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ARTICLE

Demographic consequences of changes in environmental periodicity

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Abstract

The fate of natural populations is mediated by complex interactions among vital rates, which can vary within and among years. Although the effects of random, among-year variation in vital rates have been studied extensively, relatively little is known about how periodic, nonrandom variation in vital rates affects populations. This knowledge gap is potentially alarming as global environmental change is projected to alter common periodic variations, such as seasonality. We investigated the effects of changes in vital-rate periodicity on populations of three species representing different forms of adaptation to periodic environments: the yellow-bellied marmot (*Marmota flaviventer*), adapted to strong seasonality in snowfall; the meerkat (*Suricata suricatta*), adapted to inter-annual stochasticity as well as seasonal patterns in rainfall; and the dewy pine (*Drosophyllum lusitanicum*), adapted to fire regimes and periodic post-fire habitat succession. To assess how changes in periodicity affect population growth, we parameterized periodic matrix population models and projected population dynamics under different scenarios of perturbations in the strength of vital-rate periodicity. We assessed the effects of such perturbations on various metrics describing population dynamics, including the stochastic growth rate, log λ_S. Overall, perturbing the strength of periodicity had strong effects on population dynamics in all three study species. For the marmots, log λ_S decreased with increased seasonal differences in adult survival. For the meerkats, density dependence buffered the effects of perturbations of periodicity on log λ_S. Finally, dewy pines were negatively affected by changes in natural post-fire succession under stochastic or periodic fire regimes with fires occurring every 30 years, but were buffered by density dependence from such changes under presumed more frequent fires or large-scale disturbances. We show that changes in the strength of vital-rate periodicity can have diverse but strong effects on population dynamics across different life histories. Populations buffered from inter-annual vital-rate variation can be affected substantially by

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changes in environmentally driven vital-rate periodic patterns; however, the effects of such changes can be masked in analyses focusing on inter-annual variation. As most ecosystems are affected by periodic variations in the environment such as seasonality, assessing their contributions to population viability for future global-change research is crucial.

KEYWORDS
fire regimes, matrix population model, perturbation, population viability analysis, seasonality, vital-rate periodicity

INTRODUCTION

Effects of inter-annual changes in vital rates on population dynamics have been widely studied (e.g., Aberg, 1992; Frederiksen et al., 2008; Frick et al., 2010; Hunter et al., 2010; Keith et al., 2008). However, there remains a knowledge gap regarding how populations respond to changes in the periodic, nonrandom patterns of vital-rate variation. This is despite the fact that a majority of species live in periodically varying environments and show demographic responses and adaptations to such periodicity, with vital-rate patterns recurring predictably through time (Marra et al., 2015; Panda et al., 2002; Varpe, 2017). Seasonality is one important source of nonrandom vital-rate variation. In numerous ecosystems, reproduction and survival strongly depend on seasonal rainfall (Altwegg & Anderson, 2009; Dickman et al., 1999) or temperature (Cordes et al., 2020; Lebl et al., 2011; McNutt et al., 2019; Oli & Armitage, 2004; Paniw et al., 2020). Changes in such seasonal weather patterns can strongly affect population dynamics. For example, perturbations in rainfall patterns led to immediate and strong changes in the population size of the Serengeti lions (*Panthera leo*) (Packer et al., 2005). Additionally, increases in seasonal rainfall (Buettner et al., 2007) and temperature (Woodroffe et al., 2017) have been found to negatively affect reproduction in wild dogs (*Lycaon pictus*). Other forms of vital-rate periodicity can also strongly influence population dynamics. For instance, disturbance-adapted species typically show life-cycle adaptation to the periodic occurrence of extreme climatic events (Beissinger, 1995; Caswell & Kaye, 2001; Silva et al., 1991) and to periodic changes in habitat structure after disturbances (Lennartsson & Oostermeijer, 2001; Evans et al., 2010; Paniw, Quintana-Ascencio, et al., 2017). Vital-rate periodic patterns can also occur on a much longer time scale (Park, 2019). For example, as a consequence of both abiotic and biotic factors, many populations of rodents, such as voles and lemmings, display periodic cycles in vital rates and consequently abundances (see Oli, 2019 and references therein).

Despite increasing evidence that assessing periodic changes in vital rates is critical to gaining a mechanistic understanding of population dynamics (Hostetler et al., 2015; Marra et al., 2015; Paniw et al., 2019), most structured population models use annual data to project populations through time and assume random inter-annual variation in demography when projecting population fates (e.g., Hunter et al., 2010) or assessing which taxa are most vulnerable to environmental variation (e.g., Doak et al., 2005; Franco & Silvertown, 2004; McDonald et al., 2017; Pfister, 1998). This is predominantly due to a lack of high-resolution data, both on species demography because of inaccessible periods of the life cycle (e.g., hibernation or migration), and on environmental covariates accurately representing conditions in given periods (Kleiven et al., 2018). However, vital rates often change nonlinearly across different states of the environment, often as a result of environment–density interactions (Hostetler et al., 2015; Paniw et al., 2019). For example, Bassar et al. (2016) showed that brook trout (*Salvelinus fontinalis*) population decline was mainly caused by higher mean summer temperatures decreasing the survival of young trout, and that density feedbacks could buffer the decline. Therefore, pooling vital rates across seasons or across years for species inhabiting periodic environments, or omitting multiyear periodic changes in population dynamics might obscure underlying processes affecting population dynamics, with possible implications for management (Caswell, 2001; Hostetler et al., 2015). Understanding such underlying processes is increasingly important given the predicted changes in environmental periodicity under global environmental change (Donat & Alexander, 2012; Xu et al., 2013).

In spite of an increasing effort to include periodic vital rates into population models (e.g., Guimarães et al., 2020; Hostetler et al., 2015; Paniw et al., 2019), the effects of changes in periodicity in vital rates per se on population dynamics remain largely unexplored. To bridge this knowledge gap, we assessed the effects of changes in vital-rate periodicity in three different species with a periodic life cycle: (i) the yellow-bellied marmot

(*Marmota flaviventer*), adapted to strong seasonality in snowfall, which determines the hibernation period; (ii) the meerkat (*Suricata suricatta*), a social mongoose living in the Kalahari desert where seasonality and inter-annual stochasticity in rainfall affect vital rates; and (iii) the dewy pine (*Drosophyllum lusitanicum*), a fire-adapted carnivorous plant, in which vital rates are affected by changes in fire periodicity and vary across post-fire habitat states following fire. Although the life history of dewy pines is not strictly periodic (i.e., following a pattern recurring predictably across years) under stochastic fire regimes, the succession of environmental states 4–5 years post-fire leads to periodic patterns in vital rates. These three species show different forms of adaptations to periodic environmental patterns that are broadly representative of a large number of taxa. In addition, they represent different life-history strategies to cope with inter-annual environmental variation, with the two animal species buffering to various degrees vital rates strongly influencing population fitness from environmental variations (Maldonado-Chaparro et al., 2018; Paniw et al., 2019); and natural dewy-pine populations relying heavily on seed germination from the seed bank induced by fire disturbance, with rather weak consequences for population dynamics of inter-annual fluctuations in vital rates (Paniw, Quintana-Ascencio, et al., 2017). Consequently, studying their responses to perturbations in the strength of periodic patterns will help to clarify the importance of considering periodic variation in vital rates when studying the dynamics and viability of populations. For each species, we estimated period-specific vital rates and subsequently built periodic demographic models. We then performed stochastic simulations in which we used several perturbations of vital-rate periodicity to assess the effects of these perturbations on the stochastic population growth rate.

