Supporting Information

Demographic consequences of changing environmental periodicity, *Ecology*

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Appendix S4 - Simulation parameters, recorded variables, and additional results.

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.

Initial parameters

For the marmots, we used $\mathbf{n}_0$ = (12, 11, 9, 7) as an initial population vector representing the number of juveniles, yearlings, and non-reproductive and reproductive adults at the beginning of winter in 2016. For the meerkats, we used $\mathbf{n}_0$ = (0, 8, 34, 13), representing the number of juveniles, subadults, and adult helpers and dominants at the beginning of the dry season 2016. The initial density $dens_0$ = 2.1 for the density-dependent simulations was obtained from the last available season of the observed data (dry season 2016). For the dewy pine, we used an initial population vector representing the population after a fire: $\mathbf{n}_0$ = (1000, 0, 0, 0, 0), that is, a population consisting of 1000 seeds in the seed bank, and an initial aboveground density of 0.

Annual and stochastic growth rates

The annual population growth rate log λ was computed using

$$\text{annual} \log \lambda = \log(N_{t+1}/N_t) \qquad \text{(Equation S1)}$$

with N_t the number of individuals in year t and N_{t+1} the following year. We then obtained the stochastic growth rate log λ_S by averaging log λ across the 100 simulated years using

$$\log \lambda_S = \frac{\log(N_T/N_0)}{T} \qquad \text{(Equation S2)}$$

with N_T the number of individuals at year 100, N_0 the initial number of individuals in the populations, and T the total number of years (see Caswell 2001, Tuljapurkar, Horvitz, and Pascarella 2003, and the R code).

Density

For the simulations performed at constant average density, we used the mean population density across the whole dataset (7.1 indiv./km^2) for the meerkat population. For the dewy pine, we averaged aboveground density for each site (i.e., both natural sites and the human-disturbed site) and each TSF (see Table S1), and assigned the right average density to the right MPM at each time step. For example, for simulations with a disturbance in TSF_2 and with non-disturbed vital rates taken from the naturally fire-disturbed site A, we used a density of 34 in TSF_1, 4.1 in TSF_2, and 5.3 from TSF_3 until the next fire.

In the density-dependent simulations, we computed density at every time step. For the meerkat, we used

$$\text{density} = 2 \times \frac{N_t}{\text{population range}} \qquad \text{(Equation S3)}$$

with N_t the number of individuals at time t. Population range was originally obtained by calculating the 95% kernel utilization distribution using the GPS locations of meerkat burrows (see Cozzi et al. 2018). To predict population range based on the projected population, we used a linear mixed model (LMM, using the *lmer* function from the *lme4*

R package; Bates et al. 2015) to test for the effect of the season on population range, as well as the simple and quadratic effects of three density-dependent variables: average group size, number of females, and number of dominants. We included as well the interactions between season and the three density-dependent variables aforementioned, and added a random effect of the year on the average population range (see the R code). The model selection (using the *dredge* function from the *MuMIn* R package; Bartoń 2020) showed that population range was best predicted by the number of dominant individuals in the population (see Table S2). As the data was collected on female individuals only, we multiplied the population size by two in order to obtain the total number of individuals in the population, assuming an even sex ratio (Ozgul et al. 2014).

For the dewy pine, we used

$$\text{density site } S = \frac{N_{t,S}}{\text{total area of site } S} \qquad \text{(Equation S4)}$$

to update the aboveground density each year in each TSF habitat state, with $N_{t,S}$ being the aboveground population size at time t in site S, and the total area being determined by the study area in site S. In addition, to avoid issues of population density explosion, we constrained the number of seeds in the seed bank to a maximum of 4000 individuals, and the number of seedlings to a maximum of 1700 individuals (i.e., twice the maximum number observed in the study; see the R code).

