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Jessica Johnson
Candidate

Biology
Department

This thesis is approved, and it is acceptable in quality and form for publication:

Approved by Thesis Committee:

Dr. Seth Newsome; Dr. Jennifer Rudgers, Chairperson(s)

Dr. Joseph Cook

**SENSITIVITIES OF DRYLAND MAMMALS TO
MEAN AND VARIANCE IN ARIDITY**

by

JESSICA C. JOHNSON

**B.A., ENVIRONMENTAL STUDIES,
UNIVERSITY OF COLORADO,
BOULDER, 2012**

THESIS

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Jessica C. Johnson

B.A., Environmental Studies, University of Colorado, 2012

M.S., Biology, University of New Mexico, 2022

ABSTRACT

An important component of evaluating the consequences of climate change is to understand not only how climate trends, such as warming, affect species abundance but also how increasing climate variability will change population abundances. Studies on species' sensitivities to interannual variability are rare because they require long-term data collected either over naturally variable climate conditions or within direct manipulations of year-to-year variability. Physiology, functional traits, and diet composition related to resource acquisition or reproduction may be valuable predictors of species sensitivities to changes in both climate mean and variability. We predicted that species with certain physiologies, such as large body mass, and functional traits such as caching, would be less sensitive to aridification in mean climate while strategies, and large litter sizes and flexibility in storage of reserves as fat, would facilitate benefits from increases in the variance of aridity by enabling populations to boom in 'good' years. We integrated new and published physiological, trait, and diet data with 30 years of small mammal abundance data over highly variable natural climate conditions to test this

hypothesis for two common dryland ecosystem types in the southwestern US. Our results revealed we revealed that species with certain physiologies (larger mass and larger variation in mass) were less sensitive to aridification in mean climate, and that species with certain physiologies, traits, and diet composition (smaller mass, smaller variation in mass, larger variation in percentage body fat in the spring, less litters per year, and higher percentage of annual plants in diet) benefited from increases in the variance of aridity. In sum, this study demonstrates that the life history and functional traits as well as foraging strategies of small mammals can provide a generalizable framework to predict the sensitivities of population abundance to both non-stationary components of climate change: the mean and the variance.

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INTRODUCTION

Evaluating the consequences of climate change requires that we understand not only how climate trends, such as warming, affect species abundance but also how increasing climate variability will change population sizes (1–3). Long-term data on population abundance can yield important predictions on how populations respond to warming temperatures and altered precipitation regimes of the future (4,5). Importantly, population abundance may not respond to climate variables linearly because of threshold or lagged responses to climate extremes.

Nonlinearities detect a population's sensitivity to the variance component of climate variables. Specifically, concave nonlinearity indicates that more variance in climate will reduce abundance, because population abundance declines at one or both climate extremes, as occurs with typical temperature optimum curves (6–8). In contrast, convex nonlinearity signals benefits of variance to population abundance because one or both climate extremes drive increases in abundance. Importantly, when both the average climate and climate variability change in concert, there may be unexpected population sensitivities to dual changes in mean and variance (9).

Understanding these potentially complex sensitivities of populations to climate change can inform predictions on future population sizes to guide management and conservation decisions (10,11). Moreover, the integration of life history or other traits with climatically driven abundance trends could uncover generalizable patterns in the traits and strategies that drive species sensitivities to mean and variance in climate (12,13). Therefore, when analyses detect historical influences of climate on population abundance with unique sensitivities among species or populations, a key next step is to evaluate the proximate mechanisms predicting these species-specific

climate sensitivities (14), which can improve understanding of the factors that predict whether a population will be a winner or loser under climate change.

Although relationships between climatic variables and the population abundances of multiple species can detect population-level climate sensitivities to climate means, variance, and their interaction (15,16), studies on species' sensitivities to interannual variability are rare. Such work requires long-term data collected either over naturally variable climate conditions or within direct manipulations of interannual variability (17–19). For example, the influences of climate and land cover on bird abundance in the central United States were strongly species-specific, indicating that shifting climate conditions will likely produce ecological winners and losers. For instance, northern bobwhites and prairie warblers were predicted to increase in abundance in a future climate, whereas blue-winged warblers were predicted to decline (20). The integration of species traits could allow researchers to generalize these patterns for other bird communities. Recent work on plant and animal communities in California identified winners and losers during a severe drought; plants and birds were less affected by drought than mammals. Importantly, the small mammal species that declined most during the drought were largest in size, while rarer, smaller-bodied species increased in abundance (21). These results suggest that species' traits or other characteristics, such as body size, could provide generalizable predictors of populations or species that will be winners or losers under climate change.

Physiology, functional traits, and diet composition related to resource acquisition or reproduction, such as body size, may be valuable predictors of

species sensitivities to changes in climate variability, as well as to a changing mean climate or single extreme event, such as drought (22,23). Functional traits, defined as measurable properties of organisms that strongly influence fitness, can reflect alternative strategies for coping with limited resources and stressful environmental conditions, including climate-related stressors (24). Functional traits have effectively predicted how plant species respond to climate or other environmental perturbations, such as soil nutrient overloads. For example, uncommon plant species increased in abundance under nutrient additions when traits, such as specific leaf area, leaf toughness and thickness, plant height, or leaf turnover favored rapid growth under fertilization, proving a direct link between traits and species-specific sensitivity to resource addition (25). For animals, hibernation can allow an escape from cold winters, both torpor and hibernation can help small mammal species avoid heat and mortality under food scarcity, and nests or burrows can shelter against predators and stabilize the microclimate (26,27). A traits-based approach may return robust generalizations that cannot be achieved from the detection of winner and loser species alone, opening a window on global predictions that could circumvent the need for long-term data collection on every species in order to predict future dynamics (28–30).

Relatively few studies have linked animal traits to species' sensitivities to environmental change, and no prior studies, to our knowledge, have considered animal traits as predictors of sensitivity to interannual *variability* in climate. Example animal studies that have linked traits to species' sensitivities have demonstrated that seabirds with larger wingspans could forage further for resources than small

wingspan species, and larger bodied bird species expend less metabolic energy than smaller bodied species; therefore larger body size made these taxa less sensitive to sea surface temperatures (31,32). Additionally, aquatic macroinvertebrates with drought-resistant eggs or drought-tolerant larvae can withstand drought and heat more than those lacking resistance or tolerance traits (33), and bee body size and physiological tolerance to heat and desiccation predicted bee responses to changing mean aridity (Kazenel et al., in review) (34). Among the few mammal studies linking species traits and sensitivities to climate variables, a global analysis of non-volant mammals revealed less sensitivity to changes in mean annual temperatures for species that reproduced and recruited rapidly or used diverse habitat types (35). Studies thus far have primarily focused on average trait values and changes in average climate, but variability in the traits or strategies of a population, (i.e., reflecting flexibility in diet composition or phenology), may be very important to animal success in a variable environment. The use of life history and foraging traits and strategies as predictors of population sensitivities to long-term climate has high potential to uncover robust, generalizable projections about the factors that define winners versus losers under future climates (36).

The goals of our study were to characterize the physiology, functional traits, and foraging strategies (including diet composition) of a diverse community of small mammals to evaluate these variables as predictors of climate sensitivities from a long-term 30 year dataset of abundance records in two common dryland ecosystems of central New Mexico (37,38). We generally hypothesized that certain traits and strategies would make species more or less sensitive to mean aridity (change in the

mean climate), and others would allow species to benefit (or decline) from increased variance in aridity (39–41). **Hypotheses** (Table 1). Specifically, for **physiology**, (i) we predicted species with larger average body mass would be more sensitive to mean aridity because they require more resources to build body mass when drier mean climate limits resource availability (42). In contrast, we predicted (ii) small body mass and (iii) higher variation in percentage body fat should both increase the potential benefits of variance in aridity because smaller species and those that can nimbly adjust stores of body fat can quickly capitalize on resource booms (43–46). For **life history traits**, we predicted that species with rapid reproductive strategies, (iv) such as producing more litters per year, should benefit from an increase in variance in aridity because they can rapidly increase population abundance during resource pulses because increases are not constrained by low reproductive effort (47). For **diet composition**, (v) we predicted that granivorous species would benefit from variance in aridity because during wet years, resource pulses can greatly increase production of highly nutritious seeds (48–50). Similarly, (vi) species consuming a higher mean percentage of annual plants or (vii) with higher dietary $\delta^{13}\text{C}$ stable isotope signatures (indicative of more C_3 than C_4 plants in their diet) would benefit from variance in aridity because extreme rain pulses create large pulses in annual C_3 forbs (51–53). Additionally, (viii) species with heavy investment in seed-caching should be *less* sensitive to increasing mean aridity because they store seeds, providing a buffer against resource scarcity (51,54), and (ix) caching species should benefit more from variance in aridity than non-caching species because they can secure and store resource pulses. Finally, (x) we predicted that

species with more variable $\delta^{15}\text{N}$ stable isotope values, indicating more flexibility in trophic position, should benefit from an increase in variance in aridity because diet plasticity provides opportunities to capitalize on seasonal pulses in resources by consuming both plants and arthropods (55–57).

