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7 **Running heading:** Marmot phenotypic plasticity

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9 # Environmentally Induced Phenotypic Variation in Wild Yellow-

10 # Bellied Marmots

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25    Phenotypic plasticity, the ability of an individual to modify its phenotype according to

26    the conditions it experiences, is a source of between individual variation and a

27    mechanism by which individuals can cope with environmental change. Plasticity is

28    expected to evolve in response to environmental heterogeneity, such as seasonality and

29    year-to-year variation. We aimed to characterize the patterns of phenotypic change in

30    morphological (body mass), life-history (reproductive success and litter size), and social

31    (embeddedness) traits of female marmots, in response to climatic and social variation.

32    We used data collected over 36 years on a population of yellow-bellied marmots

33    (*Marmota flaviventris*) studied in Colorado. We used mixed effect models to explore the

34    phenotypically plastic responses and tested for individual variation in the mean trait

35    values (i.e., intercept) and in plasticity (i.e., slope). We showed that all examined traits

36    were plastic and that the population's average plastic response often differed: 1)

37    between spatially distinct colonies that varied systematically in the timing of snowmelt;

38    2) among age classes; and 3) between females with different previous reproductive

39    experiences. Moreover, we showed individual differences in June mass and pup mass

40    plasticity. We suggest that plasticity plays a key role buffering the effects of continuous

41    changes in environmental conditions.

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47    Phenotypic responses to varying environmental conditions can be mediated through

48    genetically based mechanisms across generations (i.e., micro-evolutionary process) or

49    through phenotypic plasticity (Charmantier et al. 2008). Phenotypic plasticity, the ability of

50    a genotype (i.e., an individual) to express different phenotypes as a function of the

51    environmental conditions experienced (Bradshaw 1965; Pigliucci 2001), is a ubiquitous and

52    widely documented phenomenon in natural populations (Gotthard and Nylin 1995). Plastic

53    responses, such as those entailing changes in an individual's behavioral, morphological, or

54    physiological traits, constitute important sources of variation in natural populations (Sultan

55    2000; Sultan and Spencer 2002). Moreover, plasticity may be adaptive (Pigliucci 2001),

56    may be altered by natural selection (Gotthard and Nylin 1995), and may have significant

57    effects at different levels of ecological organization (Miner et al. 2005; Vindenes et al.

58    2008). Due to its evolutionary and ecological importance, there has been an increased

59    interest in understanding the types and sources of such environmentally induced phenotypic

60    variation (Gotthard and Nylin 1995).

61    Phenotypic expression of morphological, physiological and behavioral traits can be

62    continuously affected by external factors such climate and other inter-annual environmental

63    variation (i.e., precipitation, food availability) within the lifetime of an individual. Climatic

64    variation occurs naturally over time; however, present rates of warming temperatures are

65    unprecedented and known to affect many species (Parmesan 2006). Global warming has

66    induced shifts in the geographical distribution and has altered the timing of life history

67    events of species (Parmesan and Yohe 2003). Additionally, it has been proposed recently

68    that warming temperatures have affected: 1) the mean body size of a number of species

69    (Gardner et al. 2011; Sheridan and Bickford 2011) including marine fish (Thresher et al.

3

70  2007), lizards (Chamaille-Jammes et al. 2006), birds (Yom-Tov 2001), and mammals

71  (Yom-Tov, Yom-Tov and Jarrell 2008); and 2) the behavior of organisms (Biro et al. 2010).

72  Given that both morphological and behavioral traits respond to climatic variation, and are

73  ecologically important because they affect an individual's life history and therefore

74  population growth (Chevin et al. 2010), it is important to ask if such changes are the result

75  of phenotypically plastic responses (i.e., environmentally induced variation). Additionally,

76  it is important to know whether individuals differ in their responses to environmental

77  variation (i.e., among individual variation in plasticity--Brommer et al. 2005; Nussey et al.

78  2005a, 2005b) since it is a requirement of evolution of plasticity.