Table S1 - Site- and TSF-specific average aboveground density used in the simulations performed at constant average density for the dewy pine. We computed the average density per site and per TSF, and used these values in the corresponding site-TSF combination MPMs, keeping the same density value every time a given MPM was used in the simulations at constant density.

Site	TSF	Density
Human-disturbed	TSF_1	4.9
	TSF_2	4.1
	TSF_3	1.8
Naturally fire-disturbed A	TSF_1	34
	TSF_2	23
	TSF_3	5.3
Naturally fire-disturbed B	TSF_1	6.4
	TSF_2	3.7
	TSF_3	4.1

Table S2 - Model fitted to estimate the population range of the meerkat population. The best model for population range according to the AICc selection was the model with an effect of the number of dominant females in the population, with a random effect of the year on the mean estimate.

Covariate	Estimate	Standard error (SE)
Intercept	2.9	0.21
Number of dominants	0.049	0.013

Effect of perturbing vital-rate periodicity on the variance of 100 annual stochastic growth rates var(log λ) and the quasi-extinction probability p_{qext}

We assessed the effect of perturbing vital-rate periodic patterns on the variance of 100 annual stochastic growth rate var(log λ) and the quasi-extinction probability p_{qext} for three species: the yellow-bellied marmot, the meerkat, and the dewy pine.

To compute the quasi-extinction probability, for each simulation, we kept track of an eventual extinction event by using a binary variable: we assigned 1 to a simulation if the population went extinct within 100 years, 0 otherwise. For the marmots and the meerkats population we set the quasi-extinction threshold at a population size of 15% of the minimum observed size or 15% of the minimum observed number of reproductive individuals. For the marmots, this corresponded to six individuals in total or one reproductive adult; for the meerkats, it was the equivalent of 20 individuals in total or five dominants. For the dewy pines, we used a conservative threshold of five aboveground individuals and 50 seeds in the seed bank, corresponding to 50% of the lowest number of individuals observed.

For the marmots, the perturbations in the strength of vital-rate seasonality did not largely affect the variance in annual growth rates var(log λ) (Fig. S1). On the other hand, the effect of such changes on the extinction probability of the population in each scenario followed the same pattern as that of the effect of changes in vital-rate seasonality on log λ_S. The marmot population was under extinction risk only when seasonality was high in reproductive adult survival ($p_{qext} = 0.05$), as this vital rate influences most population dynamics (Paniw et al. 2020; Appendix S8: Fig. S1a and S1b). While reproductive-adult summer survival is generally high in this marmot population (Armitage and Downhower 1974; Armitage 1991), winter survival can vary greatly due to a combination of biotic and abiotic factors occurring during hibernation and in the previous growing period (Van Vuren 2001; Schwartz and Armitage 2003; Cordes et al. 2020; Montero et al 2020). Therefore, a high or low seasonality in adult survival and the associated consequences on marmots population dynamics are mainly determined by decreases or increases, respectively, in winter survival compared to summer survival.