METHODS

Small Mammal Abundance

Small mammals have been censused as part of the Sevilleta Long-Term Ecological Research (LTER) program since 1989 (58,59). Twice annually (May and October) until Oct 2021, we set Sherman live-traps (7.62x9.53x30.48cm); H.B. Sherman Traps, Inc.; Tallahassee, FL) with rolled oats as bait across six webs. Each web has twelve 100-m transects containing 12 traps, which radiate out from a central point that contains four central traps facing each cardinal direction; each web has 148 total traps (Parmenter et al. 2003)(60). Three webs are in Chihuahuan Desert shrubland dominated by *Larrea tridentata* (creosote bush), and three webs are in Chihuahuan Desert grassland dominated by *Bouteloua eriopoda* (black grama grass). The traps were typically opened for three consecutive nights per trapping event (range 2-4 consecutive nights, $x = 3.12$). We measured morphometrics of captured animals including body, tail, ear, and hindfoot length, reproductive condition (scrotal testes, lactating and/or pregnant females, or non-reproductive), and body mass (g). Data were collected for target (diurnal) rodent species (listed in Table 2). All capture and handling methods adhered to ethical guidelines and were approved by the University of New Mexico Animal Care and Use Committee (#19-200940-MC) and occurred under a U.S. Fish and Wildlife Special Use permit

(#SEV_LTER_2022_1). We estimated consumer densities per km² by dividing the number of unique individuals for each species captured during each trapping event by the total number of trapping nights and by web size (0.031416 km²). We also used a second dataset that consisted of two trapping webs located along the shrubland-grassland ecotone adjacent to the long-term core webs described above. Trapping occurred monthly during the new moon from March–November from 2013–2021, dependent on weather conditions. All SEV-LTER data are publicly available through the Environmental Data Initiative (EDI) data portal.

Physiology

We used measurements of body mass (g) from the seasonal dataset to calculate average body mass and coefficient of variation (*CV*) for each species. Body condition was measured during the monthly trapping bouts (2013–2021) via quantitative magnetic resonance (QMR) using an EchoMRI™ 3-in-1 composition analyzer (Echo Medical Systems, Houston, TX) (61). Specifically, we used measurements of body fat (g) to estimate the percentage of body fat for each individual by dividing measured fat by body mass. From these data, we calculated mean percentage body fat in the spring (March–June) or fall (July–Nov) to match the seasonal rodent abundance estimates, and we used these data to calculate the *CV* in percent body fat as a standardized metric of variability in the trait for each species (Appendix C. Tables 3–8).

Functional Traits

We compiled information on small mammal functional and life history traits from the published literature (descriptions provided in Table 3). Type of seed

caching was grouped into the following levels: 2=larder caching, 1=scatter caching, 0=does not cache (62–64) and represented animals varying in their types of food storage and allocation (65,66). We used average litter size (range: 2 - 5 offspring per litter; 62,67–70) and number of litters per year (range: 1–9 litters per year; (62,64,67,68,71,72) to capture differences in reproductive strategies (36,73). Breeding season length (6 months versus 12 months; (62,68,69,74,75) captured reproductive capacity (Appendix C. Tables 3-8).

Diet Composition and Foraging Strategies

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values give information on diet composition for small mammals (46,54). Specifically, lower values of $\delta^{13}\text{C}$ indicate more consumption of C_3 plants versus C_4 plants due to their unique carbon signatures: C_3 plants have lower $\delta^{13}\text{C}$ values (-9 to -19‰) than C_4 plants (-22 to -35‰)(76). Low values of $\delta^{15}\text{N}$ indicate a lower trophic position, based on assumptions about the trophic fractionation of $\delta^{15}\text{N}$ (77). We measured carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values from blood plasma which were collected once a month from March through November spanning from spring of 2013 through fall of 2021(78). Blood plasma was separated from red blood cells via centrifugation at 10,000 rpm for 10 minutes to determine small mammal diet within two-week time frames (46,79,80). Blood plasma was then directly pipetted into pre-weighed tin capsules, which were dried at 50°C for >24 h and weighed again to estimate plasma mass. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured with a Costech 4010 elemental analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (Bremen, Germany) at the University of New Mexico Center for Stable

Isotopes (Albuquerque, NM). Isotope data are reported in delta notation (δ) as parts per mil (‰): $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where R_{sample} and R_{standard} are the relative ratios of the heavy and light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in a sample and standard respectively. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are referenced against international standards Vienna Pee-Dee belemnite (VPDB) and atmospheric nitrogen (AIR) respectively. Measured isotope values were calibrated against an international reference standard (USGS-40) using internal reference materials run alongside plasma samples to correct for instrument drift within and between analytical runs. Repeated measurements of reference materials yielded an analytical precision of (\pm SD) of $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. From these data, we determined mean and CV of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each species.

We also compiled data from the literature to index other aspects of diet (Appendix C. Tables 3-8). Degree of granivory was ranked into the following levels: 4=consumed almost exclusively, 3=primary food source, 2=common fallback food, 1=occasionally consumed (63,68,81,82). Using data from a prior examination of gut contents from the two habitats where rodents were captured at the Sevilleta (63), we included information on the estimated average percentage of annuals plants in each species' diet ranging from 0-100%, split by habitat and across seasons (spring and fall) (63,83,84) to analyze the cost or benefit of a higher percentage of annuals over perennials (Tables S2-S7). Finally, our predictors that were not normally distributed as determined using Shapiro-wilk testing were log-transformed to obtain normal distribution and de-emphasize outliers(93), full details provided in Table 8.

Climate Context

The Sevilleta LTER supports a network of 10 meteorological (met) stations, and we used the closest station to our trapping webs that had climate data collected since 1989. Met station 40 was within 5 km of both sets of trapping webs (-106.691, 34.3592)(85). We used an integrated aridity index that incorporates both heat temperature and precipitation into a single variable, the Standardized Precipitation Evaporation Index (SPEI). We used daily temperature and precipitation data to estimate SPEI, here after referred to as the aridity index at seasonal (6-month) or annual (12-month) temporal scales (86,87). SPEI6 ended May 31 or Sept 30, corresponding to the spring or fall seasonal trapping bouts. SPEI12 ended Sept. 30 at the end of the water year (<SPEI>package cran.r-project.org/package=SPEI) (88).

Climate Sensitivity Functions

Using a set of 25 candidate mixed effects general linear models (Appendix D, Table 9), we determined the best model for each mammal species x ecosystem combination (i.e., for each mammal species' population) using model selection procedures on models fit with maximum likelihood. Our model set included models with time lags to account for appropriate response times for small mammal abundance to track to climate-altered food resources. Time lags were created by incorporating a one-step time lag into each suite of models, both for the 6-month (lag was 6 months) and 12-month SPEI integrations (lag was one year) that corresponded to our small mammal trapping seasons. Candidate models also differed in the shape of the climate sensitivity function. We considered models with a linear function to detect a response only to mean aridity (see Fig. 1, linear). We

considered models with nonlinear response curves (quadratic or cubic) to detect a response to mean aridity and variance in aridity (see methods in Rudgers et al. 2018 for more details and Fig. 1, nonlinear) (9). All models included season (spring/fall) and web identity as random effects with temporal autocorrelation (autoregressive 1 was best fit) to account for repeated measures on the same web. All models were fit by maximum likelihood using the function `lme` in the package `<nml>` (89). Within the candidate model set for each mammal population, we evaluated and ranked models using the second order Akaike Information Criterion (AIC_c) (90). From the top model, we extracted parameter estimates as metrics of each population's Climate Sensitivity Function (CSF) see also (91) using the R function `emmeans` in the package `emmeans` (92). CSF parameters are the coefficients of the best fit CSF for each individual population (species x ecosystem combination) including the linear, quadratic, and cubic coefficient estimates and their SE. If a population's best model was linear, then quadratic and cubic terms were set to zero, and if the quadratic model was best, then the cubic parameter estimate was set to zero.