79      Yellow-bellied marmots (*Marmota flaviventris*) are 3–5 kg diurnal, facultatively social,

80  hibernating sciurid rodents, which hibernates for 7–8 months (Armitage 1991). During the

81  active season (from mid-April or early May to August or September), individuals must gain

82  sufficient body mass to survive hibernation, as well as have sufficient fat stored to allow

83  them to survive until food resources become available, and have sufficient body condition

84  to reproduce the next year during the mating season which occurs immediately after

85  emergence (Armitage 1998). Because individual marmots may become philopatric, it is

86  possible to monitor all individuals in the population within their lifetime. This creates the

87  ability to identify between-individual variation of phenotypic traits.

88      We explore how female phenotypes changed in response to variation in multiple

89  environmental factors, and how this response varied among individuals. We used 36 years

90  of data, from 1975 to 2011, on a population of yellow-bellied marmots, *Marmota*

91  *flaviventris*, living in and around the Rocky Mountain Biological Laboratory (RMBL) in

92  western Colorado, where temperatures during the spring increased and summers

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93   precipitation has largely varied widely (Fig. 1). Specifically, we examined how climatic

94   conditions experienced by individuals during hibernation (i.e., winter), emergence from

95   hibernation (i.e., spring) and active season (i.e., summer), affected a set of labile traits that

96   vary during the lifetime of the individual and that describe the ability of an individual to

97   effectively obtain food resources from the environment, establish social relationships and

98   reproduce thus providing essential information on fitness and population dynamic.

99      To do so, we first focused on body mass (in June, in August and pup mass at

100  emergence), a morphological trait known to be influenced by temperature and precipitation

101  (Sheridan and Bickford 2011) and that affects marmot life history and demography

102  (Armitage et al. 1976; Ozgul et al. 2010). Second, we focused on reproductive traits

103  (reproductive success and weaned litter size) known to be important fitness components

104  and be influenced by climate change (Tafani et al. 2013). Finally, we evaluated how social

105  cohesion, which we measured as embeddedness--a trait known to influence dispersal

106  decisions (Blumstein et al. 2009), varied in response to these environmental and social

107  variables.

108     We know that the environmental conditions at RMBL have varied over time (Fig. 1). If

109  morphological, reproductive, and behavioral traits are potentially affected by environmental

110  conditions,  and the morphological variation identified since 2000 in the marmot population

111  is not a result of selection (Ozgul et al. 2010), we hypothesize that phenotypic plasticity can

112  be a mechanism that explains the phenotypic variation observed in the last decades.

113  Furthermore, due to the lack of evidence of selective pressures on body mass (Ozgul et al.

114  2010), we expected to see among individual variation in body mass plasticity. For

115  reproductive traits, since they strongly influence demography and are thus potentially

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canalized against temporal variation (Stearns and Kawecki 1994), we expect to observe less

plasticity and no individual variation in plasticity (i.e. no significant differences 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 response at both the population and

individual level. Finally, since behavioral reactions depend on the individual's past

environment (Dingemanse and Wolf 2013), we expected to see some plasticity in social

cohesion among individuals. .

## MATERIALS AND METHODS

*Monitoring and measurement of biological variables.*—Yellow-bellied marmots at the

RMBL, marmots are patchily distributed between elevations of 2700 to 3100 m.a.s.l.

(Armitage 2003a), leading to spatially distinct colonies that varied systematically in the

timing of snowmelt (up-valley versus down-valley; Van Vuren and Armitage 1991;

Schwartz et al. 1998).

Since 1962, marmots were live-trapped 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. Marmots were ear-tagged the first 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) categories: non-reproductive, nipples prominent, and reproductive (i.e., 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 a week after being seen

139    above ground for the first time (i.e., emergence date). Behavioral observations were

140    conducted from mid-April to early September, and social interactions were recorded

141    following an all occurrence sampling scheme (details in Wey and Blumstein 2010). For

142    each individual interaction, we recorded the type (i.e., affiliative or agonistic), the initiator

143    and recipient, location, and time of interaction.