MATERIALS AND METHODS

Study systems and data collection

We studied the effect of perturbations in the strength of vital-rate periodicity on the population dynamics of three species inhabiting different periodic environments: yellow-bellied marmots, meerkats, and dewy pines. The yellow-bellied marmot population thrives at high altitudes in the Rocky Mountains, where winters are long, 7–8 months on average (Edic et al., 2020; Inouye et al., 2000). Marmots survive the winter (mid-September to mid-April/May) in hibernation and reproduce during the short summer growing season (Armitage, 2014). Long winters are responsible for a great part of marmot mortality, but overwinter mortality is largely dependent on summer mass gain (Cordes et al., 2020), which is influenced by age and the location of the marmot colony in the valley where marmots live (Heissenberger et al., 2020). Mortality in marmots is also driven by predation, especially in early spring, when marmots emerge from burrows to mate (Armitage, 2014). Mortality due to predation depends on various factors, including sociality (Montero et al., 2020), but can be hard to dissociate from mortality caused by climatic factors (Armitage, 2014; Schwartz & Armitage, 2002; Schwartz & Armitage, 2005; Van Vuren, 2001). The between-year variation in these biotic and abiotic factors can lead to important fluctuations in winter survival, whereas summer survival generally remains high, particularly for adult females (Armitage, 1991; Armitage & Downhower, 1974). Additionally, although marmot vital rates vary strongly among seasons (Van Vuren & Armitage, 1991), previous studies on the marmot population have found no effect of population density on vital rates (Armitage, 1973; Armitage et al., 2011; Paniw et al., 2020). This makes marmots an ideal system in which to study the effects of seasonal perturbations on vital rates, independent of density-dependent mechanisms.

The meerkat population inhabits an arid environment characterized by a dry and a wet season and is adapted to seasonal patterning, but also to high inter-annual variability in rainfall (Clutton-Brock, Gaynor, et al., 1999). This stochasticity in the rainfall pattern has led to a bet-hedging strategy in which reproduction, although highest in the wet season, can happen throughout the year in particularly wet years and may cease altogether in particularly dry years (Bateman et al., 2013; Clutton-Brock, Maccoll et al., 1999). Therefore, unlike in the marmot population, no demographic processes in the meerkat population are restricted to a certain season, but some vary seasonally (e.g., higher pup survival, individual growth, and emigration in the wet season; English et al., 2012; Ozgul et al., 2014; Russell et al., 2002). Meerkat groups are characterized by a dominant pair monopolizing reproduction (Clutton-Brock et al., 2010) and subordinates helping to raise the young and guarding the territory (Clutton-Brock et al., 2001; Clutton-Brock et al., 2008). Consequently, vital rates strongly differ between social statuses (Paniw et al., 2019; Sharp & Clutton-Brock, 2011). Moreover, the population dynamics of the meerkats are strongly density dependent. Dominant female reproductive success increases with population density, whereas helper emigration is highest at lower densities (Bateman et al., 2013; Paniw et al., 2019). At the same time, meerkat population dynamics are largely influenced by interactions between the environment and density (Paniw et al., 2019), with vital rates displaying season-specific responses to density-dependent factors (Bateman et al., 2012; Ozgul et al., 2014; Paniw et al., 2022). The presence of both strong density feedbacks and environment–density interactions in meerkats enabled us to study how density dependence can mediate population responses to vital-rate seasonality.

Finally, the dewy pine is an early-successional carnivorous subshrub. Dewy pines in natural heathland habitat have adapted to recurrent fire regimes, where the seed bank is a key life-history stage and its dynamics vary strongly with fire occurrence; and all remaining vital rates vary strongly with inter-annual periodic post-fire habitat succession, whereas inter-annual weather fluctuations have a relatively small effect on this variation (Paniw, Quintana-Ascencio, et al., 2017). Aboveground plants are killed by fire, whereas heat and vegetation removal trigger the germination of a persistent soil seed bank (Cross et al., 2017; Gómez-González et al., 2018; Paniw, Quintana-Ascencio, et al., 2017). Seedlings then mature and do not reproduce until at least 2 years after fire. Similar to meerkats, density dependence mediates responses to vital-rate periodicity in dewy pines. Sprouting shrubs increase seedling survival and flowering probability of mature individuals in early post-fire stages (Paniw, Salguero-Gómez, & Ojeda, 2017). However, in later post-fire stages, aboveground density of dewy pines and other plant species negatively affects the number of dewy-pine seedlings and seed germination rates (Correia & Freitas, 2002; Gómez-González et al., 2018). As dewy pines are inferior competitors in heathlands (Garrido et al., 2003), resprouting shrubs rapidly overgrow them after a fire. Aboveground dewy pines thus die out 4–6 years after fire, and the population persists through a soil seed bank (Paniw, Quintana-Ascencio et al., 2017). However, natural dewy-pine populations are facing changes in both fire regimes and post-fire habitat succession due to anthropogenic pressures, including a combination of periodic vegetation removal (through frequent illegal burning and mechanistic means) and heavy browsing following fires. These latter, typically persistent, small-scale perturbations remove competing vegetation and allow aboveground individuals to persist over a longer period and recruit continuously, thus decreasing the importance of seed-bank dynamics (Paniw, Quintana-Ascencio et al., 2017). These perturbations therefore effectively delay post-fire habitat succession and increase population sensitivity to year-to-year environmental fluctuations. Such anthropogenic perturbations to the periodicity of fire regimes are common (e.g., Breininger et al., 2018; Menges & Dolan, 1998; Quintana-Ascencio et al., 2003; see also Pausas & Keeley, 2014 and references therein), but their consequences for population viability remain relatively unexplored.

The yellow-bellied marmot (*Marmota flaviventer*)

Demographic data

Demographic data have been collected since 1962 in a continuously monitored population living at 2900 m above sea level (asl) in the upper East River Valley near Gothic, Colorado, USA (38°58′ N, 106°59′ W). In this study, we used 41 years (1976–2016) of individual data from nine colonies located at the center of this area (Armitage, 2014). Individuals were live trapped each year throughout their summer active season, and ear marked in the first capture event (Armitage, 1991). Sex, age, mass, and reproductive status were recorded for each individual (Armitage et al., 1976; Armitage & Downhower, 1974; Schwartz et al., 1998). Following previous studies, we used data for females only, because most young males disperse from their natal colony, and knowledge on maternity (and consequently number of recruits) is more accurate than on paternity (Ozgul et al., 2010).

Life cycle and vital rates

We considered four life-history stages: juvenile (J; 0–1 year old), yearling (Y; 1–2 years old), nonreproductive adult (N; >2 years and not reproducing), and reproductive adult (R; >2 years and reproducing) (Ozgul et al., 2009; Figure 1a). In the winter period (August–June), juveniles and yearlings respectively grow to yearlings and adults, and adults can change reproductive status. Reproductive adults then breed during the summer period (June–August). Therefore, we considered the following seasonal vital rates: seasonal survival, transitions to and between adult stages (from winter to summer only), and recruitment (from summer to winter only; see Appendix S1: Figure S1 for further details).