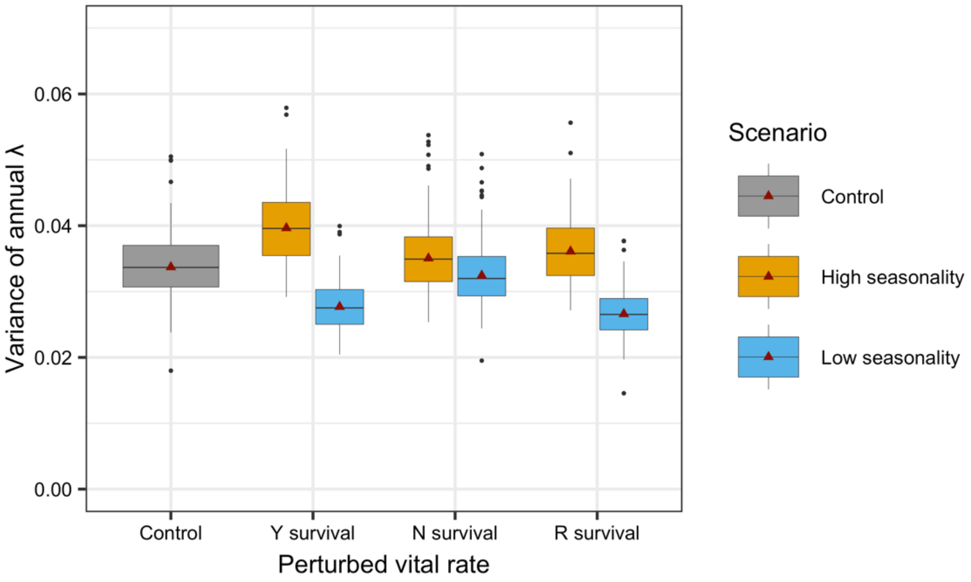

Figure S1 – Effect of perturbing vital-rate seasonality on the variance of the population growth rate in marmots. We tested the effect of a perturbation in the strength of the seasonal pattern (high or low seasonality) of the survival of yearlings (Y), and non-reproductive (N) and reproductive adults (R) on the variance in 100 annual population growth rates, var(log *λ*), with the red triangles representing the mean and the whiskers the 2.5th and 97.5th percentiles.

For the meerkats, unlike for the stochastic growth rate log λ_S, perturbing the vital-rate seasonal pattern led to important changes in the variance in annual growth rates var(log *λ*), even when density dependence was included in the projections (Fig S2). Overall, the effect of changing vital-rate seasonality on the variance in annual growth rates var(log *λ*) was opposite to its effect on the stochastic growth rate log λ_S, as expected from theory (Tuljapurkar 1982). In the control scenario, var(log *λ*) was higher in the density-dependent projections compared to the average-density projections (0.039 [0.026, 0.054] and 0.019 [0.014, 0.025], respectively; Fig. S2). Although changes in subadult survival and dominant recruitment seasonality largely affected the population growth rate, such changes did not affect its variance as greatly. Only a high seasonality in dominant recruitment at average density slightly decreased var(log *λ*) compared to the control scenario (0.0070 [0.0051, 0.010]). In addition, at constant average density, we observed large opposite effects of changes in seasonal patterns of dominant survival (0.030 [0.024, 0.038] with increased seasonality and 0.0055 [0.0041, 0.0067] with decreased seasonality), helper emigration (0.0064 [0.0048, 0.0081] with increased seasonality and 0.034 [0.027, 0.041] with decreased seasonality), and helper-to-dominant transition (0.0064 [0.0050, 0.0082] with increased seasonality and 0.034 [0.027, 0.041] with decreased seasonality). When we included density dependence, the same pattern emerged but only the negative effects of a lower seasonality in dominant survival (0.015 [0.012, 0.020]) and a higher seasonality in helper emigration and transition to dominant (respectively 0.020 [0.015, 0.026] and 0.020 [0.014, 0.027]) were clear.

In meerkats, extinction did not occur in any of the simulations.