Predictors of Climate Sensitivity

Our goal was to generalize beyond species identities by evaluating physiology, traits, and diet composition as **predictors** of population sensitivities to natural variation in climate over our 31-year time series. Therefore, we built statistical models to evaluate the relative importance of each physiological, diet, or behavioral strategy to test hypotheses. We used a separate model for grassland vs. shrubland mammal species to account for the likelihood that traits and strategies differed between the two ecosystem types. Models took the form of CSF parameter~

species' strategy or trait value, using each population as a data point (grassland, $N=15$ species, shrubland $N=15$ species). These regression models were weighted by the accuracy of climate sensitivity functions for each species' population by using the SE of the CSF parameter estimate as a model weight (Table 10). To evaluate the relative importance of traits and strategies as predictors of climate sensitivity, we also ranked the candidate set of trait/strategy models within each ecosystem, using the second order Akaike Information Criterion (AIC_c) (90). Additionally, we compared meaningful pairs of uncorrelated predictors in multiple regression analyses, but no pairs significantly predicted climate sensitivities, likely due to lack of statistical power in the multivariate trait analysis. We used R statistical software for all data analyses (88).

RESULTS

Climate Sensitivity Functions

More than half (60%) of the 30 small mammal populations had nonlinear climate sensitivities, indicating that population abundance was sensitive to variance in the aridity index (Fig. 1; Table 11). Of these variance-sensitive populations, thirteen populations (43%) had complex climate sensitivity functions that predict abundance is sensitive to the interaction between a drier climate and increasing variance in the aridity index. Of the populations with complex sensitivity functions, five were projected 'winners' under a future drier and more variable climate because they had a cubic response that predicted an increase in abundance with larger interannual climate variance under a hot and dry climate. In contrast, eight populations were projected 'losers' under the future drier and more variable climate

because they had a cubic response that predicted a decrease in abundance with higher interannual climate variance under a hot and dry climate.

In addition, for five populations (17%) both mean and variance were important, but did not interactively influence population abundance as indicated by nonlinear, but monotonic sensitivities to climate variance, making it difficult to designate as a winner or loser because of future uncertainty on whether mean or variance in climate will be the stronger climate change. Two of these populations were predicted to benefit from increasing variance in aridity, but also decline under a drier mean climate because of their convex-up but upward trending response curves (Fig. 1; Table 12). Two populations were predicted to benefit from increasing variance in aridity and increase under a drier future climate (Fig. 1; Table 12), because of their convex-up but downward trending quadratic response curves. Finally, one population (Fig. 1; Table 12), was predicted to decline with increasing variance in aridity and decline under drier climate because of the concave-down and upward trending quadratic response curve (*Peromyscus truei*, shrubland population).

The remaining populations (40%) had linear climate sensitivities that predict changes in abundance with only changes in mean aridity (Fig. 1; Table 12). Nine populations were predicted to lose under a drier future climate, because they had a positive linear response to SPEI, indicating they have higher abundance when the climate is cold and wet (high or positive SPEI), while three populations were predicted to win under a drier future climate, because they had a negative linear response to SPEI, indicating they have higher abundance when the climate is hot and dry (low or negative SPEI).

Some species had unique climate sensitivities in the grassland versus shrubland habitats (Fig. 2). For example, the best fit model for *Onychomys arenicola* (Mearn's grasshopper mouse) in the grassland was significant linear sensitivity to the annual aridity index, suggesting a decrease in population size when the climate was hot and dry (Fig. 2A). The shrubland population also showed a linear response to the annual aridity index, suggesting an increase in population size when the climate was hot and dry (Fig. 2B).

Predictors of Sensitivity to Climate Mean

The only factors that were significant predictors of small mammal species' climate sensitivities to **mean aridity** (linear component of climate sensitivity) were average body mass and CV body mass. We predicted that species with larger average body mass would be more sensitive to mean aridity because they require more resources to build body mass when drier mean climate limits resource availability (42). Results indicated that average body mass was an important predictor of climate sensitivity, correlating with larger species increasing in abundance with a hotter and drier climate in the shrubland habitat (negative linear, Fig. 3A). The largest species in both habitats was *Dipodomys spectabilis* (Banner-tailed kangaroo rat; body mass ~123 g), which increased in abundance with a drier mean climate in the shrubland. The smallest species in both habitats, *Perognathus flavus* (Silky pocket mouse; body mass ~7 g), declined in abundance with a drier mean climate in the shrubland. Unexpectedly, variation in body mass was an important predictor of climate sensitivity, correlating with species that have higher variation decreasing in abundance with a hotter and drier climate in the shrubland

habitat (negative linear, Fig. 2A). The species with the highest variation in body mass was *Dipodomys spectabilis* ($CV=3.42$), which increased in abundance with a drier mean climate in the shrubland. The species with the lowest variation in body mass across both habitats, *Perognathus flavus* ($CV=0.194$), decreased in abundance with a drier mean climate in the shrubland.

Predictors of Sensitivity to Climate Variance

The following factors were significant predictors of small mammal species' climate sensitivities to **variance in aridity** (quadratic component of climate sensitivity), in order of importance: average body mass, CV body mass, litters per year, CV in percentage body fat during the spring season and percentage of annual plants in diet (Table 13). We predicted that species with smaller body mass would benefit from variance in aridity because small species can more easily capitalize on resource booms and build their body mass than larger species (43–46). Results indicated that average body mass was also an important predictor of climate sensitivity to variability, correlating with larger species decreasing in abundance with an increasingly variable climate in both habitats (negative quadratic, Fig. 2A), where *Dipodomys spectabilis* did not benefit while *Perognathus flavus* benefited from variance in aridity for both populations.

Unexpectedly, results also indicated that variation in body mass was also an important predictor of climate sensitivity to variability, correlating with species with higher variation decreasing in population abundance with an increasingly variable climate in both habitats (negative quadratic, Fig. 2A-B), where *Dipodomys spectabilis* did not benefit while *Perognathus flavus* benefited from variance in aridity

for both populations. Interestingly, because the larger species with more variation in body mass increased in population abundance under a hot and dry climate, but also did not benefit from increasingly variability, it is hard to designate if they will win or lose under both an increasingly drier and more variable climate.

However, for physiological predictors we had predicted that species with higher variation in percentage body fat would benefit from variance in aridity because species that can nimbly adjust stores of body fat can quickly capitalize on resource booms (43–46). Results indicated that variation in percentage body fat in the spring season was an important predictor of climate sensitivity, correlating with species with higher variation increasing in abundance with an increasingly variable climate in both habitats (positive quadratic, Fig.3D). The species with the highest variation in percentage body fat across both habitats in the spring was *Perognathus flavus* ($CV= 0.0005$), which benefited from variability for both their grassland and shrubland populations. The species that had the lowest variation across both habitats in the spring was *Peromyscus truei* (Pinon mouse, $CV=0.0000127$), which did not benefit from variability for both their grassland and shrubland populations.

For functional traits or life history strategies, we predicted that species that produce more litters per year would benefit from variance in aridity because they can rapidly increase population abundance during resource pulses since increases are not constrained by low reproductive effort (47). Results indicated that the number of litters per year was an important predictor of climate sensitivity, correlating with species that produce more litters per year decreasing in abundance with an increasingly variable climate in both habitats, (negative quadratic, Fig. 3C). The species with the most litters

per year was *Reithrodontomys montanus* (Plains harvest mouse, ~9 litters/year), which did not benefit from climate variability in either grassland or shrubland habitats. In contrast, the species that had the least litters per year was *Perognathus flavus* (~1 litter/year), which benefited from variability in both grassland and shrubland populations.

For foraging strategies, we predicted that species with a higher percentage of annuals in their diet, would benefit from an increase in variance in aridity because extreme rain pulses create large pulses in annual C₃ forbs (51–53). Results indicated that having a higher percentage of annuals in the shrubland habitat was an important predictor, correlating with species that have a higher percentage of annual plants in their diets increasing in population abundance when the climate was increasingly variable (positive quadratic, Fig. 3E). One of species that has the highest percentage of annuals in their diet in the shrubland was *Perognathus flavus* (90%), which benefited from variability for their shrubland population in the spring. The species that had the least percentage of annuals in their diets was *Dipodomys spectabilis* (7%), which did not benefit from variability for their shrubland population in the spring.