The meerkat (*Suricata suricatta*)

Demographic data

Data on birth, death, emigration, recruitment and social status have been collected by frequently visiting (one to three times per week) wild groups of individually marked meerkats in the Kuruman River Reserve,

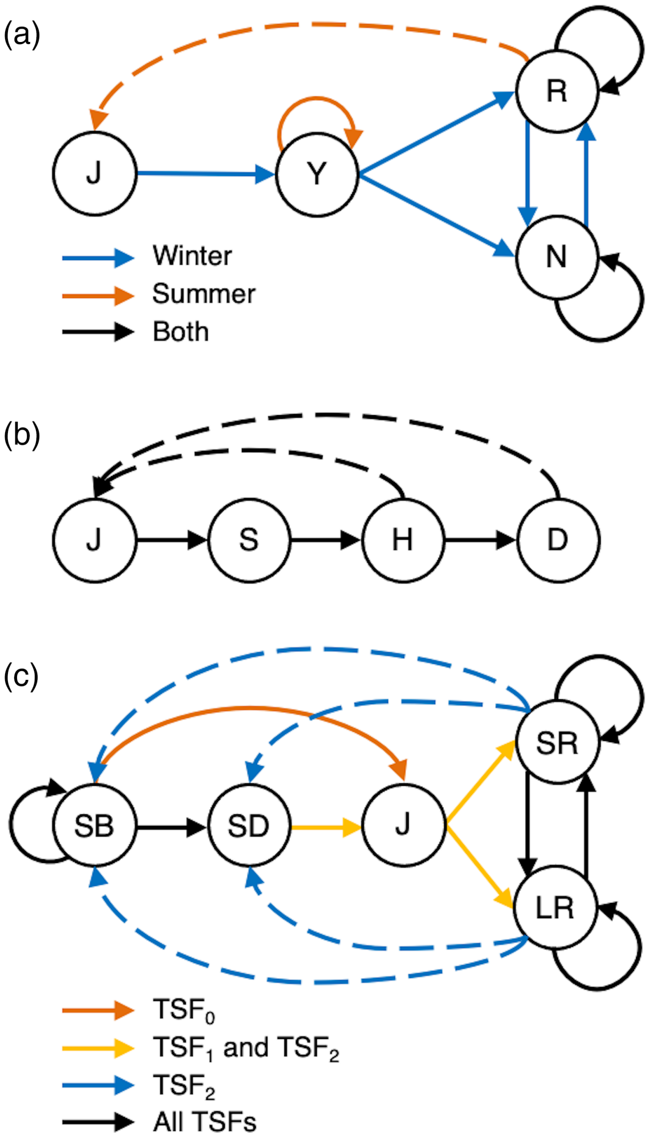

FIGURE 1 Periodic life cycles of the three study systems. The three life cycles represent the periodic transitions among life-history stages (solid arrows) and reproduction (dashed arrows) of our study systems. Different arrow colors indicate whether transitions/reproduction occur in a specific period (season or time-since-fire [TSF] state) or in all seasons or TSFs. (a) The marmot life cycle was split between the winter hibernation period (winter-to-summer transition, August–June) and the summer breeding season (summer-to-winter transition, June–August). Individuals can transition between juvenile (J), yearling (Y), and nonreproductive (N) and reproductive adult (R) stages. (b) The meerkat life cycle was split into the dry fall/winter (dry-to-wet transition, April–October) and wet spring/summer (wet-to-dry transition, October–April) seasons. Individuals can transition between juvenile (J), subadult (S), helper (H), and dominant (D) stages. (c) The dewy-pine life cycle consists of yearly transitions between time-since-fire habitat states (TSF$_0$ to TSF$_1$, TSF$_1$ to TSF$_2$, etc.). Individuals germinate from the seed bank (SB) and can transition among seedling (SD), juvenile (J), small (SR), and large reproductive individual (LR) stages.

South Africa (26°58′ S, 21°49′ E) (Clutton-Brock et al., 1998; Clutton-Brock et al., 2008). For this study, we used 20 years of individual data (1997–2016) to estimate stage-specific vital rates (Bateman et al., 2011; Ozgul et al., 2014). We used data on females only, because data on males (especially male dispersal) is limited. However, this should not introduce any bias into the analysis, given the even sex ratio in a meerkat population, and lack of sexual dimorphism (Ozgul et al., 2014). Population density was calculated as the number of individuals per km^2 of population range at each census (see Bateman et al., 2011 and Cozzi et al., 2018 for more details).

Life cycle and vital rates

Following previous studies (Ozgul et al., 2014), the meerkat life history was characterized by the following stages: juvenile (J; 0–6 months), subadult (S; 7–12 months), adult helper (H; >12 months with a subordinate status) and dominant (D; >12 months with a dominant status) (Figure 1b). We used 6-month intervals in order to represent the dry (April–October) and wet (October–April) seasons characterizing the meerkats habitat. The life cycle is therefore comprised of 6-month seasonal transitions, determined by the following vital rates: seasonal survival, helper emigration, probability of transition from helper to dominant status, and recruitment, all occurring in both seasons (see Appendix S1: Figure S2 for more details).

The dewy pine (*Drosophyllum lusitanicum*)

Demographic data

In this study, we used data collected during nine annual censuses between April 2011 and April 2019 on dewy-pine populations occurring in three sites of southern Spain and facing different types of post-fire disturbance: human disturbed (i.e., heavy persistent browsing; hereafter disturbed populations; Sierra Retin A: 36°10′ N, 5°51′ W) or natural (i.e., little browsing; hereafter natural populations; Sierra Carbonera: 36°12′ N, 5°21′ W and Sierra Retin B: 36°11′ N, 5°49′ W). Both types of populations burn, although fires may occur less frequently in heavily human-disturbed populations (see Paniw, Quintana-Ascencio et al., 2017). The seed bank-related vital rates (seed germination or stasis) were estimated from seed-burial and greenhouse-germination experiments (see Paniw, Quintana-Ascencio et al., 2017 for details). In natural populations, most seeds (93%) go into the seed bank and survive (85%) until the next fire. Conversely, in disturbed populations, a substantial proportion of seeds (13%) does not enter the seed bank but rather goes into continuous recruitment, whereas the seeds entering the seed bank have a lower survival (60%) (see Appendix S2: Table S7 for more details). Population density was calculated as the number of aboveground dewy pines per 1-m^2 within a study transect in each site and each post-fire habitat state.

Life cycle and vital rates

The life cycle of the dewy pine consists of 1-year transitions characterized by time since last fire (TSF) (Ojeda et al., 1996; Paniw, Quintana-Ascencio et al., 2017; Figure 1c). After a fire (TSF_0), seeds germinate from the seed bank (SB) and become seedlings (SD) or juveniles (J). During the year following the fire (TSF_1), surviving seedlings and juveniles reach their adult size (small, SR, or large, LR, reproductive) and are able to reproduce from the second year after the fire (TSF_2). We estimated the following vital rates: seed-bank transitions, survival of aboveground stages and transitions among them, and reproductive parameters (i.e., flowering probability, number of flowering stalks, and number of flowers per stalk) (see Appendix S1: Figure S4 for more details).

