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Original Article

Age and location influence the costs of compensatory and accelerated growth in a hibernating mammal

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INTRODUCTION

Compensatory mechanisms are well-documented responses to environmental challenges in which individuals compensate for a low body condition by modifying their behavior or physiology (Metcalfe and Monaghan 2001). Formally, compensatory growth is restricted to immature individuals who have not yet reached adult body size (Dobson and Homes 1984; Metcalfe and Monaghan 2001; Johnsson and Bohlin 2006; Morshedi et al. 2017). However, species occupying highly seasonal environments, where body fat accumulation has profound fitness consequences (Monclús et al. 2014; Blumstein et al. 2016), may exhibit accelerated growth, whereby adults gain weight faster to compensate for high mass loss during periods of poor resource availability (i.e., a bad seasonal start). Both can be viewed as compensatory strategies.

Compensatory strategies are often observed in the patterns of individual growth, particularly after periods of nutritional deficiency (Metcalfe and Monaghan 2001), as well as in species where individuals must reach a critical body size within a restricted time limit, such as for hibernation or reproduction (Arendt 1997). For instance, lab-reared rats had an 80% increase in growth rate when compared with controls after the restoration of an essential amino acid in their diet (Ishida et al. 2011). Likewise, wild brown trout (*Salmo trutta*) that underwent varying periods of food deprivation (ranging from 2 to 4 weeks) grew significantly faster than controls, increasing both in weight and body length (Johnsson and Bohlin 2005, 2006). A large body size in trout may enhance overwinter survival (Bull et al. 1996) and reproductive development (Bohlin et al. 1994). Thus, compensatory growth is probably necessary for

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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 (Ferreri and Taylor 1996; Maldonado-Chaparro et al. 2017).

Despite potential benefits, compensatory growth may also be costly, leading to suboptimal somatic functioning and lifetime consequences that may impact individual fitness. Human babies that grew rapidly to compensate for low birth weight are more likely to have higher blood pressure and adult hypertension (Erikksson et al. 2000), as well as reduced IQ (Estourgie-van Burk et al. 2009). Compensating individuals may exhibit impaired associative learning (Fisher et al. 2006), dampened immune responses (Lochmiller and Deerenberg 2000), and decreased exploratory behavior (Krause and Naguib 2011), which may limit an individual's ability to locate resources and potential mates. Bone growth and density may also be compromised (Carrier and Leon 1990; Leterrier and Constantin 1999). In fathead minnows (*Pimephales promelas*), faster-growing individuals had reduced critical swimming speed (Kolok and Oris 1995), which may increase their vulnerability to predators. Individuals growing rapidly probably spend more time foraging and, consequently, less time being vigilant or protected in shelters, increasing predation risk (Mangel and Stamps 2001). In this respect, Johnsson and Bohlin (2006) described significantly lower recapture rates of compensating wild brown trout, suggesting an overall lower survival for individuals with rapid growth in the wild.

Conversely, a number of studies did not find an effect of compensatory growth on a variety of physiological and fitness-related measures, such as immunocompetence in the damselfly *Ischnura verticalis* (Dmitriew et al. 2007), reproductive success in female guppies, *Poecilia reticulata* (Auer 2010), and pre-breeding flight performance in zebra finches, *Taeniopygia guttata* (Criscuolo et al. 2011). However, lower postbreeding flight performance was later observed in these compensating finches (Criscuolo et al. 2011), suggesting that studies may not capture the effects of compensatory growth if focused on specific life stages. In conclusion, the costs of compensatory growth may be species-specific and may become apparent in various life stages.

Although an increase in growth rate is a well-investigated compensatory strategy across a variety of taxa, the majority of studies focus on physiological effects and biomedical consequences (Metcalfe and Monaghan 2001). Few studies focus on the evolutionary and ecological consequences of compensatory growth or have been conducted in the wild (Johnsson and Bohlin 2006). One of the few examples is a study by Maldonado-Chaparro et al. (2017), who showed that compensatory growth may play a key role in the population dynamics of yellow-bellied marmots (*Marmota flaviventer*) by allowing populations to persist in seasonal and unpredictable environments. In yellow-bellied marmots, body mass is highly correlated with survival (discussed below); thus, a constantly changing environment may favor disparities in individual growth rates. This study complements the findings in Maldonado-Chaparro et al. (2017) by estimating the costs of compensatory growth on yellow-bellied marmots at the individual level.

