Supporting Information

Demographic consequences of changing environmental periodicity, *Ecology*

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Appendix S8 - Elasticities of the population growth rate to vital rates and post-fire habitat states.

Data (Conquet et al. 2022a) are available in Dryad at https://doi.org/10.5061/dryad.hhmgqnkkc and code (Conquet et al. 2022b) is available in Zenodo at https://doi.org/10.5281/zenodo.7078560.

Previous studies have assessed the influence of the mean and variance of different vital rates to stochastic population dynamics in the marmots (Maldonado-Chaparro et al. 2018; Paniw et al. 2020), meerkats (Paniw et al. 2019), and dewy pines (Paniw, Quintana-Ascencio et al. 2017). However, each study for each system used different approaches. Here we wanted to assess how sensitive each system is to changes in inter-annual (or habitat-state specific) variation in vital rates using a common approach of stochastic elasticities. This allows us to compare these elasticities to the perturbations of the strength of periodicity more systematically across the three systems.

Marmots and meerkats

To assess the importance of vital rates in shaping the dynamics of the marmot and meerkat populations, we calculated the stochastic elasticity (E^S) of the population growth rate (λ) as well as its elasticity to the mean ($E^{S\mu}$) and standard deviation ($E^{S\sigma}$) of each vital rate, following Tuljapurkar, Horvitz, and Pascarella (2003). We projected the dynamics of each population 100 times for 1000 years. For each vital rate x_i and each year t (sampled randomly among the years in the study period), we used seasonal vital rates to parameterize an unperturbed annual Matrix Population Model (MPM), $\mathbf{A}_t$, and a perturbed MPM $\mathbf{P}_t$ with (1) $x_{i,t} = x_{i,t} + \mu_i$ to calculate the elasticity of λ to the mean $E^{S\mu}$, (2) $x_{i,t} = x_{i,t} + (x_{i,t} - \mu_i)$ to calculate the elasticity of λ to the standard deviation $E^{S\sigma}$, or (3) $x_{i,t} = x_{i,t} + x_{i,t}$ to calculate the stochastic elasticity of λ, E^S. We calculated the elasticity of λ to each vital rate using

$$E \; = \lim_{T \to \infty} \left(\frac{1}{T}\right) \sum_{t\,=\,1}^{T} \frac{\mathbf{v}_{i,t} \times \mathbf{C}_{ij,t} \times u_{j,t-1}}{\lambda_t \times [\mathbf{v}_t, \mathbf{u}_t]} \qquad \text{(Equation S1)}$$

for $T = 500$, using only the last 500 years of the simulation to remove the transient dynamics.

We computed the perturbation matrix $\mathbf{C}_{i,t} = \mathbf{A}_t - \mathbf{P}_t$ for each vital rate x_i and each year t. We obtained the left and right eigenvectors $\mathbf{u}_t$ and $\mathbf{v}_t$ by performing respectively forward and backward projections of the population vector $\mathbf{n}_t$ using the unperturbed MPM $\mathbf{A}_t$ (see the R code for more detail).

Following Morris et al. (2008), we calculated the “relative effect of variability” to evaluate the proportion of the stochastic elasticity E^S attributed to changes in the variability of a given vital rate category (i.e., survival, transitions, recruitment, and emigration). That is, for each category of vital rates, we computed the ratio $\sum_j E_j^{S\sigma} / \sum_v \left(E_v^{S\mu} + E_v^{S\sigma}\right)$, where j is a vital rate in a given category, v is a vital rate among all categories, and $E^{S\mu}$ and $E^{S\sigma}$ are the elasticities of the population growth rate to the mean and standard deviation of a given vital rate (see the R code).

For all vital rates in both the marmot and meerkat populations, the elasticities of the population growth rate λ to the standard deviation $E^{S\sigma}$ were largely smaller than the elasticities to the mean $E^{S\mu}$ (Fig. S1a and S1c). This is supported by the relative effect of variability of all vital-rate categories, which shows a small contribution of the elasticity to the standard deviation $E^{S\sigma}$ to the stochastic elasticity E^S (Fig. S1b and S1d). A low sensitivity of λ to the variation of vital rates confirms previous results (Paniw et al. 2019; Paniw et al. 2020) suggesting that the marmot and meerkat populations are buffered against large inter-annual fluctuations in all vital rates (Pfister 1998; Morris et al. 2008; Hilde et al. 2020).

