Seasonal Effects of Environmental Change on Yellow-Bellied Marmot Population Dynamics

Running title: Seasonal mechanisms of population dynamics

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ABSTRACT

Environmental factors drive the persistence of natural populations by causing complex, covarying responses in demographic processes (*i.e.*, survival, growth, and reproduction). As most natural populations inhabit seasonal environments, overlooking seasonal differences in this covariation may obscure the mechanisms that buffer or amplify population responses to environmental change. We investigated how environment-driven covariation of seasonal demographic processes affects population dynamics using 40 years of individual-based data from a population of yellow-bellied marmots (*Marmota flaviventer*). We first used a factor-analytic

approach to jointly model demographic processes as a function of a latent variable describing yearly environmental quality. We then parameterized, perturbed, and projected into the future a seasonal population model that explicitly incorporated the covarying demographic responses to the environment. The projections were based on various scenarios of environmental change, including changes in the trend and temporal patterning of environmental quality. We show that, although demographic processes in both the summer and winter season contributed to population fitness, yearly environmental quality exerted the strongest effect on winter demography only. Simultaneous, negative responses to declining average environmental quality of winter survival and mass and reproductive-status change resulted in an increased risk of population quasi-extinction, regardless of summer demography. We emphasize that assessing seasonal demographic effects is key to understanding population persistence in the face of environmental change and should receive much more attention in ecological theory and conservation management.

INTRODUCTION

Effects of environmental change on survival, growth, and reproduction are typically investigated based on annual transitions among life-history stages in structured population models (Paniw, Ozgul, & Salguero-Gómez, 2018; Salguero-Gómez et al., 2016). However, all natural ecosystems show some level of seasonal fluctuations in environmental conditions, and numerous species have evolved life cycles that are cued to such seasonality (Ruf, Bieber, Arnold, & Millesi, 2012; Varpe, 2017). For example, most temperate- and many arid-environment species show strong differences in survival and growth among seasons, with reproduction being confined mostly to one season (Childs, Coulson, Pemberton, Clutton-Brock, & Rees, 2011; Rushing et al., 2017; Woodroffe, Groom, & McNutt, 2017). Species with highly adapted, seasonal life cycles

are likely to be particularly vulnerable to environmental change, even if they are relatively long-lived (Campos et al., 2017; Jenouvrier et al., 2012; Paniw, Maag, Cozzi, Clutton-Brock, & Ozgul, 2019). This is because adverse environmental conditions in one season may carry-over to the next season in which key life-history events (e.g., reproduction) occur, and can negate positive season-specific environmental effects (Marra, Cohen, Loss, Rutter, & Tonra, 2015). For instance, in species where individual traits such as body mass determine demographic rates, environment-driven changes in the trait distribution in one season can affect trait-dependent demographic rates in the next season (Bassar, Letcher, Nislow, & Whiteley, 2016; Paniw et al., 2019). Investigating annual dynamics, averaged over multiple seasons, may, therefore, obscure the mechanisms that allow populations to persist under environmental change.

Despite the potential to gain a more mechanistic view of population dynamics, modeling the effects of seasonal environmental change is an analytically complex and data-hungry endeavor (Bassar et al., 2016; Benton, Plaistow, & Coulson, 2006). This is in part because multiple environmental factors that change throughout the year can interact with each other and individual-level (e.g., body mass) or population-level factors (e.g., density dependence) to influence demographic rates (Benton et al., 2006; Lawson, Vindenes, Bailey, & van de Pol, 2015; Ozgul, Oli, Olson, Blumstein, & Armitage, 2007; Paniw et al., 2019; Töpper et al., 2018). One major analytical challenge for population ecologists is that typically only a small subset of potential environmental drivers of population dynamics are known and measured (Ehrlén, Morris, von Euler, & Dahlgren, 2016; Teller, Adler, Edwards, Hooker, & Ellner, 2016). Another challenge is that key environmental factors simultaneously affect multiple demographic rates causing them to covary within and among seasons (Maldonado-Chaparro, Blumstein, Armitage, & Childs, 2018; Paniw et al., 2019). Positive environment-driven covariation in demographic

rates can then amplify the population-level effects of environmental change (Jongejans, de Kroon, Tuljapurkar, & Shea, 2010; Robert, Bolton, Jiguet, & Bried, 2015). Antagonistic demographic responses on the other hand can buffer populations from environmental change (Knops, Koenig, & Carmen, 2007; Van de Pol et al., 2010); for instance, when population-level effects of decreased reproduction are offset by increases in survival or growth (Connell & Ghedini, 2015; Reed, Grøtan, Jenouvrier, Sæther, & Visser, 2013; Villellas, Doak, García, & Morris, 2015). Thus, explicit consideration of environment-driven patterns in demographic covariation can allow to gain a fuller picture of population persistence in a changing world. Such a consideration remains scarce (Ehrlén & Morris, 2015; Ehrlén et al., 2016) but see (Bassar et al., 2016; Compagnoni et al., 2016).