Yellow-bellied marmots are ground-dwelling sciurids and obligate hibernators (Armitage and Downhower 1974). During their short active season (~5 months), marmots must accumulate and maintain adequate fat stores to prepare for the energetic demands of hibernation (Armitage 1998), when they lose about half of their body mass (Armitage et al. 1976). Body mass prior to immergence determines whether adult females will successfully wean a litter (Blumstein et al. 2016) and is a strong predictor of overwinter survival in both young and adult marmots (Monclús et al. 2014). Consequently, long summers lead to population growth because marmots have more time to gain mass prior to immergence. This effect is expected to escalate due to climatic changes because long summers have been increasing in frequency (Ozgul et al. 2010). Moreover, larger marmots are less affected by predators and have increased energetic efficiency during hibernation and greater flexibility in diet (Armitage 2014).

Due to the strong effect of body size on individual fitness, marmots starting the active season with small body size and low weight are likely to compensate through increased growth rate, and the capacity for this plastic response was shown in previous studies (Maldonado-Chaparro et al. 2015, 2017). Body length is positively associated with the capacity to accumulate fat stores in marmots (Armitage 1999); thus, it is advantageous for young marmots to have a larger skeletal frame by the end of the active season. Most structural growth occurs in the first two active seasons of yel- low-bellied marmots (Cardini and Tongiorgi 2003); therefore, it is juveniles and yearlings (second active season) that may exhibit compensatory growth.

Adult marmots, however, may also exhibit compensatory strategies regarding fat accumulation and somatic growth. Several factors influence mass loss during hibernation and starvation in early spring, such as the hibernacula location and the duration of snow cover (details in Armitage 2014); harsh conditions may result in a high depletion of fat stores. In addition, the marmot gastrointestinal tract atrophies during hibernation, and recovers its functioning size during the active season through high mitotic activity (Hume et al. 2002). After emergence, adults must therefore not only begin to rebuild fat reserves, but also recover from muscle deterioration and damage incurred to organ systems. In this regard, adult marmots may be challenged by the limited time available to gain mass, particularly if they had high winter mass loss, and may increase the rate of mass gain accordingly.

Here, we used long-term data collected in a wild population of yellow-bellied marmots to investigate the impact of rapid mass gain on components of individual fitness. Specifically, we tested how annual survival and longevity may be affected by rapid mass gain (including compensatory growth in juveniles and yearlings and accelerated growth in adults). Longevity may be associated with lifetime reproductive success because older individuals have more chances to rear offspring, potentially increasing reproductive output (Roff 1993). We predicted that individuals exhibiting a high rate of mass gain during their lifetime would have reduced lifespans. Regarding the annual survival of different life stages, we predicted that the costs of rapid mass gain are lower in adults than in juveniles or yearlings due to the competing energetic demands of structural growth faced by the young cohorts.

MATERIALS AND METHODS

Study site

We studied a wild population of yellow-bellied marmots located in and around the Rocky Mountain Biological Laboratory (38°57'N, 106°59'W; 2900 m elevation) in Crested Butte, Colorado. Individuals 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; the movement between colonies is uncommon. Overall, the up-valley colonies are exposed to a harsher environment than the down-valley colonies (Armitage 2014). Snowpack in spring ranges from being 0.5 to 1 m deeper in northernmost than southernmost colonies (Van Vuren and Armitage 1991), and snowmelt occurs on average 12 days later at up-valley sites, resulting in a delayed start to the vegetation-growing period as compared with down-valley (Blumstein et al. 2004).

Data collection

From 2002 to 2015, we observed colonies on most days of their 5-month active season and aimed to livetrap all individuals biweekly. Most juveniles (pups) are livetrapped 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, Newport, KY) for permanent identification and their dorsal pelage is marked with black Nyanzol fur dye to enable identification from afar (more details in Blumstein 2013).

