1   **Seasonal Effects of Environmental Change on Yellow-Bellied Marmot**

2   **Population Dynamics**

3   <u>Running title</u>: Seasonal mechanisms of population dynamics

4   <u>Authors</u>: Maria Paniw[1], Dylan Childs[2], Kenneth B Armitage[3], Daniel T Blumstein[4,5], Julien

5   Martin[6], Madan Oli[7], Arpat Ozgul[1]

6

7   *1 - Department of Evolutionary Biology and Environmental Studies, University of Zurich,*
8   *Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*
9   *2 - Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN,*
10   *UK*
11   *3 - Ecology & Evolutionary Biology Department, The University of Kansas, Lawrence, KS 66045-7534,*
12   *USA*
13   *4 - Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles,*
14   *CA 90095, USA*
15   *5 - The Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA*
16   *6 - School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, UK*
17   *7 - Department of Wildlife Ecology, University of Florida, Gainesville, FL 32611, USA*
18
19
20   [*]<u>Corresponding author</u>: Tel.: +34-671-246-338; email: maria.paniw@ieu.uzh.ch; ORCID ID: 0000-0002-
21   1949-4448
22

23   **ABSTRACT**

24   Environmental factors drive the persistence of natural populations by causing complex,

25   covarying responses in demographic processes (*i.e.*, survival, growth, and reproduction). As

26   most natural populations inhabit seasonal environments, overlooking seasonal differences in this

27   covariation may obscure the mechanisms that buffer or amplify population responses to

28   environmental change. We investigated how environment-driven covariation of seasonal

29   demographic processes affects population dynamics using 40 years of individual-based data from

30   a population of yellow-bellied marmots (*Marmota flaviventer*). We first used a factor-analytic

31 approach to jointly model demographic processes as a function of a latent variable describing

32 yearly environmental quality. We then parameterized, perturbed, and projected into the future a

33 seasonal population model that explicitly incorporated the covarying demographic responses to

34 the environment. The projections were based on various scenarios of environmental change,

35 including changes in the trend and temporal patterning of environmental quality. We show that,

36 although demographic processes in both the summer and winter season contributed to population

37 fitness, yearly environmental quality exerted the strongest effect on winter demography only.

38 Simultaneous, negative responses to declining average environmental quality of winter survival

39 and mass and reproductive-status change resulted in an increased risk of population quasi-

40 extinction, regardless of summer demography. We emphasize that assessing seasonal

41 demographic effects is key to understanding population persistence in the face of environmental

42 change and should receive much more attention in ecological theory and conservation

43 management.

44 **INTRODUCTION**

45 Effects of environmental change on survival, growth, and reproduction are typically investigated

46 based on annual transitions among life-history stages in structured population models (Paniw,

47 Ozgul, & Salguero-Gómez, 2018; Salguero-Gómez et al., 2016). However, all natural

48 ecosystems show some level of seasonal fluctuations in environmental conditions, and numerous

49 species have evolved life cycles that are cued to such seasonality (Ruf, Bieber, Arnold, &

50 Millesi, 2012; Varpe, 2017). For example, most temperate- and many arid-environment species

51 show strong differences in survival and growth among seasons, with reproduction being confined

52 mostly to one season (Childs, Coulson, Pemberton, Clutton-Brock, & Rees, 2011; Rushing et al.,

53 2017; Woodroffe, Groom, & McNutt, 2017). Species with highly adapted, seasonal life cycles

2

54 are likely to be particularly vulnerable to environmental change, even if they are relatively long-

55 lived (Campos et al., 2017; Jenouvrier et al., 2012; Paniw, Maag, Cozzi, Clutton-Brock, &

56 Ozgul, 2019). This is because adverse environmental conditions in one season may carry-over to

57 the next season in which key life-history events (e.g., reproduction) occur, and can negate

58 positive season-specific environmental effects (Marra, Cohen, Loss, Rutter, & Tonra, 2015). For

59 instance, in species where individual traits such as body mass determine demographic rates,

60 environment-driven changes in the trait distribution in one season can affect trait-dependent

61 demographic rates in the next season (Bassar, Letcher, Nislow, & Whiteley, 2016; Paniw et al.,

62 2019). Investigating annual dynamics, averaged over multiple seasons, may, therefore, obscure

63 the mechanisms that allow populations to persist under environmental change.

64 　　　　Despite the potential to gain a more mechanistic view of population dynamics, modeling

65 the effects of seasonal environmental change is an analytically complex and data-hungry

66 endeavor (Bassar et al., 2016; Benton, Plaistow, & Coulson, 2006). This is in part because

67 multiple environmental factors that change throughout the year can interact with each other and

68 individual-level (e.g., body mass) or population-level factors (e.g., density dependence) to

69 influence demographic rates (Benton et al., 2006; Lawson, Vindenes, Bailey, & van de Pol,

70 2015; Ozgul, Oli, Olson, Blumstein, & Armitage, 2007; Paniw et al., 2019; Töpper et al., 2018).

71 One major analytical challenge for population ecologists is that typically only a small subset of

72 potential environmental drivers of population dynamics are known and measured (Ehrlén,

73 Morris, von Euler, & Dahlgren, 2016; Teller, Adler, Edwards, Hooker, & Ellner, 2016). Another

74 challenge is that key environmental factors simultaneously affect multiple demographic rates

75 causing them to covary within and among seasons (Maldonado-Chaparro, Blumstein, Armitage,

76 & Childs, 2018; Paniw et al., 2019). Positive environment-driven covariation in demographic

3

77   rates can then amplify the population-level effects of environmental change (Jongejans, de

78   Kroon, Tuljapurkar, & Shea, 2010; Robert, Bolton, Jiguet, & Bried, 2015). Antagonistic

79   demographic responses on the other hand can buffer populations from environmental change

80   (Knops, Koenig, & Carmen, 2007; Van de Pol et al., 2010); for instance, when population-level

81   effects of decreased reproduction are offset by increases in survival or growth (Connell &

82   Ghedini, 2015; Reed, Grøtan, Jenouvrier, Sæther, & Visser, 2013; Villellas, Doak, García, &

83   Morris, 2015). Thus, explicit consideration of environment-driven patterns in demographic

84   covariation can allow to gain a fuller picture of population persistence in a changing world. Such

85   a consideration remains scarce (Ehrlén & Morris, 2015; Ehrlén et al., 2016) but see (Bassar et al.,

86   2016; Compagnoni et al., 2016).

87   A flexible framework to model population responses to environment-driven demographic

88   covariation are integral projection models (IPMs; Ellner, Childs, & Rees, 2016). Seasonal IPMs

89   are an extension of periodic matrix population models (Caswell, 2001, ch. 13 and references

90   therein) (Ripley & Caswell, 2006), and simultaneously project trait distributions and population

91   dynamics across seasons. The construction of IPMs is typically done by fitting simple models

92   describing demographic rates as functions of a continuous state variable (e.g., body mass) and

93   (environmental) covariates. Thus, this framework can integrate demographic covariation in

94   response to environmental drivers (Hindle et al., 2018; Merow et al., 2014; Rees & Ellner, 2009).

95   IPMs are increasingly used to project population dynamics under environmental change (Paniw

96   et al., 2019; Paniw, Quintana-Ascencio, Ojeda, & Salguero-Gómez, 2017b; Simmonds &

97   Coulson, 2015); however, periodic IPMs have been developed in only a few cases (Bassar et al.,

98   2016; Paniw et al., 2019), despite their potential to provide a mechanistic understanding of

4

99   seasonal carry-over effects (Harrison, Blount, Inger, Norris, & Bearhop, 2010; Hostetler, Sillett,

100   & Marra, 2015).

101   Here, we investigated the population-level effects of environment-driven seasonal

102   covariation among trait-mediated demographic rates (*i.e.*, collectively referred to as demographic

103   processes), capitalizing on 40 years (1976-2016) of individual-based data from a population of

104   yellow-bellied marmots (*Marmota flaviventer*). Yellow-bellied marmots have adapted to a highly

105   seasonal environment; individuals spend approximately eight months in hibernation during the

106   cold winter (September/October-April/May), and use the short summer season (April/May-

107   September/October) to reproduce and replenish fat reserves (Fig. 1). One challenge that the

108   marmot study shares with numerous other natural systems is the identification of key proximal

109   environmental factors driving population dynamics. In marmots such factors are numerous and

110   affect population dynamics through complex, interactive pathways (Maldonado-Chaparro, Read,

111   & Blumstein, 2017; Oli & Armitage, 2004), which include interactions with phenotypic-trait

112   structure (Ozgul, Childs, Oli, Armitage, & Blumstein, 2010). As a result, measures of

113   environmental covariates (e.g., temperature) have previously shown little effect on the

114   covariation of marmot demographic processes (Maldonado-Chaparro et al., 2018). To address

115   this challenge, we used a novel method, a hierarchical factor analysis (Hindle et al., 2018), to

116   model the covariation of demographic processes as a function of a shared measure of latent

117   environmental quality (*i.e.*, environmental condition at a given time point), quantified in a

118   Bayesian modeling framework. We then built seasonal stage-, mass-, and environment-specific

119   IPMs for the marmot population and used prospective stochastic perturbation analyses and

120   population projections to assess how environmental change may affect population dynamics via

121   the observed demographic covariation.