Assessing the effects of perturbations in the strength of vital-rate periodicity on population dynamics

For each species, we used the demographic data to model periodic differences in vital rates for each life-cycle stage using generalized linear models and mixed models (GLMs for the deterministic vital rates in dewy pines and GLMMs for all other vital rates; with the *glm* and *glmer* functions of the R packages *stats* (R Core Team, 2020) and *lme4* (Bates et al., 2015), respectively; see Appendix S2 and Appendix S3). We then used the predictions of these models to parameterize periodic matrix population models (MPMs) and project the population dynamics for 100 years according to two scenarios—control and perturbed—to assess the effect of changes in vital-rate periodicity on the stochastic growth rate ($\log \lambda_S$), the variance of 100 annual growth rates ($\text{var}(\log \lambda)$), and the probability of quasiextinction (p_{qext}, i.e., the ratio of simulations leading to quasiextinction out of 500 simulations, with a threshold set at 15% of the minimum observed abundance or number of reproductive individuals for the marmot and meerkat populations, and at 50% of the minimum observed aboveground or seed-bank abundance for the dewy pines; see Appendix S4). These three metrics have been shown to provide a good approximation of the potential fate of populations under environmental change (e.g., Hunter et al., 2010; Trotter et al., 2013). Below, we provide an overview of the modeling process, the details of which can be found in Appendices S2 and S3.

Modeling the vital rates

To assess how vital rates differed among periodic environmental states, we modeled vital rates as functions of season for the marmots and meerkats and of post-fire habitat states (TSF) for the dewy pines. For all three study systems, we estimated stage-specific survival, probability of transition to another stage (binomial distribution), and reproductive output (Poisson distribution). Moreover, we estimated the helper emigration probability in the meerkat population, as well as the dewy-pine flowering probability (binomial distribution). System-specific details can be found in Appendix S2. We incorporated stochastic year effects as random effects in all appropriate models. These random effects modeled year-specific differences among vital-rate averages for the dewy pines and among season-specific averages (i.e., random slopes) for the marmots and meerkats. For the meerkats and dewy pines, we also incorporated the fixed effect of density on vital rates (Appendix S2). We did not do so for the marmots, as no density dependence has been found in previous studies (Armitage, 1973; Armitage et al., 2011; Paniw et al., 2020).

For each modeled vital rate, we first used the *r.squaredGLMM* function of the *MuMIn* R package (Bartoń, 2020) to select the best random-effect structure when appropriate (i.e., testing whether a random effect on the average vital rate and the slope between seasons outperformed a random effect on the average vital rate only). We subsequently selected the best fixed-effect variables using the Akaike information criterion (AIC) corrected for small sample size (AIC_c) (*AICctab* function of the *bbmle* R package; Bolker and R Development Core Team, 2020). This enabled us to determine the most parsimonious model, accounting for the number of model parameters (Burnham et al., 2010). In case of a nonsignificant difference in AIC_c values between two models (i.e., $\Delta AIC_c < 2$), we picked the model with fewer parameters, unless another model was more biologically relevant (see Appendix S3: Figure S1). Appendix S2 shows the details of the model selection approach. For models using a Poisson distribution, we tested for overdispersion and underdispersion in the best model according to the AIC_c and subsequently fitted overdispersed and underdispersed models with a quasi-Poisson distribution (see Appendix S2). All analyses were performed using

R 4.0.3 (R Core Team, 2020) via RStudio 1.4.1103 (RStudio Team, 2021). Data (Conquet et al., 2022a) are available in Dryad and R scripts (Conquet et al., 2022b) are available in Zenodo.

Projecting population dynamics

Marmot and meerkat populations: seasonal dynamics

For the meerkats and marmots, we projected population dynamics under changing patterns of vital rates that differed among seasons in a given year. That is, regardless of the fixed effect, vital rates for which the year random effect in the GLMM was applied both on the mean vital-rate estimate (i.e., the model intercept) and the difference between seasons. For the marmots, we therefore assessed the population responses to changes in the seasonal patterns of yearling and nonreproductive and reproductive adult survival. For the meerkats, we did so for subadult, helper, and dominant survival, helper emigration, transition from helper to dominant, and helper and dominant recruitment.

We used year-specific vital-rate predictions from the most parsimonious model to build periodic MPMs for each season (as described in Caswell, 2001, chapter 13). The matrix product of these periodic MPMs enabled us to compute the annual population projection matrix and subsequently the stochastic realized population growth rate, log λ_S (Appendix S4). We then simulated population dynamics by projecting MPMs representing low-seasonality (LS) and high-seasonality (HS) years for each of the aforementioned vital rates. Half of all years for which a vital rate was estimated were considered as LS and the other half as HS. That is, for a given vital rate, we defined the threshold between LS and HS years as the 50th percentile of all year-specific absolute differences between seasons (see Appendix S5 for details). In addition, we used a control scenario, in which we projected the population dynamics using MPMs representing both HS and LS years indistinctly (i.e., using all years; see Appendix S6: Figure S1a for an overview of the seasonal simulations workflow).

We performed 500 simulations, each starting with the same population vector, and projected the population dynamics for 100 years (see Appendix S4). For each simulation, we randomly selected 100 years corresponding to each scenario (LS, HS, or control). In each step of the simulation, all vital rates were predicted based on the same randomly selected year. This allowed us to maintain within-year vital-rate correlation. The predicted vital rates were then used to build the corresponding period-specific MPM.

Dewy-pine population: multiyear habitat succession and periodicity in fire regimes

We characterized transitions among life-history stages and demographic parameters in dewy pines following a succession of five post-fire habitat states (TSF_0 to $TSF_{>3}$), where plants remained in $TSF_{>3}$ until a fire disturbance set the population back to TSF_0. We simulated two distinct types of fire regimes, each with two frequencies: (1) periodic burning occurring systematically every 15 or 30 years, and (2) stochastic fires occurring on average every 15 or 30 years. In all simulations, dewy pines transitioned deterministically through the first four post-fire states, TSF_0 to TSF_3. Under periodic fires, once in the fifth state, $TSF_{>3}$, the population remained in that state until the next fire (15 or 30 years after the previous fire) and then transitioned to TSF_0. Under stochastic fires, the population can transition from $TSF_{>3}$ to TSF_0 conditional on fire frequency (*p*) (Paniw, Quintana-Ascencio et al., 2017). Under stochastic fire regimes, and after TSF_3, the dewy-pine life history is therefore not strictly periodic. However, studying the consequences of perturbations in vital-rate patterns on dewy pines can be done using tools such as periodic MPMs and Markov chains, which are commonly used to study periodic population dynamics (Caswell, 2001, chapter 13). The Markov-chain approach to model the sequence of post-fire habitats (see Appendix S7) has been applied in a wide range of systems to model the probability of recurrent disturbance regimes, for example in the case of hurricanes or fires (e.g., Evans et al., 2010; Horvitz et al., 2005; Morris et al., 2006; Pascarella & Horvitz, 1998; Quintana-Ascencio et al., 2003; Trauernicht et al., 2016; Tuljapurkar & Haridas, 2006). In addition to the different periodic patterns in fire regimes, we perturbed periodic patterns in habitat succession in natural heathlands by introducing an additional human disturbance (i.e., using vital rates from populations under a browsing-induced disturbance) first only in the years of the last post-fire state ($TSF_{>3}$), and then increasingly in the previous states (i.e., in $TSF_{3 \text{ and } >3}$, in $TSF_{2,3 \text{ and } >3}$, etc.) until all post-fire states of a natural population were perturbed.