From the repeated measurements of body mass from all individuals captured in 2002–2014 (11 729 measurements), we fitted linear mixed-effects models to predict 31 July body mass for juveniles, 1 June body mass for yearlings and adults, and 15 August body mass for all ages—dates that reflect the bulk of the marmot growing season for the respective age classes. Briefly, individual identity, year, and site were included as random effects, generating individual- and year-specific intercept and slope predictions (best linear unbiased predictors, BLUPs) that allowed individual mass values to be standardized. We predicted body mass as a function of date, taking into consideration the individual identity, year of capture, and site (further details in Maldonado-Chaparro et al. 2015 and Ozgul et al. 2010). By extracting BLUPs, we had more accurate predictions of individualized body mass than those generated by linear regression (Martin and Pelletier 2011). Our confidence in these individual mass predictions is affected by the number of repeated measurements of body mass throughout the year, and this is another reason to prefer BLUPs to residuals from simple linear regression analyses.

We then calculated adult and yearling seasonal growth as the proportion of individual mass gain per season by dividing individual body mass on 15 August by the body mass on 1 June. Juvenile relative seasonal growth was calculated as the proportion of individual mass gain per season by dividing individual body mass on 15 August by the body mass on their emergence date from the maternal burrow.

Yellow-bellied marmot social structure is matrilineal; males defend one or several breeding-age females, and most males that have survived their first hibernation (yearlings) disperse (Armitage and Downhower 1974; Armitage 1998). Because males disperse, we focused on females in this study, for which we have a larger data set and are able to monitor throughout their lives. Approximately half of the female yearlings disperse (Armitage 1998), challenging our capacity to estimate longevity and annual survival for dispersers. Because dispersal is mostly restricted to yearlings (1-year olds), the longevity analysis included exclusively females that reached at least the second year of life. We calculated longevity as the age of each individual at its last capture/observation. In the studied population, the probability of recapturing an adult marmot is higher than 98% (Ozgul et al. 2006, 2007), providing high confidence in our estimates of longevity.

Because juveniles, yearlings, and adults are subjected to different selective pressures (Petelle et al. 2013; Armitage 2014), we studied annual survivorship separately for each group. Annual survival was a binary outcome in our models, where an individual would receive a score "0" if it was not trapped or observed in the following years. Individuals with uncertain birth dates were removed from all analyses. For the yearling data set, annual survival and dispersal may be confounded because individuals that dispersed may have been designated dead. Therefore, we are cautious with our inferences made from the results of this specific analysis.

Statistical analyses

To test the impact of relative seasonal growth on annual survival, we fitted generalized linear models (GLM) with binomial error structures to the juvenile and yearling data sets and fitted a generalized linear mixed-effects model (GLMM) with binomial error structures to the adult data set. Because individual relative seasonal growth is calculated per year, the adult model was a GLMM with individual identity as a random effect because adults were sampled for multiple years. Juveniles and yearlings represent, respectively, the first and second year of a marmot's life, so each individual had one value of relative seasonal growth for each of these life stages.

The juvenile and yearling models included relative seasonal growth, August mass, number of annual mass measurements, year, position in valley, the interactions between position in valley with relative seasonal growth and August mass, and the interaction between relative seasonal growth and August mass. The model for adults included random effects of individual identity and fixed effects of relative seasonal growth, August mass, number of annual mass measurements, year, position in valley, quadratic age, the interactions between position in valley with relative seasonal growth and August mass, and the interaction between relative seasonal growth and August mass. The number of annual mass measurements was included in the models to control for sampling effort and thus correct for bias in mass estimation, as well as any other sampling bias.

Continuous variables were centered and standardized. We evaluated the assumptions of the models by plotting histograms and qq plots of residuals. We experimented with different optimizers to ensure that our mixed models converged. Detailed information about the models can be found in Heissenberger et al. (2020).

We fitted two GLMs with a Poisson error structure to study the long-term effect of compensatory growth exhibited during the juvenile and yearling life stages on longevity. For these two models, we used the data of females from extinct cohorts that reached at least 2 years of life. Juvenile and yearling seasonal growth were analyzed in separate models, and both models included the fixed effects of relative seasonal growth, August mass, number of annual mass measurements, year, position in valley, and three interactions of: position in valley with relative seasonal growth; position in valley with August mass; and relative seasonal growth with August mass. We tested for overdispersion by running additional quasi-Poisson models, which account for extra variance by fitting an additional dispersion parameter. Residual deviances did not change between the models and dispersion parameters were less than 1, indicating underdispersion.

