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Long-term changes in abundances of Sonoran Desert lizards reveal complex responses to climatic variation

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Abstract

Understanding how climatic variation affects animal populations and communities is essential for addressing threats posed by climate change, especially in systems where impacts are projected to be high. We evaluated abundance dynamics of five common species of diurnal lizards over 25 years in a Sonoran Desert transition zone where precipitation decreased and temperature increased across time, and assessed hypotheses for the influence of climatic flux on spatiotemporal variation in abundances. We repeatedly surveyed lizards in spring and summer of each year at up to 32 sites, and used hierarchical mixture models to estimate detection probabilities, abundances, and population growth rates. Among terrestrial species, abundances of a short-lived, winter–spring breeder increased markedly by an estimated 237%–285% across time, while two larger spring–summer breeders with higher thermal preferences declined by up to 64%. Abundances of two arboreal species that occupy shaded and thus sheltered microhabitats fluctuated but did not decline systematically. Abundances of all species increased with precipitation at short lag times (1–1.5 years) likely due to enhanced food availability, but often declined after periods of high precipitation at longer lag times (2–4 years) likely due to predation and other biotic pressures. Although rising maximum daily temperatures (T_{max}) are expected to drive global declines of lizards, associations with T_{max} were variable and weak for most species. Instead, abundances of all species declined with rising daily minimum temperatures, suggesting degradation of cool refugia imposed widespread metabolic or other costs. Our results suggest climate warming and drying are having major impacts on lizard communities by driving declines in species with traits that augment exposure to abiotic extremes and by modifying species interactions. The complexity of patterns we report indicates that evaluating and responding to the influence of climate change on biodiversity must consider a broad array of ecological processes.

KEYWORDS

Aridlands, climate change, ectotherms, *N*-mixture models, population trends, precipitation, Sonoran Desert, temperature

1 | INTRODUCTION

Understanding how climatic variation influences the dynamics of animal populations and communities is important for assessing threats posed by climate change and guiding conservation and adaptation strategies. In arid and semiarid environments (aridlands), climate change could have particularly severe effects on communities by increasing the frequency of extreme events and because the velocity of climate change may be higher in these often resource-limited systems (Easterling et al., 2000; Kerr, 2008; Loarie et al., 2009; Smith, 2011). In aridlands, small changes in precipitation can have large and rapid effects on plant productivity and exert a complexity of direct and indirect effects on communities at varying trophic levels and lag times (Beatley, 1969; Holmgren et al., 2006; Knapp et al., 2015; Lima, Stenseth, & Jaksic, 2002). When coupled with biotic interactions such as competition and predation (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013), small changes in precipitation and temperature can have large effects on animal communities, which has broad implications given aridlands cover >40% of land on Earth but have been the focus of few long-term studies.

In arid southwestern North America, recent evidence of climate change is pervasive and expected to intensify (Cook, Ault, & Smerdon, 2015; Garfin, Jardine, Merideth, Black, & LeRoy, 2013; Overpeck & Udall, 2010; Seager et al., 2007). Such signs include extreme drought and temperature events that have dominated regional climates recently and been linked to marked declines in vital and population growth rates in the few vertebrate populations that have been monitored recently (Barrows, 2006; Cruz-McDonnell & Wolf, 2015; Flesch, 2014; Flesch, Hutto, van Leeuwen, Hartfield, & Jacobs, 2015; Gedir, Cain, Harris, & Turnbull, 2015; Lovich et al., 2014; Moses, Frey, & Roemer, 2012; Zylstra, Steidl, Jones, & Averill-Murray, 2013). Although such patterns include both ectotherms and endotherms, climate flux could have particularly severe effects on ectotherms such as reptiles because they are active only within narrow sets of thermal conditions that vary with the physiology and behavior of individual species (Angilletta, 2009; Deutsch et al., 2008), and because ectotherms can incur large metabolic costs as the environment warms (Huey et al., 2009; Kearney, Shine, & Porter, 2009). In sunny, open environments, diurnal lizards sustain preferred body temperatures by selecting sun, shade, and substrates of varying temperatures (Cowles & Bogert, 1944; Huey, 1982), which moderates but may not eliminate the effects of rising environmental temperatures (Huey et al., 2009; Sinervo et al., 2010). Such behaviors involve retreating to thermal refugia to avoid lethally high temperatures (Dunham, 1993; Sheldon, Yang, & Tewksbury, 2011; Sinervo et al., 2010) and to limit the costs of maintenance metabolism during periods of seasonal dormancy and nocturnal inactivity (Bennett, 1982; Dunham, Grant, & Overall, 1989; Huey, 1982). Thus, for lizards, rising temperatures linked to climate change could constrain foraging, growth, reproduction, and other critical life-history processes in ways that reduce vital and population growth rates and increase extinction risks (Huey et al., 2009; Kearney, 2013; Kearney et al., 2009; Levy, Buckley, Keitt, & Angilletta, 2016; Sinervo et al., 2010). Evaluating these threats and understanding how they are influencing communities, however, requires long-term, multispecies datasets that are rarely available.

