1   **Assessing seasonal demographic covariation to understand environmental-**

2   **change impacts on a hibernating mammal**

3

4   Authors: Maria Paniw[1,2], Dylan Childs[3], Kenneth B Armitage[4], Daniel T Blumstein[5,6], Julien

5   Martin[7,8], Madan K. Oli[9], Arpat Ozgul[1]

6   *1 - Department of Evolutionary Biology and Environmental Studies, University of Zurich,*
7   *Winterthurerstrasse 190, CH-8057 Zurich, Switzerland, arpat.ozgul@ieu.uzh.ch*
8   *2 - Ecological and Forestry Applications Research Centre (CREAF), Campus de Bellaterra (UAB) Edifici*
9   *C, ES-08193 Cerdanyola del Vallès, Spain, m.paniw@creaf.uab.cat*
10   *3 - Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN,*
11   *UK, d.childs@sheffield.ac.uk*
12   *4 - Ecology & Evolutionary Biology Department, The University of Kansas, Lawrence, KS 66045-7534,*
13   *USA, marmots@ku.edu*
14   *5 - Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles,*
15   *CA 90095, USA, marmots@ucla.edu*
16   *6 - The Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA*
17   *7 - School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, UK,*
18   *8 – Department of Biology, University of Ottawa, Ottawa, K1N 9A7, Canada, julien.martin@uottawa.ca*
19   *9 - Department of Wildlife Ecology, University of Florida, Gainesville, FL 32611, USA, olim@ufl.edu*
20

21   [*]Corresponding author: Tel.: +34-671-246-338; email: maria.paniw@ieu.uzh.ch; ORCID ID: 0000-0002-
22   1949-4448
23

24

25

26

27

28

29

30

31

32

ABSTRACT

Natural populations are exposed to seasonal variation in environmental factors that simultaneously affect several demographic rates (survival, development, reproduction). The resulting covariation in these rates determines population dynamics, but accounting for its numerous biotic and abiotic drivers is a significant challenge. Here, we use a factor-analytic approach to capture partially unobserved drivers of seasonal population dynamics. We use 40 years of individual-based demography from yellow-bellied marmots (*Marmota flaviventer*) to fit and project population models that account for seasonal demographic covariation using a latent variable. We show that this latent variable, by producing positive covariation among winter demographic rates, depicts a measure of environmental quality. Simultaneous, negative responses of winter survival and reproductive-status change to declining environmental quality result in a higher risk of population quasi-extinction, regardless of summer demography where recruitment takes place. We demonstrate how complex environmental processes can be summarized to understand population persistence in seasonal environments.

47   **INTRODUCTION**

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

49   based on annual transitions among life-history stages in structured population models (Salguero-

50   Gómez et al., 2016; Paniw et al., 2018). However, all natural ecosystems show some level of

51   seasonal fluctuations in environmental conditions, and numerous species have evolved life cycles

52   that are cued to such seasonality (Ruf et al., 2012; Varpe, 2017). For example, most temperate-

53   and many arid-environment species show strong differences in survival and growth among

54   seasons, with reproduction being confined mostly to one season (Childs et al., 2011; Rushing et

55   al., 2017; Woodroffe et al., 2017). Species with highly adapted, seasonal life cycles are likely to

56   be particularly vulnerable to environmental change, even if they are relatively long-lived

57   (Jenouvrier et al., 2012; Campos et al., 2017; Paniw et al., 2019). This is because adverse

58   environmental conditions in the non-reproductive season may carry-over and negate positive

59   environmental effects in the reproductive season in which key life-history events occur (Marra et

60   al., 2015). For instance, in species where individual traits such as body mass determine

61   demographic rates, environment-driven changes in the trait distribution in one season can affect

62   trait-dependent demographic rates in the next season (Bassar et al., 2016; Paniw et al., 2019).

63   Investigating annual dynamics, averaged over multiple seasons, may, therefore, obscure the

64   mechanisms that allow populations to persist under environmental change.

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

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

67   endeavor (Benton et al., 2006; Bassar et al., 2016). This is in part because multiple

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

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

3

70 influence season-specific demographic rates (Benton et al., 2006; Lawson et al., 2015; Ozgul et

71 al., 2007; Paniw et al., 2019; Töpper et al., 2018). One major analytical challenge for ecologists

72 is that typically only a small subset of the numerous biotic and abiotic drivers of important life-

73 history processes are known and measured continuously (Teller et al., 2016); and this challenge

74 is amplified in seasonal models where more detail on such drivers may be required while

75 biological processes such as hibernation are cryptic to researchers (van de Pol et al., 2016).

76 Assessing whether the available information provides meaningful measures of biological

77 processes is another challenge. Nonlinear interactions among the myriad of biotic and abiotic

78 factors are common in nature, and teasing apart their effects on natural populations requires

79 detailed and long-term data (Benton et al., 2006; Paniw et al., 2019), which is not available for

80 most systems (Salguero-Gómez et al., 2015; 2016).