To study the relation between adult relative mass gain and longevity, we fitted a trivariate model of relative mass gain, August mass, and log-transformed longevity. Such a model allowed us to estimate the correlation at the individual level between longevity and annual relative mass gain, longevity and annual mass in August, and between annual relative mass gain and mass in August. To avoid selective disappearance biases, we restricted our analysis to adult females (2 years or older) from extinct cohorts only. To facilitate model convergence and allow for comparison across traits, all variables were scaled with a mean of 0 and a variance of 1. For relative seasonal growth and August mass, the number of annual mass measurements, position in valley, age, and age squared were fitted as fixed effects to correct for sampling effort, environmental, and aging effects on mass traits. Year was fitted as a random effect to take into account annual variation in environmental conditions affecting body mass. For longevity, position in valley was included as a fixed effect. We fitted individual identity as a random effect for all three traits. Because each individual has only one observation for longevity, we fixed the longevity residual variance at 0, allowing us to estimate the covariation between longevity and mass traits at the individual level.

Models were fitted using a Bayesian approach with MCMCglmm (Hadfield 2010). We used flat priors at the correlation level for individual identity effect (i.e., parameter expanded prior: V = diag(3)*0.002, nu = 4, alpha.mu = rep(0,3), alpha.V = diag(3)*1000). Priors for year random effects were uninformative (V = 1 and nu = 0.002). The prior for the residual variance was uninformative for annual relative mass gain and mass in August and fixed at 0 for longevity (V = diag(c(1, 1, 0.002), nu = 2.002, fix = 3). The trivariate model was run for 2 050 000 iterations with a thinning of 2000 and a burn-in period of 50 000 iterations, which, for all parameters, produced autocorrelation coefficients <0.1. Running three separate bivariate models provided quantitatively similar results.

All analyses were performed using R software version 3.6.1 (R Development Core Team 2019) and the following packages: lme4 (Bates et al. 2015), optimx (Nash and Varadhan 2011; Nash 2014), lmerTest (Kuznetsova et al. 2016), and MCMCglmm (Hadfield 2010).

RESULTS

Annual survival

Between 2002 and 2014, we collected a total of 5309 body mass measurements from 668 females. From those, we calculated 666 relative seasonal growth values from 348 up-valley females and 559 from 320 down-valley females. Separating individuals by life stages, we calculated 643 relative seasonal growth values from juveniles (332 up-valley vs. 311 down-valley), 229 from yearlings (131 up-valley vs. 98 down-valley), and 353 from 130 adults (203 from 84 up-valley adults vs. 150 from 46 down-valley adults), which ranged in age from 2 to 12 years (median = 4, interquartile range = 2–5). Sample size was small (less than 13 individuals) in 2011 for yearlings and in 2002, 2003, and 2013 for adults; therefore, data from these years were excluded from the analysis of the respective age class.

In the juvenile data set, there were significant effects of position in valley ($P < 0.001$) and August mass ($P < 0.001$) on juvenile survival (Table 1). Juveniles located up-valley and with higher August mass were more likely to survive to the next year. The number of annual mass measurements was positively associated with survival ($P < 0.001$; Table 1). There were no significant effects of relative seasonal growth or of any interaction on juvenile survival. The juvenile model had a marginal and conditional R^2 of 0.39.

For yearlings, the interaction between relative seasonal growth and position in valley was significantly associated with annual survival ($P = 0.018$; Table 1). Up-valley yearlings that exhibited high relative seasonal growth were less likely to survive to the next year, whereas down-valley yearlings that gained more mass had increased likelihood of survival (Figure 1). The number of annual mass measurements was positively associated with survival ($P < 0.001$; Table 1). There were no significant effects of August mass or August mass interactions with relative seasonal growth and position in valley. The yearling model had a marginal and conditional R^2 of 0.60.

Adults residing up-valley had a lower likelihood of survival ($P = 0.024$; Table 1). With the exception of the significant positive association between the annual number of mass measurements and adult survival ($P < 0.001$; Table 1), no other variables had a significant effect. The adult model had a marginal and conditional R^2 of 0.31.