A flexible framework to model population responses to environment-driven demographic covariation are integral projection models (IPMs; Ellner, Childs, & Rees, 2016). Seasonal IPMs are an extension of periodic matrix population models (Caswell, 2001, ch. 13 and references therein) (Ripley & Caswell, 2006), and simultaneously project trait distributions and population dynamics across seasons. The construction of IPMs is typically done by fitting simple models describing demographic rates as functions of a continuous state variable (e.g., body mass) and (environmental) covariates. Thus, this framework can integrate demographic covariation in response to environmental drivers (Hindle et al., 2018; Merow et al., 2014; Rees & Ellner, 2009). IPMs are increasingly used to project population dynamics under environmental change (Paniw et al., 2019; Paniw, Quintana-Ascencio, Ojeda, & Salguero-Gómez, 2017b; Simmonds & Coulson, 2015); however, periodic IPMs have been developed in only a few cases (Bassar et al., 2016; Paniw et al., 2019), despite their potential to provide a mechanistic understanding of

seasonal carry-over effects (Harrison, Blount, Inger, Norris, & Bearhop, 2010; Hostetler, Sillett, & Marra, 2015).

Here, we investigated the population-level effects of environment-driven seasonal covariation among trait-mediated demographic rates (*i.e.*, collectively referred to as demographic processes), capitalizing on 40 years (1976-2016) of individual-based data from a population of yellow-bellied marmots (*Marmota flaviventer*). Yellow-bellied marmots have adapted to a highly seasonal environment; individuals spend approximately eight months in hibernation during the cold winter (September/October-April/May), and use the short summer season (April/May-September/October) to reproduce and replenish fat reserves (Fig. 1). One challenge that the marmot study shares with numerous other natural systems is the identification of key proximal environmental factors driving population dynamics. In marmots such factors are numerous and affect population dynamics through complex, interactive pathways (Maldonado-Chaparro, Read, & Blumstein, 2017; Oli & Armitage, 2004), which include interactions with phenotypic-trait structure (Ozgul, Childs, Oli, Armitage, & Blumstein, 2010). As a result, measures of environmental covariates (e.g., temperature) have previously shown little effect on the covariation of marmot demographic processes (Maldonado-Chaparro et al., 2018). To address this challenge, we used a novel method, a hierarchical factor analysis (Hindle et al., 2018), to model the covariation of demographic processes as a function of a shared measure of latent environmental quality (*i.e.*, environmental condition at a given time point), quantified in a Bayesian modeling framework. We then built seasonal stage-, mass-, and environment-specific IPMs for the marmot population and used prospective stochastic perturbation analyses and population projections to assess how environmental change may affect population dynamics via the observed demographic covariation.

METHODS

Study species

Yellow-bellied marmots are large, diurnal, burrow-dwelling rodents, occupying montane regions of the western North America (Armitage, 2003; Frase & Hoffmann, 1980). They experience strong seasonal fluctuations in environmental conditions (Armitage, 2014). The biology of yellow-bellied marmots in Colorado is described in detail by Armitage (2014). Our study was conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38° 57' N, 106° 59' W). Climatic conditions in both winter and summer have been shown to influence reproduction and survival in the subsequent season (Lenihan & Van Vuren, 1996; Van Vuren & Armitage, 1991). These climatic effects on the demography of yellow-bellied marmots are mediated through body mass, with heavier individuals more likely to survive hibernation and reproduce in summer (Armitage, Downhower, & Svendsen, 1976; Ozgul et al., 2010). Population dynamics of marmots are therefore likely to be susceptible to changes in seasonal patterns of environmental drivers. However, numerous interacting climatic factors, such as temperature extremes, snowfall, and length of snow cover, determine both winter and summer environmental conditions, and their effect on marmot demography have been shown to be difficult to disentangle (Inouye, Barr, Armitage, & Inouye, 2000; Schwartz & Armitage, 2002; Schwartz & Armitage, 2005).