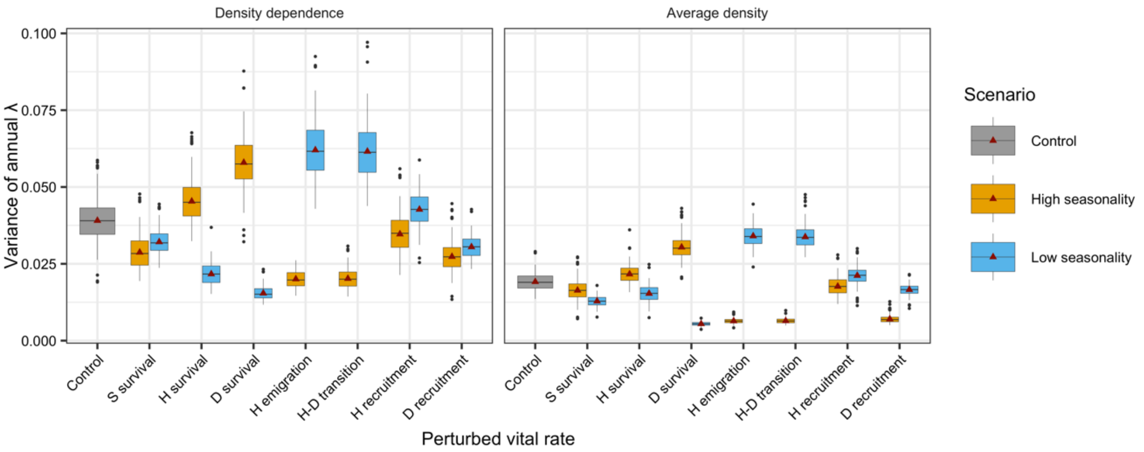

Figure S2 – Effect of perturbing vital-rate seasonality on the variance of the population growth rate in meerkats. We tested the effect of a perturbation in the strength of the seasonal pattern (high or low seasonality) of the survival of subadults (S), helpers (H), and dominants (D), helper emigration, helper-to-dominant transition, and helper and dominant recruitment on the variance in 100 annual population growth rates, var(log *λ*). We performed simulations with density-dependent dynamics (left panel) or at constant average density (right panel). The red triangles represent the mean for each boxplot, and the whiskers the 2.5th and 97.5th percentiles.

For dewy pines, unlike the stochastic growth rate log λ_S, the variance of annual growth rates var(log *λ*) was only affected by the introduction of a browsing perturbation in $TSF_{2, 3, \text{ and } >3}$ at average density under periodic fires occurring every 15 years. Under these conditions, the variance of annual growth rates increased to 0.46 [0.38, 0.55] on average under the perturbed scenario compared to 0.26 [0.17, 0.35] in the control scenario (Fig. S3a).

While in the control scenario the probability of quasi-extinction p_{qext} was 0 under all disturbance regimes, the dewy-pine population was at risk of extinction even when perturbing vital rates only in the last post-fire state ($TSF_{>3}$), both at average density and with density dependence (Fig. S3b). However, the probability of extinction differed among fire regimes and between the two scenarios with respect to density dependence. At average density (Fig. S3b, right panel), extinction probability increased with the number of perturbed post-fire states for all fire regimes. This probability was overall higher under periodic and stochastic fires occurring every 30 years, where the risk of extinction strongly increased when perturbing only $\mathrm{TSF}_{>3}$ ($p_{\mathrm{qext}} = 0.99$ and $p_{\mathrm{qext}} = 0.97$, respectively). On the other hand, this increase was smaller under stochastic fires occurring every 15 years on average ($p_{\mathrm{qext}} = 0.79$) and much reduced under periodic fires occurring every 15 years ($p_{\mathrm{qext}} = 0.20$). However, the observed differences among disturbance regimes faded when increasing the number of perturbed post-fire states, and the extinction probability reached 1 in all scenarios when perturbing all TSFs. With density dependence (Fig. S3b, left panel), extinction probability increased sharply when perturbing only $\mathrm{TSF}_{>3}$ under periodic or stochastic fires occurring every 30 years ($p_{\mathrm{qext}} = 0.96$ and $p_{\mathrm{qext}} = 0.95$, respectively), but density feedbacks buffered the dewy-pine population from extinction compared to the average-density scenario under periodic fires occurring every 15 years ($p_{\mathrm{qext}} = 0.74$ when perturbing all TSFs). With stochastic fires occurring every 15 years on average, density dependence did not change the effect of the perturbation of vital rates on extinction probability in $\mathrm{TSF}_{>3}$ only and $\mathrm{TSF}_{3\ \mathrm{and}\ >3}$ but buffered the population from extinction when introducing a browsing perturbation earlier in the post-fire habitat succession ($p_{\mathrm{qext}} = 0.89$ when perturbing all TSFs; Fig. S3b).