Longevity

We calculated a total of 189 annual growth rates for 76 adult females with known longevity collected between 2002 and 2015. For both models assessing the effects of juvenile and yearling seasonal growth on longevity, no variable had a significant effect (Table 2). The juvenile model had a marginal and conditional R^2 of 0.26. The yearling model had a marginal and conditional R^2 of 0.30.

For the trivariate model assessing adult survival, we first found that longevity was not correlated with August mass (r [with 95% credible intervals] = 0.302 [−0.037/0.507]; Table 3) or with relative seasonal growth ($r = 0.025$ [−0.558/0.759]; Table 3). Second, the among-individual variance in relative seasonal growth was extremely small or not different from 0 (0.057 [0.000/0.247]). Third, relative seasonal growth and August mass were not correlated at the individual level (0.067[−0.677/0.639]) nor at the year level (0.100[−0.466/0.713]) but were strongly correlated at the residual level (0.832[0.754/0.878]; Table 3).

DISCUSSION

We found that the relationship between relative seasonal growth and survival for yearlings depended on location. Yearlings residing up-valley that had high relative seasonal growth were less likely to survive to the next year, whereas down-valley yearlings with high relative seasonal growth had higher survival. Despite the bulk of growth occurring in the two young cohorts (Cardini and Tongiorgi 2003), we found that relative seasonal growth was associated with annual survival only in yearlings. Yearlings are therefore likely the age class with the highest susceptibility to the costs of accelerated growth, potentially because it is the developmental phase in which the conflicting demands of structural growth versus fat accumulation are the greatest. However, this potential developmental dilemma should be further explored in future studies.

Juveniles appear to have no significant costs associated with rapid growth, and the lack of a clear relationship between rapid growth and survival may be attributed to the critical importance of body mass for offspring survival. Gestation in yellow-bellied marmots lasts 32 days, followed by a month-long weaning period. Juveniles do not emerge above ground until mid-June to July (Armitage 1998), which is about a month later than yearlings. As a result,

Table 1

Results from generalized linear and mixed-effects models describing the variation in female survival by age class and variable. Parameters in bold are considered significant

	Juveniles		Yearlings		Adults	
Fixed effect	Estimate ± SE	*P*	Estimate ± SE	*P*	Estimate ± SE	*P*
Intercept	0.19 ± 0.45	0.668	1.92 ± 1.04	0.064	2.50 ± 0.55	<0.001
Relative seasonal growth	0.18 ± 0.18	0.321	0.84 ± 0.62	0.179	−0.16 ± 0.33	0.623
August mass	0.59 ± 0.16	**<0.001**	−0.26 ± 0.32	0.413	0.44 ± 0.26	0.093
Position in valley (up-valley)	1.30 ± 0.25	**<0.001**	−0.38 ± 0.69	0.579	−0.78 ± 0.34	**0.024**
Age	—		—		−1.97 ± 3.13	0.529
Age2	—		—		−4.66 ± 2.67	0.081
Year (2002)	0		0		—	
Year (2003)	0.23 ± 0.63	0.716	−0.63 ± 0.95	0.510	—	
Year (2004)	−0.71 ± 0.48	0.139	0.49 ± 1.01	0.626	0	
Year (2005)	−1.04 ± 0.55	0.059	1.48 ± 1.01	0.144	−0.22 ± 0.62	0.728
Year (2006)	−0.77 ± 0.49	0.118	−0.68 ± 0.94	0.472	−0.23 ± 0.61	0.700
Year (2007)	−1.70 ± 0.49	<0.001	−1.59 ± 0.88	0.073	−0.50 ± 0.61	0.412
Year (2008)	−1.54 ± 0.52	0.003	−1.16 ± 1.24	0.352	−1.45 ± 0.59	0.015
Year (2009)	−0.74 ± 0.51	0.150	−1.04 ± 1.02	0.308	−0.70 ± 0.63	0.268
Year (2010)	−2.75 ± 0.56	<0.001	−2.31 ± 1.06	0.029	−2.66 ± 0.66	<0.001
Year (2011)	−0.89 ± 1.05	0.393	—		−1.76 ± 0.78	0.024
Year (2012)	−1.42 ± 0.54	0.008	15.93 ± 1022.87	0.988	−1.10 ± 0.75	0.145
Year (2013)	−1.58 ± 0.51	0.002	−2.66 ± 1.00	0.008	—	
Year (2014)	−3.31 ± 0.68	<0.001	−3.47 ± 1.10	0.002	−2.40 ± 0.86	0.005
No. of mass measurements	0.84 ± 0.11	**<0.001**	1.11 ± 0.24	**<0.001**	0.73 ± 0.18	**<0.001**
Relative seasonal growth × August mass	−0.05 ± 0.12	0.693	−0.35 ± 0.26	0.183	−0.23 ± 0.14	0.093
Relative seasonal growth × Position in valley	−0.40 ± 0.27	0.137	−1.36 ± 0.57	**0.018**	0.15 ± 0.34	0.672
August mass × Position in valley	−0.20 ± 0.23	0.378	0.06 ± 0.49	0.899	−0.04 ± 0.32	0.902
Random effect (individual ID)	—				Variance (0.00)	SD (0.00)