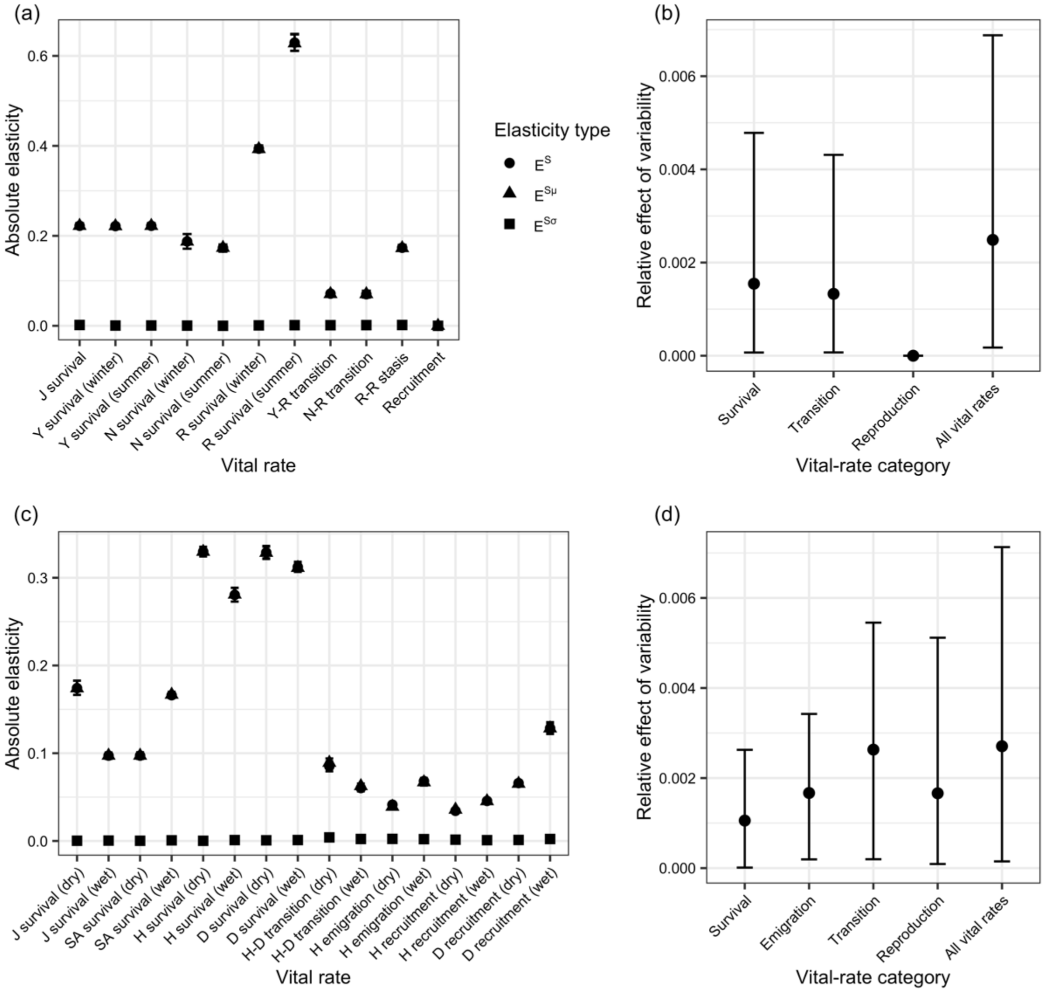

Figure S1 – Elasticities of the population growth rate and relative effect of variability in the marmot and meerkat populations. We calculated the absolute stochastic elasticity E^S of the population growth rate λ to each vital rate of the marmot and meerkat populations ((a) and (c), points). In addition, we calculated the absolute elasticities to the mean $E^{S\mu}$ and standard deviation $E^{S\sigma}$ of the vital rates ((a) and (c), triangles and squares). For all vital rates in both populations, the elasticity to vital rate variability was largely smaller than that to the mean vital rate. This is confirmed by the small relative effect of variability for each vital-rate category ((b) and (d)), which represents the part of E^S attributed to vital-rate variability.