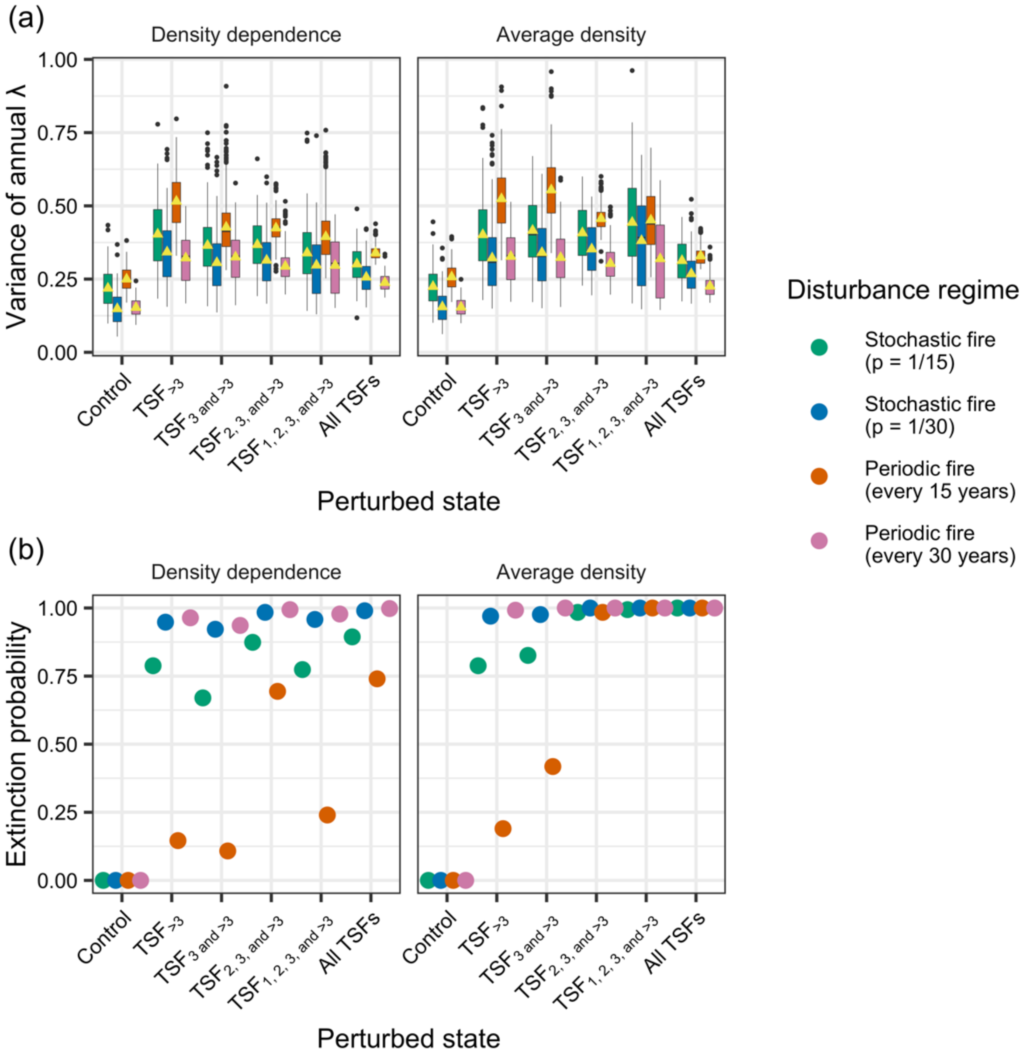

Figure S3 – Effect of perturbing vital-rate periodicity on the variance of the population growth rate and the probability of quasi-extinction in dewy pines. We projected the dewy-pine population dynamics under four different disturbance regimes: stochastic fires occurring every 15 or 30 years on average, and periodic fires occurring every 15 or 30 years. Under these fire regimes, we tested for the effect of a human-induced perturbation in different combinations of states in the sequence of post-fire habitats (TSF_0 to $TSF_{>3}$) on two metrics: (a) the variance in 100 annual population growth rates, var(log λ), with the yellow triangles representing the mean and the whiskers the 2.5th and 97.5th percentiles; and (b) the quasi-extinction probability, p_{qext}. We performed simulations with density-dependent dynamics (left panels) or at constant average density (right panels).

