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Environmentally induced phenotypic variation in wild yellow-bellied marmots

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

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

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

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

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

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

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

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

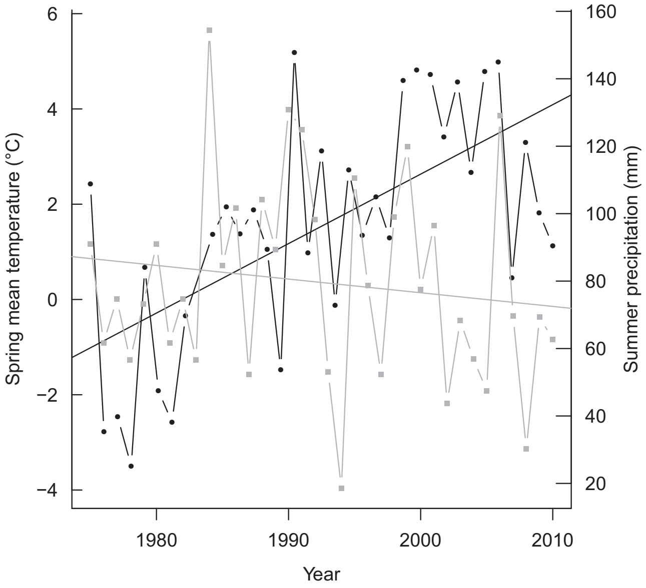

Fig. 1.—Yearly variation (with temporal trend) in mean spring temperature (°C; in black) and in summer precipitation (mm; in gray) at the Rocky Mountain Biological Laboratory (RMBL), Colorado.

Materials and Methods

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

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

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

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

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

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

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

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

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

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

RESULTS

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

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

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

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

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

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

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

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

[a] Indicates *t*-values.

[b] Indicates *Z*-value.

DISCUSSION

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

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

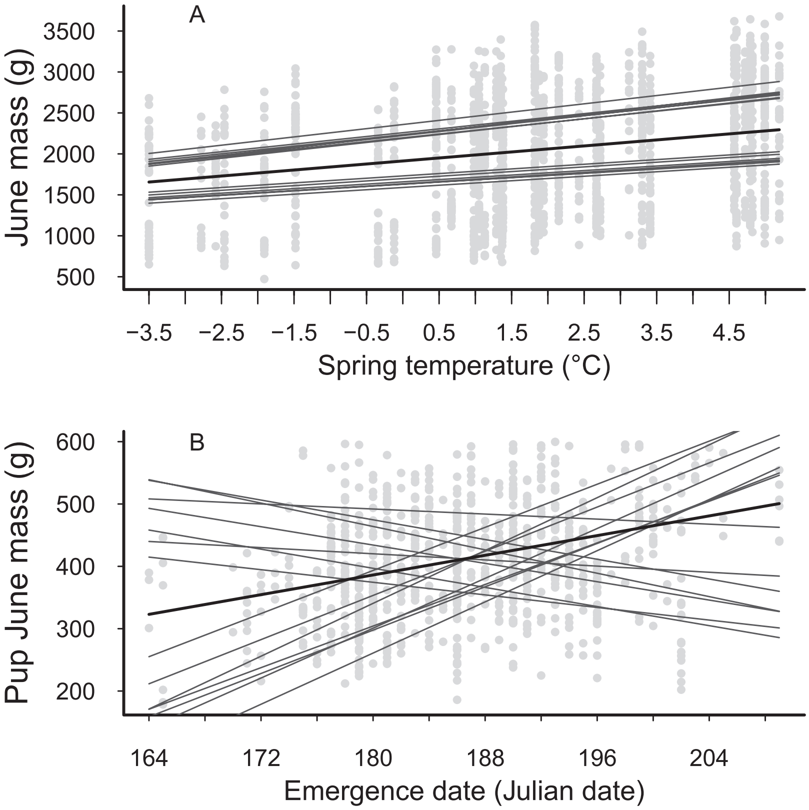

Fig. 2.—Reaction norm patterns of morphological and reproductive traits in yellow-bellied marmots (*Marmota flaviventris*). Black lines represent the mean population plastic response, and gray lines represent individual-level plastic responses. For the sake of clarity, in a) and b), plastic responses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

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

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

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

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

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

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

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

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

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

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

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

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SUPPORTING INFORMATION

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

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

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

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

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