Notably, the primary species that had populations that contained predictors of their climate sensitivities included *Dipodomys spectabilis*, *Perognathus flavus*, *Peromyscus truei* and *Reithrodontomys montanus*. Interestingly, of these four species, some had populations where their abundances responded to climate more instantaneously by increasing or decreasing within the same year those certain climate conditions occurred and included both populations of *Perognathus flavus*

and *Reithrodontomys montanus*, but only the *Dipodomys spectabilis* grassland population and *Peromyscus truei* shrubland population. Conversely, the *Dipodomys spectabilis* shrubland population and *Peromyscus truei* grassland populations had a delayed response, with their populations increasing or decreasing a year after certain climate conditions occurred indicating that there are species and population-level differences in how quickly these population sizes can change in response to climatic conditions. For all the predictors we examined, none correlated with the sensitivity of population abundance to the interaction between climate mean and variance, because no relationships with cubic parameters of CSFs were significant. The following predictors were also tested but were not statistically significant for any parameters of climate sensitivity ($P > 0.05$): % fat (spring and fall) and CV fall, caching, litter size, breeding season length, $\delta^{13}\text{C}$ values and CV, $\delta^{15}\text{N}$ values and CV, granivory, % annuals in grassland (spring and fall) and % annuals in shrubland (fall).

DISCUSSION

Climate Sensitivities of Dryland Small Mammal Species

Our results demonstrated that by incorporating a nonlinear approach to linking population abundance to long-term climate data, that most small mammal species' population abundances are sensitive to either mean aridity or variance in aridity. To our knowledge, this is the first study to detect such potential interactive effects of dual changes in the mean and variance in aridity on small mammal abundance using time series data because we looked at multiple aspects of climate including lagged effects and evaluated multiple species on a population-level. There

was a surprising sensitivity to variance, with 60% of populations having nonlinear sensitivities, suggesting that mean and variance interactions could be important to predicting the future. We speculate that one of the quadratic responses was not observed because for that type of response, mean and variance would not benefit populations, and in this highly variable and stochastic environment, mean and variance should always have additive effects on this community's population abundance. The 30% of populations that were more sensitive to mean aridity, with decreased population abundances when the climate was hotter and drier, and the 27% of populations more sensitive to a variance in aridity, with decreased population abundances when the climate was more variable, had physiological, trait and diet composition predictors that drove their sensitivities making them ecological 'losers'. For the predictors that drove these climate sensitivities, 73% of the populations had traits that predicted a sensitivity to variance in aridity, while only 27% predicted a sensitivity to mean aridity.

Predictors of Sensitivity to Climate Mean

Fewer traits were correlated with a sensitivity to mean aridity. Because these species are desert animals adapted to a warmer climate, their traits have potentially made these species more sensitive to variability than mean aridity. Conversely, there may be other traits and factors that were not included that may have predicted more sensitivities to mean aridity (47,94). Typically, trait-based analysis can be limited by the number of traits analyzed, and therefore expanding upon this study with more traits could reveal more sensitivities to mean aridity. For example, of our predictors we did not have any that were life history traits, rather only predictors that

were physiological and diet or foraging strategies were significant. Therefore, incorporating more life history traits may potentially provide more results.

Of the few significant predictors correlated with a sensitivity to climate mean, two correlated with a sensitivity to both mean aridity and variance in aridity, body mass and variation in body mass.

Physiology. *Dipodomys spectabilis* (Banner-tailed kangaroo rat), had the highest average body mass and largest variation of body mass, while *Perognathus flavus* (Silky pocket mouse) had the smallest mass and lowest variation in mass. During more variable seasons, small mammal species that can shift to storing food resources as body fat, will have the strongest survival advantage, therefore, size can negatively affect the larger species because they require more resources to build-up their body mass, which is reflected in larger species also having the highest variability in body mass (54). The negative effect of body size on survivorship for small mammals was documented in a study evaluating the reduction of average body size in a community of small mammals in Portal, AZ, that historically also had *Dipodomys spectabilis* and *Perognathus flavus* as their largest and smallest species, respectively (95,96). Ultimately, within Portal, AZ, a catastrophic disturbance resulted in local extirpation of the largest species, and because energy use was shown to not be uniform across body size in small mammal communities despite utilizing similar resources, the smallest species was able to rebound while the largest did not (42,97). Researchers have long speculated that there is relationship between mammal body size and/or mass with a sensitivity to increasing climate change, but some studies have been unable to link this trait to climate sensitivity

(98,99), or for example, did not find a relationship between interspecific differences in pika mass and climate sensitivity (100), therefore our results have expanded upon these existing studies to provide more exhaustive evidence of the generalization that animal species with larger body masses and higher variation may be susceptible to population declines from variance in aridity, but increases from a drier mean climate, making it difficult to designate them as winners or losers under a future a drier and more variable climate.

Predictors of Sensitivity to Climate Variance

Our remaining three significant predictors correlated with sensitivity to variance in aridity alone, variation in percentage body fat in the spring season, number of litters produced per year, and percent of annuals in diet in the shrubland in the spring season.

Physiology

Average percentage body fat varied by season, ranging from 4-9% in the spring and 4-11% in the fall. *Perognathus flavus* had the highest variation in their percentage body fat in the spring while *Peromyscus truei* (Pinon mouse) had the lowest variation in percentage body fat. *Perognathus flavus* has highly individualized diets that enable them to switch to more specialized diets to minimize inter- and intra-specific competition during years when their abundance increases dramatically (79,80). For example, the Sevilleta's monthly LTER trapping dataset revealed that this species will increase their individual dietary specialization by expanding their foraging strategies to include more resources when resource availability declines, enabling them to have high dietary plasticity that could mirror fluctuations in fat

content. Having this dietary advantage allows for flexibility therefore, when variance in aridity increases they are able to adapt to forage on the increased diversity of different food sources, expanding their individual niche width thereby increasing their fitness (46). Additionally, this species has a relationship between food ration and torpor with lower body mass resulting in longer torpor. Under colder and wetter conditions, more food resources exist enabling this species to increase their initial cache storage which will help them increase their abundance by avoiding longer torpor if they have enough food availability to increase their average percent body fat. Lower variation would indicate the inability to increase their average body mass, so the higher food availability increases the variation, and lower availability from increases in mean aridity supports the evidence that this species declined in abundance with mean aridity but benefited from variance in aridity (101).

Peromyscus truei had the least amount of variation in percentage body fat across both seasons, and because they do not cache food resources but instead store their food resources endogenously, they have consistently higher body fat, indicating they work to always maintain a certain level of fat content (102). Seasonal food resource constraints can impact other taxa, such as ungulates encountering weather seasonality that is common in the Mediterranean where poorer feeding conditions will later shift to enhanced vegetative conditions, thereby providing animals with highly variable body conditions between these shift in resource pulses (103).

Therefore, our results further support the generalization that larger variation in percentage body fat will allow animal species to benefit from variance in aridity which provides necessary pulses in resources to counteract low resource conditions

from increasing mean aridity.

Functional traits

Number of litters produced within a year (breeding season) greatly varied by species. *Reithrodontomys montanus* (Plains harvest mouse) had the highest average number of litters produced per year, while *Perognathus flavus* had the lowest number of litters per year. Species that are polyestrous and can reproduce multiple times a breeding season often wait for optimal environmental conditions to produce ample food resources prior to entering reproduction (94,104). However, if climate variability will make conditions unpredictable and less productive then species may delay reproduction, reducing the number of litters produced in a breeding year or skip reproduction altogether, with studies finding that litters per season will decrease with drought (47). Our results support this notion by detecting a much greater cost to species reliant on producing more litters to maintain population size. With an increasingly more variable climate, species that decrease vital reproductive effort because they are shorter-lived species may see abundance declines with an variance in aridity, relative to the longer lived species that can either maintain their population size through less reproductive effort under drought conditions or can reduce their metabolism until optimal conditions are met in later seasons or years (47,105). Our results can help support other analyses that have tried to examine effects of drought on reproduction, helping enhance predictions on species such as copperhead snakes that are known to be reliant on optimal climate conditions for reproduction but have reproductive output that is difficult to determine despite being iteroparous by providing evidence that species more reliant on heavy reproductive output may decrease in

abundance with a more variable climate (106).