Seasonal demographic rates and trait transitions

For this study, we focused on the population dynamics of eight major colonies continuously monitored since 1976 (Armitage, 2014; Supporting Material S1). Each year, marmots were live-trapped throughout the growing season in summer (and ear-tagged upon first capture), and their

sex, age, mass, and reproductive status were recorded (Armitage & Downhower, 1974; Schwartz, Armitage, & Van Vuren, 1998). We focused on seasonal demographic processes of females only. All young males disperse from their natal colonies, and female immigration into existing colonies is extremely rare; as such, local demography can be accurately represented by the female segment of the population (Armitage, 2010). We classified female marmots by age and reproductive status: juveniles (< 1 year old), yearlings (1 year old), and non-reproductive (≥ 2 years old; not observed pregnant or with offspring) and reproductive adults (≥ 2 years old; observed pregnant or with offspring) (Armitage & Downhower, 1974).

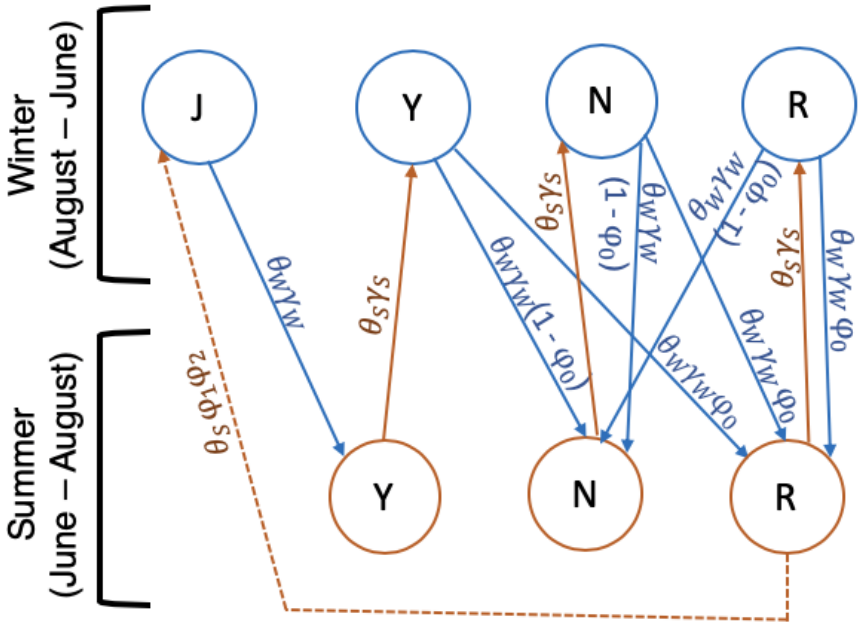

Figure 1: Seasonal life-cycle transitions modelled for yellow-bellied marmots. The two seasons correspond to the main periods of mass loss (winter) and gain (summer). Solid and dashed arrows represent discrete-time stage transitions and recruitment, respectively. Transitions among winter (W) and summer (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 mixed effects models in a Bayesian framework and include body mass and a common latent variable representing environmental quality as covariates.

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

individuals can be measured and has been shown to be a good estimate of pre-hibernation mass (Maldonado-Chaparro et al., 2017). Body-mass estimates on the two specific dates were obtained using linear mixed effect models as described in Ozgul *et al*. (2010; see also Maldonado-Chaparro et al., 2017). Body mass of juvenile females was estimated for August 15.

Modelling demographic and mass change (trait-transition) rates

We jointly modeled all seasonal demographic and mass change rates (*i.e.*, demographic processes) as a function of stage and body mass - or mother's mass in the case of juvenile mass - at the beginning of a season, using a Bayesian modeling framework (Table 1; Supporting Material S1). All mass estimates were cube-root transformed to stabilize the variance and improve the normality of the residuals in the Gaussian submodels (Maldonado-Chaparro et al., 2017). We fitted all demographic-process submodels as generalized linear mixed effects models (GLMMs). We assumed a binomial error distribution (logit link function) for the probability of winter (θ_W) and summer (θ_S) survival and of probability of reproducing (*i.e.*, being in the reproductive adult stage at the beginning of summer; φ_0); a Poisson error distribution (log link function) for the number of recruits (φ_1); and a Gaussian error distribution (identity link) for the masses (z^*) at the end of each season (Table 1). Mass-change (*i.e.*, mass gain or loss) rates (γ) were then defined as functions of current (z) and next (z^*) mass using a normal probability density function. For the juvenile mass distribution (φ_2), the density function depended on the mother's mass (z_M) (see below; Supporting Material S2).

