs between accelerated mass gain and other bodily functions may be more evident in this cohort. Rapid growth early in life appears to be favored in homeotherms by selection due to the high juvenile mortality attributed largely to predation pressure (Arendt, 1997). Offspring body mass has been shown to strongly influence offspring survival in birds and mammals and ultimately drive population growth (Ronget et al., 2017). In line with this finding, mortality rates due to predation are highest in juvenile yellow-bellied marmots; this age category also exhibits the highest mortality during hibernation (Armitage & Downhower, 1974). While compensatory growth was previously not found in juvenile yellow-bellied marmots emerging late in the active season (Monclús et al., 2014), we observe the highest variation in individual growth rates in the juvenile cohort (pers. obs.). However, compensatory growth was found in female adults and yearlings (Maldonado-Chaparro et al., 2015).

In this study, we aimed to quantify the potential costs of rapid growth on annual survival and longevity in a wild population of yellow-bellied marmots. Specifically, we tested how survival and longevity may be affected by rapid growth in different life stages. While we predicted that

rapidly growing adults may demonstrate increased annual survival, juveniles and yearlings may have lower survival due to the added demands of structural growth. Also, we expected that individuals exhibiting accelerated growth for several years may have reduced lifespan due to the cumulative somatic costs of rapid growth.

Materials and methods

Study site

Yellow-bellied marmots in and around Gothic, Colorado at the Rocky Mountain Biological Laboratory (38°57'N, 106°59'W; 2900 m elevation; Armitage, 2014) have been extensively studied starting in 1962. Populations reside in either 'up-valley' or 'down-valley' colonies that vary in phenology and associated ecological factors, such as elevation, snowmelt date, and length of the vegetative growth period (Blumstein et al., 2004). Down-valley and up-valley sites differ by an elevational gradient of 165 m, and emigration between colonies is extremely rare. The majority of individuals located down-valley emerge an average of fourteen days earlier from hibernation than individuals up-valley due to delayed snowmelt, and consequentially face a shorter active season (Blumstein et al., 2004).

Data collection

Since 2002, we observed colonies on most days of their five-month active season and aimed to live-trap all individuals every other week. Most juveniles are live trapped within a week of emergence, and all individuals are regularly sexed and weighed. All marmots are given two uniquely numbered metal ear tags (Monel self-piercing fish tags #3, National Band and Tag) for

permanent identification and their dorsal pelage is marked with black Nyanzol fur dye to enable identification from afar (e.g., Blumstein, 2013).

From repeated measurements of body mass, we fitted a linear mixed effects model to predict 1 June and 15 August body mass (Ozgul et al. 2010; Maldonado-Chaparro, et al., 2015).

We assumed that an individual did not survive the winter if it was not trapped/observed by the end of the summer and if the individual further failed to be identified in subsequent trappings/observations the following season. Thus, we calculated longevity as the age of each individual at last observation.

Virtually all male and about half of female yearlings disperse (Armitage, 1998). Thus, for yearlings and adults our analyses focused on non-dispersing females because we were certain of their age. We inferred dispersal if animals disappeared within 10 days of their group's litter emergence, although this date may vary with year and colony location (Blumstein et al., 2009). Individuals for which the date of birth or death was not known were therefore assumed to have dispersed, and were removed from the data set.

Statistical analyses

Because juveniles (animals born that year), yearlings (animals who have survived their first hibernation), and adults (animals who have survived ≥ 2 hibernations) are subjected to slightly different selective pressures (e.g., Petelle et al., 2013), and because most of the structural growth is restricted to juveniles and yearlings (Armitage, 2014), we analyzed each group separately.

We fitted generalized linear mixed effects models with binomial error structures in lme4 (Bates et al., 2015), using optimx (Nash & Varadhan, 2011; Nash, 2014) and lmerTest (Kuznetsova et al., 2016) to test hypotheses about annual survival utilizing R software (R

Development Core Team, 2013). Models included random effects of ID and fixed effects of mass gain rate, number of annual mass measurements, year, position in valley, and the interaction between mass gain rate and position in valley. Juveniles suffer high predation rates and this raises an important computational issue; we may have only a single mass measurement for them. Thus, for juveniles, we fitted two models, one including all juveniles and one limited to juveniles with three or more measurements. For adults, we added the fixed effect of age and the interaction between mass gain rate and age.