SD, standard deviation; SE, standard error.

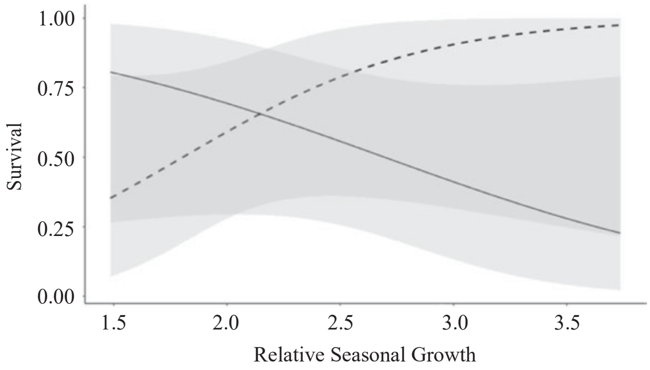

Figure 1

The effect of the interaction between position in valley and relative seasonal growth on annual survival in yearlings. Dashed line represents individuals residing down-valley; continuous line represents individuals residing up-valley. Plot was generated using predicted probabilities from generalized linear model. Buffers represent the 95% confidence interval.

juveniles have an extremely short period to gain mass. Due to their smaller size, juveniles also possess a smaller surface area to volume ratio, losing more mass than yearlings at lower temperatures (Armitage et al. 2003), which leads to high mortality during hibernation (Armitage and Downhower 1974). In this respect, juveniles are both at a greater time and size disadvantage when compared with yearlings and probably have the most to gain from increased seasonal growth. In fact, August mass was significantly associated with juvenile survival, and this relationship between offspring body mass and offspring survival has been observed in other mammals and birds (Ronget et al. 2017).

We found that relative seasonal growth had no effect on adult survival. Adults have completed the bulk of skeletal growth and attained full size; thus, they do not face the same developmental conflict in resource allocation as the younger cohorts. This finding is in line with our prediction that the costs of rapid mass gain would be lower in adults than in juveniles or yearlings.

The influence of valley position in the effects of relative seasonal growth on survival for yearlings suggests that environmental differences between up-valley and down-valley are selecting for different growth strategies. As mentioned above, whereas down-valley yearling survival was positively associated with compensatory growth, costs were evident in up-valley yearlings. Marmots in our up-valley sites live in an overall harsher environment, characterized by higher elevation, longer hibernation, and a shorter vegetative growth period (Blumstein et al. 2004). The majority of up-valley individuals hibernate about 14 days longer than down-valley marmots and, therefore, face a shorter active season (Blumstein et al. 2004). Costs of compensatory growth are likely higher in harsher environments, where any difference in body maintenance investment may directly affect individual fitness.