Disentangling the effects of season and density in shaping meerkat population responses to changing seasonality

To disentangle the roles of season and density in shaping meerkat population dynamics, we first assessed whether density consistently varied with season. We therefore modeled density as a function of the season using a simple linear model. We found that density did not consistently differ between seasons (Table S3) but showed a lot of variability, especially in the dry season (Fig. S4). We next explored how much seasonal variation in population dynamics can be attributed to variation in density. Therefore, we fitted vital-rate models without a season effect and repeated population simulations analogous to the ones presented in the main text. That is, we removed the covariate season from the best models in which it was present as a fixed or random effect, for each vital rate, and projected the meerkat population using seasonal time steps but assuming no seasonal differences in vital rates (i.e., using the same vital-rate value for both seasons). For the projections, we used vital-rate specific highly- or little-seasonal years from models fitted with both season and density.

Table S3 - Model fitted to assess the relationship between season and density. We modeled density as a function of season using a linear model. Density did not differ between seasons.

Covariate	Estimate	Standard error (SE)	P-value
Intercept (dry season)	7.11	0.51	5.88e-16 ***
Wet season	-0.0080	0.73	0.991

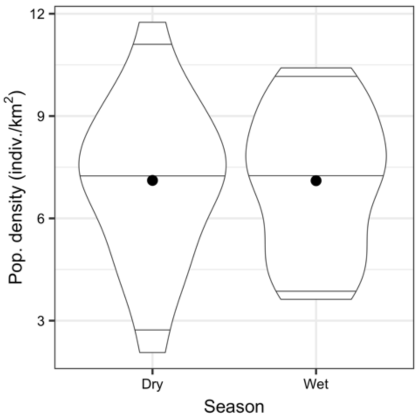

Figure S4 – Meerkat seasonal population density. The violin plots represent the distribution of meerkat population densities in the dry and wet seasons. Density does not vary between seasons, but varies between years, especially in the dry season. The dots represent seasonal means, and the horizontal lines the 2.5th, 5th, and 97.5th percentiles, respectively.