We fitted a generalized linear mixed effect model to study overall longevity utilizing a subset of longitudinal data. We included random effects of ID and fixed effects of year, number of annual mass measurements, position in valley, age, and the interaction between mass gain rate and age, and mass gain rate and position in valley. Continuous variables were scaled due to exceptional differences between parametric values, and a Poisson distribution was inferred.

We evaluated assumptions of mixed effects models by plotting histograms and qq plots of residuals. Transformations were not needed, as residuals were normally distributed and qq plots revealed a linear residual pattern. Additionally, untransformed models yielded lower AIC (Akaike information criterion) values than models incorporating transformed variables, suggesting an overall better fit.

Results

Annual survival

Between 2002-2014, we collected a total of 1,289 body mass measurements from 688 females, 708 observations from 363 up-valley females and 581 observations from 325 down-

valley females. There were 643 mass measurements from juveniles, 239 from yearlings, and 407 from 142 adults, which ranged in age from 2 years to 14 years.

In the full juvenile data set, there were no significant effects of mass gain rate on annual survival (Table 1a). However, there were annual effects and a weak positive effect of valley position on overwinter survival ($p = 0.062$). Juvenile marmots born up-valley had a greater overwinter survival probability than those born down-valley. When we restricted the analysis to include only 396 juveniles possessing three or more mass measurements, there were some significant annual effects on overwinter survival, a positive effect of living up-valley on survival ($p = 0.012$), and a weak interaction between mass gain rate and position in valley ($p = 0.069$) (Table 1b). Up-valley female juveniles that exhibited accelerated growth were less likely to survive the winter, although living up-valley had a positive effect on overwinter survival.

After controlling for annual effects, yearlings that lived up-valley and that gained mass more quickly had reduced survival (Table 2). Overall, up-valley yearlings were more likely to survive to the next year.

After controlling for annual effects, adults benefited from rapid growth; older adults that gained more mass had increased survival (Table 3). Overall, older animals were less likely to survive.

Longevity

322 longitudinal mass measurements for 72 females were collected throughout 2002-2014. Only individuals that had at least one annual mass measurement for each year of life were included in the analysis.

After controlling for the effects of year and sampling bias, we found no effect of mass gain rate ($p = 0.902$) on lifespan length. Age had a positive effect on longevity ($p = 0.010$). Position in valley had no effect on lifespan length ($p = 0.188$), and there were no significant interactive effects between mass gain rate and age ($p = 0.759$) or mass gain rate and position in valley ($p = 0.724$) (Table 4).

Discussion

Overall, and somewhat surprisingly, we found annual costs of compensatory growth in yearlings and to some extent in juveniles—two cohorts that were still undergoing structural and somatic growth. However, we found benefits of compensatory growth in older female marmots. The value of compensatory growth depends upon a variety of factors, such as the social environment, time in the year, temperature, food availability, and individual intrinsic factors such as physiological state and age (Nicieza & Metcalfe, 1997). Variation in growth rates are also expected in response to time restrictions imposed on development, a common constraint in seasonal environments (Dmitriew, 2011).

In both yearlings and the restricted sample of female juveniles, there were interactive effects between mass gain rate and position in valley. Individuals in this younger cohort residing up-valley that gained mass more rapidly were less likely to survive to the next year in comparison with slower-growing individuals. The importance of valley position suggests an influence of one or more key environmental factors that differs between down-valley and up-valley colonies. Compensation is a dynamic process and varies with the local environment (Metcalfe & Monaghan, 2001). Prior work has shown that the higher-elevation marmots have adjusted their

life history trajectories by having smaller litters and enhanced annual survival may reflect this (Maldonado-Chaparro et al., 2015).