81   Overcoming the challenges in parameterizing seasonal population models is important

82 because a robust projections of such models require assessing the simultaneous effects of biotic

83 and abiotic factors on several demographic rates, causing the latter to covary within and among

84 seasons (Maldonado-Chaparro et al., 2018; Paniw et al., 2019). Positive environment-driven

85 covariation in demographic rates can amplify the population-level effects of environmental

86 change. For instance, Jongejans et al. (2010) demonstrated that positive covariation in survival

87 and reproduction in several plant populations magnified the effect of environmental variability

88 on population dynamics and increased extinction risk. On the other hand, antagonistic

89 demographic responses, either due to intrinsic tradeoffs or opposing effects of biotic/abiotic

90 factors, can buffer populations from environmental change (Knops et al., 2007; Van de Pol et al.,

91 2010); for instance, when population-level effects of decreased reproduction are offset by

92 increases in survival or growth (Connell & Ghedini, 2015; Reed et al., 2013; Villellas et al.,

93   2015). Thus, explicit consideration of patterns in demographic covariation can allow for a fuller

94   picture of population persistence in a changing world. Such a consideration remains scarce

95   (Ehrlén & Morris, 2015; Ehrlén et al., 2016; but see Bassar et al., 2016; Compagnoni et al.,

96   2016).

97   Here, we investigated the population-level effects of seasonal covariation among trait-

98   mediated demographic rates (*i.e.*, collectively referred to as demographic processes), capitalizing

99   on 40 years (1976-2016) of individual-based data from a population of yellow-bellied marmots

100 (*Marmota flaviventer*). Our main aims were to (i) efficiently model demographic covariation in

101 the absence of knowledge on its underlying drivers and (ii) characterize the seasonal mechanisms

102 through which this covariation affects population viability. Yellow-bellied marmots have

103 adapted to a highly seasonal environment; individuals spend approximately eight months in

104 hibernation during the cold winter (September/October-April/May), and use the short summer

105 season (April/May-September/October) to reproduce and replenish fat reserves (Fig. 1). One

106 challenge that the marmot study shares with numerous other natural systems is the identification

107 of key proximal biotic and abiotic factors driving population dynamics. In marmots such factors

108 are numerous and affect population dynamics through complex, interactive pathways

109 (Maldonado-Chaparro et al., 2017; Oli & Armitage, 2004), which include interactions with

110 phenotypic-trait structure (Ozgul et al., 2010). As a result, measures of environmental covariates

111 (e.g., temperature or resource availability) have previously shown little effect on the covariation

112 of marmot demographic processes (Maldonado-Chaparro et al., 2018). To address this challenge,

113 we used a novel method, a hierarchical factor analysis (Hindle et al., 2018), to model the

114 covariation of demographic processes as a function of a shared latent variable, quantified in a

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

116   integral projection models (IPMs; Ellner et al., 2016) for the marmot population, which allowed

117   us to simultaneously project trait distributions and population dynamics across seasons. We used

118   prospective stochastic perturbation analyses and population projections to assess how the

119   observed demographic covariation mediated population viability.

120   **METHODS**

121   *Study species*

122   Yellow-bellied marmots are an ideal study system to assess the effects of seasonal covariation in

123   demographic rates on population viability. These large, diurnal, burrow-dwelling rodents

124   experience strong seasonal fluctuations in environmental conditions, and their seasonal

125   demography has been studied for > 40 years (Armitage, 2014). Our study was conducted in the

126   Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38°

127   57' N, 106° 59' W). Climatic conditions in both winter and summer have been shown to

128   influence reproduction and survival in the subsequent season (Lenihan & Van Vuren, 1996; Van

129   Vuren & Armitage, 1991). In addition, predation is major cause of death in the active summer

130   season (Van Vuren, 2001; Maldonado-Chaparro et al., 2017) and may be particularly severe

131   shortly before (Bryant & Page, 2005) or after hibernation (Armitage, 2014), especially in year

132   with heavy snow (Blumstein, pers. obs.). The effects of these factors on the demography of

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

134   survive hibernation, reproduce in summer, and escape predation (Armitage et al.,1976; Ozgul et

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

136   seasonal patterns of biotic and abiotic drivers. However, numerous interacting climatic factors,

137   such as temperature extremes and length of snow cover, determine both winter and summer

138   environmental conditions. The effects on marmot demography of these climatic factors, and of

139   interactions between climate and predation (the latter mostly a cryptic process) have been shown

140   to be difficult to disentangle (Schwartz & Armitage, 2002; Schwartz & Armitage, 2005).

