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Title: Shifts in competitive structures can drive variation in species' phenology

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ABSTRACT

Characterizing patterns and drivers of species' responses to various environmental contexts is useful in determining their adaptive capacity to the consequences of ongoing global environmental change. For many species, a well-documented response to anthropogenic climate change is a shift in the timing of their key life-history events or phenology. Often, these phenological shifts are associated with changes in abiotic factors used as proxies for resource availability or other suitable conditions. However, less is known about how species' interactions that can lead to resource limitation influence phenological responses. Using long-term experimental data on small mammals monitored in the southwestern United States, we show that altered competitive landscapes can drive shifts in breeding timing and duration, and that, relative to a dominant competitor, other species exhibit less specific responses to environmental factors. These results suggest that plasticity of phenological responses, that is often described in the context of annual variation in abiotic factors, can occur in response to biotic context as well. Additionally, in response to competitive pressures, species may employ adaptive strategies, such as low phenological synchrony, to compensate for the adverse demographic impacts of mismatched resource and species' phenology. Variation in phenological responses under different biotic conditions shown here further demonstrate that shifting biotic interactions are rampantly occurring in many natural systems and a more nuanced understanding of its impacts on population dynamics is useful to better understand and predict biodiversity patterns in a changing world.

INTRODUCTION

Characterizing species' responses to various environmental conditions is useful in determining their sensitivity and adaptive capacity to the consequences of ongoing global environmental change (Glick et al., 2011). Among the known responses to climate change, shifts in phenology or the timing of key life-history events of organisms, are the most well-documented (Cohen et al., 2018; Roslin et al., 2021; Walther et al., 2002). Often, the timing of important phenological events (e.g., reproduction) match with periods of high resource availability to support high fitness and survival costs (Bradshaw & Holzapfel, 2007; Buss et al., 2021; Forchhammer et al., 1998; Helm et al., 2013; Reed et al., 2013; Walther et al., 2002). Fitness costs of reproduction are often attributed to the increased energetic demands of maintaining and developing reproductive organs and behaviors (Visser & Both, 2005) and survival costs are incurred from increased predation risk (Audzijonyte & Richards, 2018; Kelt et al., 1995). To avoid unfavorable conditions during the reproductive period, species may use abiotic (i.e., temperature, day length, precipitation) and biotic cues (i.e., flowering, prey availability) to regulate and shape reproductive phenology (Denny et al., 2014; Kenagy & Bartholomew, 1981; Wolkovich et al., 2014).

Timing reproductive activities to overlap with periods of high resource availability is important for consumer species. Thus, many studies assess phenological drivers related to either reliable environmental cues of resource availability or biotic cues related directly to the emergence or abundance of prey (i.e., resource) species (DeLucia et al., 2012; Gordo & Sanz, 2005; Pearce-Higgins & Yalden, 2004). In fact, decoupled resource and consumer phenology often has negative implications for successful production and survival of offspring (Thackeray et al., 2010; Wann et al., 2019). However, resource availability is determined by more than just the intrinsic population dynamics of predator and prey. Competition from other species can deplete

important resources and create resource limitation even when resource supply is initially high and can negatively impact individuals and populations. In fact, demographic rates were found to be lower for those that initiate their biological activities (i.e., breeding) after their competitors (Carter & Rudolf 2022). Thus, plasticity of species' phenology under different biotic contexts could have important implications for interpreting observed phenological changes as ecosystems increasingly undergo turnover in their component species. However, it is unclear whether plasticity exists to allow shifts in a species' phenology when a competitor is absent.

While competition has the potential to impact reproductive timing and investment, it may not similarly impact all individuals within a species, especially for species where variation in the degree and type of offspring investment depends on the sex of the parent (Mysterud et al., 2008). In general, female animals play a primary role in provisioning offspring from conception until birth or hatching. In mammals, this period of primary responsibility for offspring provisioning is lengthened through lactation. Because female mammals are energetically and nutritionally providing for their own increased resource needs and those of their offspring, females may be particularly sensitive to the effects of resource depletion caused by interspecific competition. In contrast, males for many mammal species are frequently uninvolved in offspring rearing. Their enhanced energetic demands during this period are due to acquiring and defending females from other conspecifics (Ostfeld 1985), and thus, may be largely influenced by intraspecific competition for mates. These differences in reproductive constraints and pressures may also be reflected in their use and sensitivity to environmental cues. With logical support for sex-specific phenological responses, it is therefore important that such sources of variation are considered when assessing the effects of competition on reproductive phenology. However, data that allow

sex-specific assessment of competitive effects on phenology in dynamic environments are often limited.

Long-term field experiments, where sex-specific differences in reproductive investments of species are largely known and competitive networks are explicitly manipulated, are well-suited for investigating the role of competition in driving reproductive phenology (Ernest et al., 2016; Kelt et al., 1995, Mysterud et al., 2008; Ostfeld, 1985). In long-term field experiments where dominant competitors are removed, the effect of their loss on the reproductive phenology of other species in the system can be evaluated by comparing the reproductive parameters of a focal species in control and treatment set-ups during different temporal contexts. Here, we used long-term data on small mammals monitored in an experimental field site near Portal, Arizona to assess the effects of competition on reproductive phenology. This long-term experiment (1977 to present) in the southwestern USA generates fine-scale (monthly) data on desert rodents under different biotic contexts. The experiment involves the removal of a dominant competitor, the kangaroo rats (*Dipodomys* spp.), in a subset of the experimental plots (hereafter referred to as exclosure plots). In this study, we compared the breeding phenology of desert pocket mice (*Chaetodipus penicillatus*) and Bailey's pocket mice (*C. baileyi*) in control and exclosure plots. Specifically, we determined periods of significant change in the monthly proportions of breeding male and female individuals in both plot types. We also assessed the sex-specific responses to abiotic conditions, and intra- and inter-specific competition of both species in each plot type (control and exclosure). In doing so, we can gain a more robust understanding of phenological responses to environmental factors, which may vary in future landscape and climate change scenarios.