144

145    *Body mass estimation.* —We used a linear mixed effect model with a restricted maximum

146    likelihood (REML) method to adjust each non-pup female's body mass to a specific date by

147    fitting it as a function of a linear and quadratic effect of day of the year (Ozgul et al. 2010;

148    Martin and Pelletier 2011). We included identity (ID, as an intercept), the individual mass

149    gain rate ("Day x ID"), year, and colony as random effects. We then used the predicted

150    values of yearly individual intercepts and slopes (provided by best linear unbiased

151    predictors, BLUPs) to adjust individual mass on 1 June and 15 August for each year.

152    Despite the uncertainty around BLUPs (Hadfield et al. 2010), the mixed model approach

153    provides adjusted body masses that are more accurate than those generated from a linear

154    regression for each individual (Martin and Pelletier 2011). We used 5,599 body mass

155    measurements from 1,448 female-years (mean = 3.86 masses per individual per year;

156    range: 1–20). For pups (pup mass), we used a similar model to estimate their body mass at

157    emergence (the 1st day a pup from a litter was seen above ground during the reproductive

158    season) based on 7,172 body masses from 2,277 pups (mean = 3.14 masses per individual;

159    range: 1–18).

160

161 *Reproductive traits.* —Every summer, and for each adult female, we noted the weaning

162 success (0 – failed to wean a litter, 1 – weaned a litter) and the size of the litter produced

163 (number of pups that emerged from the natal burrow). The female's prior reproduction is

164 the reproductive status (weaning and number of offspring) of the individual in the previous

165 year.

166

167 *Sociality.* —For each non-pup female, we used embeddedness, the degree to which an

168 individual is well integrated to other individuals in the group (Moody and White 2003), as a

169 measure of social cohesion (details in Blumstein et al. 2009). We used affiliative

170 interactions to construct social networks for each social group in the colony sites each year.

171 Within each social group, we calculated the embeddedness of each individual for each year

172 by converting the social matrix into a symmetric, undirected matrix and then applying the

173 Moody and White (2003) cohesive blocking algorithm, as implemented in the igraph

174 package v. 0.6.5-2 (Csardi and Nepusz 2006) in R software (R Core Team 2013).

175

176 *Quantifying environmental variation.* —We used a set of 7 climatic variables and 2 social

177 variables to describe the environmental conditions experienced by the marmots (see

178 definitions in Supporting Information S1). Winter (WMT) and spring (SMT) mean

179 temperatures (°C) were obtained from the RMBL weather station (106º59.588'N, 38º773'W

180 at 2900 m) from 1975 to 2011. The length of the growing season (LGS) was calculated as

181 number of days from the first day of bare ground to the first mean daily temperature below

182 0ºC. Summer (i.e., June and July) precipitation (SP) records were obtained from the

183 National Oceanic and Atmospheric Administration weather station in Crested Butte (9.5 km

184 from RMBL at 2700 m). As a measure of vegetation productivity of the valley, we used a

185 NDVI (normalized difference vegetation index), obtained from satellite images from the

186 Global Inventory Modelling and Mapping Studies (GIMMS) corrected dataset for a period

187 spanning from 1981 to 2006 (Tucker et al. 2005). The NDVI values for April (ANDVI) and

188 July (JNDVI) for each year were used to reflect the seasonal variation in food availability

189 within and among years.

190    We used two different indices of social environment. First, we estimated the yearly

191 colony size (CS) as the number of non-pup individuals from both sexes present in a colony

192 in the current year (including individuals that potentially disperse). Second, within each

193 colony, we estimated the yearly non-pup group size (GS) from 2002 to 2011 using a

194 network approach based on marmots observed at least 5 times within a year. To do so, we

195 used a random walk algorithm (Rosvall and Bergstrom 2008) to determine the number and

196 identity of the non-pup marmots that belonged to a particular group. We based group

197 assignments on the individual's current space-use overlap (Smith, Strelioff, Blumstein,

198 unpublished data), and on the proportion of time that a pair of individuals was seen together

199 (based on livetrapping and observation data). This was calculated over a period of one

200 active season (i.e., April through September).