141

142   *Seasonal demographic rates and trait transitions*

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

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

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

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

147   et al., 1998). 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). Thus, we focused on seasonal

150   demographic processes of females only. We classified female marmots by age and reproductive

151   status: juveniles (< 1 year old), yearlings (1 year old), and non-reproductive (≥ 2 years old; not

152   observed pregnant or with offspring) and reproductive adults (≥ 2 years old; observed pregnant

153   or with offspring) (Armitage & Downhower, 1974).
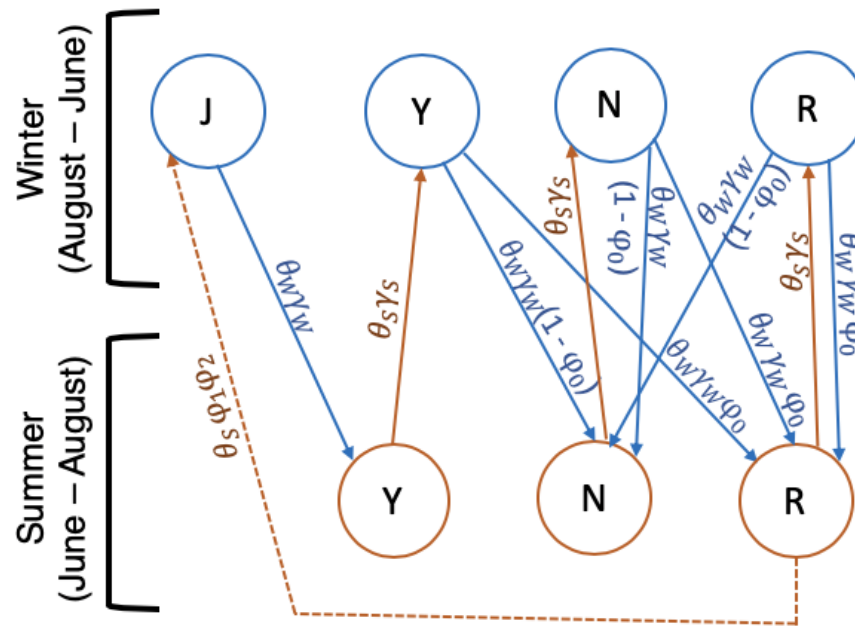
154

Figure 1: Seasonal life-cycle transitions modelled for yellow-bellied marmots. The two seasons correspond to the main periods of mass loss (winter) and gain (summer). Solid and dashed arrows represent discrete-time stage transitions and recruitment, respectively. Transitions among winter (W) and summer (S) stages (marked by arrows in different colors) depend on demographic rates (survival [θ], reproduction [φ_0], and recruitment [φ_1]) and trait transitions (mass change [γ], and offspring mass [φ_2]). Stages are: juveniles, J, yearlings, Y, non-reproductive adults, N, and reproductive adults, R. All stage-specific demographic rates and trait transitions are modeled using generalized linear mixed effects models in a Bayesian framework and include body mass and a common latent variable representing environmental quality as covariates.

163

164   We determined demographic rates (survival, reproduction, and recruitment) for two discrete

165   growing seasons: winter (August - June) and summer (June - August) (Fig. 1), delineating the

166   main periods of mass loss and gain, respectively (Maldonado-Chaparro et al., 2017). We

167   assumed that females that permanently disappeared from a colony had died. This measure of

168   apparent survival may overestimate the death of yearlings in the summer, which disperse from

169   their natal colonies (Van Vuren & Armitage, 1994). At the same time, the intensive trapping

170   protocol ensured a high capture probability of yearlings (Oli & Armitage, 2004), decreasing the

171   discrepancies between their apparent and true survival.

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

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

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

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

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

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

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

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

180   population (Ozgul et al., 2010).

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

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

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

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

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

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

187   estimated using linear mixed effect models. These models were fitted for each age class and

188   included the fixed effect of day-of-year on body mass, and the random effects of year, site and

189   individual identity on the intercept and on the day-of-year slope (for details see Ozgul *et al.*,

190   2010; Maldonado-Chaparro et al., 2017). Body mass of juvenile females was estimated for

191   August 15.

192

193   *Modelling covariation in demographic processes – latent-variable approach*

9

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

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

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

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

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

199   2017). We fitted all demographic-process submodels as generalized linear mixed effects models

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

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

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

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

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

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

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

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

208   To model temporal covariation in seasonal demography in the absence of explicit

209   knowledge on key biotic or abiotic drivers of this covariation, we used a factor-analytic

210   approach. This approach has recently been proposed by Hindle and coauthors (2018) as a

211   structured alternative to fit and project unstructured covariances among demographic processes

212   when factors explaining these covariances are not modeled. We implemented this novel

213   approach parameterizing a model-wide latent variable (Q_y) which affected all demographic

214   processes in a given year (y) (for details see Supporting Material S1 and Hindle *et al.*, 2018). Q_y

215   was incorporated as a covariate in all seven demographic-process submodels (Table 1). Year-

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

217   associated β_q slope parameters then determine the magnitude and sign of the effect of Q_y on a

218   given, season-specific demographic process (Table 1). To make the Bayesian model identifiable,

219   we constrained the standard deviation of Q_y to equal 1 and arbitrarily set the β_q for summer

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

221   correlations of demographic processes with θ_S.