METHODS

Data Curation and Manipulation

We used time-series data on rodents and environmental variables collected at an experimental field site near Portal, Arizona (31°56'20.29"N 109° 4'47.44"W) to determine the effects of biotic context (presence of kangaroo rats) and abiotic factors (temperature, NDVI, precipitation) on the reproductive phenology of two pocket mice species (*C. penicillatus* and *C. baileyi*). We used rodents as model species in this study because male and female reproductive investments of rodents are largely known (Mysterud et al., 2008). Moreover, desert rodents are especially ideal for answering questions about phenological plasticity given the resource-limited environment they inhabit, which may drive variation in their responses to both biotic and abiotic factors.

In this study, we used data collected from 1988 to 2014, because this is the longest period when the experimental treatments were consistent for the most plots. We used data obtained from control plots, where all rodents including kangaroo rats have access, and exclosure plots, where all other rodents were allowed access through smaller holes in the fences surrounding the plots. More detailed description of the experimental plots is discussed elsewhere (Ernest et al. 2016). All plots were sampled monthly, and the sex, species, and reproductive condition of individuals were recorded.

Rodent data- We assembled a dataset on the observed total abundance and counts of reproductive *C. baileyi* and *C. penicillatus* in Portal, Arizona using the 'portalr' package (Christensen et al., 2019). We created subsets of the data for each type of plot (control and exclosure) and sex (male and female). In calculating the proportion of reproductive individuals, we considered those that had testes described to be scrotal (descended), recently scrotal, or had

minor signs of scrotal testes as reproductive males. We considered individuals that were described to be pregnant (after palpating the belly), and/or those with either red and/or enlarged nipples, and/or those with swollen and/or plugged vaginas as reproductive females. To limit the introduction of biases in our dataset through the inclusion of juveniles, we identified a minimum threshold of the body mass for the breeding individuals (McLean and Guralnick, 2020) for each species and sex (i.e., *C. baileyi* male= 16 g, *C. baileyi* female= 21 g, *C. penicillatus* male= 10 g, *C. penicillatus* female= 12 g). We filtered out individuals that had a body mass below the threshold for each group.

Environmental data- We used monthly data on NDVI (an index of plant greenness), mean temperature (°C), cumulative precipitation (millimeters) that fell during warm or cool months (calculated as the sum of precipitation on days > or < 4 °C), and biomass data of *C. baileyi*, *C. penicillatus*, and all species of *Dipodomys*. We manipulated data to obtain lagged values (lag =1 month) of all abiotic variables. We explored the effects of time lagged variables and time accumulation effects of precipitation because climate affects vegetation dynamically through temporal processes (Ding et al., 2020; Wen et al., 2019). We assumed that the cumulative effect of precipitation is three months (90 days) given the aridity of the system (Ma et al., 2021). We used biomass data of *C. baileyi*, *C. penicillatus*, and all species of *Dipodomys* as proxies for competitive effects.

Data Analysis

We built generalized additive models (GAMs) to characterize the reproductive phenology of male and female *C. baileyi* and *C. penicillatus* in different biotic contexts, and to determine the relationship between the proportion of breeding individuals with abiotic and biotic factors.

We also built GAMs to characterize the reproductive phenology of kangaroo rats so that we could compare any shifts in the breeding phenology of *Chaetodipus* spp. with that of the dominant competitor. We pooled all data on *Dipodomys* spp. monitored in the site (*D. ordii*, *D. merriami*, *D. spectabilis*) and focused only on their timing in control plots, where we have adequate observation data on the group.

We used GAMs because they are appropriate for fitting data that may exhibit non-linear trends and associations (Pedersen et al. 2019), a dynamic typical of species' phenology that wax and wane through time. Here, we fitted species-, sex-, and treatment-specific models to different subsets of the dataset. For example, we built a separate model for data on male *C. penicillatus* in control plots. We built models that included terms for abiotic factors (terms for NDVI, warm and cool precipitation, and mean monthly temperature with lag of zero and one), a proxy for intraspecific competition (i.e., population biomass), and for interspecific competition (i.e., biomass of competitors). We built separate models for all combinations of data. These models followed the general form:

$$Y \sim Binomial\ (n\ , p) \quad \text{(Eqn. 2)}$$

$$logit\ (p) = \alpha + \sum_{m=1}^{2} f_m(T_m) + \sum_{k=1}^{10} (\beta_k X_k) \quad \text{(Eqn. 3)}$$

In Eqn. 2, Y is the number of breeding individuals, which follows a binomial distribution with the parameters *n* (number of independent trials, e.g., total number of males) and p (probability of success, e.g., proportion of breeding males). In Eqn. 3, p is modeled as a function of the intercept (α), the smooth function for month ($f_1(T_1)$), which was parameterized using cubic cyclic regression splines (Pederson et al. 2019), the smooth function for year ($f_2(T_2)$), which was parameterized using Gaussian process smooths (Wood 2006), and linear terms for the effects of

abiotic and biotic predictors (β_k). We used Pearson's correlation coefficient (r) to test for collinearity among the predictors included in the models ($|r| < 0.5$). We standardized all predictors by centering each value on the mean and dividing them by two standard deviations (Gelman, 2008) to facilitate interpretation of results. All models were implemented in a restricted maximum likelihood (REML) framework using the 'mgcv' package ver 1.8-31 (Wood and Wood 2015) in R ver 4.1.1 (R Core Team, 2021). Data (10.5281/zenodo.7301687) and code (10.5281/zenodo.7327503) used to conduct data analyses are archived in Zenodo.