To describe environment-driven temporal covariation in seasonal demography in the absence of explicit knowledge on environmental drivers, we quantified a model-wide latent variable (Q_y) affecting all demographic processes in a given year (y) (Table 1). One latent

variable was enough to capture covariation among the demographic processes (Supporting Material S1). Details of the parameterization of Q_y can be found in Supporting Material S1 (see also Hindle *et al*., 2018). Briefly, this covariate effectively estimates the overall annual environmental quality that affects the various demographic processes simultaneously, thereby capturing correlated responses (within and among seasons) to environmental fluctuations (Hindle et al., 2018). In the absence of causal variables that can be directly measured, Q_y was incorporated as a covariate in all seven demographic-process submodels; and the year-specific values of Q_y were drawn from a normal distribution with mean = 0 and SD =1. Higher Q_y indicate a better quality of the environment in a given year, and the associated β_q slope parameters determine the magnitude and sign of the effect of Q_y on a given, season-specific demographic process (Table 1). Thus, similar to large-scale environmental indices such as NAO or ENSO, Q_y captures to what extent a bad ($Q_y < 0$) or good ($Q_y > 0$) environment is likely to affect both summer and winter demography. To make the Bayesian model identifiable, we constrained the standard deviation of Q_y to equal 1 and arbitrarily set the β_q for summer survival (θ_S) to be positive. The β_q of the remaining submodels can, therefore, be interpreted as correlations of demographic processes with θ_S due to environmental variation.

Aside from the environmental covariate Q_y simultaneously affecting all demographic processes, we included a random year effect ($\varepsilon_{Ysubmodel}$) as a covariate in each submodel. This year effect accounted for additional temporal variation not captured by Q_y. We also tested for the effect of population density (measured as total abundance, abundance of adults, or abundance of yearling and adults) in all submodels. However, like previous studies, we could not detect any clear density effects (Armitage, 1984; Maldonado-Chaparro et al., 2018).

The prior distributions of the Bayesian model and posterior parameter samples obtained are detailed in Supporting Material S1. For each demographic-process submodel, we chose the most parsimonious model structure by fitting a full model that included all covariates (mass, stage, and Q_y) and two-way interactions between mass and stage and stage and Q_y, and retaining only those parameters for which the posterior distribution (± 95 % C.I.) did not overlap 0 (Table 1; Table S2.1).

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. The logit link, for winter survival as an example, corresponds to $1^{-(1/1+\exp(-\theta W))}$. *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^*)	$z_J^* = \alpha_{0z*J} + \beta_{zz*J} \times z_M + \beta_{qz*J} \times Q_y[\text{year}] + \varepsilon_{yz*J}[\text{year}]$	$\aleph(z_J^*, \tau_{z*J})$

Seasonal Integral Projection Models

We used the most parsimonious models of demographic processes (Table 1) to parameterize density-independent, stage-mass-structured, seasonal and environment-specific Integral Projection Models (IPMs) (Easterling, Ellner, & Dixon, 2000; Ellner et al., 2016). For each stage a, the IPMs track the number of individuals (n_a) in the mass range [z, z+dz] at time t. The fate of these individuals at time t+1 is described by a set of coupled integral equations, which differ for each season and are a function of the latent environmental variable Q_y. In the winter season, individuals can survive (θ_W) and change mass (γ_W) according to their stage, mass, and environment. Conditional on survival, juveniles (J) transition to yearlings (Y), while all other stages are distributed to either the reproductive (R) or non-reproductive (N) adult stage at the beginning of summer, depending on the stage-specific probability of reproducing (φ_0). During the summer season, individuals in stages Y, N, and R survive (θ_S) and change mass (γ_S) according to their stage and mass at the beginning of summer and according to the environment; but, in summer, transitions to another stage do not occur. Reproductive individuals (R) of a given mass also produce $\varphi_1/2$ female juveniles (J), *i.e.*, half of the total number of recruits. Female recruits are distributed across z mass classes by the end of summer, given by φ_2. The mathematical descriptions of the IPMs for the winter and summer seasons are provided in Supporting Material S2.