Foraging Strategies

P. flavus had one of the highest percentage of annuals in the spring season in the shrubland in their diets compared with *Dipodomys spectabilis* that had one the the lowest percentages. *Perognathus flavus* relies heavily on foraging annual forbs over perennial grasses and shrubs in comparison to the other species in this community (63). Annual forbs can delay their germination during years that precipitation is more variable, helping them to remain a reliable food source for *Perognathus flavus* in spite of a variable climate, thereby creating a unique advantage for this species to benefit from increasing variance in aridity (53,107). Though increasing mean aridity and variance in aridity may be negatively impacting native and perennial grass species, our results have detected a benefit from a reliance on annual forbs with increasing climate variability indicating animal species such as lagomorphs that primarily utilize annuals may increase in population abundance (108).

Though all five of our predictors correlated with a sensitivity to variance in aridity, and 40% of these predictors correlated with an importance of mean and variance, we did not have any significant predictors to detect a sensitivity to the *interaction* of mean and variance in aridity on species population abundance. Therefore, we still lack good predictors of sensitivity to the most complex and difficult part of the future to predict. Future considerations should evaluate a larger variety of predictors to further inform projections on population abundances and individual sensitivities to the interaction of mean and variance in aridity.

CONCLUSION

By integrating physiological, functional traits, and diet measurements with 30 years of small mammal abundance data over highly variable natural climate conditions we revealed that species with certain physiologies (larger mass and larger variation in mass) were less sensitive to aridification in mean climate, and that species with certain physiologies, traits and diet composition (smaller mass, smaller variation in mass, larger variation in percentage body fat in the spring, less litters per year, and higher percentage of annual plants in diet) benefited from increases in the variance of aridity. Our results show the multitude of complex variables allowing these populations to be resilient to climate variability and boom in 'good' years in two common dryland ecosystem types in the southwestern US. Through these generalizations, we have gained important insights into which life history traits and strategies are the best predictors of species' past, present, and future climate sensitivities.

APPENDICES

Appendix A. Hypotheses Testing

Appendix B. Target Species List

Appendix C. Predictor Descriptions and Data

Appendix D. Climate Sensitivity Function Model Structure and Parameters

Appendix E. CSF Model Selection and Predictor Response Rankings

Appendix A. Hypothesis Testing

Table 1. Hypothesis tests for traits and strategies as predictors of the sensitivity of small mammal abundance to mean or variance in aridity, based on climate sensitivity functions determined from long-term abundance and climate data. Predictions that were supported by data analysis as statistically significant ($P < 0.05$) are indicated in bold; *n/a* indicates a prediction for which there was no strong *a priori* hypothesis from the literature.

	Predictor of sensitivity	Hypothesized to benefit under	Support
(i)	Large body mass	Lower mean aridity	no
(ii)	Small body mass	Greater variance in aridity	yes
(iii)	Variation in body fat	Greater variance in aridity	yes
(iv)	Litters per year	Great variance in aridity	no
(v)	Granivory	Greater variance in aridity	no
(vi)	Annual plants	Greater variance in aridity	yes
(vii)	Higher $\delta^{13}\text{C}$ values	Greater variance in aridity	no
(viii)	Caching	Greater mean aridity	no
(ix)	Non-caching	Lower variance in aridity	no
(x)	Variation in $\delta^{15}\text{N}$ values	Greater variance in aridity	no
(<i>n/a</i>)	Variation in body mass	<i>n/a</i> (greater mean and variance)	yes

Appendix B. Target Species List

Table 2. Species code definitions for our target species from Order Rodentia selected for this analysis; this table includes each species code which are similar to USDA plant codes that use the first 2 letters of the genus and first 2 letters of the species for ease of data recording during the identification process, mammalian Family name, mammalian Genus name, mammalian Species name and the common vernacular name for each species.

Species Code	Family	Genus	Species	Common Name
DIME	Heteromyidae	<i>Dipodomys</i>	<i>merrami</i>	Merriam's Kangaroo Rat
DIOR	Heteromyidae	<i>Dipodomys</i>	<i>ordii</i>	Ord's Kangaroo Rat
DISP	Heteromyidae	<i>Dipodomys</i>	<i>spectabilis</i>	Banner-tailed Kangaroo Rat
PGFL	Heteromyidae	<i>Perognathus</i>	<i>flavescens</i>	Plains Pocket Mouse
PGFV	Heteromyidae	<i>Perognathus</i>	<i>flavus</i>	Silky Pocket Mouse
ONAR	Cricetidae	<i>Onychomys</i>	<i>arenicola</i>	Mearn's Grasshopper Mouse
ONLE	Cricetidae	<i>Onychomys</i>	<i>leucogaster</i>	Northern Grasshopper Mouse
PEBO	Cricetidae	<i>Peromyscus</i>	<i>boylii</i>	Brush Mouse
PEER	Cricetidae	<i>Peromyscus</i>	<i>eremicus</i>	Cactus Mouse
PELE	Cricetidae	<i>Peromyscus</i>	<i>leucopus</i>	White-footed Mouse
PEMA	Cricetidae	<i>Peromyscus</i>	<i>maniculatus</i>	American Deer Mouse
PENA	Cricetidae	<i>Peromyscus</i>	<i>nasutus</i>	Northern Rock Mouse
PETR	Cricetidae	<i>Peromyscus</i>	<i>truei</i>	Pinyon Mouse
REME	Cricetidae	<i>Reithrodontomys</i>	<i>megalotis</i>	Western Harvest Mouse
REMO	Cricetidae	<i>Reithrodontomys</i>	<i>montanus</i>	Plains Harvest Mouse

Appendix C. Predictor Descriptions and Data

Table 3. Small mammal predictor descriptions that include the name of the predictors that were selected for this analysis, the category of each predictor, and the description of the empirical data and/or ranking process used for the analyses.

Predictor	Category	Description	References
Caching behavior	Trait	2=deep caching, 1=shallow caching, 0=does not cache	(62–64)
Insectivory	Diet	4=insects almost exclusive food source, 3= primary food source, 2= common fallback food, 1= occasionally consumed	(81)
Granivory	Diet	4=seeds almost exclusive food source, 3=primary food source, 2=common fallback food, 1=occasionally consumed	(63)(82)(68) (81)
Annuals	Diet	percentages of annuals in gut content by habitat and season	(63)
Body mass	Physiology	average mass (g)	(59)
% Fat	Physiology	average (%) fat; split across spring and fall	(78)
CV body mass	Physiology	CV of body size in grams	(59)
CV % body fat	Physiology	CV of percentage body fat	(78)
$\delta^{13}\text{C}$	Diet	average isotopic carbon values	(78)
$\delta^{15}\text{N}$	Diet	average isotopic nitrogen values	(78)
CV $\delta^{13}\text{C}$	Diet	CV of isotopic carbon values	(78)
CV $\delta^{15}\text{N}$	Diet	CV of in isotopic nitrogen values	(78)
Litter size	Trait	average litter size	(68)(70)(69) (67)(62)
Breeding season length	Trait	total number of breeding months (from literature and SEV empirical data)	(78)((68)(62) (69)(74)
Litters per year	Trait	average distinct litters per year	(62)(67)(71)(64) (72)

Table 4. Physiology data

species	avg. body mass	CV body mass	avg. % fat spring	avg. % fat fall	CV fat spring	CV fat fall
DIME	41.34795	0.880777	5	4	3E-05	7.81E-05
DIOR	48.36669	1.151165	4	5	3.25E-05	0.001212
DISP	123.0126	3.42001	5	4	0.000127	3.59E-05
ONAR	19.63737	1.033166	8	6	7.09E-05	7.68E-05
ONLE	21.37797	1.578341	6	5	0	6.20E-05
PEBO	22.11739	0.790485	NA	NA	NA	NA
PGFL	8.55	0.711014	6	NA	NA	NA
PGFV	7.292902	0.193607	6	6	0.000488	0.000242
PEER	19.57786	0.695042	7	6	0	6.67E-05
PELE	22.21649	0.837333	NA	11	NA	1.41E-05
PEMA	18.20833	1.62233	NA	NA	NA	NA
PENA	20.94444	0.314176	NA	NA	NA	NA
PETR	21.35093	0.497571	9	7	1.27E-05	3.17E-06
REME	10.4	0.565255	8	7	3.39E-05	3.21E-05
REMO	8.311475	0.292706	NA	8	NA	0

Table 5. Functional Trait data

species	Degree of caching	Litter size	Litters/year	Breeding season length
DIME	1	3	2	12
DIOR	1	4	2	8
DISP	2	2	2	12
ONAR	0	4	3	9
ONLE	0	4	4	6
PGFL	2	4	2	6
PGFV	2	4	1	8
PEBO	0	3	3	12
PEER	0	2	3	12
PELE	0	5	3	8
PEMA	0	5	8	12
PENA	0	3	3	6
PETR	0	4	8	10
REME	0	4	8	10
REMO	0	4	9	12