201

202    *Analysis of phenotypic responses.*—To test for phenotypically plastic responses, we

203 used a "reaction norm approach", which relates the phenotypic expression of an individual

204 to an environmental gradient (Pigliucci 2001). Such a framework allows us to calculate the

205 expected trait value in the mean environment (i.e., intercept or 'I'), the phenotypic change

206 per unit of change of the environment (i.e., slope or 'E'), individual differences in the

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207  plastic response (i.e., individual by environment interaction or 'I x E'; Nussey et al. 2007),

208  and correlations among an individual's intercept and slope ($r_{ES}$). We used repeated-

209  measures for an individual across multiple years to fit generalized linear mixed models

210  (GLMMs) for each of our dependent variables: June mass, August mass, pup mass,

211  weaning success, litter size, and embeddedness. We used a Gaussian distribution (identity

212  link-function) to fit each of our models, except for weaning success, for which we used a

213  binomial distribution (logit link-function). We scaled the variables (by subtracting the mean

214  and dividing the centered value by two standard deviations following Gelman 2008) to

215  facilitate comparison of the model coefficients within and between analyses (Nussey et al.

216  2007). We constructed and analyzed the mixed effect models in two stages.

217      The goal of the first stage was to identify, for each model, the significant environmental

218  effects (i.e., I and E). We did not test for variation in individual plasticity during this step to

219  avoid over-fitting the model (see Zuur et al. 2009 for model selection approaches). For each

220  dependent variable, we constructed the maximum model that included all biologically

221  meaningful explanatory variables in the fixed-effect component (Table 1). We included as

222  random effects: 1) female identity, to control for repeated measures on individuals; 2) year,

223  to control for unexplained annual variation in the climate and social environment

224  covariates; and 3) group identity (i.e., the identity of the social group to which a marmot

225  belongs), to control for repeated measures on groups. Then, using a backwards-stepwise

226  approach (Zuur et al. 2009), we excluded the least significant fixed effect and refit the

227  model until we obtained the minimum fitted model in which all the explanatory variables

228  were significant at the 5% level. Significance of fixed effects was estimated using the

229  Satterthwaite's approximation for degrees of freedom in the lmerTest package v. 2.0-3 in R

230   (Kuznetsova et al. 2013). Random effects were not tested at this stage and only included to

231   correct for the hierarchical structure of the data.

232       In the second stage we evaluated, for each variable in the minimum fitted model,

233   patterns of variation in individual plasticity. Specifically we tested to see if there was: 1)

234   among individual variation of the trait value in the mean environment (i.e., I, fitted with

235   individual identity [ID]); 2) individual variation in plasticity (i.e., I x E, fitted as

236   environment x ID); and 3) a significant correlation between the trait value in the mean

237   environment and plasticity at the individual level (i.e., $r_{ES}$, fitted as the correlation between

238   ID and environment x ID). The significance of each random effect was tested by

239   performing a Likelihood Ratio Test (LRT; Pinheiro and Bates 2000), where we compared

240   models with and without the specific random effect of interest fitted using a REML

241   approach. All analyses were implemented in R v. 3.0.2 (R Core Team 2013) and the R

242   package lme4 (Bates et al. 2013).

243

244                                    **RESULTS**

245   *Trends in climate.* —In general, over time, our study site was getting warmer but also had

246   an increase in food availability (Supporting Information S2). For the period from 1975 to

247   2011, winter mean temperatures increased by $0.105 \pm 0.020$°C (SE) per year ($r^2 = 0.439, t_{34}$

248   $= 5.330, P < 0.0001$), and spring mean temperatures increased by $0.150 \pm$ °C per year ($r^2 =$

249   $0.383, t_{32} = 4.636, P < 0.0001$; Fig. 1). The growing season shortened by $0.734 \pm 0.290$