122   **METHODS**

123   *Study species*

124   Yellow-bellied marmots are large, diurnal, burrow-dwelling rodents, occupying montane regions

125   of the western North America (Armitage, 2003; Frase & Hoffmann, 1980). They experience

126   strong seasonal fluctuations in environmental conditions (Armitage, 2014). The biology of

127   yellow-bellied marmots in Colorado is described in detail by Armitage (2014). Our study was

128   conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory,

129   Gothic, Colorado (38° 57' N, 106° 59' W). Climatic conditions in both winter and summer have

130   been shown to influence reproduction and survival in the subsequent season (Lenihan & Van

131   Vuren, 1996; Van Vuren & Armitage, 1991). These climatic effects on the demography of

132   yellow-bellied marmots are mediated through body mass, with heavier individuals more likely to

133   survive hibernation and reproduce in summer (Armitage, Downhower, & Svendsen, 1976; Ozgul

134   et al., 2010). Population dynamics of marmots are therefore likely to be susceptible to changes in

135   seasonal patterns of environmental drivers. However, numerous interacting climatic factors, such

136   as temperature extremes, snowfall, and length of snow cover, determine both winter and summer

137   environmental conditions, and their effect on marmot demography have been shown to be

138   difficult to disentangle (Inouye, Barr, Armitage, & Inouye, 2000; Schwartz & Armitage, 2002;

139   Schwartz & Armitage, 2005).

140

141   *Seasonal demographic rates and trait transitions*

142   For this study, we focused on the population dynamics of eight major colonies continuously

143   monitored since 1976 (Armitage, 2014; Supporting Material S1). Each year, marmots were live-

144   trapped throughout the growing season in summer (and ear-tagged upon first capture), and their

145   sex, age, mass, and reproductive status were recorded (Armitage & Downhower, 1974;

146   Schwartz, Armitage, & Van Vuren, 1998). We focused on seasonal demographic processes of

147   females only. All young males disperse from their natal colonies, and female immigration into

148   existing colonies is extremely rare; as such, local demography can be accurately represented by

149   the female segment of the population (Armitage, 2010). We classified female marmots by age

150   and reproductive status: juveniles (< 1 year old), yearlings (1 year old), and non-reproductive ($\geq$

151   2 years old; not observed pregnant or with offspring) and reproductive adults ($\geq$ 2 years old;

152   observed pregnant or with offspring) (Armitage & Downhower, 1974).
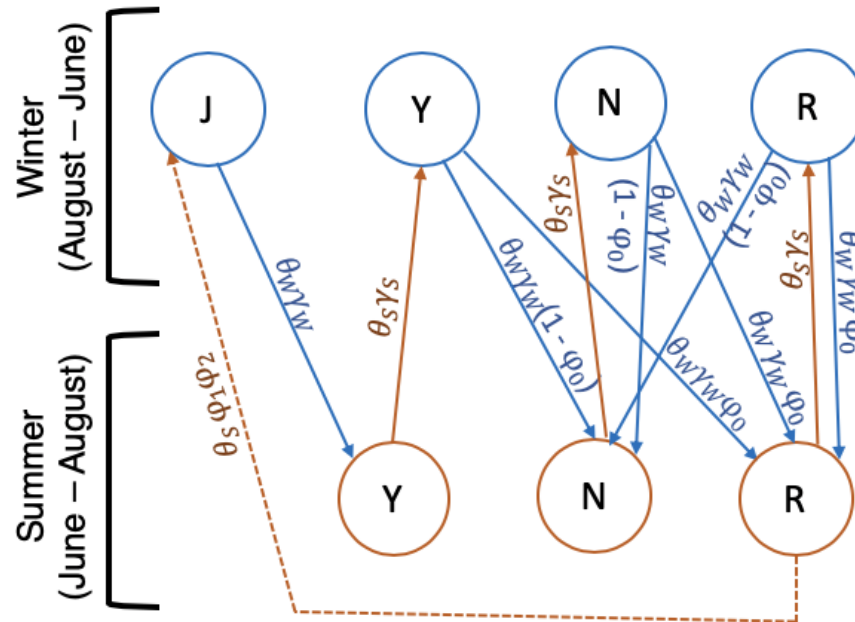
153

154   **Figure 1**: Seasonal life-cycle transitions modelled for yellow-bellied marmots. The two seasons correspond to the

155   main periods of mass loss (winter) and gain (summer). Solid and dashed arrows represent discrete-time stage

156   transitions and recruitment, respectively. Transitions among winter (W) and summer (S) stages (marked by arrows

157   in different colors) depend on demographic rates (survival [θ], reproduction [φ_0], and recruitment [φ_1]) and trait

158   transitions (mass change [γ], and offspring mass [φ_2]). Stages are: juveniles, J, yearlings, Y, non-reproductive

159   adults, N, and reproductive adults, R. All stage-specific demographic rates and trait transitions are modeled using

160   generalized mixed effects models in a Bayesian framework and include body mass and a common latent variable

161   representing environmental quality as covariates.

162

163   We determined all demographic rates of females (survival, reproduction, and recruitment) for

164   two discrete growing seasons: winter (August - June) and summer (June - August) (Fig. 1).

165   Although marmots begin emerging from hibernation in April and some do not hibernate until

166   October (Armitage, 2014), the two seasons delineate the main periods of mass loss and gain,

167   respectively (Maldonado-Chaparro et al., 2017). We assumed that females that permanently

168   disappeared from a colony had died. This measure of apparent survival may overestimate the

169   death of yearlings in the summer, which disperse from their natal colonies (Van Vuren &

170   Armitage, 1994). At the same time, the intensive trapping protocol ensured a high capture

171   probability of yearlings (Oli & Armitage, 2004), decreasing the discrepancies between their

172   apparent and true survival.

173   Female marmots give birth to one litter from mid-May to mid-June. In our population

174   model, females ≥ 2 year of age that survived the winter were considered reproductive adults at

175   the beginning of summer if they were observed to be pregnant of with pups, or non-reproductive

176   adults otherwise (Fig. 1). Upon successful reproduction, weaned offspring emerge from burrows

177   ca. 35 days after birth (Armitage et al., 1976); we therefore defined recruitment as the number of

178   female juveniles weaned by reproductive females that survive the summer (Fig. 1). The sex ratio

179   of female:male recruits was assumed to be 1:1 (Armitage & Downhower, 1974). Observations

180   and pedigree analyses allowed to determine the mother of each new juvenile recruited into the

181   population (Ozgul et al., 2010).

182   To assess changes in body mass from one season to the next, we estimated body mass of

183   every female at the beginning of each season: June 1 (beginning of the summer season when

184   marmots begin foraging) and August 15 (beginning of the winter season in our models when

185   foraging activity decreases). Mid-August is the latest that body mass for the vast majority of

8

186 individuals can be measured and has been shown to be a good estimate of pre-hibernation mass

187 (Maldonado-Chaparro et al., 2017). Body-mass estimates on the two specific dates were obtained

188 using linear mixed effect models as described in Ozgul *et al.* (2010; see also Maldonado-

189 Chaparro et al., 2017). Body mass of juvenile females was estimated for August 15.

190

191 *Modelling demographic and mass change (trait-transition) rates*

192 We jointly modeled all seasonal demographic and mass change rates (*i.e.*, demographic

193 processes) as a function of stage and body mass - or mother's mass in the case of juvenile mass -

194 at the beginning of a season, using a Bayesian modeling framework (Table 1; Supporting

195 Material S1). All mass estimates were cube-root transformed to stabilize the variance and

196 improve the normality of the residuals in the Gaussian submodels (Maldonado-Chaparro et al.,

197 2017). We fitted all demographic-process submodels as generalized linear mixed effects models

198 (GLMMs). We assumed a binomial error distribution (logit link function) for the probability of

199 winter (θ_W) and summer (θ_S) survival and of probability of reproducing (*i.e.*, being in the

200 reproductive adult stage at the beginning of summer; φ_0); a Poisson error distribution (log link

201 function) for the number of recruits (φ_1); and a Gaussian error distribution (identity link) for the

202 masses (z^*) at the end of each season (Table 1). Mass-change (*i.e.*, mass gain or loss) rates (γ)

203 were then defined as functions of current (z) and next (z^*) mass using a normal probability

204 density function. For the juvenile mass distribution (φ_2), the density function depended on the

205 mother's mass (z_M) (see below; Supporting Material S2).