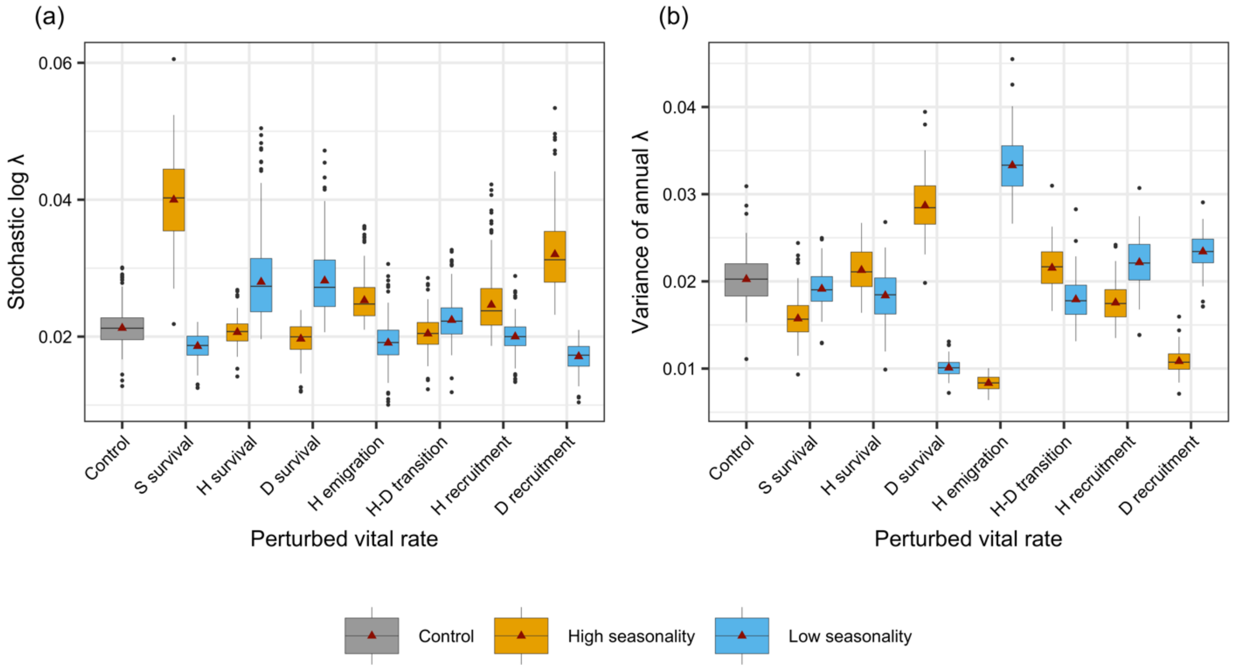

Figure S5 – Effect of perturbing vital-rate seasonality on the stochastic growth rate and variance of the population growth rate in meerkats, without the seasonal vital rates. We fitted vital-rate models without the effect of season and projected the population assuming no seasonal differences in vital rates and under years of high or low seasonality in the survival of subadults (S), helpers (H), and dominants (D), helper emigration, helper-to-dominant transition, and helper and dominant recruitment (taken from models fitted with the effect of season and density). We assessed the effects of these scenarios on (a) the stochastic growth rate log λ_S and (b) its variance across 100 years, var(log λ). The red triangles represent the mean for each boxplot, and the whiskers the 2.5th and 97.5th percentiles.

Projecting the meerkat population picking years of higher seasonality in subadult survival increased the stochastic population growth rate to 0.040 [0.027, 0.052] on average, compared to 0.021 [0.017, 0.027] in the control scenario (Fig. S5a). This effect is probably due to a strong positive effect of a high overall subadult survival on population dynamics in highly-seasonal years, outweighing the effects of density dependence. Compared to simulations with both season and density, we found no effects of highly- or little-seasonal years in dominant recruitment when ignoring the effect of season. These results show that neither season alone nor density alone shape meerkat population responses to environmental variation, and that environment-density interactions, and potentially correlations among vital rates, play a key role in such responses.

Without the effect of season, the variance of 100 annual growth rates var(log λ) responded strongly to less scenarios of picking years of increased or decreased seasonality in vital rates compared to the projections at constant average density (Fig. S2, right panel), but to more of these scenarios compared to the projections with both season and density dependence (Fig. S2, left panel). Projecting the meerkat population dynamics under years of higher or lower seasonality in subadult survival did not affect var(log λ) (Fig. S5b). However, compared to the control scenario (0.020 [0.015, 0.026] on average), picking years of higher and lower seasonality in emigration respectively decreased (0.0083 [0.0064, 0.010]) and increased var(log λ) (0.033 [0.027, 0.040]). In addition, projections under years of higher seasonality in dominant recruitment and lower seasonality in dominant survival both decreased the variance of annual growth rates (on average, 0.011 [0.0084, 0.014] and 0.010 [0.0083, 0.012] respectively). In sum, when ignoring seasonal differences in vital rates, compared to projections including season and density, density dependence only partly buffered the population from strong variations in the annual growth rate across 100 years. Similar to our findings for the stochastic growth rate (Fig. S5a), environment-density interactions thus play an important role in determining the variation of annual growth rates.

References – Appendix S4

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