250   days per year ($r^2 = 0.134, 34_{df}, t = -2.528, P = 0.016$), as a result of a significant earlier start

251   of permanent snow cover. Growing season finished $1.16 \pm 0.163$ days earlier per year ($r^2 =$

252   $0.587, 34_{df}, t = -7.125, P < 0.0001$), although it also showed trends of an earlier snow melt

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253    $(-0.318 \pm 0.218, r^2 = 0.030, 35_{df}, t = -1.459, P = 0.154)$. Precipitation during the summer

254    did not decrease significantly over time $(-0.406 \pm 0.482$ mm per year, $r^2 = -0.008, 34_{df}, t = -$

255    $0.841, P = 0.406$, Fig. 1). During the period from 1981 to 2005, April food availability

256    increased slightly, $0.006 \pm 0.002$ NDVI per year $(r^2 = 0.214, 23_{df}, t = 2.748, P = 0.011)$,

257    whereas July food availability did not change $(0.002 \pm 0.002$ NDVI per year, $r^2 = -0.02$,

258    $24_{df}, t = 0.717, P = 0.480)$.

259

260    *Population level phenotypic response.* —Across the study period, we found difference in

261    rate and the direction at which the changes in the phenotype take place (i.e., value and sign

262    of the slope-Table 2, see Supporting Information S3 for non-significant effects). At the

263    population level, we identified positive and negative responses to changes in environmental

264    variables. June mass exhibited a positive response to spring temperature, i.e., females were

265    heavier in June when spring temperatures were warmer (Table 2; Fig. 2a). The effect of the

266    length of growing season on August body mass exhibited a negative pattern (Table 2). In

267    this case, female August mass increased with shorter growing seasons. Among the

268    reproductive traits, weaning success was positively correlated with spring temperatures,

269    whereas the number of weaned pups increased with increases in maternal June mass, and

270    when there were fewer individuals in the colony (Table 2). Pup mass was positively

271    correlated with emergence date (Table 2). Finally, embeddedness increased as group size

272    increased (Table 2).

273        In addition to variation in the pattern of plasticity, we found significant differences in

274    the mean plastic response between spatially distinct colonies (up-valley versus down-

275    valley), age category, and reproductive status. Female marmots living up-valley had smaller

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276   litters than females living down-valley. Also, up-valley females were smaller during the

277   spring season than down-valley females, but at the end of the season (i.e., August) up-

278   valley females were heavier (Table 2). In general, adult females that had reproduced the

279   year before compared to females that did not reproduce are: 1) heavier in early season, 2)

280   had greater weaning success the current year, and 3) were more socially cohesive (Table 2).

281   Finally, yearling females appeared to be the most socially cohesive among females of all

282   age categories (Table 2).

283

284   *Individual level phenotypic response.* —At the individual level, individuals differed in the

285   mean (i.e., intercept) June mass, August mass, and litter size, as indicated by the significant

286   random effect of female identity (Table 3). We identified significant individual variation in

287   the plasticity (i.e., the slope) of female June mass as a function of spring temperature (Table

288   3; Fig. 2a), and pup body mass as a function of date of emergence (Table 3; Fig. 2b).

289   Finally, we found a significant positive correlation, at the individual level, between

290   intercept and the effect of spring temperature on female June mass (Table 3; Fig. 2a).

291

292                                    **DISCUSSION**

293       Our results showed that all measured phenotypic traits of female yellow-bellied

294   marmots were affected by multiple environmental factors, and that the observed variation

295   may be explained by phenotypically plastic responses. In general, female marmots: 1)

296   exhibited significant population-level phenotypic plasticity in their morphological, life

297   history, and social traits across environments; 2) varied in their individual average response

298   (i.e., intercept); and, for two traits, 3) varied in the degree of individual plasticity (i.e.,

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299  slope). The mean response differed between: 1) spatially distinct colonies that varied

300  systematically in the timing of snowmelt (up-valley versus down-valley); 2) age categories;

301  and 3) females with prior reproductive experiences. Our finding is consistent with an

302  expectation that most quantitative traits have some degree of phenotypic plasticity

303  (Pigliucci 2001).