Table 6. Diet composition (foraging strategy) data

species	granivory	% annuals grassland spring	% annuals grassland fall	% annuals shrubland spring	% annuals shrubland fall
DIME	3	NA	NA	32	33
DIOR	3	62	88	NA	0
DISP	2	7	NA	7	NA
ONAR	1	36	67	86	50
ONLE	2	NA	NA	NA	NA
PGFL	4	NA	NA	NA	NA
PGFV	4	90	83	90	0
PEBO	3	NA	NA	NA	NA
PEER	2	NA	NA	NA	NA
PELE	3	NA	NA	NA	NA
PEMA	3	NA	NA	NA	NA
PENA	3	NA	NA	NA	NA
PETR	3	100	NA	100	100
REME	3	NA	NA	33	NA
REMO	3	NA	NA	NA	NA

Table 7. Diet composition data

species	$\delta^{13}\text{C}$	$CV \delta^{13}\text{C}$	$\delta^{15}\text{N}$	$CV \delta^{15}\text{N}$
DIME	-19.3472	-0.27814	8.982564	0.264908
DIOR	-18.9853	-0.31182	8.319016	0.181352
DISP	-20.1731	-0.2918	7.724173	0.239161
ONAR	-18.7115	-0.20424	9.38317	0.115404
ONLE	-19.0438	-0.04608	9.65625	0.063167
PGFL	NA	NA	NA	NA
PGFV	-20.471	-0.22185	8.221889	0.144936
PEBO	-19.176	-0.37894	8.166667	0.17619
PEER	-18.6259	-0.24499	8.12963	0.223187
PELE	-14.525	-0.51441	8.225	0.189894
PEMA	NA	NA	NA	NA
PENA	NA	NA	NA	NA
PETR	-20.4778	-0.16041	8.267151	0.285731
REME	-19.1382	-0.29329	8.794186	0.132318
REMO	-18.5167	-0.34733	9.7	0.237457

Table 8. Log transformed data

species	mass	cvmass	cvfatspr	cvfatfall	lpy	cache	gran	littersize	blength
DIME	1.616	-0.055	-4.522	-4.110	0.301	0.301	0.477	0.477	1.079
DIOR	1.685	0.061	-4.490	-2.917	0.301	0.301	0.477	0.602	0.903
DISP	2.090	0.534	-3.896	-4.450	0.301	0.477	0.301	0.301	1.079
ONAR	1.293	0.014	-4.150	-4.110	0.477	0.000	0.000	0.602	0.954
ONLE	1.330	0.198	NA	-4.210	0.602	0.000	0.301	0.602	0.778
PGFL	0.932	-0.148	NA	NA	0.301	0.477	0.602	0.602	0.778
PGFV	0.863	-0.713	-3.311	-3.617	0.000	0.477	0.602	0.602	0.903
PEBO	1.345	-0.102	NA	NA	0.477	0.000	0.477	0.477	1.079
PEER	1.292	-0.158	NA	-4.180	0.477	0.000	0.301	0.301	1.079
PELE	1.347	-0.077	NA	-4.850	0.477	0.000	0.477	0.699	0.903
PENA	1.260	0.210	NA	NA	0.903	0.000	0.477	0.699	1.079
PENA	1.321	-0.503	NA	NA	0.477	0.000	0.477	0.477	0.778
PETR	1.329	-0.303	-4.900	-5.500	0.903	0.000	0.477	0.602	1.000
REME	1.017	-0.248	-4.470	-4.490	0.903	0.000	0.477	0.602	1.000
REMO	0.920	-0.534	NA	NA	0.954	0.000	0.477	0.602	1.079

Appendix D. Climate Sensitivity Function Model Structure and Parameters

Table 9. Model structure for 25 candidate mixed effects general linear models

Model
lme(SPECIES~season.fs,random=list(~1 web_id),data=smg,method="ML")
lme(SPECIES~SPEI_6+season.fs,random=list(~1 web_id,~1 year_f),data=smg,method="ML")
update(SPECIES1, ~. +I(SPEI_6^2))
update(SPECIES2, ~. +I(SPEI_6^3))
lme(SPECIES~SPEI_6lag+season.fs,random=list(~1 web_id,~1 year_f),data=smg,method="ML",na.action=na.omit)
update(SPECIES1L, ~. +I(SPEI_6lag^2))
update(SPECIES2L, ~. +I(SPEI_6lag^3))
lme(SPECIES~SPEI_6+season.fs,correlation=corAR1(form=~time),random=list(~1 web_id,~1 year_f),data=smg,method="ML")
update(SPECIES1AR, ~. +I(SPEI_6^2))
update(SPECIES2AR, ~. +I(SPEI_6^3))
lme(SPECIES~SPEI_6lag+season.fs,correlation=corAR1(form=~time),random=list(~1 web_id,~1 year_f),data=smg,method="ML")
update(SPECIES1LAR, ~. +I(SPEI_6lag^2))
update(SPECIES2LAR, ~. +I(SPEI_6lag^3))
lme(SPECIES~SPEI_12+season.fs,random=list(~1 web_id,~1 year_f),data=smg,method="ML")
update(SPECIES1, ~. +I(SPEI_12^2))
update(SPECIES2, ~. +I(SPEI_12^3))
lme(SPECIES~SPEI_12lag+season.fs,random=list(~1 web_id,~1 year_f),data=smg,method="ML",na.action=na.omit)
update(SPECIES1L_12, ~. +I(SPEI_12lag^2))
update(SPECIES2L_12, ~. +I(SPEI_12lag^3))
lme(SPECIES~SPEI_12+season.fs,correlation=corAR1(form=~time),random=list(~1 web_id,~1 year_f),data=smg,method="ML")
update(SPECIES1AR_12, ~. +I(SPEI_12^2))
update(SPECIES2AR_12, ~. +I(SPEI_12^3))
lme(SPECIES~SPEI_12lag+season.fs,correlation=corAR1(form=~time),random=list(~1 web_id,~1 year_f),data=smg,method="ML")
update(SPECIES1LAR_12, ~. +I(SPEI_12lag^2))
update(SPECIES2LAR_12, ~. +I(SPEI_12lag^3))

Table 10. CSF parameters

species	habitat	intercept	season	integration	lag	linear	quadratic	cubic
DIME	grass	0.031639	-0.00706	6	n	-0.01031	0	0
DIME	shrub	1.685131	0.122981	12	n	-3.00E-05	-0.11374	-0.00032
DIOR	grass	0.472426	0.156132	12	n	0.115347	-0.06085	-0.07344
DIOR	shrub	0.180688	0.004676	12	y	-0.13619	-0.04572	0.03011
DISP	grass	0.557356	-0.02289	12	n	-0.00776	-0.01159	0.014525
DISP	shrub	0.410038	0.008501	12	y	-0.00741	-0.03266	0.020518
ONAR	grass	0.124218	-0.02164	12	n	0.000915	0	0
ONAR	shrub	0.186032	-0.0333	12	n	-0.00702	0	0
ONLE	grass	0.004105	0.003377	12	n	-0.01024	0.007451	0
ONLE	shrub	0.015025	-0.01396	12	n	0.003155	0.013238	-0.0107
PGFL	grass	0.001876	-0.00013	6	n	0.000739	0	0
PGFL	shrub	0.001876	-0.00013	6	n	0.002088	0.002715	-0.00194
PGFV	grass	0.62634	0.203216	12	n	-0.06622	0.224371	0
PGFV	shrub	0.490685	-0.06169	12	n	0.110138	0.169876	-0.06245
PEBO	grass	-0.00024	0.013904	6	n	0.003521	0	0
PEBO	shrub	0.013218	0.018925	12	n	0.023774	0	0
PEER	grass	0.003013	-0.00278	6	n	-0.00152	0	0
PEER	shrub	0.131439	-0.13643	6	y	0.012717	0.034487	0
PELE	grass	0.0197	-0.00322	12	n	0.010585	0	0
PELE	shrub	0.026674	0.01578	12	n	0.018922	0	0
PEMA	grass	0.008335	-5.05E-06	6	n	0.000198	0	0
PEMA	shrub	0.009206	9.89E-05	12	y	-0.01493	-0.00042	0.00414
PENA	grass	-0.00282	0.004519	6	y	-0.00713	0.002028	0.003965
PENA	shrub	0.001747	0.000903	6	n	0.000601	0	0
PETR	grass	-0.00395	0.029734	6	y	-0.01323	0.00242	0.010204
PETR	shrub	0.034835	0.014834	12	n	0.008997	-0.01742	0
REME	grass	-0.00028	0.006766	6	n	0.000699	0.005503	0
REME	shrub	0.012456	0.012341	6	n	0.002342	0	0
REMO	grass	0.008769	-0.00328	12	n	-0.00266	0.006816	0.0053
REMO	shrub	0.002872	0.000905	6	n	-0.00888	0.001447	0.004696