206   To describe environment-driven temporal covariation in seasonal demography in the

207 absence of explicit knowledge on environmental drivers, we quantified a model-wide latent

208 variable (Q_y) affecting all demographic processes in a given year (y) (Table 1). One latent

9

209   variable was enough to capture covariation among the demographic processes (Supporting

210   Material S1). Details of the parameterization of Q_y can be found in Supporting Material S1 (see

211   also Hindle *et al.*, 2018). Briefly, this covariate effectively estimates the overall annual

212   environmental quality that affects the various demographic processes simultaneously, thereby

213   capturing correlated responses (within and among seasons) to environmental fluctuations (Hindle

214   et al., 2018). In the absence of causal variables that can be directly measured, Q_y was

215   incorporated as a covariate in all seven demographic-process submodels; and the year-specific

216   values of Q_y were drawn from a normal distribution with mean = 0 and SD =1. Higher Q_y

217   indicate a better quality of the environment in a given year, and the associated β_q slope

218   parameters determine the magnitude and sign of the effect of Q_y on a given, season-specific

219   demographic process (Table 1). Thus, similar to large-scale environmental indices such as NAO

220   or ENSO, Q_y captures to what extent a bad ($Q_y < 0$) or good ($Q_y > 0$) environment is likely to

221   affect both summer and winter demography. To make the Bayesian model identifiable, we

222   constrained the standard deviation of Q_y to equal 1 and arbitrarily set the β_q for summer survival

223   (θ_S) to be positive. The β_q of the remaining submodels can, therefore, be interpreted as

224   correlations of demographic processes with θ_S due to environmental variation.

225   Aside from the environmental covariate Q_y simultaneously affecting all demographic

226   processes, we included a random year effect ($\varepsilon_{Ysubmodel}$) as a covariate in each submodel. This

227   year effect accounted for additional temporal variation not captured by Q_y. We also tested for the

228   effect of population density (measured as total abundance, abundance of adults, or abundance of

229   yearling and adults) in all submodels. However, like previous studies, we could not detect any

230   clear density effects (Armitage, 1984; Maldonado-Chaparro et al., 2018).

231   The prior distributions of the Bayesian model and posterior parameter samples obtained

232   are detailed in Supporting Material S1. For each demographic-process submodel, we chose the

233   most parsimonious model structure by fitting a full model that included all covariates (mass,

234   stage, and Q_y) and two-way interactions between mass and stage and stage and Q_y, and retaining

235   only those parameters for which the posterior distribution ($\pm$ 95 % C.I.) did not overlap 0 (Table

236   1; Table S2.1).

237   **Table 1:** Parameterization of the most parsimonious models describing winter (W) and summer (S)

238   demographic processes in marmots. The distributions B, N, and P correspond to the Bernoulli, normal,

239   and Poisson distributions, respectively. The logit link, for winter survival as an example, corresponds to 1-

240    $^{(1/1+\exp(-\theta_W))}$. *Stage* – life cycle stage. Q – latent environmental variable. z – season-specific mass. z_M –mass

241   of the mother.

Demographic process	Function	Likelihood distribution
Winter (W):		
Survival (θ_W)	$\text{logit}(\theta_W) = \alpha_{0\theta W} + \alpha_{a\theta W}[\text{stage}] + \beta_{z\theta W} \times z + \beta_{q\theta W} \times Q_y[\text{year}] + \varepsilon_{y\theta W}[\text{year}]$	$B(\theta_W)$
Mass next (z_W^*)	$z_W^* = \alpha_{0z*W} + \alpha_{az*W}[\text{stage}] + (\beta_{zz*W} + \beta_{zaz*W}[\text{stage}]) \times z + \beta_{qz*W} \times Q_y[\text{year}] + \varepsilon_{yz*W}[\text{year}]$	$N(z_W^*, \tau_{z*W})$
Reproduction (φ_0)	$\text{logit}(\varphi_0) = \alpha_{0\varphi 0} + \alpha_{a\varphi 0}[\text{stage}] + \beta_{z\varphi 0} \times z + \beta_{q\varphi 0} \times Q_y[\text{year}] + \varepsilon_{y\varphi 0}[\text{year}]$	$B(\varphi_0)$
Summer (S):		
Survival (θ_S)	$\text{logit}(\theta_S) = \alpha_{0\theta S} + \alpha_{a\theta S}[\text{stage}] + \beta_{z\theta S} \times z + \beta_{q\theta S} \times Q_y[\text{year}] + \varepsilon_{y\theta S}[\text{year}]$	$B(\theta_S)$
Mass next (z_S^*)	$z_S^* = \alpha_{0z*S} + \alpha_{az*S}[\text{stage}] + (\beta_{zz*S} + \beta_{zaz*S}[\text{stage}]) \times z + \beta_{qz*S} \times Q_y[\text{year}] + \varepsilon_{yz*S}[\text{year}]$	$N(z_S^*, \tau_{z*S})$
Number of recruits (φ_1)	$\log(\varphi_1) = \alpha_{0\varphi 1} + \beta_{z\varphi 1} \times z + \beta_{q\varphi 1} \times Q_y[\text{year}] + \varepsilon_{y\varphi 1}[\text{year}]$	$P(\varphi_1)$
Juvenile mass (z_J^*)	$z_J^* = \alpha_{0z*J} + \beta_{zz*J} \times z_M + \beta_{qz*J} \times Q_y[\text{year}] + \varepsilon_{yz*J}[\text{year}]$	$N(z_J^*, \tau_{z*J})$

242

243 *Seasonal Integral Projection Models*

244 We used the most parsimonious models of demographic processes (Table 1) to parameterize

245 density-independent, stage-mass-structured, seasonal and environment-specific Integral

246 Projection Models (IPMs) (Easterling, Ellner, & Dixon, 2000; Ellner et al., 2016). For each stage

247 a, the IPMs track the number of individuals (n_a) in the mass range [z, z+dz] at time t. The fate of

248 these individuals at time t+1 is described by a set of coupled integral equations, which differ for

249 each season and are a function of the latent environmental variable Q_y. In the winter season,

250 individuals can survive (θ_w) and change mass (γ_w) according to their stage, mass, and

251 environment. Conditional on survival, juveniles (J) transition to yearlings (Y), while all other

252 stages are distributed to either the reproductive (R) or non-reproductive (N) adult stage at the

253 beginning of summer, depending on the stage-specific probability of reproducing (φ_0). During

254 the summer season, individuals in stages Y, N, and R survive (θ_S) and change mass (γ_S)

255 according to their stage and mass at the beginning of summer and according to the environment;

256 but, in summer, transitions to another stage do not occur. Reproductive individuals (R) of a given

257 mass also produce φ_1/2 female juveniles (J), *i.e.*, half of the total number of recruits. Female

258 recruits are distributed across z mass classes by the end of summer, given by φ_2. The

259 mathematical descriptions of the IPMs for the winter and summer seasons are provided in

260 Supporting Material S2.

261   We numerically integrated the summer and winter IPMs using the 'midpoint rule'

262 (Easterling et al., 2000) with upper and lower integration limits of 7.8 (472 g) and 17.1 (5000 g),

263 respectively. To avoid unintended eviction of individuals from the model (*i.e.*, for a given mass

264 class z, the sum of the probabilities to transition to $z^* < 1$), we applied a constant correction (*i.e.*,

265 equally redistributing evicted individuals among all z^*) when constructing the IPMs as suggested

266   in Merow *et al.*, (2014) (see also Williams, Miller, & Ellner, 2012). For each stage-specific IPM,

267   we chose a bin size of 100 (*i.e.*, dividing masses into 100 classes), as further increasing the bin

268   size did not significantly improve the precision of estimates of the long-term population growth

269   rate. The IPMs we constructed accurately reproduced observed population dynamics from 1976-

270   2016 (Supporting Material S2).

271

272   *Sensitivity of population dynamics to seasonal demographic processes: prospective*

273   *perturbations*

274   Changes in population dynamics in response to changes in environmental fluctuations are

275   determined by the response of demographic processes to the environment and, in turn, of

276   population dynamics to demographic processes (Maldonado-Chaparro et al., 2018). To explore

277   these two sources of variation in the long-term fitness of the marmot population, we first

278   quantified the proportional change in the demographic processes (Table 1) to changes in Q_y, *i.e.*,

279     $\partial(\log \rho)/\partial Q_y$, where ρ is a demographic process. We calculated these elasticities for different

280   values of Q_y (from -1 to 1), increasing each value by 0.01 and keeping mass at its stage-specific

281   average and ε_Y fixed to the value estimated for 2015. To assess the effect of parameter

282   uncertainty on our estimates, we repeated these calculations for a sample of 1000 parameter

283   values drawn from the posterior distribution (Paniw, Quintana-Ascencio, Ojeda, & Salguero-

284   Gómez, 2017a).

285   We next assessed which demographic processes most affected the stochastic population

286   fitness under observed (1976-2016) environmental fluctuations. We used a simulation of 100,000

287   years to assess asymptotic, long-term stochastic population dynamics (see section below for

288   short-term viability simulations). Each simulation started with the population of individuals with

13

289   the standing stage and mass distribution at the beginning of the winter season in 2016. At each

290   run of the simulation, a seasonal IPM was constructed with resampled, year-specific Q_y and ε_Y

291   values. We then calculated the periodic IPM product of the winter and summer IPMs, describing

292   the demographic and trait transitions from the beginning of one winter season to the next

293   (Caswell, 2001; chapter 13). Lastly, we obtained the stochastic population growth rate, $\log\lambda s$, (a

294   measure of fitness) as the mean of the logs of annual realized population growth rates, $\lambda = n_{t+1}/n_t$,

295   where n_t and n_{t+1} are the total number of individuals in the population at time (year) t and $t+1$,

296   respectively.