Environmental harshness may not be the only factor influencing the relationship between relative seasonal growth and yearling survival. In recent years, foxes have begun to raise their litters in a down-valley site (Waser et al. 2014) and the increase in predator numbers may have strengthened selective pressure on young marmots. This environmental change would potentially lead to higher mortality of smaller-sized yearlings and to the positive selection of rapidly growing yearlings because rapid growth probably reduces size-dependent vulnerability to predators. Thus, costs to compensatory growth may vary due to the type and strength of selective pressures associated with habitat heterogeneity and environmental

Table 2

Results from generalized linear models describing variation in female longevity by the age class analyzed (juvenile and yearling)

Fixed effect	Juveniles Estimate ± SE	*P*	Yearlings Estimate ± SE	*P*
Intercept	−1.08 ± 2.10	0.609	−2.37 ± 4.44	0.593
Relative seasonal growth	0.99 ± 0.67	0.103	2.46 ± 2.03	0.225
August mass	0.001 ± 0.001	0.243	0.001 ± 0.001	0.482
Position in valley (up-valley)	−0.28 ± 1.12	0.803	−4.10 ± 2.62	0.117
Year (2002)	0		0	
Year (2003)	0.14 ± 0.25	0.576	—	—
Year (2004)	0.09 ± 0.24	0.710	0.38 ± 0.36	0.300
Year (2005)	0.16 ± 0.26	0.532	0.18 ± 0.23	0.436
Year (2006)	−0.46 ± 0.31	0.136	0.45 ± 0.31	0.138
Year (2007)	−0.13 ± 0.27	0.616	−0.11 ± 0.33	0.746
Year (2008)	−0.54 ± 0.40	0.183	−0.56 ± 0.35	0.107
Year (2009)	−0.44 ± 0.36	0.159	−0.56 ± 0.38	0.145
Year (2010)	−0.25 ± 0.36	0.493	−0.58 ± 0.37	0.122
Year (2011)	−0.84 ± 0.74	0.258	−0.87 ± 0.53	0.101
Year (2012)	−0.40 ± 0.57	0.483	−0.54 ± 0.83	0.518
Year (2013)	−0.47 ± 0.59	0.424	−0.36 ± 0.55	0.519
Year (2014)	—	—	−0.51 ± 0.57	0.369
No. of mass measurements	0.003 ± 0.04	0.947	0.03 ± 0.02	0.079
Relative seasonal growth × August mass	−0.001 ± <0.001	0.110	−0.001 ± 0.001	0.279
Relative seasonal growth × Position in valley	−0.01 ± 0.24	0.957	0.57 ± 0.54	0.289
August mass × Position in valley	<0.001 ± <0.001	0.880	0.001 ± 0.001	0.280

SE, standard error.

Table 3

Variance covariance estimates (with their 95% credible intervals) from a trivariate model of relative mass gain, mass in August, and longevity. Components of variance are on the diagonal, covariance below diagonal, and correlation above the diagonal. — indicates effects that were not fitted, 0* indicates estimates that were fixed to zero. Parameters in bold are considered significantly different from zero

	Relative mass gain	Mass in August	Longevity
Among individuals			
Relative mass gain	0.057 (0.000/0.247)	0.067 (−0.677/0.639)	0.025 (−0.558/0.759)
Mass in August	0.008 (−0.089/0.100)	**0.424 (0.232/0.629)**	0.302 (−0.037/0.507)
Longevity	0.019 (−0.108/0.170)	0.159 (−0.040/0.353)	**0.974 (0.756/1.22)**
Among years			
Relative mass gain	**0.506 (0.147/1.018)**	0.100 (−0.466/0.713)	—
Mass in August	0.047 (−0.170/0.341)	**0.198 (0.050/0.409)**	—
Longevity	—	—	—
Residual			
Relative mass gain	**0.664 (0.498/0.834)**	**0.832 (0.754/0.878)**	0*
Mass in August	**0.464 (0.335/0.590)**	**0.479 (0.348/0.591)**	0*
Longevity	0*	0*	0*

unpredictability (Álvarez and Metcalfe 2007; Maldonado-Chaparro et al. 2017).

Because juvenile marmots are the most vulnerable to predation, the increased predator pressure down-valley may be the main reason for the higher juvenile survival up-valley. In addition, human activities have disproportionately taken their toll down-valley, where we have had young marmots die inside car engines, outhouses, or get hit by cars. Predator presence also limits prey-foraging activity (Sinclair and Arcese 1995) and increases individual stress levels, which can lead to reduced prey survival (Bonier et al. 2009; Romero and Wingfield 2015).