Model Interpretation

Reproductive phenology- We characterized rodent breeding phenology by identifying periods of significant change in the proportion of breeding individuals (i.e., when the rates of change were non-zero). Here, we approximated the derivatives of the spline function for month through finite differences to determine the direction of the function (i.e., increasing or decreasing; Simpson, 2018). In this case, we estimated the rate of change in the fitted smoother (i.e., month) to identify periods when the proportion of breeding individuals increased or decreased. We interpreted periods when the rate of change in the fitted smoother for month were increasing as the onset of breeding season (i.e., when more individuals are exhibiting reproductive characteristics), and when the rate of change were decreasing as termination of breeding season (i.e., when fewer individuals are exhibiting reproductive characteristics). We also performed exploratory work on the reproductive phenology of *C. penicillatus* at different time periods of *C. baileyi* establishment in the site. *C. baileyi* colonized the site in 1995, causing major shifts in resource use and the competitive landscape, especially for *C. penicillatus* (Bledsoe and Ernest 2019, Diaz and Ernest 2022). To assess the effect of the shift in the

competitive landscape caused by this natural experiment, we also built simpler models (without terms for competition) for all species-, sex-, and treatment- specific datasets to determine the relative importance of these terms in explaining variation in breeding proportions. Details of the methods and results of these exploratory works are found in the Appendix.

Association between covariates and proportion of breeders- We examined relationships between covariates and the proportion of breeders in two ways. First, we assessed whether individuals of both pocket mice species exhibited different environmental responses under different biotic contexts. We interpreted the coefficient values based on their signs (positive or negative) to assess whether the effect of a given factor on the proportion of breeding individuals was positive or negative. Then, we compared species-specific responses in each plot to the response of the kangaroo rats to infer species-specific strategies for competition relative to the dominant competitor in the system. We used the distribution curves of the slopes estimated from models of both pocket mice species and related it to the distribution curves of the slopes from models of kangaroo rats (i.e., *Dipodomys* spp. and *C. baileyi* in control and exclosure plots, *Dipodomys* spp. and *C. penicillatus* in control and exclosure plots).

RESULTS

Both species of pocket mouse exhibited changes in their phenology when kangaroo rats are removed from the rodent community (Figs. 1 and 2). Changes included shifts in onset and duration, depending on species and sex (details below; Figs. 1 and 2). Some relationships between covariates and the proportion of breeders did not differ between control and kangaroo rat exclosure plots (Fig. 3), however, the responses of both pocket mice species to most

covariates were relatively broader than that of kangaroo rats in control plots (Fig 4a and 4b) and were narrower in exclosure plots (Fig. 4c and 4d).

Reproductive phenology of pocket mice under different biotic conditions

Female Bailey's pocket mouse (C. baileyi)- Females on control plots went into breeding condition earlier than those on exclosure plots (January to March vs. February to April, respectively; Fig 1c, e), but declines in reproductive activity occurred during similar timeframes on both exclosures and controls (June-August vs. July-Sept, respectively; Figure 1c, e). On both plots, the onset of the breeding season for female *C. baileyi* occurred later than that for females of the dominant competitor, kangaroo rats (Fig. 1a, 1c, 1e). Thus, in the absence of kangaroo rats, female *C. baileyi* delayed reproduction by ~1 month and in the presence of kangaroo rats, entered reproductive condition earlier and stayed in reproductive condition longer.

The best fit models for female *C. baileyi* on controls and exclosures overlapped in their important drivers, but also contained important differences. On control plots, female reproductive condition was positively associated with warm precipitation (lag 0) and cool precipitation (lag 1; variation explained= 66.4%; $R^2 = 0.57$; Fig. 2a). The best fit model for *C. baileyi* on exclosures also found a positive role for warm precipitation (lag 0), but not for cool precipitation. Additional important associations that emerged in the exclosure model that did not appear in the control model included a negative association with NDVI (lag 0), a positive association with NDVI (lag 1), and desert pocket mouse biomass (variation explained= 69.3%; $R^2 = 0.66$; Fig. 2a). Moreover, female *C. baileyi* in control plots exhibited a wider range of responses to some abiotic and biotic factors than kangaroo rats, and those in exclosure plots (Fig. 4a and Appendix S1 Fig. S2).

Male Bailey's pocket mouse (*C. baileyi*)- The main difference between males on controls and exclosures was a lack of a seasonal signal in the proportion of reproductive males on controls, in contrast to a weak seasonal signal on the exclosure. This suggests that in the presence of kangaroo rats, male *C. baileyi* do not follow a particular schedule when they are more likely to be reproductively active. Without kangaroo rats present, male *C. baileyi* exhibited weak seasonal reproductive behavior, with their breeding onset occurring about a month earlier than female *C.baileyi* on the same plots (Fig.1e).