297   During the simulations, we adapted the approach described in Ellner et $al.$ (2016; chapter

298   7) to calculate the elasticity of $\log \lambda s$ to changes in the mean (e_S^μ) and standard deviation (e_S^σ) of

299   stage-specific demographic processes ρ, e.g., juvenile survival. To do so, we perturbed a

300   demographic-process function for a given stage over an interval of masses [z, $z+dz$] by its mean

301   and standard deviation obtained across 40 years of observed dynamics (Supporting Material S3).

302   Observed dynamics were obtained by resampling year-specific values of Q_y and ε_Y for 1976-

303   2016 from the Bayesian model. We then built a winter or summer IPM using the perturbed vital

304   rate and obtained a new, perturbed periodic IPM product ($i.e.$, the perturbation kernel). Lastly,

305   we integrated this product into eq. 7.5.2 in Ellner et $al.$ (2016) in order to estimate e_S^μ and

306   e_S^σ from the simulations of population dynamics for T = 90,000 years ($i.e.$, discarding the first 10,

307   000 years of simulations to ensure no effect of transient population fluctuations):

$$e = E\Big[\frac{\langle v_{t+1}, C_t w_t\rangle}{\langle v_{t+1}, K_t w_t\rangle}\Big],$$

308

309   where C_t is the perturbation kernel, K_t is the unperturbed annual IPM kernel at each simulation

310   iteration t, v and w are the left and right eigenvectors associated with K at $t+1$ and t, respectively.

311   For instance, if average winter survival in a given mass interval ($i.e.$, IPM bin) for reproductive

14

312   individuals from 1976-2016 was 0.95, each winter IPM during T simulations was perturbed by

313   subtracting a focal value of winter survival from its 40-year mean; and e_s^μ was calculated by

314   integrating this perturbed IPM as C_t into the above equation. The two elasticities quantify the

315   strength of selection pressures on lower-level vital rates in stochastic environments (Haridas &

316   Tuljapurkar, 2005; Rees & Ellner, 2009). We repeated the elasticity calculations for a sample of

317   100 parameter values from the posterior distribution.

318

319   *Population viability under changes in environmental quality*

320   To assess how the combined effects of (i) seasonal demographic responses to environmental

321   fluctuations and (ii) population sensitivity to seasonal demography impact population viability,

322   we simulated population dynamics under environmental change. We ran 200 independent

323   simulations each projecting population dynamics for 50 years. The projections were based on

324   several scenarios of changes in the distribution of environmental quality, Q_y. We first created

325   base simulations (*i.e.*, no environmental change) where Q_y was picked from a normal distribution

326   with $\mu_Q = 0$ and $\sigma_Q = 1$ across all demographic processes. Next, we approximated random future

327   fluctuations in Q_y under different average environmental conditions. To do so, we sampled Q_y

328   from a normal distribution fixing the average environmental quality ($\mu_Q = -1, -0.5, 0.5, 1$) and its

329   variation ($\sigma_Q = 0.6, 1.2$) over the 50 years of projections. We then explored how a trend in μ_Q

330   would affect viability and mass distribution. To do so, we decreased the four μ_Q by 0.01 in each

331   year of the projections, keeping σ_Q unaltered. Lastly, as temporal autocorrelation in

332   environmental states can affect population dynamics (Paniw et al., 2018), we projected

333   autocorrelated changes in Q_y. That is, each year, marmots could experience either a good or bad

334   environment where Q_y was sampled from a normal distribution with either $\mu_Q = 1$ or $\mu_Q = -1$,

15

335 respectively (σ_Q was fixed at 0.6). The sequence of good and bad environments was determined

336 by a Markov chain with various autocorrelation coefficients (see Supporting Material S4 for

337 details). All simulations were repeated for a random sample of 1,000 parameters from the

338 posterior distribution to account for parameter uncertainty.

339   For all environmental-change scenarios, we recorded the probability of quasi-extinction

340 across the 200 simulations. Quasi-extinction was defined conservatively as the number of non-

341 juvenile individuals (*i.e.*, yearlings and non-reproductive and reproductive individuals) in the

342 population to be < 4, which corresponded to 10 % of their lowest observed number.

343 **RESULTS**

344 *Seasonal environment-driven covariation in demographic processes*

345 Our GLMMs showed a strong effect of environmental quality (measured by the latent variable

346 Q_y) on winter but not summer demographic processes. This effect was positive for all winter

347 demographic processes, as evidenced by the positive β_q (Fig. S1.3 in Supporting Material S1).

348 The β_q for demographic processes in the summer, however, were comparatively small and were

349 not significantly different from 0 (95 % posterior C.I.s overlapped 0). This environment-driven

350 positive covariation in demographic processes therefore indicated that Q_y provided a measure of

351 environmental quality (Hindle et al., 2018) that did not correlate with any single environmental

352 variable measured at the study site and correlated well with observed annual changes in

353 population size (Supporting Material S1).

354   In accordance with the posterior distribution of β_q parameters, only winter demographic

355 processes were significantly affected by small changes in Q_y (Fig. 2). Among the winter

356 demographic processes, changes in Q_y affected reproduction across stages the most, followed by

357 survival of juveniles (Fig. 2).
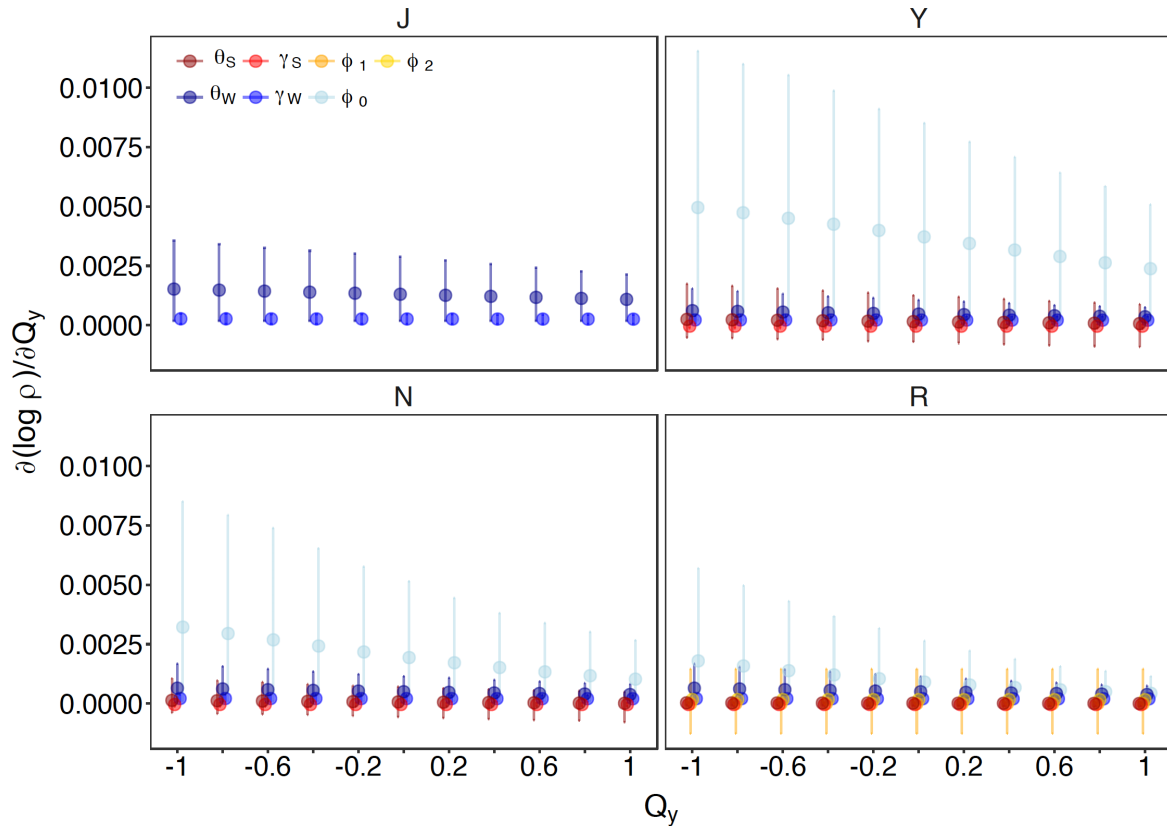
Figure 2: The sensitivity of seasonal demographic processes to environmental quality in marmots. Sensitivity is assessed as proportional changes in demographic processes, ρ, as environmental quality, Q_y, increases slightly. This sensitivity is measured with respect to different average values of Q_y and across four different life-cycle stages: juveniles (J), yearlings (Y), non-reproductive adults (N), and reproductive adults (R). The demographic processes include winter (W; blue color tones) and summer (S; red color tones) survival (θ) and mass change (γ); and probability of reproducing (φ_0), recruitment (φ_1), and juvenile mass (φ_2). Points and error bars show averages $\pm$ 95 % C.I. across 1,000 posterior parameter samples obtained from the Bayesian population model.