We numerically integrated the summer and winter IPMs using the 'midpoint rule' (Easterling et al., 2000) with upper and lower integration limits of 7.8 (472 g) and 17.1 (5000 g), respectively. To avoid unintended eviction of individuals from the model (*i.e.*, for a given mass class z, the sum of the probabilities to transition to $z^* < 1$), we applied a constant correction (*i.e.*, 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

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, logλs, (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 λs 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):

308 $$e = E[\frac{\langle v_{t+1}, C_t w_t \rangle}{\langle v_{t+1}, K_t w_t \rangle}],$$

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

individuals from 1976-2016 was 0.95, each winter IPM during T simulations was perturbed by subtracting a focal value of winter survival from its 40-year mean; and e_S^{μ} was calculated by integrating this perturbed IPM as C_t into the above equation. The two elasticities quantify the strength of selection pressures on lower-level vital rates in stochastic environments (Haridas & Tuljapurkar, 2005; Rees & Ellner, 2009). We repeated the elasticity calculations for a sample of 100 parameter values from the posterior distribution.

Population viability under changes in environmental quality

To assess how the combined effects of (i) seasonal demographic responses to environmental fluctuations and (ii) population sensitivity to seasonal demography impact population viability, we simulated population dynamics under environmental change. We ran 200 independent simulations each projecting population dynamics for 50 years. The projections were based on several scenarios of changes in the distribution of environmental quality, Q_y. We first created base simulations (*i.e.*, no environmental change) where Q_y was picked from a normal distribution with $\mu_Q = 0$ and $\sigma_Q = 1$ across all demographic processes. Next, we approximated random future fluctuations in Q_y under different average environmental conditions. To do so, we sampled Q_y from a normal distribution fixing the average environmental quality (μ_Q = -1, -0.5 , 0.5, 1) and its variation (σ_Q = 0.6, 1.2) over the 50 years of projections. We then explored how a trend in μ_Q would affect viability and mass distribution. To do so, we decreased the four μ_Q by 0.01 in each year of the projections, keeping σ_Q unaltered. Lastly, as temporal autocorrelation in environmental states can affect population dynamics (Paniw et al., 2018), we projected autocorrelated changes in Q_y. That is, each year, marmots could experience either a good or bad environment where Q_y was sampled from a normal distribution with either $\mu_Q = 1$ or $\mu_Q = -1$,

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).