222   Aside from the latent variable Q_y simultaneously affecting all demographic processes, we

223   included a random year effect ($\varepsilon_{Ysubmodel}$) as a covariate in each submodel. While Q_y captured

224   demographic covariation, the year effect accounted for additional temporal variation of each

225   demographic process not captured by Q_y. We also tested for the effect of population density

226   (measured as total abundance, abundance of adults, or abundance of yearling and adults) in all

227   submodels. However, like previous studies, we could not detect any clear density effects

228   (Armitage, 1984; Maldonado-Chaparro et al., 2018).

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

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

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

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

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

234   1; Table S1.1).

235

236

237

238

239

Table 1: Parameterization of the most parsimonious models describing winter (W) and summer (S) demographic processes in marmots. The distributions B, N, and P correspond to the Bernoulli, normal, and Poisson distributions, respectively. *Stage* – life cycle stage. *Q* – latent environmental variable. *z* – season-specific mass. z_M –mass 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^*)	$z_W^* = \alpha_{0z*W} + \alpha_{az*W}[\text{stage}] + (\beta_{zz*W} + \beta_{zaz*W}[\text{stage}]) \times z + \beta_{qz*W} \times Q_y[\text{year}] + \varepsilon_{yz*W}[\text{year}]$	$\aleph(z_W^*, \tau_{z*W})$
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^*)	$z_S^* = \alpha_{0z*S} + \alpha_{az*S}[\text{stage}] + (\beta_{zz*S} + \beta_{zaz*S}[\text{stage}]) \times z + \beta_{qz*S} \times Q_y[\text{year}] + \varepsilon_{yz*S}[\text{year}]$	$\aleph(z_S^*, \tau_{z*S})$
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^*)	$z_J^* = \alpha_{0z*J} + \beta_{zz*J} \times z_M + \beta_{qz*J} \times Q_y[\text{year}] + \varepsilon_{yz*J}[\text{year}]$	$\aleph(z_J^*, \tau_{z*J})$

Interpreting demographic covariation: latent variable as a measure of environmental quality

The latent variable, Q_y, effectively captured the covariation among the demographic processes (Supporting Material S1); therefore, using one latent variable across both seasons was sufficient. Our GLMMs showed a strong effect of Q_y on winter but not summer demographic processes. This effect was positive for all winter demographic processes, as evidenced by the positive β_q (Table S1.1). The β_q for demographic processes in the summer, however, were comparatively

12

252   small and were not significantly different from 0 (95 % posterior C.I.s overlapped 0). The

253   positive β_q indicate that Q_y effectively estimates the overall annual environmental quality or

254   suitability, capturing both biotic and abiotic processes. A positive value of Q_y then depicts an

255   environmental condition at a given time point that increases winter survival and probability of

256   reproducing and decreases mass loss (Hindle et al., 2018). The variation in Q_y was in part

257   explained by environmental variables measured at the study site, but was unrelated to population

258   density (Supporting Material S1). Negative values of Q_y were associated with longer and more

259   severe winters and a higher snow cover, while positive Q_y indicated warmer winters and springs.

260   However, as the environmental variables explained < 50 % of the variation in Q_y, the latent

261   variable captures multivariate, partly unobserved biotic and abiotic processes into a simple,

262   univariate measure of how bad ($Q_y < 0$) or good ($Q_y > 0$) environmental conditions are likely to

263   affect marmot demography.

264   Aside from the effects of environmental quality, our models are consistent with previous

265   findings on the importance of body mass and stage on yellow-bellied marmot demography

266   (Maldonado-Chaparro et al., 2017; Ozgul et al., 2010). The most parsimonious GLMMs (Table

267   S1.1) showed a positive effect of mass on all demographic processes, with the weakest effect of

268   mass on summer survival (θ_S) of reproductive adults. Survival, in particular θ_S, was highest for

269   reproductive adults; reproduction was also highest for adults that reproduced before (Fig. S1.5).

270

271   *Seasonal Integral Projection Models*

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

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

274   Projection Models (IPMs) (Easterling et al., 2000; Ellner et al., 2016). For each stage a, the IPMs

13

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

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

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

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

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

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

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

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

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

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

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

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

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

288   Supporting Material S2. Our population model assumes that past conditions affecting individuals

289   are captured by the current mass distribution and are propagated through time, allowing us to

290   assess trait- and stage-mediated demographic processes (Ozgul et al., 2010).

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

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

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

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

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

296   in Merow *et al.*, (2014) (see also Williams et al., 2012). For each stage-specific IPM, we chose a

297   bin size of 100 (*i.e.*, dividing masses into 100 classes), as further increasing the bin size did not

298   significantly improve the precision of estimates of the long-term population growth rate. The

299   IPMs we constructed accurately reproduced observed population dynamics from 1976-2016

300   (Supporting Material S2).

301

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

303   *perturbations*

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

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

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

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

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

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

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

311   average and ε_Y fixed to 0. To assess the effect of parameter uncertainty on our estimates, we

312   repeated these calculations for a sample of 1000 parameter values drawn from the posterior

313   distribution (Paniw et al., 2017).