Aside from the effects of environmental quality, our models confirmed previous findings on the importance of body mass and stage on yellow-bellied marmot demography (Maldonado-Chaparro et al., 2017; Ozgul et al., 2010; Ozgul, Oli, & Armitage, 2009). The most parsimonious GLMMs (Table 1; Table S1.1 in Supporting Material S1) showed a positive effect of mass on all demographic processes, with the weakest effect of mass on summer survival (θ_S) of reproductive

17

372   adults. Survival, in particular θ_S, was highest for reproductive adults; reproduction was also

373   highest for adults that reproduced before (Fig. S1.3 in Supporting Material S1).

374

375   *Sensitivity of population dynamics to seasonal demographic processes*

376   While environmental quality affected winter demographic processes only, our prospective

377   perturbation analyses showed that winter and summer demography equally determine long-term

378   population fitness. Stochastic elasticity analyses (e_S^{μ} and e_S^{σ}) showed that relative increases in the

379   mean (μ) of winter (θ_W) and summer (θ_S) survival for reproductive adults (R), would lead to

380   substantial relative increases of the stochastic population growth rate, $\log\lambda s$ (Fig. 3a). Highest e_S^{μ}

381   were found at intermediate and large mass classes; e_S^{μ} was negative for small masses when mass

382   changes (γ) and offspring mass (φ_2) were perturbed (Fig. S3.1a in Supporting Material S3),

383   explaining the overall small e_S^{μ} for γ and φ_2 summed over all mass classes (Fig. 3a). Overall,

384   relative changes in $\log\lambda s$ due to increases in the standard deviation of demographic processes

385   (e_S^{σ}) were much smaller compared to e_S^{μ} (Fig. 3b) and didn't differ significantly between vital

386   rates, as 95 % posterior C.I. crossed 0 (Fig. S3.1b).
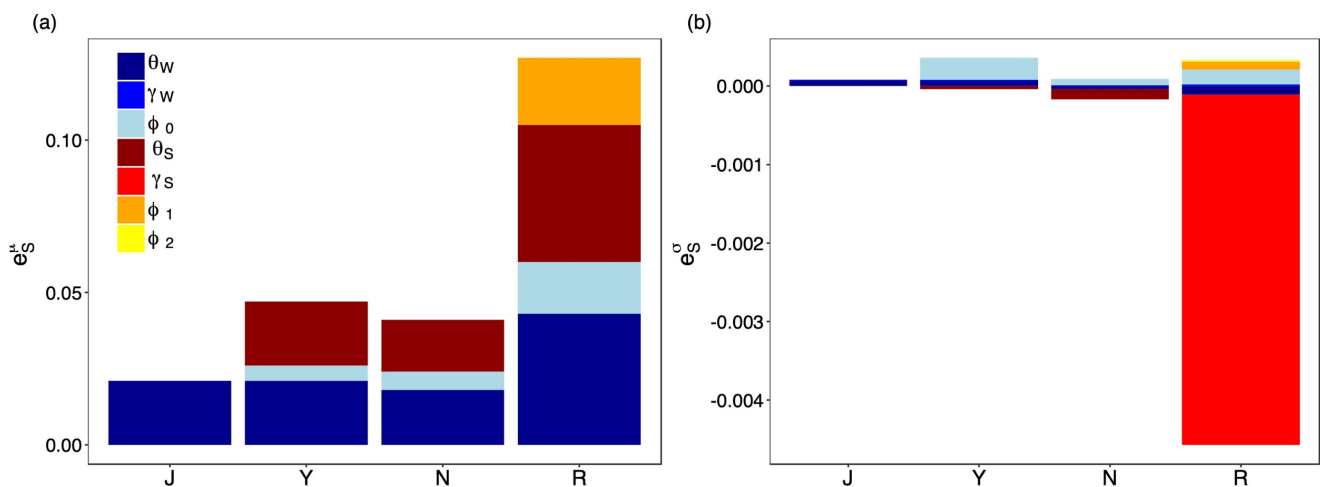

387

388   **Figure 3** Sensitivity of the average long-term population fitness to changes in the average and variability of

389   demographic processes modeled for the yellow-bellied marmots. The sensitivity measure is obtained analytically as

390   elasticities (e) of the stochastic population growth rate, log λs, to changes in (a) the mean (μ) and (b) standard

391   deviation (σ) of stage-specific demographic processes summed over all mass classes. Stages are juveniles (J),

392   yearlings (Y), non-reproductive adults (N), and reproductive adults (R). Demographic processes include winter (W)

393   and summer (S) survival (θ) and mass change (γ); reproduction (φ_0); recruitment (φ_1), and offspring mass

394   distribution (φ_2). Elasticities were calculated at the mean posterior values of parameters obtained from the Bayesian

395   demographic model.

396

397   *Population viability under changes in environmental quality*

398   While population fitness was equally sensitive to demographic processes over winter and

399   summer, environmental fluctuations strongly affected viability through winter demography.

400   Using base simulations (*i.e.*, obtaining Q_y from a normal distribution with $\mu_Q = 0$ and $\sigma_Q = 1$),

401   the probability of quasi-extinction, at an average of 0.1 [0.0, 0.3 C.I.] across posterior

402   parameters, were relatively low. Simulations of population dynamics based on scenarios of

403   environmental change resulted in substantial decreases (0 at $\mu_Q = 1$) and increases (0.9 [0.6, 1.0

404   C.I.] at $\mu_Q = -1$) in quasi-extinction, compared to base simulations, when the population

405   experienced a high and low average environmental quality (Q_y), respectively (Fig. 4). Average

406   quasi-extinction further increased and its uncertainty across posterior parameters decreased when

407   a declining trend in average environmental quality (Q_y) was simulated (Fig. S4.1). Changes in

408   the standard deviation of Q_y had comparatively little effect on quasi-extinction (Fig. 4). The

409   same was true for simulations of autocorrelated environmental fluctuations, where changes in the

410   frequency of good environmental conditions (effectively changing the average environmental

411   quality) had a strong effect on viability, while changes in the patterning of environmental states

412   had little effect (Supporting Material S4).

19
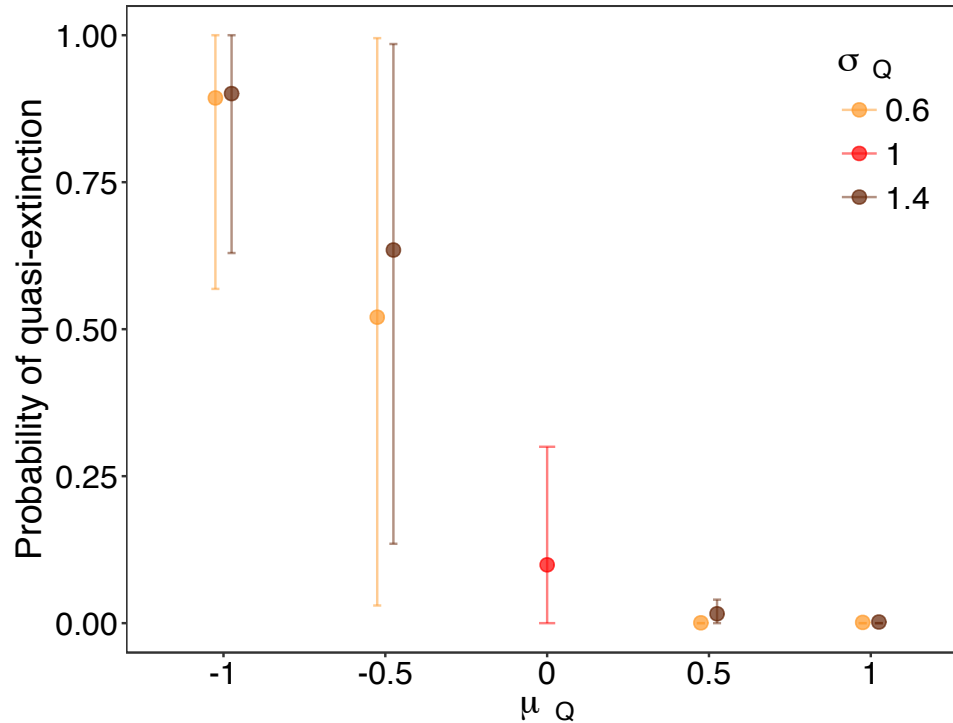
Figure 4: Probability of quasi-extinction (*i.e.*, < 4 non-juveniles in the population) of yellow-bellied marmots under different scenarios of environmental change. The scenarios consisted of projecting population dynamics for 50 years fixing a different mean (μ) and standard deviation (σ) of environmental quality (Q) in all demographic processes. Points and error bars show averages ± 95 % C.I. across 1,000 posterior parameter samples obtained from the Bayesian population model. Base simulations ($\mu_Q = 0$; $\sigma_Q = 1$) are depicted in red.

DISCUSSION

One important pathway through which environmental change can act on population dynamics is through seasonal direct and carry-over effects on survival, growth, and reproduction (Harrison et al., 2010; Paniw et al., 2019). Using a novel, factor-analytic approach to quantify environment-demography relationships, we show that positive responses in several demographic processes to winter environmental conditions can drive annual population dynamics in a winter-adapted mammal. This sensitivity to winter conditions occurs despite the fact that offspring are recruited in summer and both summer and winter demographic processes determine population fitness. As

20

428   whole-year, population-level effects of environmental change can be filtered by seasonal

429   processes in the absence of density-dependent feedbacks, we highlight the need to assess such

430   seasonal processes to gain a mechanistic understanding of population persistence (Paniw et al.,

431   2019; Picó, de Kroon, & Retana, 2002).