304

305  *Population level phenotypic plasticity patterns.* —Our marmot population showed

306  different phenotypically plastic trends across morphological, reproductive and behavioral

307  traits that can be attributed to differences in how rapidly each trait responded to

308  environmental changes. Moreover, climate conditions during hibernation and emergence

309  affected many traits in our population. Warmer winter temperatures were associated with

310  increased weaning success, a reproductive trait that was also positively affected by food

311  availability in April (measured as NDVI index) and warmer spring temperatures. Likewise,

312  females' June mass and August mass were enhanced by warmer springs and shorter

313  growing seasons, respectively. This suggests that body size and fecundity can be positively

314  affected by anthropogenic climate warming (i.e., increases in spring temperatures and early

315  timing of snow melt). These results showed an opposite  trend than that seen in other

316  species where body mass and litter size decreased with warmer temperatures (Gardner et al.

317  2011; Ohlberger 2013; Tafani et al. 2013, but see Yom-Tov et al. 2008). Thus, we suggest

318  that the observed increase in body mass, and the associated reproductive outcomes, are a

319  response to warmer temperatures that may emerge as a result of changes in physiological

320  responses that affect metabolic rates (Boyles et al. 2011) or changes in foraging strategies

321  (Van Beest and Milner 2013).

14

322    Warmer ambient temperatures may affect marmots in two ways: 1) they can facilitate

323    energy savings on metabolism,  especially during hibernation in winter, and 2) they can

324    induce an earlier snow melt thus increasing the food availability during the spring which

325    enhances individual body condition and body size. Moreover, our results revealed

326    intraspecific differences in the nature of the body mass response in habitats with different

327    phenologies. Marmots at our up-valley sites were, on average, lighter in June than down-

328    valley marmots, but, interestingly, up-valley marmots were slightly heavier in August than

329    down-valley marmots. This finding suggests a mechanism that enables adult marmots to

330    compensate for a bad start. Furthermore, pups born up-valley were heavier than those born

331    down-valley after controlling for variation explained by litter size and other variables, but

332    up-valley females weaned smaller litters than down-valley females. Within population

333    differences in the plastic response may result from some level of genetic adaptation in

334    response to climate change (Bradshaw et al. 2006; Bradshaw and Holzapfel 2008; Husby et

335    al. 2011), which would be inferred if spatially distinct colonies differed genetically within a

336    population. Although  it is possible that such genetic differences among colonies in our

337    population might have appeared in the last decade, we have not previously identified

338    them (Schwartz and Armitage 1980). Therefore, the observed differences are likely to be

339    driven mostly by local environmental conditions. Thus, we suggest that differences in

340    microclimatic conditions can affect life history traits within populations and can trigger

341    differences in a population's mean phenotypic response.

342    Variation in the social environment can trigger phenotypically plastic responses. Colony

343    size, which can be interpreted as a measure of local density, can modify intraspecific

344    competition experienced by an individual, thus affecting reproductive and foraging

15                                                  - -

345  decisions (Parker and Begon 1986). Our results indicate that, at low local densities, females

346  can increase their litter size through phenotypic plasticity. For instance, female marmots

347  living in small groups can increase their per capita offspring production (Armitage 1986),

348  perhaps as a result of decreased competition within and among matrilines (Armitage

349  2003b). In general, a female's litter size allocation decisions depend on the predicted

350  competitive environment of their adult offspring and on her body condition (Mousseau and

351  Fox 1998; Dobson et al. 1999). In our study, females in better body condition in June were

352  more likely to wean larger litters; though, because body size is often correlated with

353  reproductive output (Lindström 1999), we can expect increases in body size to positively

354  affect weaning success. Likewise, a female's body mass is positively associated with

355  increases in colony size. This result may differ from the negative relationship between body

356  size and local abundance expected from intraspecific competition (Begon et al. 1986).