We used TFS-specific vital-rate predictions from our models and rates on seed-bank dynamics described in previous studies (Paniw, Quintana-Ascencio et al., 2017) to build MPMs for each TSF. We used these MPMs to project population dynamics for 100 years using 500 simulations, in each iteration randomly sampling among MPMs describing one of the two natural populations. In addition, for each iteration in the stochastic post-fire state $TSF_{>3}$, we randomly sampled a year-specific MPM. We increased browsing pressure by replacing MPMs associated with natural habitat conditions by MPMs parameterized with vital rates estimated from human-disturbed populations, for any given TSF (see Appendix S6: Figure S1b for an overview of the periodic simulations workflow). We compared scenarios of increasing anthropogenic pressures to the control scenario (i.e., natural populations with no browsing perturbation) in each fire regime.

Population responses to vital-rate periodic patterns under density dependence

For the meerkats and dewy pines, projections of population dynamics incorporated density dependence. That is, at each iteration of the simulations, population density was estimated and used to predict vital rates and parameterize an MPM from these predictions at the next iteration (see Appendix S4 for more details). To better understand the contribution of variation in population density on the population responses to perturbations in vital-rate seasonal patterns, we also compared density-dependent projections to ones in which the density input during parameter estimation was fixed at constant average values obtained from the observed data (see Appendix S4).

Analysis of the simulations results

For all three systems and for each simulation, we recorded the stochastic growth rate log λ_S (Tuljapurkar et al., 2003). We also investigated the effect of changes in vital-rate patterns on the variance in 100 annual log λ, var(log λ), and the quasiextinction probability p_{qext} (see Appendix S4 for more details). We checked the overlap of the distributions of each metric (i.e., the mean and the 2.5th and 97.5th percentiles) across the 500 simulations between two scenarios. We considered a metric to differ between scenarios when 95% of the distributions (i.e., between the 2.5th and 97.5th percentiles) did not overlap.

Comparing population sensitivity to changes in periodic environmental patterns versus stochastic environmental variation

We compared our results from periodic population models to "classic" assessments of population fitness sensitivity to stochastic environmental variation (Morris et al., 2008). To do so, for marmots and meerkats, we computed the stochastic elasticities of the population growth rate to changes in the mean and standard deviation of vital rates (Tuljapurkar et al., 2003; Appendix S8). We then calculated the relative importance of the stochastic elasticity of the growth rate due to changes in the variability of vital rates compared with changes in their mean (Morris et al., 2008; Appendix S8).

For dewy pines, as the effects of periodic patterns consisted of changing the sequences of post-fire habitat states, we explored the link between the effects of human-induced disturbances in various post-fire habitat states and the role of these states in shaping population dynamics. We thus used the megamatrix approach to calculate the elasticity of the population growth rate to each post-fire habitat state (Pascarella & Horvitz, 1998).

RESULTS

Periodic patterns in vital rates of three study populations

Most vital rates of marmots, meerkats, and dewy pines showed significant, nonrandom periodic variation (Figure 2; for details, see Appendix S3). In marmots, survival of reproductive adults was high in summer, but dropped more than 20% in winter (Figure 2a), due to the harsh conditions marmots are exposed to during hibernation (Armitage, 2017; Cordes et al., 2020; Paniw et al., 2020). For meerkats, helper survival was lower during the wet season (Figure 2b). Reproduction and emigration mainly happen in the wet season (Doolan & Macdonald, 2009; Ozgul et al., 2014), and this seasonal pattern in helper survival is likely to be due to an increase in the number of evictions by dominant females to reduce reproductive competition (Dubuc et al., 2017; Young et al., 2006), as evicted meerkats have a lower survival rate than resident individuals (Maag, 2019). In addition, whereas most meerkat vital rates responded negatively to population density, subadult survival increased with density, and low densities had negative effects on juvenile survival and dominant recruitment in the wet season (Appendix S3: Table S1, Figures S1 and S2a). Finally, in a natural population of dewy pines, the survival probability of juvenile individuals decreased by about 80% between the third and fourth years after fire (Figure 2c), characteristic of the short lifespan of the plant in natural habitats (Paniw et al., 2015). Whereas in human-disturbed populations, despite strong between-year fluctuation, juvenile survival remained high on average. The rate of continuous germination in late TSFs was also higher in human-disturbed populations (i.e., fewer seeds entering and remaining in the seed bank; Appendix S2: Table S7). However, survival of smaller plants and the reproductive output of all adults decreased on average under human disturbances (Appendix S3: Tables S3 and S4). In both natural and perturbed dewy-pine populations, density affected most density-dependent vital rates negatively across TSFs, although the effect was stronger in perturbed habitats (Appendix S3: Tables S3 and S4, and Figure S2b). At the same time, under a browsing