Models show that male *C. baileyi* on control plots were positively associated with *C. penicillatus* biomass, and negatively associated with mean temperature (lag 0) and *C. baileyi* biomass (variation explained= 21.8%, R2 = 0.17; Fig. 2b). Male *C. baileyi* on exclosure plots did not share a similar sensitivity to mean temperature but showed a similar relationship to the other variables: a positive association with *C. penicillatus* biomass and a negative association with *C. baileyi* biomass (variation explained= 44.3%; R2 = 0.42; Fig. 2b). Moreover, male *C. baileyi* in both control and exclosure plots exhibited similar generalized responses to some abiotic factors (Fig. 4b), and more specialized responses to some biotic factors (Appendix S1: Figure S2). However, in general, they exhibited more generalized responses to both abiotic and biotic factors compared to kangaroo rats.

Female desert pocket mouse (C. penicillatus)- Females on control plots delayed their reproductive onset by nearly a month in comparison to females on exclosure plots (November to January (Fig. 3c) on control plots while those on exclosure plots were increasing around October to December (Fig. 3e)). Many breeding females left breeding condition from May to August, which was the same regardless of plot type. Thus, in the absence of kangaroo rats, female *C.*

penicillatus entered reproductive condition earlier and stayed in reproductive condition longer than females observed in exclosure plots (Fig. 3c and 3e).

Female *C. penicillatus* on control plots were positively associated with mean temperature (lag 0), warm precipitation (0), cool precipitation (lag 1), and *C. penicillatus* biomass, and negatively associated with cool precipitation (lag 0) and *C. baileyi* biomass (variation explained= 55.5%; R2 = 0.53; Fig. 2c). Female *C. penicillatus* on exclosure plots responded similarly to mean temperature (lag 0), warm precipitation (lag 0), and Bailey's pocket mouse biomass on control plots, but, additionally, was positively associated with NDVI (lag 1; Fig. 2c). Female *C. penicillatus* in both controls and exclosures exhibited relatively generalized responses to abiotic factors (Fig. 4c). Additionally, there is marginal overlap between kangaroo rat and *C. penicillatus* responses to temperature and precipitation, which may suggest differences in how these environmental cues are being viewed by both species. In contrast, their responses to biotic factors were generally similar with that of their dominant competitor, kangaroo rats (Appendix S1: Fig S2).

Male desert pocket mouse (C. penicillatus)- For male *C. penicillatus*, the end to the breeding season occurred sooner on exclosure plots than on controls. The proportions of breeding male *C. penicillatus* began increasing in January on both controls and exclosures but finished decreasing on control plots in September in comparison to August on exclosure plots (Fig. 3d). Thus, the presence of kangaroo rats resulted in a longer breeding season for male *C. penicillatus*.

Male *C. penicillatus* on both control (variation explained= 63.6%; R2 = 0.68) and exclosure (variation explained= 52.1%; R2 = 0.48) plots were generally not associated with any

predictors (Fig. 2d). However, the proportions of breeding male *C. penicillatus* on exclosure plots were negatively associated with warm precipitation (lag 1; Fig. 2d). Like male *C. baileyi*, male *C. penicillatus* in both control and exclosure plots also exhibited a relatively more generalized response to abiotic and less generalized response to biotic factors (Fig. 4d and Appendix S1: Fig S2). Finally, male *C. penicillatus* responses to most factors did not differ from the responses of their dominant competitors, *Dipodomys* spp.

DISCUSSION

Our results show that small mammals can shift the timing of their breeding phenology in response to the presence or absence of an important competitor. Differences in breeding phenology were observed between control and kangaroo rat exclosure plots for females of both species and - to some extent - males. Shifts in breeding phenology occurred in a variety of ways - changes in the timing of initiation and/or cessation of breeding season, as well as changes in the duration and degree of seasonality (or synchrony) exhibited. Our results add to our understanding of animal phenology by providing evidence that observed shifts in timing can be driven not only by shifts in abiotic cues, but also in a species' competitive environment.

While we detected shifts in breeding phenology in response to our experimental manipulation of kangaroo rats, it is not immediately clear how changes in the competitive milieu are driving changes in the breeding phenology of the two pocket mice. Models examining interactions between competition and phenology timing show that competitors that time their activities before or coincident with their main competitor exhibit higher survival rates whereas those that come afterwards tend to suffer from poorer condition and outcomes (Carter and Rudolf 2022). A similar process might explain why *C. baileyi* on controls enter reproductive condition

sooner than those on kangaroo rat exclosures since reproducing later may mean lower resource availability when kangaroo rats are present. We also see that *C. penicillatus* females initiate their reproductive season before either *C. baileyi* or the kangaroo rats initiate theirs, regardless of whether kangaroo rats are present or not. Initiating their reproductive season before these two dominant competitors is also consistent with Carter and Rudolf's (2022) simulation. However, the relatively delayed breeding onset of female *C. penicillatus* in controls, where both kangaroo rats and Bailey's pocket mouse are present (Fig 2) is not consistent with Carter & Rudolf (2022), as there should be little advantage to delaying reproduction in a more competitive environment, where you would otherwise avoid competition by initiating reproduction early.

The counterintuitive response of *C. penicillatus* may emerge from a unique aspect of its biology. Unlike the other two species, *C. penicillatus* is known to enter intermittent torpor during the winter depending upon energetic state and ambient temperature (French 1977). In this system, we note slight increases in the proportion of breeding female *C. penicillatus* in exclosure plots during winter months, suggesting that many of the individuals that do not enter torpor are in good enough condition to initiate reproductive condition. A possible explanation for *C. penicillatus*' delay in breeding in the controls could be related to decreased body condition when kangaroo rats are present - diverting more individuals into torpor and fewer into reproductive pathways. While Carter & Rudolf (2022) incorporate intraspecific variation into their model, it provides limited implications for temporal variation in the condition of individuals of species that are capable of multiple breeding seasons. Our results suggest that expanding Carter & Rudolf (2022) to incorporate individual decision-making on if and when to initiate reproductive events based on energetic condition could provide important insights into how species may shift phenology in response to changes in their competitive environment.