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

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

316   years to assess the stochastic population growth rate, $\log \lambda s$, a measure of fitness (see Supporting

317   Material S3 for details; see section below for short-term viability simulations). During the

318   simulation, we calculated the elasticity of $\log \lambda s$ to changes in the 40-year observed mean (e_S^μ)

319   and standard deviation (e_S^σ) of stage-specific demographic processes; we adapted the approach

320   described in Ellner *et al.* (2016; chapter 7) to evaluate the relative effects of these changes on log

15

321   λs (see S3 for details). The two elasticities quantify the strength of selection pressures on lower-

322   level vital rates in stochastic environments (Haridas & Tuljapurkar, 2005; Rees & Ellner, 2009).

323   We repeated the elasticity calculations for a sample of 100 parameter values from the posterior

324   distribution.

325   *Population viability under changes in environmental quality*

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

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

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

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

330   several scenarios of changes in the distribution of environmental quality, Q_y, corresponding to

331   changes in the average and standard deviation of winter length and harshness as well as

332   unobserved environmental drivers. We first created base simulations (*i.e.*, no environmental

333   change) where Q_y was picked from a normal distribution with $\mu_Q = 0$ and $\sigma_Q = 1$ across all

334   demographic processes. This was appropriate, as we found no indication of temporal

335   autocorrelation in Q_y (Supporting Material S1). Next, we approximated random future

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

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

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

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

340   year of the projections, keeping σ_Q unaltered. We also explored population-level effects of future

341   increases in the temporal autocorrelation in Q_y as detailed in Supporting Material S4. All

342   simulations were repeated for a random sample of 1,000 parameters from the posterior

343   distribution to account for parameter uncertainty.

16

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

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

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

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

348   **RESULTS**

349   *Sensitivity of population dynamics to seasonal demographic processes*

350   In accordance with the posterior distribution of β_q parameters, which did not cross 0 for winter

351   demographic processes, only winter demographic processes were significantly affected by small

352   changes in Q_y (Fig. 2). Among the winter demographic processes, changes in Q_y affected

353   reproduction across stages the most, followed by survival of juveniles (Fig. 2).
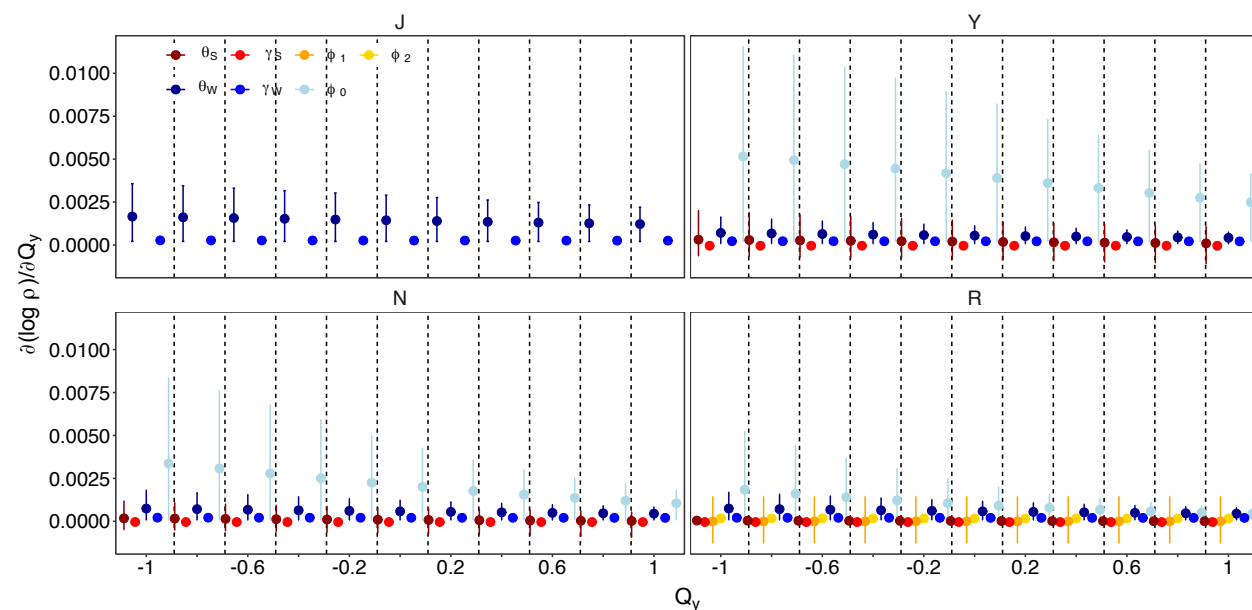

354

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

17

360   probability of reproducing (φ_0), recruitment (φ_1), and juvenile mass (φ_2). Points and error bars show averages $\pm$ 95

361   % C.I. across 1,000 posterior parameter samples obtained from the Bayesian population model.