432   Empirical studies have typically used annual models to demonstrate how positive

433   demographic covariation can amplify environmental effects on population dynamics

434   (Compagnoni et al., 2016); or how opposing demographic responses can buffer such effects

435   (Gamelon et al., 2017; Reed et al., 2013). However, in marmots, as in numerous other

436   populations (Bassar et al., 2016; Jenouvrier et al., 2018), seasonal demographic processes play an

437   important role in life-cycle dynamics (Armitage, 2017). Our prospective perturbations show that

438   changes in both mean winter and summer survival of reproductive adults have the strongest

439   effect on population fitness, confirming the critical role of this life-cycle stage (Maldonado-

440   Chaparro et al., 2018; Ozgul et al., 2009). At the same time, environmental fluctuations do not

441   affect adult survival or other demographic processes throughout the year. That is, although the

442   environment has been shown to drive particularly recruitment in numerous temperate species

443   (e.g., Bonardi, Corlatti, Bragalanti, & Pedrotti, 2017; Nouvellet, Newman, Buesching, &

444   Macdonald, 2013), such effects are not evident in marmots; here, environmental quality shows

445   little impact on summer demography, including recruitment, and little covariation with winter

446   demography. Instead, only the joint responses of demographic processes in winter are affected

447   by environmental quality. The joint effects of the sensitivity of winter demography to

448   environmental quality and the sensitivity of population fitness to winter demography then

449   determine population persistence under environmental change.

450   The seasonal effects of environmental quality on population persistence must be

451   understood in terms of the role of reproductive females in the marmot population (Ozgul et al.,

452   2009). In our simulations, a good winter quality, which has previously been shown to have the

453   strongest effect on individual survival (Armitage, Blumstein, & Woods, 2003), would, in

454   particular, result in more reproductive females in the summer. In turn, summer survival and

455   reproduction of these females are important to long- and short-term demography (Maldonado-

456   Chaparro et al., 2018; Ozgul et al., 2009), but are not driven by environmental conditions. As is

457   the case in other socially complex mammals (Morris et al., 2011), reproduction in yellow-bellied

458   marmots is governed primarily by social interactions, in particular the behavior of dominant

459   females (Armitage, 2010; Blumstein & Armitage, 1998). Even under optimal summer

460   conditions, the reproductive output of the population may not be increased as dominant females

461   suppress reproduction in younger subordinates and therefore regulate the size of colonies

462   (Armitage, 1991). Dominant females, in addition, may skip reproduction themselves if they enter

463   hibernation with a relatively low mass (Armitage, 2017). Thus, the necessity of meeting the

464   physiological requirements of hibernation profoundly affects life-history traits of yellow-bellied

465   marmots that are expressed during the active season. Here, an explicit seasonal population

466   analysis allowed us to recognize a potentially important mechanism through which the

467   environment filters demography: survival in or transition to the reproductive stage in a good

468   winter can guarantee successful reproduction in summer, in addition to direct summer processes.

469   Unlike the direct effects of seasonal survival and reproduction, trait transitions between

470   seasons had a smaller effect on annual population dynamics, even if winter mass changes were

471   mediated by environmental quality. In this sense, the prospective perturbation analyses

472   performed in our study are in agreement with retrospective analyses described by Maldonado-

473   Chaparro and colleagues (2018), who found a relatively small contribution of growth to past

474   variation in annual population growth. These relatively small effects are likely due to the fact

475   that marmots compensate for winter mass loss with increased growth in the summer, creating a

476   zero net effect on annual trait change (Maldonado-Chaparro et al., 2017). Although the strength

477   of compensatory effects may differ within seasons or among life-history stages (Monclús, Pang,

478   & Blumstein, 2014), such effects are common in rodents and other species that have a short

479   window for mass gain (Morgan & Metcalfe, 2001; Orizaola, Dahl, & Laurila, 2014), and

480   highlight the advantages of assessing seasonal dynamics when studying population-level global-

481   change effects (Bassar et al., 2016).

482   Under environmental change, the persistence of marmots was mostly affected by changes

483   in mean environmental quality, whereas changes in the variance and temporal patterning of the

484   mean showed little effects. This supports previous conclusions that yellow-bellied marmots are

485   partly buffered against increases in environmental variation (Maldonado-Chaparro et al., 2018;

486   Morris et al., 2008) or autocorrelation (Engen et al., 2013). Further support for demographic

487   buffering comes from the fact that changes in the mean environmental quality most strongly

488   affected those demographic processes to which the stochastic population growth rate was least

489   sensitive. That is, yearlings gaining reproductive status in particular, albeit contributing relatively

490   little to population dynamics, contributed strongly via environment-driven effects. It is well

491   known that in species where vital rates of adults are relatively buffered, juveniles are much more

492   sensitive to environmental variation (Gaillard & Yoccoz, 2003; Jenouvrier et al., 2018).

493   Although demographic buffering has been investigated in other animals (Bjørkvoll et al., 2016;

494   Morris et al., 2008; Pfister, 1998; Rotella, Link, Chambert, Stauffer, & Garrott, 2012), we are, to

495   the best of our knowledge, the first to show that it is likely to persist across the seasonal

496   environments and different masses for a high-altitude specialist; see Jenouvrier *et al*., (2018) for

497   similar analyses in a long-lived bird.

498   Our results emphasize that declines in environmental quality in one season alone can

499   strongly affect annual population dynamics of a mammal highly adapted to seasonal

500   environments and buffered from environmental variation. Therefore, positive demographic

501   covariation under environmental change may threaten populations even if it affects demographic

502   process to which the stochastic growth rate is least sensitive, *i.e.*, processes that are under low

503   selection pressure (Coulson, Gaillard, & Festa-Bianchet, 2005; Iles, Rockwell, & Koons, 2019).

504   Studies of global change ecology that focus on the effects of environmental factors on

505   demographic processes considered to strongly affect both short- and long-term population

506   dynamics may therefore miss the important role of seasonal demographic covariation. In

507   addition, such seasonal mechanisms are potentially critical for conservation management (Paniw

508   et al., 2019) but would be missed by annual-step analyses where demographic processes are

509   averaged across the entire year (Hostetler et al., 2015).

510   Given the strong overlap of our results with previous findings and overall robust model

511   performance, the factor analytic approach we used to quantify environment-driven covariation in

512   demographic processes appears to be a promising alternative to approaches linking specific vital

513   rates directly to environmental drivers (Evans & Holsinger, 2012; Hindle, Pilkington,

514   Pemberton, & Childs, 2019; Hindle et al., 2018). In the case of yellow-bellied marmots, where

515   demographic rates were relatively easy to parameterize and the assumption of positive

516   covariation holds in part due to a lack of density feedbacks, the factor analytic approach can be

517   used effectively to assess population-level effects of perturbing a global measure of

518   environmental quality. In cases where environment-demography relationships are more complex

519   and include negative demographic covariation (e.g., where trade-offs dominate), this approach

520   may find limited applications. However, positive covariation of demographic patterns is common

521   (Jongejans et al., 2010; Paniw et al., 2019); and, given the short time series of most demographic

522   datasets (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016) or little knowledge on the

523   actual environmental drivers of population dynamics (Pol et al., 2016; Teller et al., 2016), the

524   factor analytic approach can be particularly useful in comparative studies.

525   Most species inhabit seasonal environments. Under global environmental change, it may

526   therefore be critical to understand how seasonality patterns mediate persistence of natural

527   populations. Our analyses point to an important role of seasonal differences in demographic

528   covariance in driving population responses to environmental change. Novel methods such as the

529   factor analytic approach allow researchers to overcome some challenges associated with such

530   mechanistic approaches, and we encourage more seasonal demographic analyses across different

531   taxa.

ACKNOWLEDGMENTS

541

542   **AUTHOR CONTRIBUTIONS**

543   K.B.A., D.T.B., and M.O. led the long-term study and data collection; M.P., D.C., and A.O.

544   conceived the ideas for the paper and designed the analyses; M.P. conducted the analyses with

545   substantial help from J.M.; M.P. wrote the manuscript; all authors discussed the results and

546   commented on the manuscript.

547

548   **DATA AVAILABILITY**

549   The datasets generated and analyzed during the current study as well as the R scripts to run all

550   analyses are available in the *Dryad* repository, [PERSISTENT WEB LINK TO DATASETS].

551   **REFERENCES**

552   Armitage, K. B. (1984). Recruitment in yellow-bellied marmot populations: kinship, philopatry,

553   and individual variability. In J. O. Murie & G. R. Michener (Eds.), *The Biology of Ground-*

554   *Dwelling Squirrels* (pp. 377–403), Lincoln: Univ. Nebraska Press.

555   Armitage, K. B. (1991). Social and population dynamics of yellow-bellied marmots: results from

556   long-term research. *Annual Review of Ecology and Systematics*, 22, 379–407.

557   Armitage, K. B. (2003). Observations on plant choice by foraging yellow-bellied marmots.

558   *Oecologia Montana*, 12, 25–28.