The most immediate and often-cited cost of accelerated growth fueled by heightened foraging activity is increased predation risk (Mangel & Stamps, 2001). Predation on juveniles at one of our down-valley sites has been comparatively high during much of this study and the reduced overall survival may reflect this increased exposure. Selection for rapid growth in juveniles to outgrow vulnerability to predation may further drive variability in growth rates (Arendt, 1997).

As might be expected, older animals were less likely to survive to the next year. However, older animals that gained more mass were more likely to survive. At eight years of age, regardless of valley position, female marmots begin to lose body mass (Kroeger et al., in review). This reduced body mass may lead to reduced over-winter survival; aging animals that gain more mass throughout the season may thus improve their chances for survival.

The conflicting demands of structural growth vs. fat accumulation might make juveniles and yearlings more vulnerable to over-winter mortality as a consequence of insufficient fat reserves. Compensating individuals, such as up-valley juveniles that are weaned on average 8 days later than down-valley juveniles (Armitage, 2014), or up-valley yearlings that emerge later from hibernation than down-valley yearlings, may face a greater time constraint on mass gain and thus may trade-off the accumulation of fat stores over sufficient structural growth.

However, as our results indicate, failing to allocate sufficient resources to bone growth may also be costly (Arendt & Wilson, 2000). In fledgling gulls, bone development is traded off in favor of prioritizing rapid growth (Carrier & Leon, 1990), and in humans, bone mineral density has been shown to correlate with survival, and serves as a strong proxy of good health

(Johansson et al., 1998). While greater body size may increase fasting tolerance (Millar & Hickling, 1990), reduced starvation resistance has been shown in faster-growing individuals (Gotthard et al., 1994). Marmots that grew more rapidly over the summer may similarly be less tolerant to an extended period of food deprivation that is further compounded by longer up-valley winters.

Our results indicate that there are short-term costs for young marmots that exhibit accelerated growth, but there appear to be no long-term consequences. On the contrary, it has been suggested that rapidly-growing individuals may not pay the full price of compensation until later in life (Metcalf & Monaghan, 2001), although results of long-term studies on the effects of accelerated growth are mixed. Reduced long-term survival rates in rapidly growing individuals have been found in various species, including a population of lizards (Olsson & Shine, 2002) and numerous studies of lab-raised rodents (Rollo, 2002). Furthermore, taller humans may be afflicted by increased rates of disease including coronary heart disease, diabetes, and cancer, and may lead overall shorter lives (Samaras & Elrick, 1999). On the other hand, a study in wild bighorn ewes found no longevity effects of prolonged growth, although reproductive fitness was negatively impacted (Marcil-Ferland et al., 2013). However, these ewes also experience a seasonal cycle of mass gain during the summer and subsequent mass loss during the winter (Pelletier et al., 2007), whereas modern humans and laboratory rodents are presumed to have relatively consistent access to food year-round.

Increased metabolic output due to increased growth rate may produce more reactive oxygen species (ROS) in the body that can cause cumulative cellular damage (Finkel & Holbrook, 2000). The “free radical theory” is of primary interest in the biology of aging (Finkel & Holbrook, 2000). Over time, these oxygen metabolites could depreciate organ function; coupled with the

complications of older age, anatomical efficiency could be severely compromised. Studies have found evidence linking reactive oxygen species in the body to effects on lifespan (Harman & Eddy, 1979).

The yellow-bellied marmot has evolved in a seasonal subalpine environment subject to alternating periods of food stress and abundance. As marmots are obligate hibernators, the active season is spent fervently accumulating fat reserves. Therefore, rapid mass gain, followed by extreme reduction in body mass, is a life-history strategy that marmots have adopted in order to cope with the demands of a seasonal climate. This fluctuation in body mass is therefore an annual cycle; such seasonal variations in body mass may be adaptive in species facing unpredictable environmental conditions (Hodges et al., 2006). As has been proposed in wild brown trout, in which no consequences of accelerated growth were found within the time frame of the study, yellow-bellied marmots may have evolved a “buffering” ability against extreme variations in food availability (Johnsson & Bohlin, 2005). Adaptation to the physiological stresses associated with such periodic rapid mass gain and loss may have occurred in this species, safeguarding individuals against cumulative long-term consequences, such as shortened lifespan. The ecological consequences of rapid growth are more likely to be paid in the short-term, as opposed to long-term costs operating on the cellular and physiological levels (Metcalf & Monaghan, 2001). Accordingly, we observed short-term ecological consequences to increased growth rate in the form of reduced annual survival, but the absence of long-term consequences suggests a lack of cumulative cellular damage, or the possible existence of buffering somatic maintenance mechanisms in this species.