357  However, in populations where food is not a limiting resource, such as the yellow-bellied

358  marmots we study (Blumstein 2013), we might expect individuals to increase their mean

359  body size regardless of local population size.

360       Additionally, our results indicated that within colonies social group size is positively

361  associated with social structure. In species in which group size fluctuates annually, like the

362  marmots we study, an individual's ability to establish social relationships with other

363  individuals might affect its fitness (Sibly 1983). Therefore, individuals should increase their

364  affiliative interactions with other group members to maintain group cohesion until the cost

365  of living in a group outweighs the advantages of group living (Sueur et al. 2011). Such

366  plasticity in social behavior varied among age categories and reproductive status. Thus,

367  yearling females may increase their group cohesion as a way to remain philopatric and

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368    increase their direct fitness (Blumstein et al. 2009), whereas older females increase their

369    amicable behaviors and cohesiveness as a way to increase their ability to recruit younger

370    individuals (Armitage 2011; Armitage et al. 2011). Furthermore, females that reproduced

371    the year before (i.e., mothers) are more socially cohesive, perhaps because they can play a

372    role as promoters of social cohesiveness (Armitage 2011; Armitage et al. 2011).

373

374    *Individual level variation in the phenotypic response.* —Females differed in their mean

375    phenotypic response (i.e., intercept) for three of the evaluated traits (June mass, August

376    mass, and litter size). This variation can occur as a result of biological differences, such as

377    reproductive status and age, or as a result of genetic differences between individuals. Also,

378    such differences could emerge from individual-specific previously experienced ecological

379    conditions (so-called permanent environment effect, Kruuk and Hadfield 2007), or they

380    could emerge from variation in individual quality (Nussey et al. 2007; Dingemanse et al.

381    2010; Dingemanse and Wolf 2013). Future studies will be required to determine which is

382    important in this population.

383    We found among-individual variation in the slope (i.e., I x E) of June mass as a function

384    of spring temperature, and pup mass as a function of date of emergence, indicating that

385    individuals can respond differently to the changes in the current environmental conditions.

386    In both cases, differences may emerge as a consequence of differences in the internal state

387    of the individual, because of variation in individual-specific habitat use (Dingemanse and

388    Wolf 2013), or because of intraspecific competition for resources (Wolf et al. 2008).

389    Specifically, individual variation in pup mass plasticity may result from the pup's internal

390    state and non-genetic maternal effects, whereby the mother can shape the offspring's

391    phenotype according to the environment in which the pup develops (Mousseau and Fox

392    1998; Lindström 1999). Assuming the existence of some genetic variation, the presence of

393    individual differences in plasticity creates the opportunity for selection and evolution of

394    plasticity in body mass with environmental changes.

395         Finally, there was a positive correlation between intercept and slope for June mass

396    plasticity, which means that heavier females in June can express larger plastic responses

397    than lighter females. Thus, we suggest that warmer springs lead to heavier females that can

398    get disproportionally larger than smaller females. Correlations among intercept and slope

399    may also indicate that plasticity is heritable (Nussey et al. 2007) and therefore can be

400    subject to natural selection. In contrast, the lack of among-individual differences in

401    plasticity (shown by the non-significant I x E) in August mass, weaning success, litter size,

402    and embeddedness, suggests that there could be physiological or genetic constraints on

403    plasticity. Even though we did not evaluate underlying genetic differences in the plastic

404    response (i.e., G x E), individual variation in plasticity can maintain phenotypic variation at

405    the population level, therefore fostering population stability and persistence (Dingemanse

406    and Wolf 2013).