Appendix E. CSF Model Selection and Predictor Response Rankings

Table 11. Top model by population

species	habitat	top model
DIME	grass	linear (-)
DIME	shrub	cubic (-)
DIOR	grass	cubic (-)
DIOR	shrub	cubic (+)
DISP	grass	cubic (+)
DISP	shrub	cubic (+)
ONAR	grass	linear (+)
ONAR	shrub	linear (-)
ONLE	grass	quadratic (+)
ONLE	shrub	cubic (-)
PGFL	grass	linear (+)
PGFL	shrub	cubic (-)
PGFV	grass	quadratic (+)
PGFV	shrub	cubic (-)
PEBO	grass	linear (+)
PEBO	shrub	linear (+)
PEER	grass	linear (-)
PEER	shrub	quadratic (+)
PELE	grass	linear (+)
PELE	shrub	linear (+)
PEMA	grass	linear (+)
PEMA	shrub	cubic (+)
PENA	grass	cubic (+)
PENA	shrub	linear (+)
PETR	grass	cubic (+)
PETR	shrub	quadratic (-)
REME	grass	quadratic (+)
REME	shrub	linear (+)
REMO	grass	cubic (+)
REMO	shrub	cubic (+)

Table 12. Total CSF population count

model	population count
linear (+)	9
linear (-)	3
quadratic (+ down)	2
quadratic (+ up)	2
quadratic (- up)	1
quadratic (- down)	0
cubic (-)	8
cubic (+)	5

Table 13. Predictor responses and rankings

Trait	Location	Linear Response	Quadratic Response	Cubic Response	Ranking of Importance	p-value
(Log) average body mass	Grass	NS	S (-)	NS	1	p=0.0043
(Log) average body mass	Shrub	S (-)	S (+)	NS	1	p = 0.0323 and quad p=0.0013
(Log) CV body mass	Grass	NS	S (-)	NS	2	p= 0.0014
(Log) CV body mass	Shrub	S (-)	S (-)	NS	2	linear p=0.0395 and quad p=0.0056
(Log) litters per year	Both	NS	S (-)	NS	3	p= 0.0270
(Log) CV % body fat (spring)	Both	NS	S (+)	NS	4	p=0.0001
% annual plants	Shrub	NS	S (+)	NS	5	p= 0.0265

Linear: (+) declines under mean aridity; (-) = inclines under mean aridity

Quadratic: (+) = benefits from variance in aridity; (-) cost from variance in aridity

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FIGURES

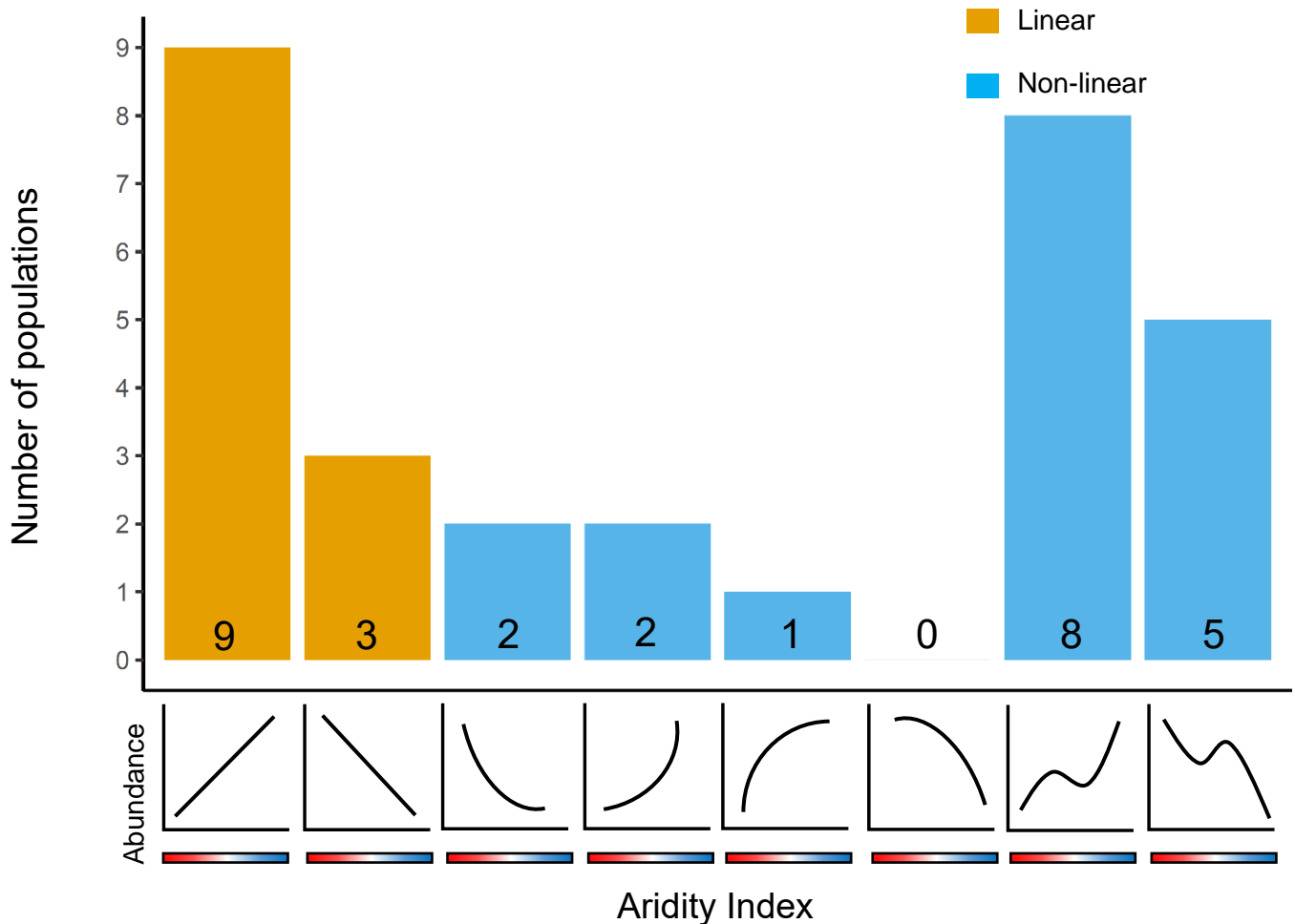


Figure 1. Number of populations with each type of Climate Sensitivity Function (CSF) for small mammal species in grassland or shrubland habitats of the Sevilleta National Wildlife Refuge (SEV-LTER Program data). Each CSF shape is represented by an accompanying cartoon illustrating the general relationship between population abundance and the SPEI Aridity Index, which ranges from hot/dry (negative SPEI - red) to cold/wet (positive SPEI - blue). Small mammal populations with linear sensitivities are predicted to change only with changes in the mean aridity index, but not the variance. Populations with nonlinear CSFs are predicted to be sensitive to changes in interannual variance in the aridity index, and, depending on the CSF shape, may or may not also be sensitive to a change in the mean.