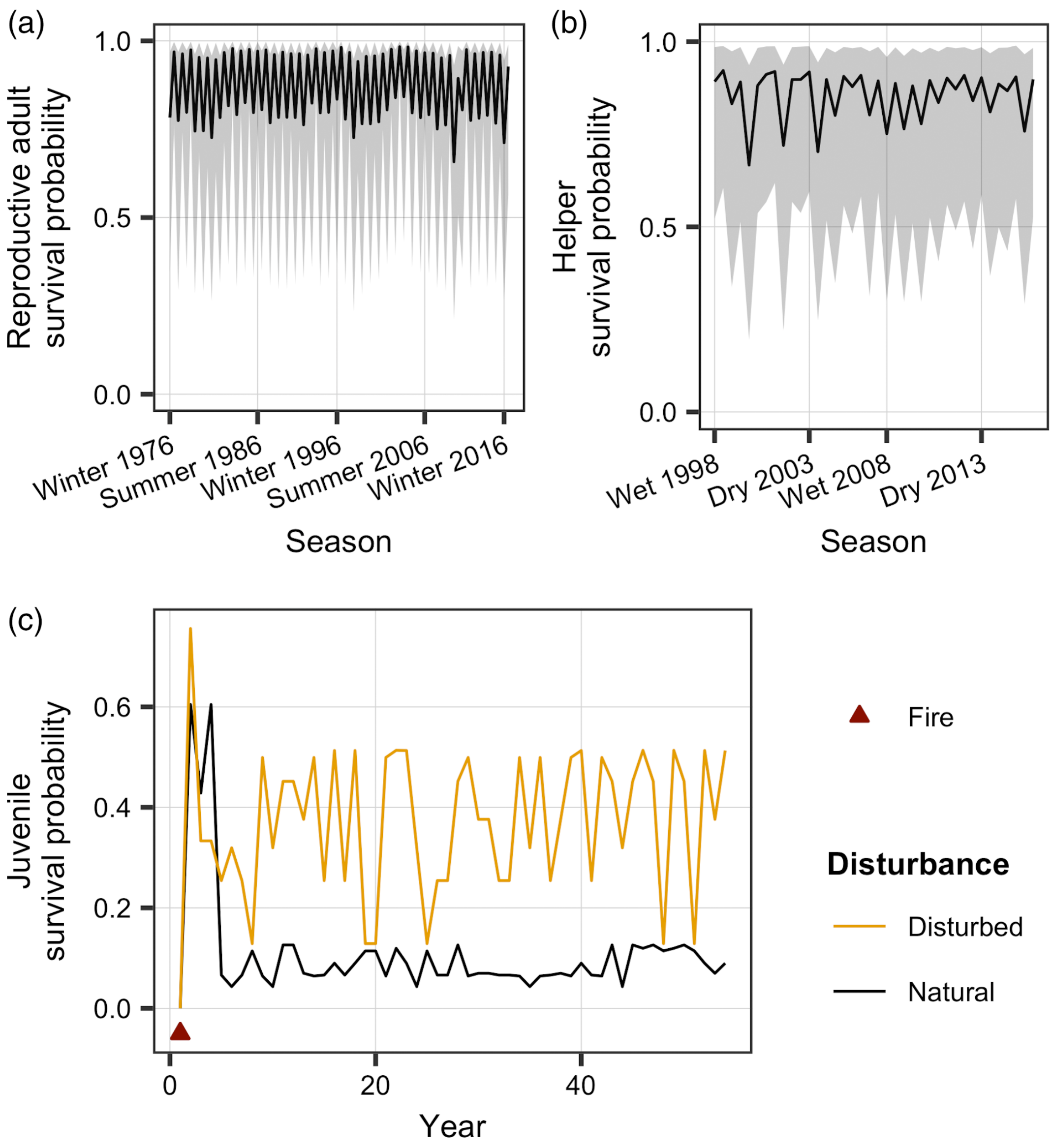

FIGURE 2 Vital-rate periodicity across time. (a) In marmots, reproductive adult survival greatly varies between summer and winter, with a stable pattern across the 40 years of study. (b) In meerkats, vital rates, including helper survival, are not strictly seasonal as in marmots, but can vary strongly between the dry and wet seasons as a response to stochastic inter-annual rainfall patterns. Lines show the average estimates, shaded areas show the 95% confidence intervals and were obtained using the *predictInterval* function from the *merTools* R package (Knowles & Frederick, 2020). (c) In natural dewy-pine populations under stochastic fires occurring on average every 30 years, individuals (here juveniles) typically have a lower survival rate, and survival decreases predictably with time.

perturbation, survival of seedlings and small individuals increased with dewy-pine density, suggesting a facilitation mechanism in perturbed environmental conditions (Paniw, Salguero-Gómez, & Ojeda, 2017).

Effects of perturbations in the strength of vital-rate periodicity on population dynamics

Population dynamics (log λ_S) of all three species were significantly affected by perturbations of the periodic pattern of at least one vital rate (Figure 3; see Appendix S4 for results on variance of log λ_S). Higher periodic fluctuations in vital rates could affect population dynamics positively (in the case of yellow-bellied marmots), be strongly mediated by density feedbacks (for meerkats), or may only show an effect in a specific environmental context (in the case of dewy pines).

For marmots, in the control scenario (i.e., simulations that sample randomly from LS and HS years), log λ_S was above 0 (0.056 [0.032, 0.078] on average; Figure 3a), suggesting a slightly increasing population (Paniw et al., 2020). In addition, perturbing the strength of the

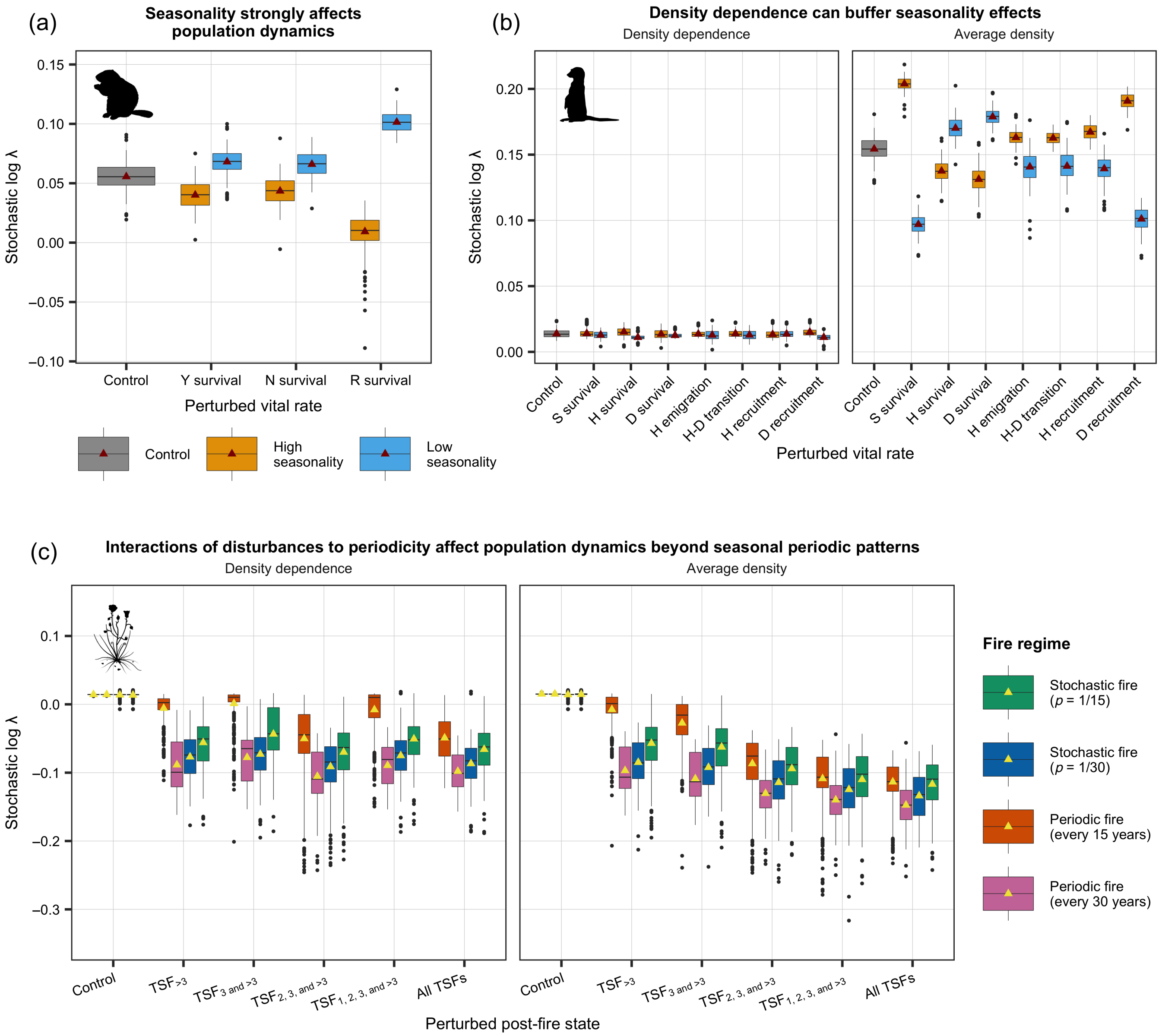

FIGURE 3 Effect of perturbations in the strength of vital-rate periodic patterns on the population dynamics of marmots, meerkats, and dewy pines. We assessed the effect of a perturbation in the strength of vital-rate periodicity on the stochastic population growth rate log λ_S of three species: (a) For the marmots, we assessed the effect of a high or low seasonality in yearling (Y) and nonreproductive (N) and reproductive (R) adult survival on log λ_S. (b) For the meerkats, we assessed the effect of a high or low seasonality in subadult (S), helper (H), and dominant (D) survival, helper emigration, helper to dominant transition, as well as helper and dominant recruitment. (c) For the dewy pines, we assessed the effect of changing periodic habitat succession by projecting the population under four different fire regimes: periodic or stochastic fires occurring every 15 or 30 years. In addition, to assess the consequences of changing post-fire vital-rate periodicity, we introduced a human-induced disturbance in various combinations of the five post-fire habitat states (from $TSF_{>3}$ only to all time-since-fire [TSFs]). For meerkats and dewy pines, simulations were performed including density dependence in vital rates [(b) and (c), left panels] or keeping density constant at its average value [(b) and (c), right panels]. The triangle on each boxplot represents the mean, and the boxplot whiskers the 2.5th and 97.5th percentiles.