Males of both pocket mice species also exhibited changes in reproductive timing in response to altered competitive environments. Male *C. penicillatus* in control plots were going into and out of the breeding season longer than those on exclosures while *C. baileyi* males exhibited a weak seasonal signal when kangaroo rats were absent. Decreased phenological synchrony, in the form of longer periods of increase and decrease for *C. penicillatus* (Fig 3) and a lack of seasonal signal for *C. baileyi* (Fig. 1) in control plots, may have been a competitive strategy of these pocket mice to offset costs of delayed breeding relative to kangaroo rats (Carter and Rudolf 2022). However, these changes may also be consistent with previous knowledge on the advantages obtained by males of various species when they are always reproductively ready, or are close to being ready, when opportunities to breed arise (Laaksonen et al., 2002; Mysterud et al., 2008). This may especially be important in highly seasonal environments where it may be energetically impossible for females to breed year-round, and so males may enter the breeding season earlier and leave it later than females (Bronson, 1985). Alternatively, a shortened breeding season may also be an adaptive strategy by males under stressful conditions. In this system, male *C. penicillatus* on exclosure plots may opt to not increase energy allocation for breeding when environmental conditions are not optimal for females since the metabolic consequences of breeding under adverse conditions can adversely impact future demographic success (Descamps et al. 2007, Lane et al. 2010)

Within-species phenological synchrony, which occurs when there is low variation in the timing of a biological event for a given species, may arise from consistent responses among individuals to external cues (i.e., shared responses to environmental factors at a given time scale). Rudolf and Carter (2022) posit that the implications of low and high phenological synchrony are dependent on competitive context. In this case, there is potentially a benefit to

high synchrony (i.e., shorter breeding period and/or specific responses to environmental cues) in some groups (e.g., female kangaroo rats) and low synchrony (i.e., longer breeding period and/or less specific responses to environmental cues) in others (e.g., male kangaroo rats and *C. baileyi* males on controls). However, given the nature of our data, it is not immediately clear how to quantify the strength of intraspecific synchrony. If intraspecific synchrony is driven by individuals exhibiting strong and consistent responses to drivers, then the model results may provide some insights into the degree of intraspecific synchrony. Consistent with the impression of higher synchrony, female kangaroo rats exhibit strong responses to environmental variables with narrower distribution curves for parameter estimates, and thus, low within-species variability in their environmental responses (Fig 4). In contrast, both pocket mice species exhibited a broader range of responses to external stressors (Fig 4). This larger variation in the parameter estimates was generally consistent on both exclosures and controls and across males and females, suggesting that high intraspecific variability in these species may not be driven specifically by the direct impacts of competition with kangaroo rats. This may mean that these pocket mice exploit environmental conditions that are underutilized by kangaroo rats as an adaptive strategy. Consequently, this may facilitate population-level shifts in phenological timing in response to changes in competitive context. While shifts in biotic context appear to drive changes in the breeding phenology of both pocket mice, these had a subtle impact on the structure of the best fit model on controls versus exclosures. Important environmental drivers on control plots were generally also important on exclosure plots but the strength and significance of some drivers changed depending on the biotic context. What this may mean for the interoperability of models fit under one biotic context for predicting phenology in other biotic contexts is currently unclear but bears further investigation.

Overall, the variation in the phenological responses of desert rodents under different biotic conditions that we have documented here highlight the important role of species interactions in driving phenology. While these results cannot distinguish whether the impacts of competition occur through resource depletion, behavioral interference, or other impacts of the kangaroo rats, these results show that removing a competitor can influence a species' phenology. Future studies that can tease apart these direct and indirect impacts may be useful in developing a robust understanding of the effects of competition in species' phenology. By recognizing that competitive landscapes can influence the responses of breeding individuals, we gain a more nuanced understanding of one of the key biological phenomena that can alter ecosystem dynamics.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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FIGURE LEGENDS

Figure 1. Reproductive phenology of female (left panel) and male (right panel) kangaroo rats in control plots (top panel), and Bailey's pocket mice in control (middle panel) and exclosure (bottom panel) plots in an experimental field site near Portal, Arizona. Plots show estimated smooths of the month term from species-, sex-, and treatment-specific generalized additive models (GAMs). Blue and red shading indicates periods of significant increase and decrease in breeding proportions, respectively. In cases where seasonal patterns or periods of significant increase or decrease could not be estimated from the model, raw data on proportion of breeding individuals were plotted (male *Dipodomys* spp. and *C. baileyi*; B, D).

Figure 2. Association between select abiotic and biotic factors with the proportion of reproductive female (left panel) and male (right panel) Bailey's pocket mouse (top panel) and desert pocket mouse (bottom panel) in control and kangaroo rat exclosure plots.

Figure 3. Reproductive phenology of female (left panel) and male (right panel) kangaroo rats in control plots (top panel), and desert pocket mice in control (middle panel) and exclosure (bottom panel) plots in an experimental field site near Portal, Arizona. Details on the configuration of these plots are like Figure 1.

Figure 4. Distribution curves of the abiotic covariate slope estimates indicating the response of female (left panel) and male (right panel) Bailey's pocket mouse (top panel) and desert pocket mouse (bottom panel) in control and kangaroo rat exclosure plots, compared to kangaroo rat estimates. Curves indicate the normal distribution with mean equal to the point estimate, and standard deviation equal to the standard error of the coefficients.