While there are costs to rapid growth (Arendt, 1997), various growth rates may confer the same fitness (Mangel & Stamps, 2001). The persistence of variation in mass gain rates of

yellow-bellied marmots and the fact that median mass gain rates are slightly higher in surviving juveniles and yearlings despite evidence of costs to compensating individuals suggests that the benefits of compensatory growth outweigh the costs in this species. Considering the central role mass gain plays in marmot life history, and the predictive strength of late season mass on overwinter survival, we may expect compensatory growth to not only persist in populations of this long-lived sciurid and other species that face similar time constraints on development, but to play a dynamic role in buffering populations against seasonal stressors. This may be of critical importance for numerous species in light of a rapidly changing climate.

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Table 1. A) Results of generalized mixed effects model explaining variation in juvenile female annual survival ($N = 643$); B) analysis restricted to juveniles with ≥ 3 annual mass measurements ($N = 396$).

	Variable	Estimate	SE	<i>z</i>	<i>p</i>
<u>A)</u> Fixed effect	Intercept	-1.19	0.810	-1.47	0.141
	Mass Gain Rate	0.184	0.181	1.02	0.307
	Position in Valley [up]	1.88	0.890	2.11	0.0352
	Mass Gain Rate x Position in Valley [up]	-0.320	0.263	-1.21	0.225
	Variable	Estimate	SE	<i>z</i>	<i>p</i>
<u>B)</u> Fixed effect	Intercept	-1.09	1.01	-1.08	0.281
	Mass Gain Rate	0.317	0.219	1.45	0.281
	Position in Valley [up]	2.91	1.16	2.51	0.281
	Mass Gain Rate x Position in Valley [up]	-0.616	0.338	-1.82	0.281

Table 2. Results of generalized mixed effects model explaining variation in yearling female annual survival ($N = 239$).

	Variable	Estimate	SE	<i>z</i>	<i>p</i>
Fixed effect	Intercept	-3.48	2.23025	-1.561	0.119
	Mass Gain Rate	1.82	1.19553	1.525	0.127
	Position in Valley [up]	5.39	2.51313	2.144	0.0321
	Mass Gain Rate x Position in Valley [up]	-2.53	1.16324	-2.170	0.0300

Table 3. Results of generalized mixed effects model explaining variation in adult female annual survival ($N = 407$).

	Variable	Estimate	SE	<i>z</i>	<i>p</i>
Fixed effect	Intercept	4.27	2.71	1.575	0.115
	Mass Gain Rate	-1.93	1.92	-1.008	0.313
	Age	-1.26	0.478	-2.629	0.00857
	Mass Gain Rate x Age	0.948	0.36231	2.615	0.00892
	Position in Valley [up]	-1.12	2.20176	-0.507	0.612
	Mass Gain Rate x Position in Valley [up]	-0.171	1.61238	-0.106	0.916
	Variable	Variance	SD		
Random effect	Individual ID	0.326	0.571		

Table 4. Results of linear mixed effects model explaining variation in female longevity
($N = 322$).

	Variable	Estimate	SE	<i>z</i>	<i>p</i>
Fixed effect	Intercept	1.70	2.71	1.58	0.115
	Mass Gain Rate	0.0153	1.92	-1.01	0.313
	Age	0.249	0.478	-2.63	0.00857
	Mass Gain Rate x Age	-0.0293	0.362	2.62	0.00892
	Position in Valley [up]	-0.125	2.20	-0.507	0.612
	Mass Gain Rate x Position in Valley [up]	0.0216	1.61	-0.106	0.916
	Variable	Variance	SD		
Random effect	Individual ID	0.0651	0.255		

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