407         In conclusion, we showed that long-term, individual-based studies provide unique

408    insights into phenotypic plasticity and may allow us to predict how climate changes can

409    affect the fate of natural populations. Female marmots responded to environmental

410    variation through phenotypically plastic responses, and importantly, plasticity of some traits

411    differed among individuals, which could enhance the population's potential to adapt to a

412    warming environment. Individual differences in our population suggests that further studies

413    could explore the relative importance of genetic and environmental effects in accounting

414 for these patterns. While we did not evaluate the adaptive value of plasticity, anthropogenic

415 climate change will place individuals in a different selective regime, with potential

416 consequences to individual fitness, population genetics, and population dynamics. More

417 importantly, our findings suggest that phenotypic responses have direct conservation

418 implications regarding the importance of the environment in the maintenance of natural

419 variation within a population, and they encourage further exploration of interactive effects

420 of plasticity of morphological, life history, and social traits in population dynamics.

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27

**FIGURE LEGENDS**

611 **FIG. 1.**— Yearly variation (with temporal trend) in spring mean temperature (°C; in black)

612 and in summer precipitation (mm; in grey) at the Rocky Mountain Biological Laboratory

613 (RMBL).

614

615 **FIG. 2.** — Reaction norm patterns of morphological and reproductive traits in yellow-

616 bellied marmots. Black lines represent the mean population plastic response, and gray lines

617 represent individual-level plastic responses. For the sake of clarity, in a and b, only 14

618 individuals' plastic responses are illustrated. These were chosen from females with the

619 highest and lowest slopes and were estimated from models in Table 2 using population

620 means for all other parameters.

621                                   **TABLES**

622    **TABLE 1.**— Fitted fixed effects in the Linear Mixed Models (LMM) for each of the

623    six evaluated traits. The fixed effects are: Winter temperature (WMT), Spring

624    temperature (SMT), April NDVIS (ANDVI), Colony size (CS), Age category (AC),

625    Previous reproductive status (PRS), Valley (V), June body mass (JBM), Summer

626    precipitation (SP), Length of growing season (LGS), July NDVI (JNDVI), Litter size

627    (WLS), Pup Emergence date (PED), Pup sex (Sex), Group size (GS). Valley indicates

628    differences in the altitudes of the spatial location of a marmot in its natural

629    environment (Up and Down-Valley).Variables in bold are the fixed effects that

630    remained in the final mixed model.

631

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

632

Table 2. Estimates of significant fixed effects obtained through a linear mixed effect

634   model for yellow-bellied marmot females. The reference categories for the (*) factors

635   are: Valley [Down-Valley]; Age Category [Adults]; Reproduce previous year [No]; In

636   the case of pup body mass, Sex [Female]. *Z*-value is reported for binomial models and

637   *t*-values for Gaussian models.

638

| *Fixed effects* | Estimate | *SE* | $t^a$, $z^b$ | *P*-value |
|---|---|---|---|---|
| June mass (*n* = 1418 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* = 1424; 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 x 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; 151 females; 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; 176 females; 21 groups; 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 |

640　　Table 3. Estimates of random effects obtained through a linear mixed effect model for

641　　June and August female body mass. Proportion of variance explained (PVar) was

642　　estimated as the ratio of a variance component over sum of the variance components.

643　　$r_{E\text{-}S}$ represent the correlation between ID and "spring temperature x ID".

| *Random effects* | Estimate | PVar | LRT | *P*-value |
|---|---|---|---|---|
| June mass (*n* = 1418 observations; 591 females; 34 years) | | | | |
| Year | 0.007 | 0.192 | 224.78 | < 0.001 |
| ID (intercept) | 0.013 | 0.336 | 319.28 | < 0.001 |
| Spring mean temperature x ID (slope) | 0.002 | 0.054 | 8.11 | 0.018 |
| $R_{E\text{-}S}$ | 0.60 | | 30.91 | < 0.001 |
| Residual | 0.016 | | | |
| August mass (*n* = 1424 observations; 593 females; 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; 34 years) | | | | |
| Year | 0.267 | | 15.0 | < 0.001 |
| ID | 0.202 | | 2.13 | 0.140 |
| Weaned litter size (*n* = 339 observations; 151 females; 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 x ID (Slope) | 0.286 | 0.534 | 65.71 | < 0.001 |
| Residual | 0.163 | | | |
| Embeddedness (*n* = 429 observations; 176 females; 21 groups; 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 | | | |

644