FIGURES

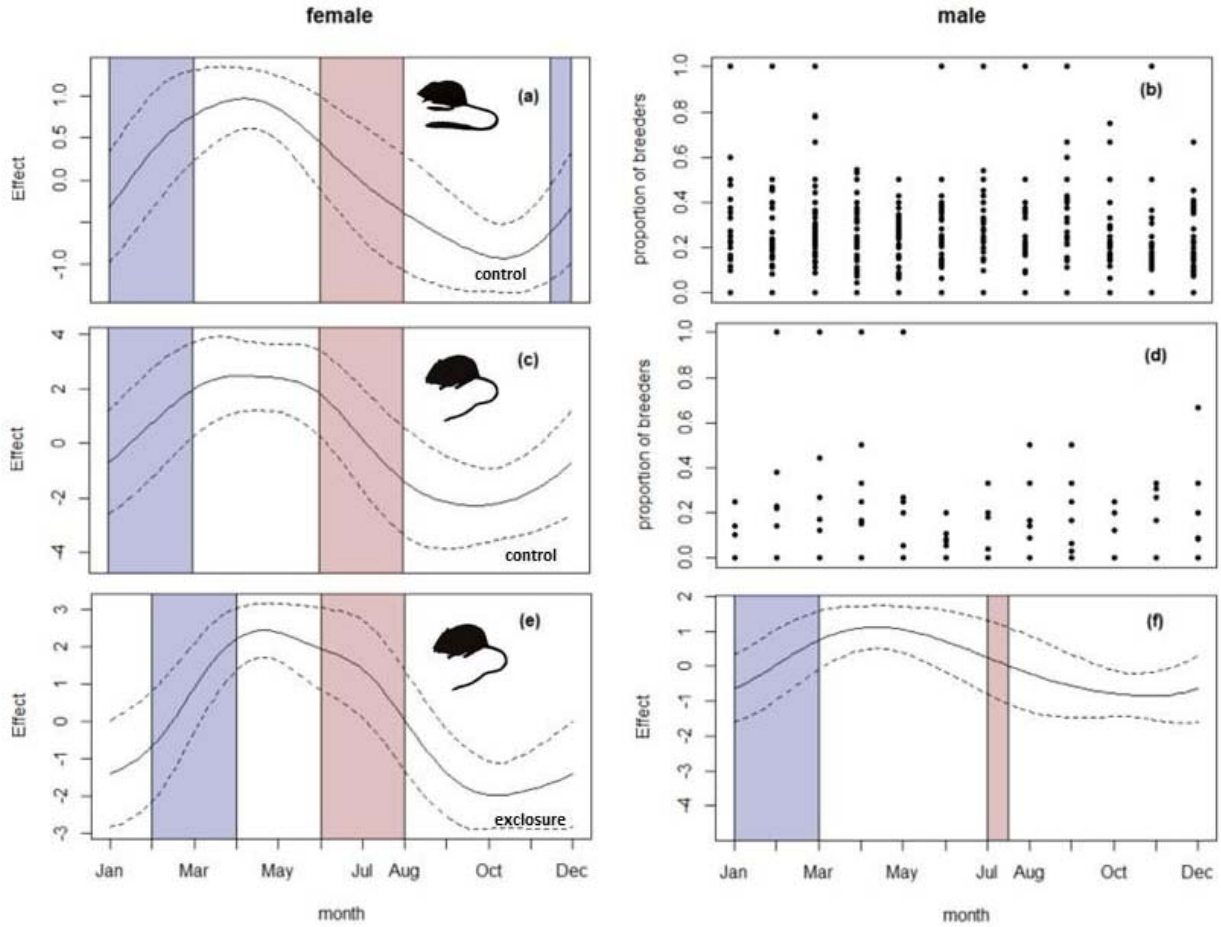

Figure 1.