362

363   While environmental quality affected winter demographic processes only, our

364   prospective perturbation analyses showed that winter and summer demography equally

365   determine long-term population fitness. Stochastic elasticity analyses (e_S^{μ} and e_S^{σ}) showed that

366   relative increases in the mean (μ) of winter (θ_W) and summer (θ_S) survival for reproductive

367   adults (R), would lead to substantial relative increases of the stochastic population growth rate,

368   logλs (Fig. 3a). Highest, positive e_S^{μ} were found at intermediate and large mass classes, and e_S^{μ}

369   was negative for small masses when mass changes (γ) and offspring mass (φ_2) were perturbed

370   (Fig. S3.1a in Supporting Material S3). This explained the overall small e_S^{μ} for γ and φ_2 summed

371   over all mass classes (Fig. 3a). Overall, relative changes in logλs due to increases in the standard

372   deviation of demographic processes (e_S^{σ}) were much smaller compared to e_S^{μ} (Fig. 3b) and didn't

373   differ significantly between vital rates, as 95 % posterior C.I. crossed 0 (Fig. S3.1b).
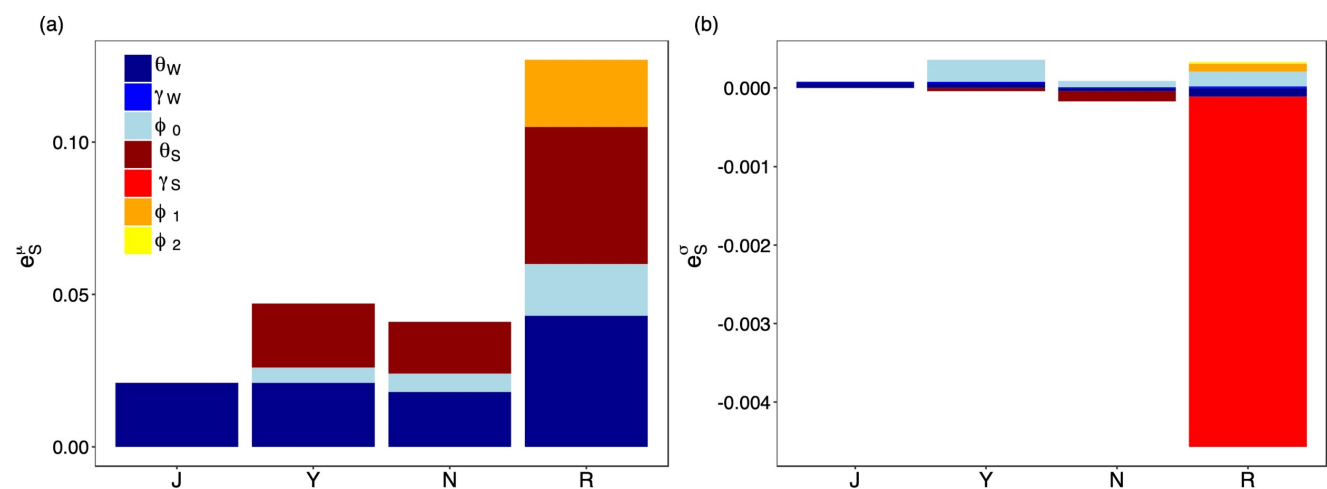

374

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

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

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

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

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

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

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

382 demographic model.

383

384 *Population viability under changes in environmental quality*

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

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

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

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

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

390 environmental change, corresponding in part to changes in winter length and harshness, resulted

391 in substantial changes to viability. Quasi-extinction decreased (0 at $\mu_Q = 1$) and increased (0.9

392 [0.6, 1.0 C.I.] at $\mu_Q = -1$), compared to base simulations, when the population experienced a high

393 and low average environmental quality (Q_y), respectively (Fig. 4). Average quasi-extinction

394 further increased and its uncertainty across posterior parameters decreased when a declining

395 trend in Q_y was simulated (Fig. S4.1). Changes in the standard deviation (Fig. 4) and

396 autocorrelation (Fig. S4.2) of Q_y had comparatively little effect on quasi-extinction.
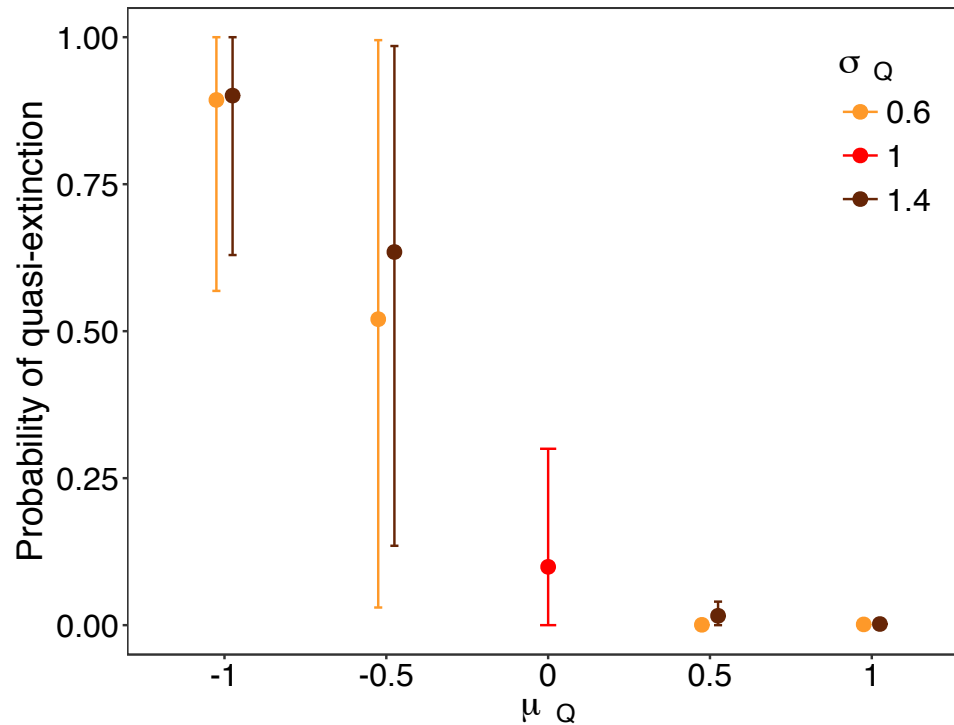
19