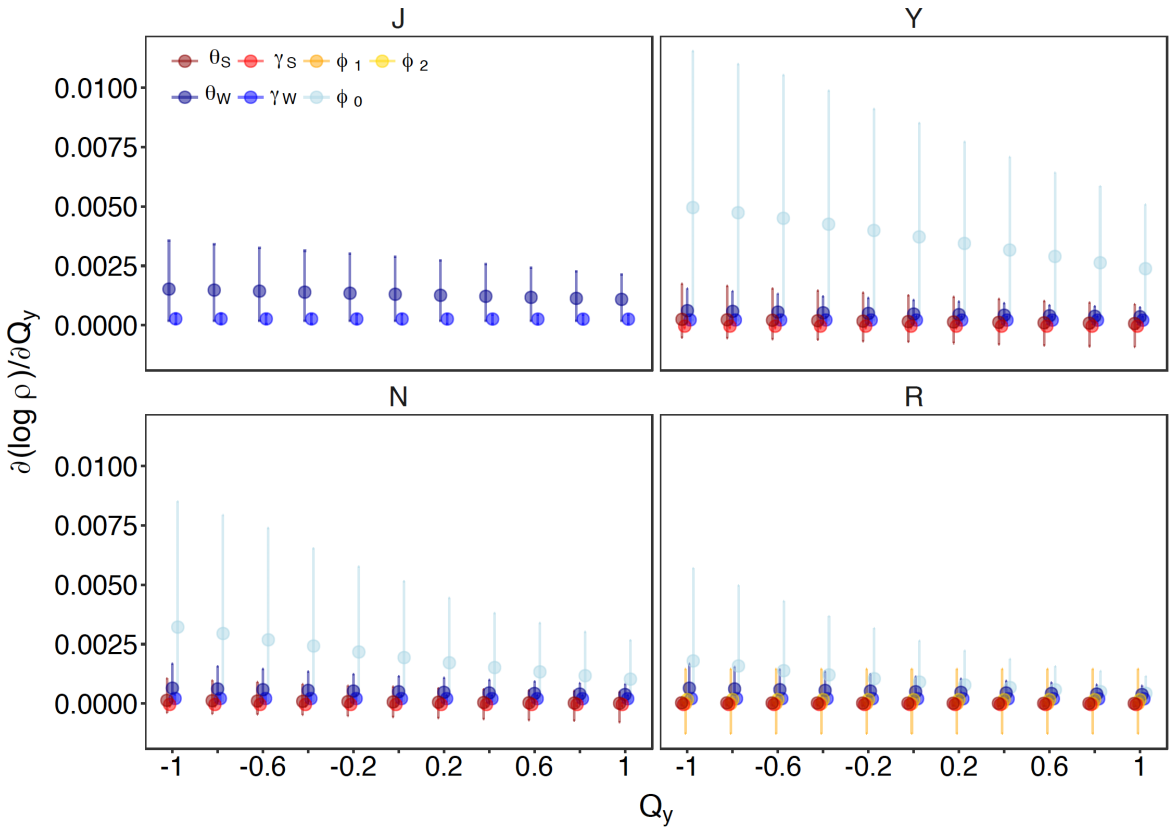

Figure 2: The sensitivity of seasonal demographic processes to environmental quality in marmots. Sensitivity is assessed as proportional changes in demographic processes, ρ, as environmental quality, Q_y, increases slightly. This sensitivity is measured with respect to different average values of Q_y 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 ± 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

adults. Survival, in particular θ_S, was highest for reproductive adults; reproduction was also highest for adults that reproduced before (Fig. S1.3 in Supporting Material S1).

Sensitivity of population dynamics to seasonal demographic processes

While environmental quality affected winter demographic processes only, our prospective perturbation analyses showed that winter and summer demography equally determine long-term population fitness. Stochastic elasticity analyses (e_S^{μ} and e_S^{σ}) showed that relative increases in the mean (μ) of winter (θ_W) and summer (θ_S) survival for reproductive adults (R), would lead to substantial relative increases of the stochastic population growth rate, logλs (Fig. 3a). Highest e_S^{μ} were found at intermediate and large mass classes; e_S^{μ} was negative for small masses when mass changes (γ) and offspring mass (φ_2) were perturbed (Fig. S3.1a in Supporting Material S3), explaining the overall small e_S^{μ} for γ and φ_2 summed over all mass classes (Fig. 3a). Overall, relative changes in logλsdue to increases in the standard deviation of demographic processes (e_S^{σ}) were much smaller compared to e_S^{μ} (Fig. 3b) and didn't differ significantly between vital rates, as 95 % posterior C.I. crossed 0 (Fig. S3.1b).