Dewy pines

For the dewy-pine population, we assessed the response of the stochastic growth rate log λ_S to perturbations in each post-fire habitat state (TSF_0 to $TSF_{>3}$). Therefore, we calculated the elasticity of lambda to each post-fire state using the megamatrix approach as described by Pascarella and Horvitz (1998). We used five post-fire state-specific annual MPMs $\mathbf{A}_{1\text{–}5}$ to parameterize a 25 X 25 block-diagonal matrix $\mathbf{A}_{15}$, with $\mathbf{A}_1$, …, $\mathbf{A}_5$ on the diagonal and zeros elsewhere, using the function *bdiag* from the R package *Matrix* (Bates and Maechler 2021). Then, using a post-fire state transition matrix, **C**, containing probabilities of transitioning between two post-fire states (see Appendix S7) and a 5 X 5 identity matrix $\mathbf{I}_5$, we built the megamatrix **M** using

$$\mathbf{M} = (\mathbf{C} \otimes \mathbf{I}_5) \times \mathbf{A}_{15} \qquad \text{(Equation S2)}$$

Each element $m_{ij\alpha\beta}$ of the megamatrix represents the transition probability from the life-history stage *i* in the post-fire state α to stage *j* in state β. We computed the elasticity matrix **E** of **M** using the *elasticity* function from the *popbio* R package (Stubben and Milligan 2007). We then obtained the elasticities of the population growth rate λ to each post-fire state by summing the elements $e_{ij\alpha\beta}$ of **E** for each β across all *ij* and α as in

$$\sum_{ij\alpha} e_{ij\alpha\beta} = \mathbf{E}_\beta \qquad \text{(Equation S3)}$$

We replicated this analysis with 100 megamatrices, randomly sampling the annual MPM for the stochastic post-fire state $\mathbf{A}_5$ in each replication (see the R code).

The dewy-pine population growth rate was substantially more sensitive to the last post-fire state ($TSF_{>3}$) than to the other states (0.50 [0.45 ; 0.55] in $TSF_{>3}$ and 0.13 [0.11 ; 0.15] on average for the other states; Fig. S2). Paniw, Quintana-Ascencio et al. (2017) showed that the population growth rate of dewy pines is most sensitive to the mean as well as variation in seed-bank parameters and that the magnitude of the elasticity of log λ_S to seed-bank parameters increased the longer the population remains in $TSF_{>3}$. Consequently, the higher elasticity of λ to $TSF_{>3}$ arises from high elasticities to seed-bank parameters. The dewy-pine population can therefore tolerate and benefit from fluctuations in seed-bank parameters. The population is thus not as strongly buffered against inter-annual variability in vital rates as the marmot and meerkat populations.

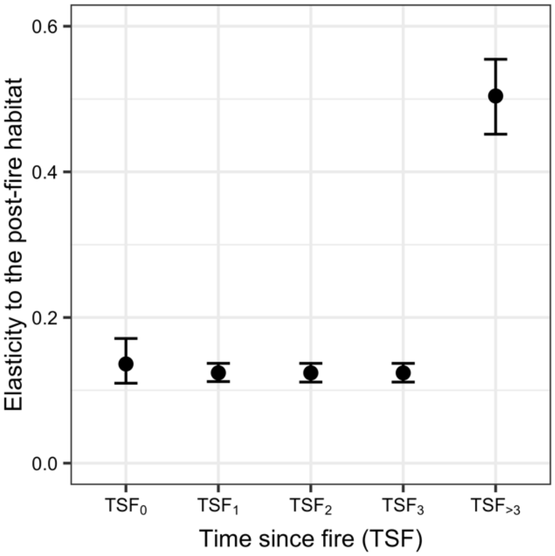

Figure S2 – Elasticity of the dewy-pine population growth rate to the post-fire states. We calculated the elasticity of *λ* to each post-fire state (TSF_0 to $TSF_{>3}$) using 100 megamatrices, following Pascarella and Horvitz (1998). The dewy-pine population was most sensitive to the last post-fire state, $TSF_{>3}$.