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, development, and reproduction (Harrison et al., 2010; Paniw et al., 2019). These effects, however, are often cryptic and therefore difficult to quantify in ecological models (Hindle et al., 2019). We use a novel, factor-analytic approach to efficiently quantify partially unobserved environment-demography relationships. This approach allows us to investigate how positive responses in several demographic processes to winter environmental conditions can drive annual population dynamics in a winter-adapted

20

412 mammal. The sensitivity to winter conditions occurs despite the fact that offspring are recruited

413 in summer and both summer and winter demographic processes determine population fitness. As

414 whole-year, population-level effects of environmental change can be filtered by season-specific

415 processes in the absence of density-dependent feedbacks, we highlight that the assessment of

416 such processes allows for a mechanistic understanding of population persistence (Picó et al.,

417 2002; Paniw et al., 2019).

418   In marmots, as in numerous other populations (Bassar et al., 2016; Jenouvrier et al.,

419 2018), seasonal demographic processes play an important role in life-cycle dynamics (Armitage,

420 2017). Our prospective perturbations show that changes in both mean winter and summer

421 survival of reproductive adults have the strongest effect on population fitness, confirming the

422 critical role of this life-cycle stage (Ozgul et al., 2009). At the same time, environmental

423 conditions do not affect adult survival or other demographic processes in the same way

424 throughout the year. That is, although the environment has been shown to drive particularly

425 recruitment in numerous temperate species (e.g., Bonardi et al., 2017; Nouvellet et al., 2013),

426 such effects are not evident in marmots; here, a higher annual environmental quality, which

427 increases all winter demographic processes, shows little impact on summer demography,

428 including recruitment. In turn, only these joint responses of winter demographic processes to

429 environmental quality determine population persistence under environmental change.

430   The complex, partially unmeasured environmental processes that cause positive

431 covariation in seasonal demographic processes can be effectively captured using a univariate,

432 latent measure of environmental quality. In our study, this latent quality correlated better with

433 observed annual population growth than any measured environmental variable (Supporting

434 Material S1). In part, a good quality depicts shorter and milder winters. Milder winters increase

21

435   food availability and the time available for vigilance, thereby decreasing predation risk (Van

436   Vuren, 2001), especially just before or after hibernation (*i.e.*, within our winter season) when

437   such risk is severe (Armitage, 2014). Predation risk in early spring also increases under high

438   snow cover, as marmots, including more experienced adult females, cannot easily retreat to their

439   burrows (Blumstein, pers. obs.). Predation is however cryptic in the system (Van Vuren, 2001).

440   Capturing the effects of unobserved environmental variation, including predation, the latent-

441   variable approach appears to be a promising alternative to modeling seasonal demographic

442   processes under limited knowledge of their drivers (Evans & Holsinger, 2012; Hindle et al.,

443   2019; Hindle et al., 2018). We note that this approach may find limited applications in cases

444   where environment-demography relationships are more complex than in the yellow-bellied

445   marmots and include negative demographic covariation (e.g., due to opposing environmental

446   effects on demographic rates or tradeoffs between these rates). However, positive covariation in

447   demographic patterns is common (Jongejans et al., 2010; Paniw et al., 2019); and, given the short

448   time series of most demographic datasets (Salguero-Gómez et al., 2015; 2016) or little

449   knowledge on the actual environmental drivers of population dynamics (van de Pol et al., 2016;

450   Teller et al., 2016), the factor-analytic approach can be particularly useful in comparative

451   studies.

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

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

454   2009). In our simulations, shorter and less sever winters (*i.e.*, a good winter quality), would

455   result in more reproductive females in the summer (Armitage et al., 2003). In turn, summer

456   survival and recruitment by these females are important to long- and short-term demography

457   (Ozgul et al., 2009; Maldonado-Chaparro et al., 2018), but are not driven by environmental

22

458   conditions. That is, although predation affects individuals in summer (Van Vuren, 2001), its

459   effects are strongest on juveniles and yearlings, while adult females are little affected (Ozgul et

460   al., 2006). At the same time, as is the case in other socially complex mammals (Morris et al.,

461   2011), reproduction in yellow-bellied marmots is governed primarily by social interactions, in

462   particular the behavior of dominant adult females (Armitage, 2010; Blumstein & Armitage,

463   1998). Even under optimal summer conditions, the reproductive output of the population may

464   not increase as dominant females suppress reproduction in younger subordinates and therefore

465   regulate the size of colonies (Armitage, 1991). Dominant females, in addition, may skip

466   reproduction themselves if they enter hibernation with a relatively low mass (Armitage, 2017).