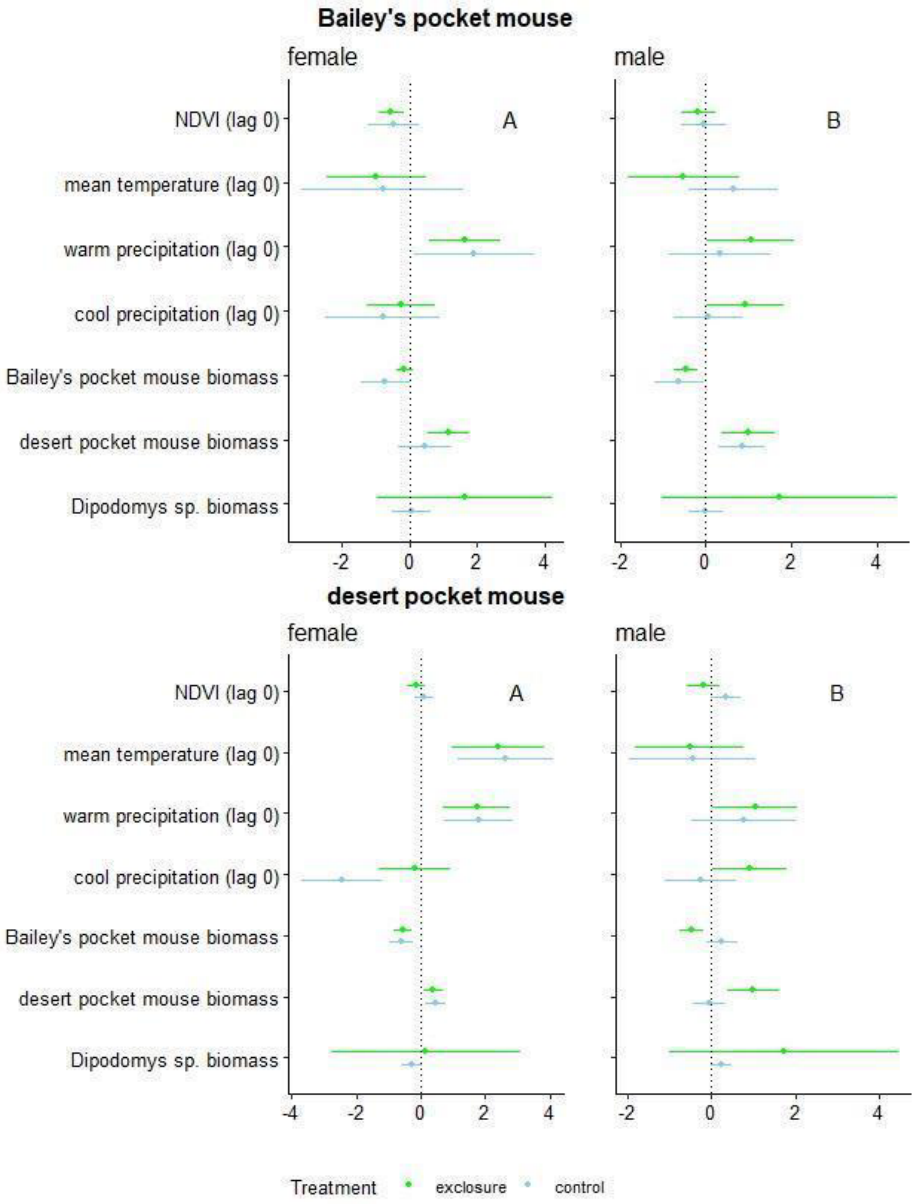
Bailey's pocket mouse
female
male
A
B
NDVI (lag 0)
mean temperature (lag 0)
warm precipitation (lag 0)
cool precipitation (lag 0)
Bailey's pocket mouse biomass
desert pocket mouse biomass
Dipodomys sp. biomass
-2
0
2
4
desert pocket mouse
female
male
A
B
NDVI (lag 0)
mean temperature (lag 0)
warm precipitation (lag 0)
cool precipitation (lag 0)
Bailey's pocket mouse biomass
desert pocket mouse biomass
Dipodomys sp. biomass
-4
-2
0
2
4
Treatment
exclosure
control

Figure 2.

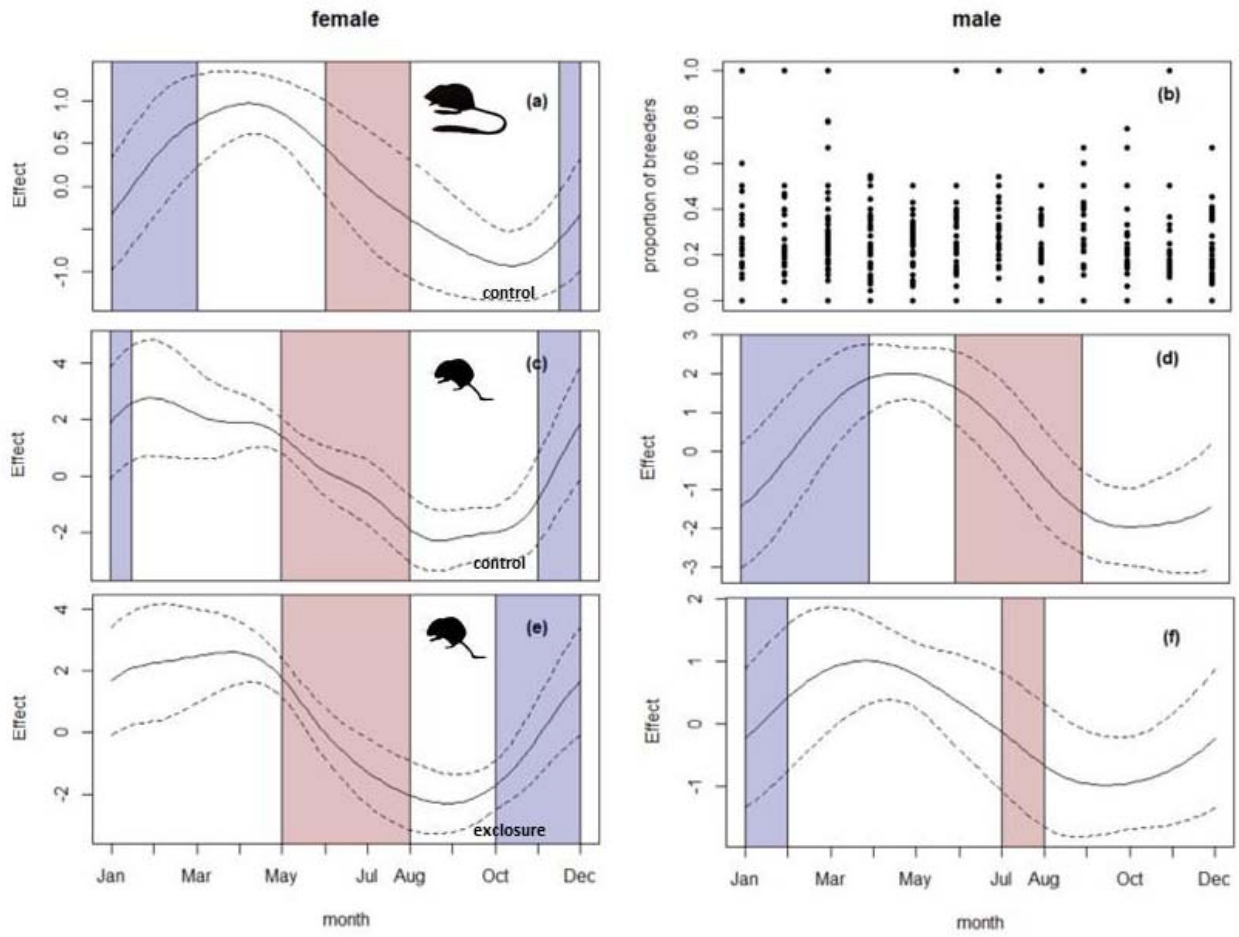
female
male
(a)
(b)
(c)
(d)
(e)
(f)
Effect
proportion of breeders
control
control
exclosure
Jan
Mar
May
Jul
Aug
Oct
Dec
month