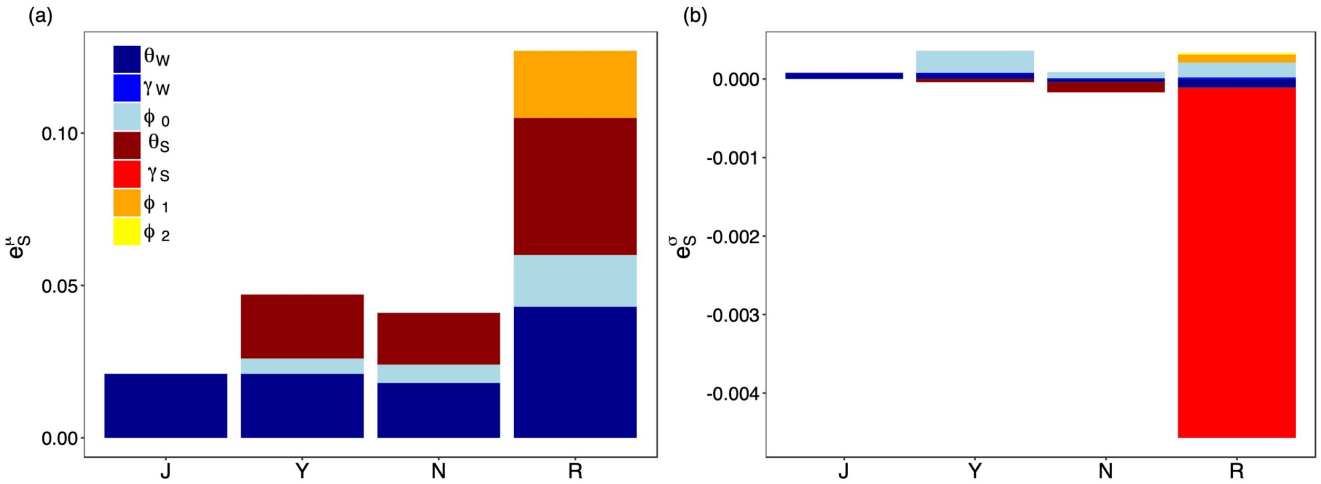

Figure 3 Sensitivity of the average long-term population fitness to changes in the average and variability of demographic processes modeled for the yellow-bellied marmots. The sensitivity measure is obtained analytically as elasticities (e) of the stochastic population growth rate, log λs, to changes in (a) the mean (μ) and (b) standard deviation (σ) of stage-specific demographic processes summed over all mass classes. Stages are juveniles (J), yearlings (Y), non-reproductive adults (N), and reproductive adults (R). Demographic processes include winter (W) and summer (S) survival (θ) and mass change (γ); reproduction (φ_0); recruitment (φ_1), and offspring mass distribution (φ_2). Elasticities were calculated at the mean posterior values of parameters obtained from the Bayesian demographic model.

Population viability under changes in environmental quality

While population fitness was equally sensitive to demographic processes over winter and summer, environmental fluctuations strongly affected viability through winter demography. Using base simulations (*i.e.*, obtaining Q_y from a normal distribution with $\mu_Q = 0$ and $\sigma_Q = 1$), the probability of quasi-extinction, at an average of 0.1 [0.0, 0.3 C.I.] across posterior parameters, were relatively low. Simulations of population dynamics based on scenarios of environmental change resulted in substantial decreases (0 at $\mu_Q = 1$) and increases (0.9 [0.6, 1.0 C.I.] at $\mu_Q = -1$) in quasi-extinction, compared to base simulations, when the population experienced a high and low average environmental quality (Q_y), respectively (Fig. 4). Average quasi-extinction further increased and its uncertainty across posterior parameters decreased when a declining trend in average environmental quality (Q_y) was simulated (Fig. S4.1). Changes in the standard deviation of Q_y had comparatively little effect on quasi-extinction (Fig. 4). The same was true for simulations of autocorrelated environmental fluctuations, where changes in the frequency of good environmental conditions (effectively changing the average environmental quality) had a strong effect on viability, while changes in the patterning of environmental states had little effect (Supporting Material S4).

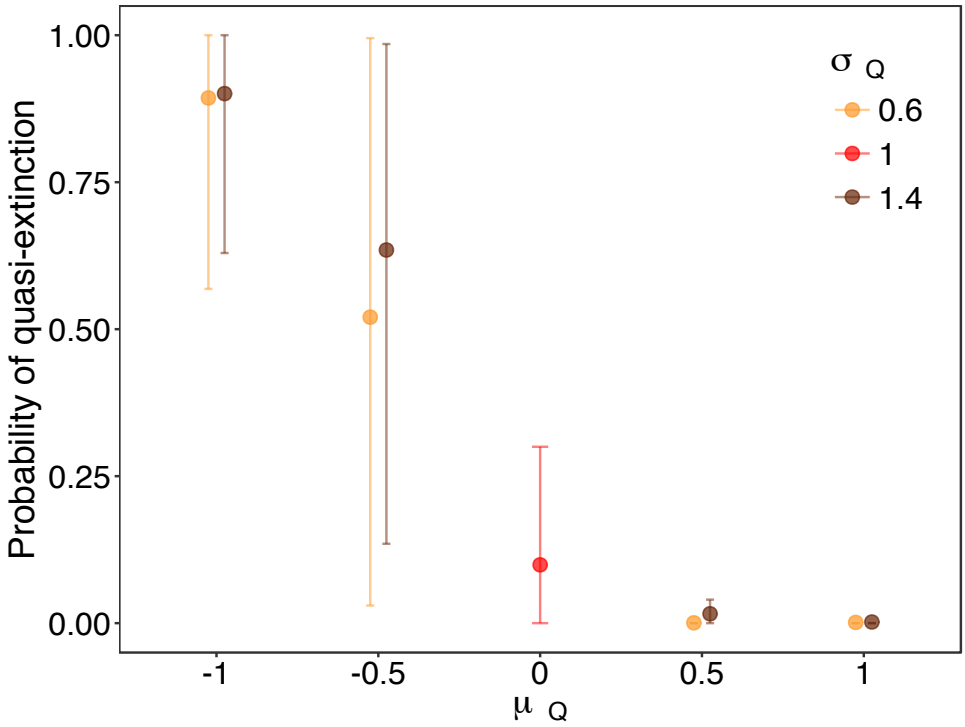

Figure 4: Probability of quasi-extinction (*i.e.*, < 4 non-juveniles in the population) of yellow-bellied marmots under different scenarios of environmental change. The scenarios consisted of projecting population dynamics for 50 years fixing a different mean (μ) and standard deviation (σ) of environmental 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

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.