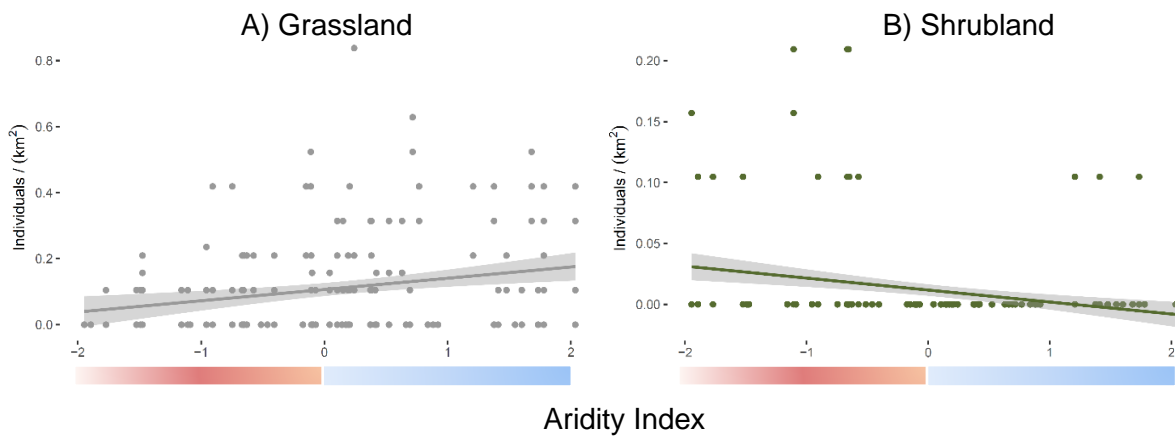


Figure 2. Climate sensitivity functions for *Onychomys arenicola* in two habitat types at the Sevilleta NWR. In the grassland (2A), abundance had a linear relationship with mean aridity indicating this population increased under cool/wet conditions and decreased under hot/dry conditions. In the shrubland (2B), their abundance also had a linear relationship with aridity but indicated this population decreased under cool/wet conditions and increased under hot/dry conditions.

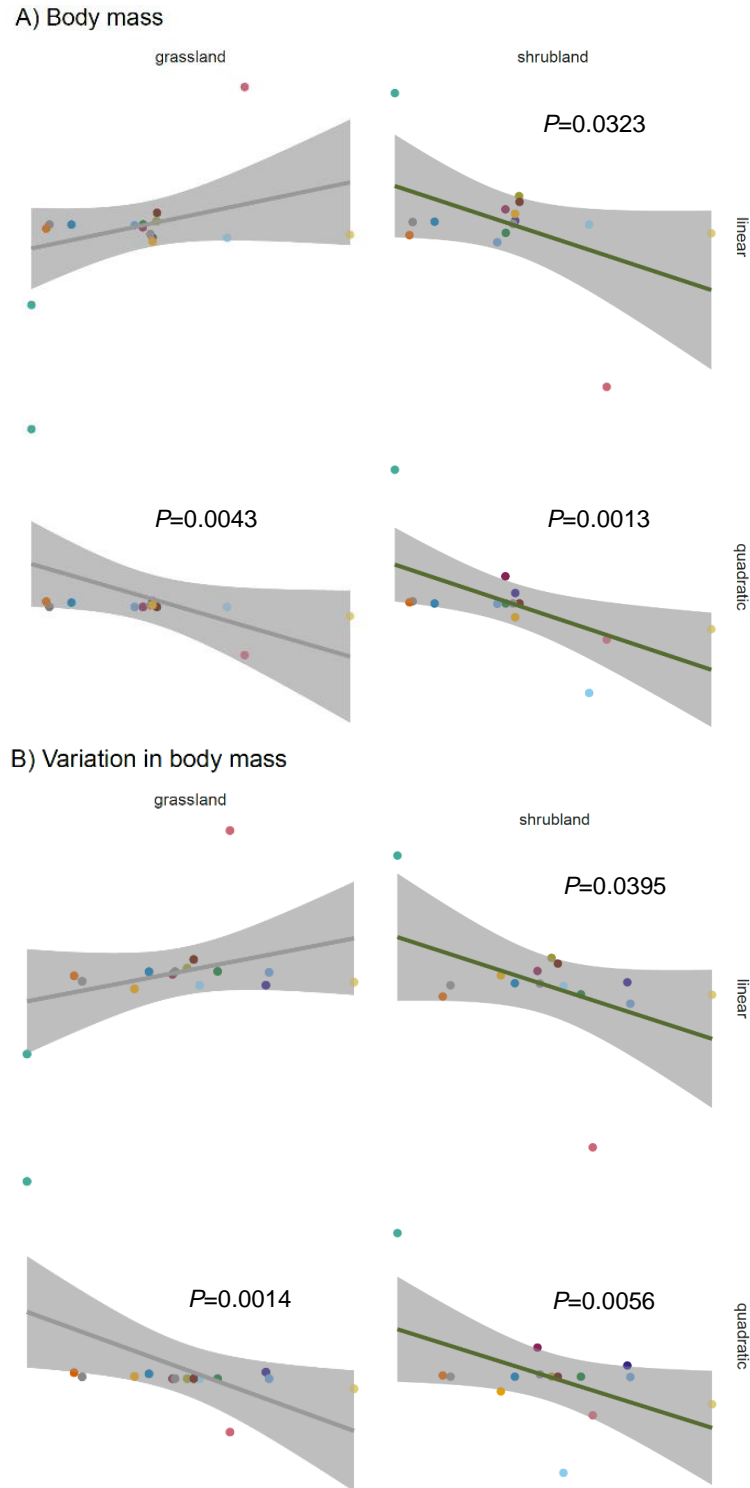
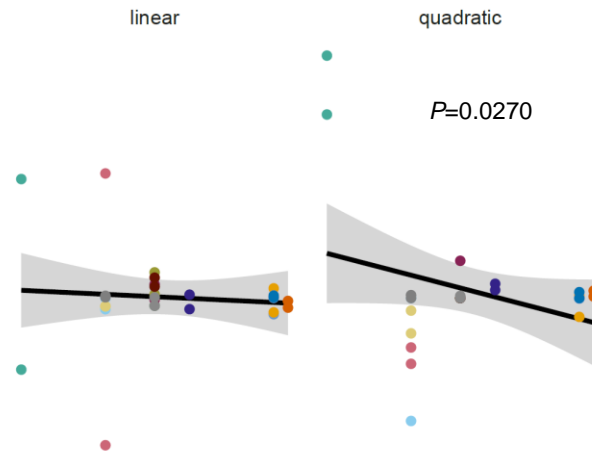
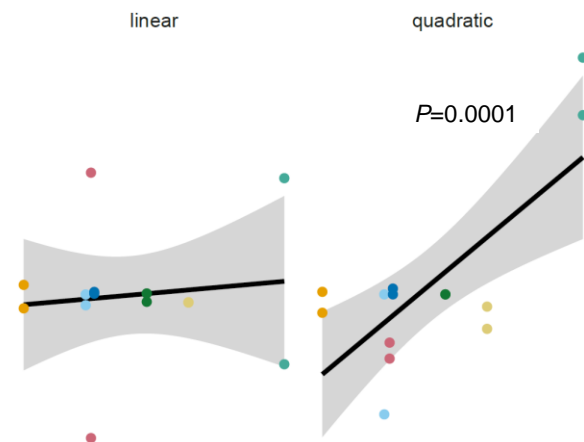


Figure 3. Small mammal traits that significantly predicted the sensitivity of population abundance to mean aridity (linear term from climate sensitivity function) and variance (quadratic) in grassland or shrubland habitat. Plots with significant ($P < 0.05$) trait relationships with linear terms of climate sensitivity functions indicate the trait increased (positive slope) or reduced (negative slope) the sensitivity of population abundance to declines under mean aridity. Traits with significant trait relationships with quadratic terms of climate sensitivity functions indicate the trait increased population abundance under greater variance in aridity (quadratic > 0 , convex) or reduced abundance under greater variance in aridity (quadratic < 0 , concave).

C) Litters per year



D) Variation in % fat spring



E) % annual plants shrubland

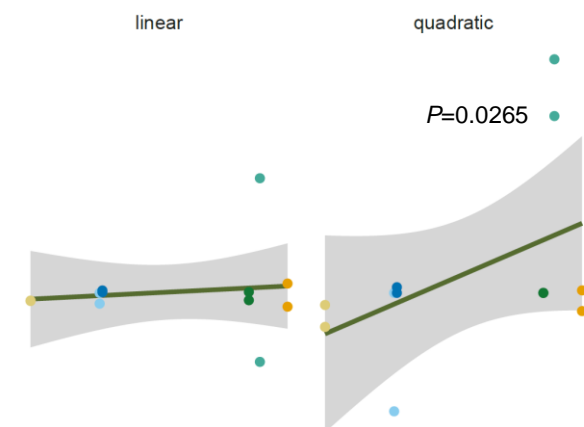


Figure 4. Small mammal traits that significantly predicted the sensitivity of population abundance to only variance in aridity in (quadratic) in both habitats. Plots with significant ($P < 0.05$) trait relationships with quadratic terms of climate sensitivity functions indicate the trait increased population abundance under greater variance in aridity (quadratic > 0 , convex) or reduced abundance under greater variance in aridity (quadratic < 0 , concave).