Figure 3.

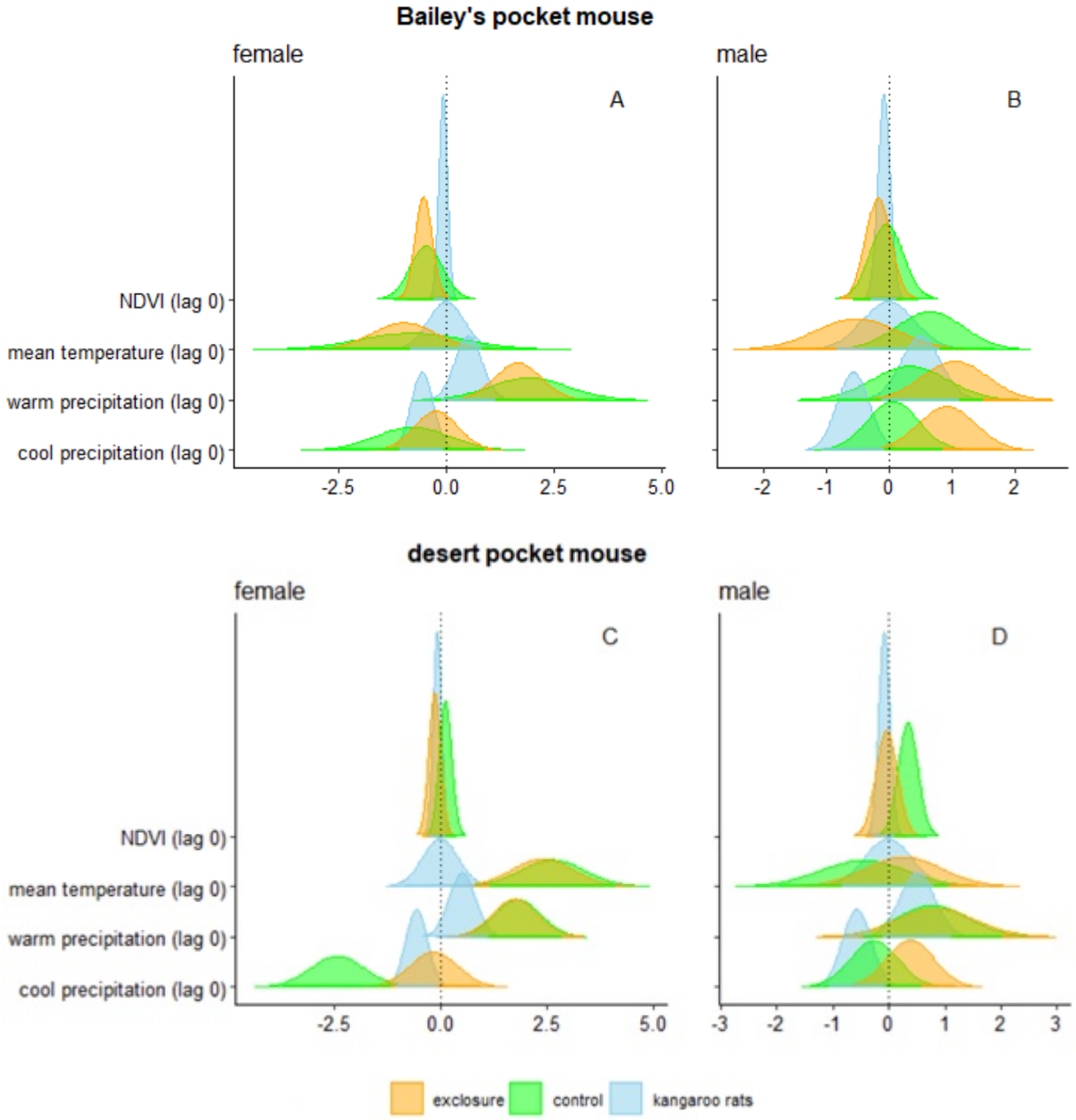
Bailey's pocket mouse
female
male
A
B
NDVI (lag 0)
mean temperature (lag 0)
warm precipitation (lag 0)
cool precipitation (lag 0)
-2.5
0.0
2.5
5.0
-2
-1
0
1
2
desert pocket mouse
female
male
C
D
NDVI (lag 0)
mean temperature (lag 0)
warm precipitation (lag 0)
cool precipitation (lag 0)
-2.5
0.0
2.5
5.0
-3
-2
-1
0
1
2
3
exclosure
control
kangaroo rats

Figure 4.