467   Thus, the necessity of meeting the physiological requirements of hibernation profoundly affects

468   life-history traits of yellow-bellied marmots that are expressed during the active season.

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

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

471   by environmental quality. These relatively small effects are likely due to the fact that marmots

472   compensate for winter mass loss with increased growth in the summer, creating a zero-net effect

473   on annual trait change (Maldonado-Chaparro et al., 2017; 2018). Although the strength of

474   compensatory effects may differ within seasons or among life-history stages (Monclús et al.,

475   2014), such effects are common in rodents and other species that have a short window for mass

476   gain (Morgan & Metcalfe, 2001; Orizaola et al., 2014), and highlight how assessing seasonal

477   dynamics can provide a mechanistic understanding of population-level global-change effects

478   (Bassar et al., 2016).

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

480   in mean environmental quality, whereas changes in the variance and temporal autocorrelation of

481   the mean showed little effects. This supports previous conclusions that yellow-bellied marmots

482   are partly buffered against increases in environmental variation (Maldonado-Chaparro et al.,

483   2018; Morris et al., 2008) or autocorrelation (Engen et al., 2013). Further support for

484   demographic buffering comes from the fact that changes in the mean environmental quality most

485   strongly affected those demographic processes to which the stochastic population growth rate

486   was least sensitive, *i.e.*, yearlings gaining reproductive status. It is well known that in species

487   where vital rates of adults are relatively buffered, juveniles are much more sensitive to

488   environmental variation (Gaillard & Yoccoz, 2003; Jenouvrier et al., 2018). Our results indicate

489   that demographic buffering (Pfister, 1998; Morris et al., 2008) likely persists across the seasonal

490   environments and different masses for a high-altitude specialist.

491   Our results emphasize that declines in environmental quality in the non-reproductive

492   season alone can strongly affect annual population dynamics of a mammal highly adapted to

493   seasonal environments. Therefore, positive demographic covariation under environmental

494   change may threaten populations even if it affects demographic process to which the stochastic

495   growth rate is least sensitive, *i.e.*, processes that are under low selection pressure (Coulson et al.,

496   2005; Iles et al., 2019). Studies that focus on the effects of environmental factors on single

497   demographic processes that strongly affect both short- and long-term population dynamics may

498   therefore underestimate the important role of seasonal demographic covariation.

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

500   therefore be critical to understand how seasonal patterns mediate persistence of natural

501   populations. Novel methods such as the factor analytic approach allow researchers to overcome

502   some challenges associated with more mechanistic approaches assessing population responses to

503   environmental change, and we encourage more seasonal demographic analyses across different

504   taxa.

ACKNOWLEDGMENTS

REFERENCES

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

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

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

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

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

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

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

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

523   Chicago Press.

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

525   *Dynamics*. Cmbridge: Cambridge University Press.

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

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

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

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

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

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

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

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

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

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

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

537   *Biology*, 22, 577–593.

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

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

540   1173–1181.

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

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

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

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

545   61–76.

546   Bryant, A. A. & Page, R. W. (2005). Timing and causes of mortality in the endangered

547   Vancouver Island marmot (*Marmota vancouverensis*). *Canadian Journal of Zoology*, 83,

548   674–682.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

564   *Animal Ecology*, 74, 789–801.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

584   Interactions between demography and environmental effects are important determinants of

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

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

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

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

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

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

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

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

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

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

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

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

597   *Naturalist*, E57–E64.

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

599   (2018). Climate change and functional traits affect population dynamics of a long-lived

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

623   *and Evolution*, 5, 99–110.

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

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

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

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

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

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

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

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

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

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

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

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

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

637   25.

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

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

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

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

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

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

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

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

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

647   466, 482-485.

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

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

650   *Naturalist*, 173, 517-530.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

670   20151529.

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

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

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

674   (2017). Spatial and temporal drivers of avian population dynamics across the annual cycle.

675   *Ecology*, 98, 2837–2850.

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

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

678   218.

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

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

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

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

683   *Conference, Cheboksary, Russia*.

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

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

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

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

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

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

690   171–183.

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

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

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

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

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

696   *Evolution*, 7, 1246–1257.

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

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

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

700   Van Vuren, D. (2001). Predation on yellow-bellied marmots (*Marmota flaviventris*). *The*

701   *American Midland Naturalist*, 145, 94–100.

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

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

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

705   57, 943–960.

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

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

708   *Letters*, 18, 1139–1152.

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

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

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

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

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

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

715   1329–1338.