559   Armitage, K. B. (2010). Individual fitness, social behavior, and population dynamics of yellow-

560   bellied marmots. I. Billick & M.V. Price (Eds.) *The Ecology of Place: Contributions of*

561   *Place-Based Research to Ecological Understanding* (pp. 132–154), Chicago: University of

562   Chicago Press.

563   Armitage, K. B. (2014). *Marmot Biology: Sociality, Individual Fitness, and Population*

564   *Dynamics*. Cmbridge: Cambridge University Press.

565 Armitage, K. B. (2017). Hibernation as a major determinant of life-history traits in marmots.

566   *Journal of Mammalogy*, 98, 321–331.

567 Armitage, K. B., Blumstein, D. T., & Woods, B. C. (2003). Energetics of hibernating yellow-

568   bellied marmots (*Marmota flaviventris*). *Comparative Biochemistry and Physiology. Part A,*

569   *Molecular & Integrative Physiology*, 134, 101–114.

570 Armitage, K. B., & Downhower, J. F. (1974). Demography of yellow-bellied marmot

571   populations. *Ecology*, 55, 1233–1245.

572 Armitage, K. B., Downhower, J. F., & Svendsen, G. E. (1976). Seasonal changes in weights of

573   marmots. *The American Midland Naturalist*, 96, 36–51.

574 Bassar, R. D., Letcher, B. H., Nislow, K. H., & Whiteley, A. R. (2016). Changes in seasonal

575   climate outpace compensatory density-dependence in eastern brook trout. *Global Change*

576   *Biology*, 22, 577–593.

577 Benton, T. G., Plaistow, S. J., & Coulson, T. N. (2006). Complex population dynamics and

578   complex causation: devils, details and demography. *Proceedings. Biological Sciences*, 273,

579   1173–1181.

580 Bjørkvoll, E., Lee, A. M., Grøtan, V., Saether, B.-E., Stien, A., Engen, S., Albon, S., Loe, L.E.,

581   & Hansen, B. B. (2016). Demographic buffering of life histories? Implications of the choice

582   of measurement scale. *Ecology*, 97, 40–47.

583 Blumstein, D. T., & Armitage, K. B. (1998). Life history consequences of social complexity a

584   comparative study of ground-dwelling sciurids. *Behavioral Ecology*, 9, 8-19.

585 Bonardi, A., Corlatti, L., Bragalanti, N., & Pedrotti, L. (2017). The role of weather and density

586   dependence on population dynamics of Alpine-dwelling red deer. *Integrative Zoology*, 12,

587   61-76.

588   Campos, F. A., Morris, W. F., Alberts, S. C., Altmann, J., Brockman, D. K., Cords, M., Pusey,

589   A., Stoinski, T. S., Strier, K. B., & Fedigan, L. M. (2017). Does climate variability influence

590   the demography of wild primates? Evidence from long-term life-history data in seven

591   species. *Global Change Biology*, 23, 4907–4921.

592   Caswell, H. (2001). *Matrix Population Models*. Sunderland: Sinauer.

593   Childs, D. Z., Coulson, T. N., Pemberton, J. M., Clutton-Brock, T. H., & Rees, M. (2011).

594   Predicting trait values and measuring selection in complex life histories: reproductive

595   allocation decisions in Soay sheep. *Ecology Letters*, 14, 985–992.

596   Compagnoni, A., Bibian, A. J., Ochocki, B. M., Rogers, H. S., Schultz, E. L., Sneck, M. E.,

597   Elderd, B. D., Iler, A. M., Inouye, D. W., Jacquemin, H., & Miller, T. E. X. (2016). The

598   effect of demographic correlations on the stochastic population dynamics of perennial

599   plants. *Ecological Monographs*, 86, 480–494.

600   Connell, S. D., & Ghedini, G. (2015). Resisting regime-shifts: the stabilising effect of

601   compensatory processes. *Trends in Ecology & Evolution*, 30, 513–515.

602   Coulson, T., Gaillard, J.-M., & Festa-Bianchet, M. (2005). Decomposing the variation in

603   population growth into contributions from multiple demographic rates. *The Journal of

604   Animal Ecology*, 74, 789–801.

605   Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: applying a new

606   structured population model. *Ecology*, 81, 694–708.

607   Ehrlén, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of

608   species under environmental change. *Ecology Letters*, 18, 303–314.

609   Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally

610   explicit structured population models of plants. *The Journal of Ecology*, 104, 292–305.

611   Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven Modelling of Structured*

612   *Populations: A Practical Guide to the Integral Projection Model*. Springer.

613   Engen, S., Sæther, B.-E., Armitage, K. B., Blumstein, D. T., Clutton-Brock, T. H., Dobson, F. S.,

614   Festa-Bianchet, M., Oli, M. K., & Ozgul, A. (2013). Estimating the effect of temporally

615   autocorrelated environments on the demography of density-independent age-structured

616   populations. *Methods in Ecology and Evolution*, 4, 573–584.

617   Evans, M. E. K., & Holsinger, K. E. (2012). Estimating covariation between vital rates: a

618   simulation study of connected vs. separate generalized linear mixed models (GLMMs).

619   *Theoretical Population Biology*, 82, 299–306.

620   Frase, B. A., & Hoffmann, R. S. (1980). Marmota flaviventris. *Mammalian Species*,135, 1–8.

621   Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of

622   environmental canalization? *Ecology*, 84, 3294–3306.

623   Gamelon, M., Grøtan, V., Nilsson, A. L. K., Engen, S., Hurrell, J. W., Jerstad, K., Phillips, A. S.,

624   Røstad, O. W., Slagsvold, T., Walseng, B., Steneth, N. C., & Sæther, B.-E. (2017).

625   Interactions between demography and environmental effects are important determinants of

626   population dynamics. *Science Advances*, 3, e1602298.

627   Haridas, C. V., & Tuljapurkar, S. (2005). Elasticities in variable environments: properties and

628   implications. *The American Naturalist*, 166, 481–495.

629   Harrison, X. A., Blount, J. D., Inger, R., Norris, R. D., & Bearhop, S. (2010). Carry-over effects

630   as drivers of fitness differences in animals. *The Journal of Animal Ecology*, 80, 4–18.

631   Hindle, B. J., Pilkington, J. G., Pemberton, J. M., & Childs, D. Z. (2019). Cumulative weather

632   effects can impact across the whole life cycle. *Global Change Biology*, in press.

633   Hindle, B. J., Rees, M., Sheppard, A. W., Quintana-Ascencio, P. F., Menges, E. S., & Childs, D.

634   Z. (2018). Exploring population responses to environmental change when there is never

635   enough data: a factor analytic approach. *Methods in Ecology and Evolution*, 147, 115.

636   Hostetler, J. A., Sillett, T. S., & Marra, P. P. (2015). Full-annual-cycle population models for

637   migratory birds. *The Auk*, 132, 433–449.

638   Iles, D. T., Rockwell, R. F., & Koons, D. N. (2019). Shifting vital rate correlations alter

639   predicted population responses to increasingly variable environments. *The American*

640   *Naturalist*, E57–E64.

641   Inouye, D. W., Barr, B., Armitage, K. B., & Inouye, B. D. (2000). Climate change is affecting

642   altitudinal migrants and hibernating species. *Proceedings of the National Academy of*

643   *Sciences of the United States of America*, 97, 1630–1633.

644   Jenouvrier, S., Desprez, M., Fay, R., Barbraud, C., Weimerskirch, H., Delord, K., & Caswell, H.

645   (2018). Climate change and functional traits affect population dynamics of a long-lived

646   seabird. *The Journal of Animal Ecology*, 87, 906–920.

647   Jenouvrier, S., Holland, M., Stroeve, J., Barbraud, C., Weimerskirch, H., Serreze, M., & Caswell,

648   H. (2012). Effects of climate change on an emperor penguin population: analysis of coupled

649   demographic and climate models. *Global Change Biology*, 18, 2756–2770.

650   Jongejans, E., de Kroon, H., Tuljapurkar, S., & Shea, K. (2010). Plant populations track rather

651   than buffer climate fluctuations. *Ecology Letters*, 13, 736–743.

652   Knops, J. M. H., Koenig, W. D., & Carmen, W. J. (2007). Negative correlation does not imply a

653   tradeoff between growth and reproduction in California oaks. *Proceedings of the National*

654   *Academy of Sciences of the United States of America*, 104, 16982–16985.

655   Lawson, C. R., Vindenes, Y., Bailey, L., & van de Pol, M. (2015). Environmental variation and

656   population responses to global change. *Ecology Letters*, 18, 724–736.

657   Lenihan, C., & Vuren, D. V. (1996). Growth and survival of juvenile yellow-bellied marmots

658   (*Marmota flaviventris*). *Canadian Journal of Zoology*, 74, 297–302.

659   Maldonado-Chaparro, A. A., Blumstein, D. T., Armitage, K. B., & Childs, D. Z. (2018).

660   Transient LTRE analysis reveals the demographic and trait-mediated processes that buffer

661   population growth. *Ecology Letters*, 23, 1353.

662   Maldonado-Chaparro, A. A., Read, D. W., & Blumstein, D. T. (2017). Can individual variation

663   in phenotypic plasticity enhance population viability? *Ecological Modelling*, 352, 19–30.