The seasonal effects of environmental quality on population persistence must be understood in terms of the role of reproductive females in the marmot population (Ozgul et al., 2009). In our simulations, a good winter quality, which has previously been shown to have the strongest effect on individual survival (Armitage, Blumstein, & Woods, 2003), would, in particular, result in more reproductive females in the summer. In turn, summer survival and reproduction of these females are important to long- and short-term demography (Maldonado-Chaparro et al., 2018; Ozgul et al., 2009), but are not driven by environmental conditions. As is the case in other socially complex mammals (Morris et al., 2011), reproduction in yellow-bellied marmots is governed primarily by social interactions, in particular the behavior of dominant females (Armitage, 2010; Blumstein & Armitage, 1998). Even under optimal summer conditions, the reproductive output of the population may not be increased as dominant females suppress reproduction in younger subordinates and therefore regulate the size of colonies (Armitage, 1991). Dominant females, in addition, may skip reproduction themselves if they enter hibernation with a relatively low mass (Armitage, 2017). Thus, the necessity of meeting the physiological requirements of hibernation profoundly affects life-history traits of yellow-bellied marmots that are expressed during the active season. Here, an explicit seasonal population analysis allowed us to recognize a potentially important mechanism through which the environment filters demography: survival in or transition to the reproductive stage in a good winter can guarantee successful reproduction in summer, in addition to direct summer processes.

Unlike the direct effects of seasonal survival and reproduction, trait transitions between seasons had a smaller effect on annual population dynamics, even if winter mass changes were mediated by environmental quality. In this sense, the prospective perturbation analyses 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

environments and different masses for a high-altitude specialist; see Jenouvrier *et al*., (2018) for similar analyses in a long-lived bird.

Our results emphasize that declines in environmental quality in one season alone can strongly affect annual population dynamics of a mammal highly adapted to seasonal environments and buffered from environmental variation. Therefore, positive demographic covariation under environmental change may threaten populations even if it affects demographic process to which the stochastic growth rate is least sensitive, *i.e.*, processes that are under low selection pressure (Coulson, Gaillard, & Festa-Bianchet, 2005; Iles, Rockwell, & Koons, 2019). Studies of global change ecology that focus on the effects of environmental factors on demographic processes considered to strongly affect both short- and long-term population dynamics may therefore miss the important role of seasonal demographic covariation. In addition, such seasonal mechanisms are potentially critical for conservation management (Paniw et al., 2019) but would be missed by annual-step analyses where demographic processes are averaged across the entire year (Hostetler et al., 2015).

Given the strong overlap of our results with previous findings and overall robust model performance, the factor analytic approach we used to quantify environment-driven covariation in demographic processes appears to be a promising alternative to approaches linking specific vital rates directly to environmental drivers (Evans & Holsinger, 2012; Hindle, Pilkington, Pemberton, & Childs, 2019; Hindle et al., 2018). In the case of yellow-bellied marmots, where demographic rates were relatively easy to parameterize and the assumption of positive covariation holds in part due to a lack of density feedbacks, the factor analytic approach can be used effectively to assess population-level effects of perturbing a global measure of environmental quality. In cases where environment-demography relationships are more complex

and include negative demographic covariation (e.g., where trade-offs dominate), this approach may find limited applications. However, positive covariation of demographic patterns is common (Jongejans et al., 2010; Paniw et al., 2019); and, given the short time series of most demographic datasets (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016) or little knowledge on the actual environmental drivers of population dynamics (Pol et al., 2016; Teller et al., 2016), the factor analytic approach can be particularly useful in comparative studies.

Most species inhabit seasonal environments. Under global environmental change, it may therefore be critical to understand how seasonality patterns mediate persistence of natural populations. Our analyses point to an important role of seasonal differences in demographic covariance in driving population responses to environmental change. Novel methods such as the factor analytic approach allow researchers to overcome some challenges associated with such mechanistic approaches, and we encourage more seasonal demographic analyses across different taxa.

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AUTHOR CONTRIBUTIONS

K.B.A., D.T.B., and M.O. led the long-term study and data collection; M.P., D.C., and A.O. conceived the ideas for the paper and designed the analyses; M.P. conducted the analyses with substantial help from J.M.; M.P. wrote the manuscript; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY

The datasets generated and analyzed during the current study as well as the R scripts to run all analyses are available in the *Dryad* repository, [PERSISTENT WEB LINK TO DATASETS].

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