seasonal pattern in survival of reproductive adults strongly affected the stochastic growth rate of the population compared with the control scenario, as expected from the key role of reproductive adult survival in shaping marmot population dynamics (Maldonado-Chaparro et al., 2018; Appendix S8: Figure S1a). A HS in reproductive-adult survival, which was driven largely by decreases in winter survival compared with summer survival (Appendix S4), decreased log λ_S to 0.0093 [−0.024, 0.036] on average and slightly elevated extinction risk (Appendix S4). In turn, log λ_S considerably increased to 0.10 [0.084, 0.12] with LS in adult survival (Figure 3a).

Last, contrary to the substantial effects of intra-annual vital-rate variability, marmot population dynamics seem buffered against inter-annual variation in all vital rates, as indicated by low elasticity of the marmot population growth rate to inter-annual standard deviation in vital rates (Appendix S8: Figure S1a,b).

For meerkats, density dependence strongly mediated the effect of vital-rate seasonality on population growth. In the control scenario (i.e., selecting years randomly among both HS and LS years), compared with log λ_S obtained at constant, average density (0.15 [0.14, 0.17]), log λ_S in the density-dependent simulations was much lower (0.014 [0.0083, 0.021] on average; Figure 3b). When we included density dependence, log λ_S was not affected by any perturbations of vital-rate seasonality. Conversely, at constant, average density, a LS in most vital rates had negative effects on log λ_S, except for helper and dominant survival. Additional analyses, where we projected population dynamics assuming no seasonality in vital rates, confirmed that environment–density interactions shape population dynamics (Appendix S4: Figure S4; see also Paniw et al., 2019).

The strength of seasonality effects under average density depended on the vital rate but were largest for subadult survival and dominant recruitment, without leading to population extinction. Compared with an average stochastic growth rate of 0.15 in the control scenario, a LS in subadult survival strongly decreased log λ_S to 0.097 [0.082, 0.11] on average; and a LS in dominant recruitment decreased it to 0.10 [0.082, 0.12]. Conversely, a HS in subadult survival increased log λ_S to 0.20 [0.19, 0.21] on average, whereas an increased seasonality in dominant recruitment increased the population growth rate to 0.19 [0.18, 0.20] on average (Figure 3b). These two vital rates strongly influence meerkat population dynamics (Paniw et al., 2019). Indeed, dominant recruitment is responsible for the greater part of meerkats' reproductive output (Clutton-Brock et al., 2010), and most subadults become helpers and thus contribute importantly to increasing the survival of young (Clutton-Brock et al., 2001; Groenewoud & Clutton-Brock, 2020). However, in contrast with previous findings identifying emigration as a key driver of meerkat dynamics (Bateman et al., 2012; Bateman et al., 2013; Paniw et al., 2019), changes in emigration seasonality did not have strong effects on the population growth rate. As in the case of the marmots, whereas intra-annual vital-rate variation under constant densities could substantially affect meerkats, changes in the standard deviation of none of the vital rates led to large changes in the population growth rate (Appendix S8: Figure S1c,d), indicating buffering.

For dewy pines, the differences in vital rates between natural and perturbed habitats led to substantial changes in growth rates under projections altering the post-fire periodic pattern of vital rates and density dependence, compared with assuming a natural habitat succession after fires (control scenario) under periodic and stochastic fire regimes (Figure 3c). Under density dependence, introducing a browsing perturbation in a natural dewy-pine population decreased the average population growth rate slightly to negative values, increasing extinction risk (Appendix S4: Figure S3b), compared with the control scenario (without browsing), where growth rates were largely positive. The changes in growth rates were similar whether the fire regime was stochastic or periodic when it occurred with a frequency of 1/15 years. More specifically, log λ_S decreased to −0.049 [−0.12, 0.013] and −0.066 [−0.14, 0.012] on average when perturbing all TSFs under a periodic and stochastic regime, respectively, compared with log λ_S of 0.014 [0.014, 0.015] and 0.013 [0.0017, 0.019] in the control scenario (Figure 3c). Changes in log λ_S were more substantial in projections of browsing perturbations at constant average density. Here, on average, log λ_S was −0.11 [−0.21, −0.067] and −0.12 [−0.20, −0.059] under a periodic and stochastic fire regime, respectively, compared with 0.015 [0.014, 0.017] and 0.015 [0.0038, 0.020] in the control scenario.

Negative effects of browsing combined with frequent large-scale fires on dewy-pine populations have been reported previously, but previous analyses omitted density feedbacks (Paniw, Quintana-Ascencio et al., 2017). Our results however demonstrate that density dependence somewhat buffered populations from the effects of the browsing perturbation under higher fire frequencies, especially under periodic fire regimes (every 15 years; Figure 3c; Appendix S4: Figure S3b). At the same time, under less frequent periodic burning (every 30 years), populations were consistently negatively affected by browsing perturbations; and the effects of density dependence disappeared (Figure 3c). Under this fire regime, log λ_S was −0.097 [−0.16, −0.039] and −0.089 [−0.16, −0.0081] at average density and with density dependence, respectively, for perturbation starting in $\text{TSF}_{>3}$, compared with 0.015 [0.014, 0.016] and 0.014 [0.013, 0.015] under natural conditions. The browsing perturbation had similar effects under stochastic fires occurring every 30 years on average (Figure 3c). This was because populations spent more years in $\text{TSF}_{>3}$ under less frequent fires, where density feedbacks are less important (Appendix S3: Table S4). The substantial effects of long-term perturbations to the period of post-fire habitat succession, starting in early post-fire years, stands in contrast with megamatrix elasticity analyses assuming no browsing and stochastic fire regimes (Pascarella & Horvitz, 1998). These latter revealed that the dewy-pine population growth rate was largely only sensitive to perturbations in the last post-fire habitat state ($TSF_{>3}$) under natural disturbances (Appendix S8: Figure S2).

DISCUSSION

Using three study systems that represent a range of life-history adaptations to periodic environments, we highlight the complex effects that changes in vital-rate periodic patterns can have on population dynamics. In each of our three study species, perturbing the strength of periodicity in various vital rates led to large changes in population dynamics, especially for vital rates strongly influencing population dynamics (Figure 3; Appendix S8). Our results suggest that, whereas according to classic sensitivity analyses our study populations are buffered from inter-annual environmental variation leading to vital-rate fluctuations (Paniw et al., 2020; Appendix S8), these populations appear to be sensitive to perturbations in the strength of vital-rate periodicity. This variety of population responses to periodic changes in environmental states—leading to periodic patterns in critical vital rates—suggests that quantifying and taking such periodicity into account when projecting population dynamics should receive more consideration in population ecology and is particularly important given widespread changes in climatic variability.