References – Appendix S8

Bates, D., and M. Maechler. 2021. “Matrix: Sparse and Dense Matrix Classes and Methods. R package version 1.3-2.” https://CRAN.R-project.org/package=Matrix.

Conquet, E., A. Ozgul, D. T. Blumstein, K. B. Armitage, M. K. Oli, J. G. A. Martin, T. H. Clutton-Brock, and M. Paniw. 2022. “Demographic consequences of changes in environmental periodicity.” Dryad, dataset. https://doi.org/10.5061/dryad.hhmgqnkkc.

Conquet, E., A. Ozgul, D. T. Blumstein, K. B. Armitage, M. K. Oli, J. G. A. Martin, T. H. Clutton-Brock, and M. Paniw. 2022b. R code for Demographic consequences of changes in environmental periodicity. Zenodo, software. https://doi.org/10.5281/zenodo.7078560.

Hilde, C. H., M. Gamelon, B.-E. Saether, J.-M. Gaillard, N. G. Yoccoz, and C. Pélabon. 2020. “The demographic buffering hypothesis: evidence and challenges.” *Trends in Ecology and Evolution* 35 (6): 523–538. https://doi.org/10.1016/j.tree.2020.02.004.

Maldonado-Chaparro, A. A., D. T. Blumstein, K. B. Armitage, and D. Z. Childs. 2018. “Transient LTRE analysis reveals the demographic and trait-mediated processes that buffer population growth.” *Ecology Letters* 21 (11): 1693–1703. https://doi.org/10.1111/ele.13148.

Morris, W. F., C. A. Pfister, S. Tuljapurkar, C. V. Haridas, C. L. Boggs, M. S. Boyce, E. M. Bruna, et al. 2008. “Longevity can buffer plant and animal populations against changing climatic variability.” *Ecology* 89 (1): 19–25. https://doi.org/10.1890/07-0774.1.

Paniw, M., D. Z. Childs, K. B. Armitage, D. T. Blumstein, J. G. A. Martin, M. K. Oli, and A. Ozgul. 2020. “Assessing seasonal demographic covariation to understand environmental-change impacts on a hibernating mammal.” *Ecology Letters* 23 (4): 588–597. https://doi.org/10.1111/ele.13459.

Paniw, M., N. Maag, G. Cozzi, T. H. Clutton-Brock, and A. Ozgul. 2019. “Life history responses of meerkats to seasonal changes in extreme environments.” *Science* 363 (6427): 631–635. https://doi.org/10.1126/science.aau5905.

Paniw, M., P. F. Quintana-Ascencio, F. Ojeda, and R. Salguero-Gómez. 2017.

"Interacting livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean carnivorous plant." *The Journal of Applied Ecology* 54 (6): 1884–1894. https://doi.org/10.1111/1365-2664.12872.

Pascarella, J.B., and C. C. Horvitz. 1998. "Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis." *Ecology* 79 (2): 547–563. https://doi.org/10.1890/0012-9658(1998)079[0547:hdatpd]2.0.co;2.

Pfister, C. A. 1998. "Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications." *Proceedings of the National Academy of Science of the United States of America* 95 (1): 213–218. https://doi.org/10.1073/pnas.95.1.213.

Stubben, C. J., and B. G. Milligan. 2007. "Estimating and analyzing demographic models using the popbio package in R." *Journal of Statistical Software* 22 (11). https://doi.org/10.18637/jss.v022.i11.

Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. "The many growth rates and elasticities of populations in random environments." *The American Naturalist* 162 (4): 489–502. https://doi.org/10.1086/378648.