Adults residing up-valley were less likely to survive to the next year. This probably can be attributed to the harsher conditions associated with longer up-valley winters (Blumstein et al. 2004). Although increased predator density may underlie reduced survival rates in down-valley juvenile marmots, adult marmots are less affected by predators primarily due to their larger body size (Armitage 2014). Additionally, the competition for resources could potentially influence individual survival directly or by interacting with other factors. However, if resource competition was the principal cause of mortality in our study area, we would expect it to negatively influence all life stages. Instead, the location affected individual survival in each age class differently.

The relationship between the number of annual mass measurements and annual survival was positive for all age classes. This variable was added to account for sampling effort because the number of captures per individual per season varies. At least three hypotheses may explain this pattern: 1) individuals captured multiple times have more access to the nutritious food used as baits in traps, which could conceivably increase their overwinter survival; 2) individuals that die during the summer have fewer captures than individuals that survived all summer; and 3) larger group sizes may occur in areas of high habitat quality; thus, animals are trapped more times. Hypothesis 1 would not be expected for at least two reasons: first, once each trapping session ends, we remove the traps but the bait remains and this creates an opportunity for trap-shy animals to access the bait and, second, given the amount of food naturally available when we trap, our subsidy (a handful of bait) is relatively limited. Hypothesis 2 might be expected to be relevant for juveniles and yearlings because few adults die during the summer. Hypothesis 3 could apply to all age groups because we aim to trap all individuals biweekly; thus, large groups may require multiple capture sessions to capture most individuals. Assuming that group size is influenced by habitat quality and that individuals in high-quality habitats have high survival, we could expect an association between the number of recaptures and survival.

Our results regarding annual survival in yellow-bellied marmots suggest that there are short-term costs for yearling marmots that exhibit accelerated growth in harsher environments, but the lack of effects on longevity could indicate that there may be no long-term consequences. By contrast, it has been previously suggested that rapidly growing individuals may not pay the full price of compensation until later in life (Metcalfe and Monaghan 2001). Evidence of long-term costs of accelerated growth is mixed. Reduced long-term survival rates in rapidly growing individuals have been found in various species, including a population of lizards (*Niveoscincus mircolepidotus*; Olsson and Shine 2002) and numerous studies of lab-raised rodents (*Rattus norvegicus* and *Mus musculus*; Rollo 2002). In contrast, a study in wild bighorn ewes (*Ovis canadensis*) found no longevity effects of prolonged growth (Marcil-Ferland et al. 2013). Similarly to marmots, the wild bighorn ewes experience a seasonal cycle of mass gain during the summer and subsequent mass loss during the winter (Pelletier et al. 2007). In this respect, it is possible that cyclical fluctuations in resource availability are relevant factors in explaining species differences with regards to growth-related effects on lifespan.

Rapid mass gain followed by an extreme reduction in body mass is a life-history strategy selected in marmots. Increased caloric uptake, such as seen in compensating individuals, should increase metabolic rate and lead to increased production of oxygen radicals that damage cells and tissues. The result of this damage may, over time, lead to reduced longevity (Finkel and Holbrook 2000; Metcalfe and Monaghan 2003; Dmitriew 2011). The lack of longevity effects in marmots could suggest the existence of buffering somatic maintenance mechanisms in this species, as has been proposed for wild brown trout (Johnsson and Bohlin 2005). Alternatively, it may indicate that the metabolic differences between compensating and noncompensating individuals are not sufficiently great enough or carried out over a long enough time scale to lead to any detectable differences in lifespan length.

In summary, we focused on two fitness correlates, individual annual survival and longevity, to assess individual fitness consequences of rapid growth. Although there are costs to rapid growth (Arendt 1997), various growth rates may confer the same fitness (Mangel and Stamps 2001). The persistence of variation in seasonal growth of yellow-bellied marmots despite evidence of costs suggests that the benefits of compensatory growth outweigh the costs at the population level. Considering the central role mass gain plays in marmot life history (Armitage 2014) and the importance body size has for the survival and fitness of an overwhelming array of species, we may expect compensatory growth to not only persist in populations of this long-lived sciurid and other species that face similar temporal constraints on development, but also to play a dynamic role in buffering populations against environmental stressors. This may be of critical importance for numerous species in light of a rapidly changing climate.

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