664   Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full

665   annual cycle research in animal ecology. *Biology Letters*, 11, 20150552.

666   Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E.,

667   Record, S., Rees, M., Salguero-Gómez, R., & McMahon, S. M. (2014). Advancing

668   population ecology with integral projection models: a practical guide. *Methods in Ecology*

669   *and Evolution*, 5, 99–110.

670   Monclús, R., Pang, B., & Blumstein, D. T. (2014). Yellow-bellied marmots do not compensate

671   for a late start: the role of maternal allocation in shaping life-history trajectories.

672   *Evolutionary Ecology*, 28, 721–733.

673   Morgan, I. J., & Metcalfe, N. B. (2001). Deferred costs of compensatory growth after autumnal

674   food shortage in juvenile salmon. *Proceedings. Biological Sciences*, 268, 295–301.

675   Morris, W. F., Altmann, J., Brockman, D. K., Cords, M., Fedigan, L. M., Pusey, A. E., Stoinski,

676   T. S., Bronikowski, A. M., Alberts, S. C., & Strier, K. B. (2011). Low demographic

677   variability in wild primate populations: fitness impacts of variation, covariation, and serial

678   correlation in vital rates. *The American Naturalist*, 177, E14–E28.

679   Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna,

680   E. M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J.-M., Horvitz, C. C.,

681   Kalisz, S., Kendall, B. E., Knight, T. M., Lee, C. T., & Menges, E. S. (2008). Longevity can

682   buffer plant and animal populations against changing climatic variability. *Ecology*, 89, 19–

683   25.

684 Nouvellet, P., Newman, C., Buesching, C. D., & Macdonald, D. W. (2013). A multi-metric

685   approach to investigate the effects of weather conditions on the demographic of a terrestrial

686   mammal, the european badger (*Meles meles*). *PloS One*, 8, e68116.

687 Oli, M. K., & Armitage, K. B. (2004). Yellow-bellied marmot population dynamics:

688   demographic mechanisms of growth and decline. *Ecology*, 85, 2446–2455.

689 Orizaola, G., Dahl, E., & Laurila, A. (2014). Compensatory growth strategies are affected by the

690   strength of environmental time constraints in anuran larvae. *Oecologia*, 174, 131–137.

691 Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., & Blumstein, D. T. (2010). Coupled

692   dynamics of body mass and population growth in response to environmental change. *Nature*,

693   466, 482-485.

694 Ozgul, A., Oli, M. K., & Armitage, K. B. (2009). Influence of local demography on asymptotic

695   and transient dynamics of a yellow-bellied marmot metapopulation. *The American*

696   *Naturalist*, 173, 517-530.

697 Ozgul, A., Oli, M. K., Olson, L. E., Blumstein, D. T., & Armitage, K. B. (2007). Spatiotemporal

698   variation in reproductive parameters of yellow-bellied marmots. *Oecologia*, 154, 95–106.

699 Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T., & Ozgul, A. (2019). Life history responses

700   of meerkats to seasonal changes in extreme environments. *Science*, 363, 631–635.

701 Paniw, M., Ozgul, A., & Salguero-Gómez, R. (2018). Interactive life-history traits predict

702   sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters*, 21, 275–286.

703   Paniw, M., Quintana-Ascencio, P. F., Ojeda, F., & Salguero-Gómez, R. (2017a). Accounting for

704   uncertainty in dormant life stages in stochastic demographic models. *Oikos* , 126, 900–909.

705   Paniw, M., Quintana-Ascencio, P. F., Ojeda, F., & Salguero-Gómez, R. (2017b). Interacting

706   livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean

707   carnivorous plant. *The Journal of Applied Ecology*, 54, 1884–1894.

708   Pfister, C. A. (1998). Patterns of variance in stage-structured populations: evolutionary

709   predictions and ecological implications. *Proceedings of the National Academy of Sciences of*

710   *the United States of America*, 95, 213–218.

711   Picó, F. X., de Kroon, H., & Retana, J. (2002). An extended flowering and fruiting season has

712   few demographic effects in a Mediterranean perennial herb. *Ecology*, 83, 1991–2004.

713   Pol, M., Bailey, L. D., McLean, N., Rijsdijk, L., Lawson, C. R., & Brouwer, L. (2016).

714   Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and*

715   *Evolution*, 7, 1246–1257.

716   Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B.-E., & Visser, M. E. (2013). Population growth

717   in a wild bird is buffered against phenological mismatch. *Science*, 340, 488–491.

718   Rees, M., & Ellner, S. P. (2009). Integral projection models for populations in temporally

719   varying environments. *Ecological Monographs*, 79, 575–594.

720   Ripley, B. J., & Caswell, H. (2006). Recruitment variability and stochastic population growth of

721   the soft-shell clam, *Mya arenaria*. *Ecological Modelling*, 193, 517–530.

722   Robert, A., Bolton, M., Jiguet, F., & Bried, J. (2015). The survival–reproduction association

723   becomes stronger when conditions are good. *Proceedings. Biological Sciences*, 282,

724   20151529.

725   Rotella, J. J., Link, W. A., Chambert, T., Stauffer, G. E., & Garrott, R. A. (2012). Evaluating the

726   demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years

727   of mark-recapture data. *The Journal of Animal Ecology*, 81, 162–173.

728   Ruf, T., Bieber, C., Arnold, W., & Millesi, E. (2012). *Living in a Seasonal World:*

729   *Thermoregulatory and Metabolic Adaptations*. Springer Science & Business Media.

730   Rushing, C. S., Hostetler, J. A., Sillett, T. S., Marra, P. P., Rotenberg, J. A., & Ryder, T. B.

731   (2017). Spatial and temporal drivers of avian population dynamics across the annual cycle.

732   *Ecology*, 98, 2837–2850.

733   Salguero-Gómez, R., Jones, O. R., & Archer, C. R., et al. (2015). The COMPADRE Plant Matrix

734   Database: an open online repository for plant demography. *Journal of Ecology*, 103, 202-

735   218.

736   Salguero-Gómez, R., Jones, O. R., Archer, C. R., et al. (2016). COMADRE: a global data base

737   of animal demography. *The Journal of Animal Ecology*, 85, 371–384.

738   Schwartz, O. A., & Armitage, K. B. (2002). Correlations between weather factors and life-

739   history traits of yellow-bellied marmots. *Proceedings of the 3rd International Marmot*

740   *Conference, Cheboksary, Russia*.

741   Schwartz, O. A., & Armitage, K. B. (2005). Weather influences on demography of the yellow-

742   bellied marmot (*Marmota flaviventris*). *Journal of Zoology*, 265, 73–79.

743   Schwartz, O. A., Armitage, K. B., & Van Vuren, D. (1998). A 32-year demography of yellow-

744   bellied marmots (*Marmota flaviventris*). *Journal of Zoology*, 246, 337–346.

745   Simmonds, E. G., & Coulson, T. (2015). Analysis of phenotypic change in relation to climatic

746   drivers in a population of Soay sheep *Ovis aries*. *Oikos*, 124, 543–552.

747   Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G., & Ellner, S. P. (2016). Linking

748   demography with drivers: climate and competition. *Methods in Ecology and Evolution*, 7,

749   171–183.

750   Töpper, J. P., Meineri, E., Olsen, S. L., Rydgren, K., Skarpaas, O., & Vandvik, V. (2018). The

751   devil is in the detail: non-additive and context-dependent plant population responses to

752   increasing temperature and precipitation. *Global Change Biology*, 24, 4657-4666.

753   Van de Pol, M., Vindenes, Y., Sæther, B.-E., Engen, S., Ens, B. J., Oosterbeek, K., & Tinbergen,

754   J. M. (2010). Effects of climate change and variability on population dynamics in a long-

755   lived shorebird. *Ecology*, 91, 1192–1204.

756   Van Vuren, D., & Armitage, K. B. (1994). Survival of dispersing and philopatric yellow-bellied

757   marmots: what is the cost of dispersal? *Oikos*, 69, 179–181.

758   Varpe, Ø. (2017). Life history adaptations to seasonality. *Integrative and Comparative Biology*,

759   57, 943–960.

760   Villellas, J., Doak, D. F., García, M. B., & Morris, W. F. (2015). Demographic compensation

761   among populations: what is it, how does it arise and what are its implications? *Ecology*

762   *Letters*, 18, 1139–1152.

763   Van Vuren, D., & Armitage, K. B. (1991). Duration of snow cover and its influence on life-

764   history variation in yellow-bellied marmots. *Canadian Journal of Zoology*, 69, 1755–1758.

765   Williams, J. L., Miller, T. E. X., & Ellner, S. P. (2012). Avoiding unintentional eviction from

766   integral projection models. *Ecology*, 93, 2008–2014.

767   Woodroffe, R., Groom, R., & McNutt, J. W. (2017). Hot dogs: High ambient temperatures

768   impact reproductive success in a tropical carnivore. *The Journal of Animal Ecology*, 86,

769   1329–1338.

770   Williams J. L., Miller T. E. X. & Ellner S. P. (2012). Avoiding unintentional eviction from

771   integral projection models. *Ecology*, 93, 2008–2014.