Among the various types of environmental patterning, seasonality is one of the most common forms (Boyce, 1979; Panda et al., 2002; Park, 2019). Numerous species have adapted to seasonal environmental patterning and show various degrees of seasonal variation in vital rates (Varpe, 2017). In general, variation in vital rates is expected to negatively affect the population growth rate (Doak et al., 2005; Tuljapurkar, 1990); but such expectations are largely based on assuming random inter-annual vital-rate variation (Tuljapurkar, 1990). Our results agree with previous studies pointing to the importance of seasonal vital-rate variation in driving population dynamics (Bassar et al., 2016; Kanno et al., 2015; Wichmann et al., 2003) depending on the direction of vital-rate responses to increasing or decreasing seasonality. For example, in species exposed to harsh winters, like marmots, an increase in environmental seasonality can be associated with large increases in winter mortality, thus leading to population decreases and increased extinction risks (Appendix S4; Albon et al., 2016), whereas a decrease in seasonality could have positive effects on populations living in such environmental conditions (van de Pol et al., 2010). Strong effects of changes in seasonal environmental patterns can also arise due to, and be amplified by, seasonal correlations between key vital rates (Jongejans et al., 2010; but see Compagnoni et al., 2016). For example, in meerkats, highly seasonal years in subadult survival mostly corresponded to years where dominant recruitment was high and helper emigration particularly low in the wet season, positively affecting the population growth rate. These important seasonal relationships in vital rates are not picked up in classic sensitivity analyses, where inter-annual vital-rate variation shows a consistently small effect on population growth rates (Appendix S8). In summary, population responses to changes in environmentally driven vital-rate patterns are largely context dependent (Töpper et al., 2018), and these contexts are masked in analyses focusing on inter-annual variation only.

Seasonality is perhaps the most known and studied form of environmental and vital-rate periodicity, but periodic patterns in vital rates occur on other scales as well (Park, 2019). The dewy pines represent a common form of such periodicity: adaptations to disturbance regimes (Brawn et al., 2001; Denslow, 1980; Pausas et al., 2004). Although many studies on disturbance-adapted plants have shown strong effects of changes in the periodic pattern of these disturbance regimes on population dynamics (Evans et al., 2010; Keith et al., 2020; Miller et al., 2019), we found no differences in dewy-pine stochastic growth rates among different fire regimes considered. Instead, dewy-pine populations were negatively affected by introducing human perturbations in the form of heavy browsing after fires, especially when starting in the early post-fire habitat states (Figure 3c; Paniw, Quintana-Ascencio et al., 2017). Such perturbations, continuously removing aboveground vegetation, effectively alter the patterning of the post-fire life cycle in dewy pines by allowing continuous seed germination (depleting the seed bank) and longer aboveground persistence of dewy pines (increasing intraspecific competition) (Brewer et al., 2021; Paniw, Quintana-Ascencio et al., 2017). This then makes populations less resilient to fire disturbances. Such detrimental effects of herbivory on populations of plants in fire-prone habitats have been found in various species (e.g., Giljohann et al., 2017; Groenendijk et al., 2011; Mandle et al., 2015; Sühs et al., 2021). In other systems, plant population persistence may be enhanced by a combination of frequent burning and herbivory (Baeza et al., 2007; Fuhlendorf et al., 2009; Galíndez et al., 2013). Whereas past research on disturbance-adapted plant species has focused on natural systems, our results highlight the importance of understanding complex interactions between disturbance regimes and environmental and anthropogenic pressures after the disturbances in human-dominated landscapes.

Regardless of the nature of periodic variation in vital rates, density-dependent processes may mediate the effects of this variation on population dynamics. In our case, this occurred for both meerkats (density feedbacks buffered both negative and positive effects of vital-rate seasonality; Figure 3b) and dewy pines (density feedbacks buffered negative effects of a browsing perturbation under more frequent than usual periodic and stochastic fires; Figure 3c). Density dependence is expected to stabilize population dynamics in the long term (Boyce et al., 2006; Sinclair & Pech, 1996); but on a shorter time frame (within the length of our projections), density dependence can be a major driver of population cycles (Radchuk et al., 2016). Numerous studies have shown the key role of density dependence in mediating vital-rate response to inter-annual variations in the environment (Bonenfant et al., 2009; Vøllestad & Olsen, 2008), making it an important factor shaping population dynamics (Coulson et al., 2001; Gamelon et al., 2017; Hansen et al., 2019). Our results on meerkats and dewy pines suggest that the role of density dependence in buffering population dynamics from inter-annual environmentally driven variation in vital rates similarly applies at the intra-annual scale.

Interactions between density and periodic environmental variation can be important drivers of context-dependent population responses to the environment, and are common in nature (e.g., Barbraud & Weimerskirch, 2003; Coulson et al., 2001; Gamelon et al., 2017). For instance, in meerkats, many vital rates show seasonal differences in their responses to important social factors such as the number of dispersing males (Paniw et al., 2022) or group size, which interact with population density but do not strongly correlate with it (Bateman et al., 2012; Ozgul et al., 2014). For disturbance-adapted species, density feedbacks may stabilize population dynamics under periodic environmental change. For dewy pines, such feedbacks may slow population declines under the most intense browsing pressures, when natural habitat succession and fire regimes are most perturbed, but have little effects on populations otherwise. Our case studies therefore suggest that, across a wide range of environmental settings, including periodic environmental variation, the effects of environment–density interactions on populations are quite context dependent (Wang et al., 2009). Nonetheless, the key role of such interactions between periodicity and density in shaping population responses to changes in periodic patterns emphasizes the need to understand the effects of environmental variation beyond assuming random stochastic environments in density-independent population projections.

In summary, our results suggest that periodic patterns in vital rates play a key role in population dynamics across a wide range of life histories, with strong population responses to changes in periodicity arising because of particularly favorable or adverse conditions in critical periods of the life cycle (Burant et al., 2019), which can be buffered or emphasized by environment–density interactions (Paniw et al., 2019). Further perturbations in vital-rate patterning are expected under global change (IPCC, 2014), potentially strongly affecting species population dynamics and persistence (Bassar et al., 2016; Beissinger, 1995; Flockhart et al., 2015). Analyses of periodic vital-rate patterns have thus far primarily focused on species for which vital rates strongly differ between periods, such as migratory and seasonally breeding species (e.g., Reid et al., 2018). However, some populations experience periodic environments that do not necessarily translate into sharp periodic differences in vital rates (e.g., Viñals-Domingo et al., 2020), and accounting for periodicity in vital-rate fluctuations in these populations may help to reveal sensitivities to changes in periodic patterns when there appears to be no effect of changes in stochastic inter-annual vital-rate variations. In conclusion, our results highlight the need for studies investigating the sensitivity of populations to changes in vital-rate patterns beyond classic analyses relying on inter-annual variations, as sensitivities to environmental periodicity will be masked in such frameworks.

AUTHOR CONTRIBUTIONS

Maria Paniw, Arpat Ozgul, and Eva Conquet designed the study. The data and insights on the study species were provided by Kenneth B. Armitage, Daniel T. Blumstein, Madan K. Oli, and Julien G. A. Martin for the marmots, Tim H. Clutton-Brock for the meerkats, and Maria Paniw for the dewy pines. The analyses were performed by Eva Conquet, with input from Maria Paniw and Arpat Ozgul. The manuscript was written by Eva Conquet, with substantial contribution to revisions from all authors.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

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

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