Despite the importance of understanding how climatic variation is influencing vertebrate communities, extracting accurate inferences from field data can be challenging, particularly for ectotherms. This is because local variation in weather can have large effects on both individual activity, and thus detection probability during sampling, and also critical life-history processes, and thus spatiotemporal changes in true abundance (Cowles & Bogert, 1944; Dunham et al., 1989). Therefore, differentiating the effects of weather on activity and abundance should improve our understanding of spatiotemporal changes in population size and factors that influence these dynamics (Kéry et al., 2009). Although such challenges are not new, analytical tools that explicitly consider the detection process when estimating temporal changes in abundances of unmarked animal populations—the only practical approach for monitoring many populations—have only recently been developed (Dail & Madsen, 2011; Kéry et al., 2009).

Here, we assess long-term abundance dynamics of five common species of diurnal lizards in the Sonoran Desert, where recent drought and extreme temperature events could be having pervasive effects. Lizards provide a useful focal system for assessing ecological responses to climatic variation because (1) they are relatively abundant and observable, (2) temperature influences activity in complex ways depending on the behavior and physiology of each species (Huey, Pianka, & Schoener, 1983; Milstead, 1967; Vitt & Pianka, 1994), and (3) in aridlands, precipitation can have marked bottom-up (via food supply) and top-down (via predation) effects on populations (Anderson, 1994; Lima et al., 2002; Rosenzweig, 1968; Walther, 2010). Thus, climatic variation could influence species differently depending on their physiology, microhabitat (e.g., terrestrial vs. arboreal), or trophic position (Huey and Tewksbury, 2009; Kearney et al., 2009; Sinervo et al., 2010), which varied among the five species we considered. Our goals were to (1) evaluate temporal variation in abundances of multiple species of lizards and estimate any systematic long-term trends, (2) evaluate hypotheses for the influence of spatiotemporal variation in local weather on population dynamics, and (3) assess how interspecific differences in species' traits contributed to dynamics.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied lizards in Organ Pipe Cactus National Monument (OPCNM), which is in the central Sonoran Desert in southern Arizona, USA. Since the late 1980s, lizards have been the focus of an intensive monitoring effort that, to our knowledge, provides the longest spatially replicated annual time-series data for a vertebrate community in arid southwestern North America. Because monitoring spanned prolonged warm-wet phases of the El Niño Southern Oscillation (ENSO; 1991–1995, 1997–1998), and recent extreme drought and temperature events, this system provides a useful opportunity to assess the influence of climatic variation on a vertebrate assemblage in arid southwestern North America.

Organ Pipe Cactus National Monument is a large (133,882 ha) reserve situated in a broad transition zone where desert woodlands of the Arizona Upland subdivision of the Sonoran Desert shift to more xeromorphic shrub-dominated desertscrub of the Lower

Colorado River Valley subdivision (Bowers, 1980; Brown, 1982; Figure 1). This transition is driven by decreasing elevation and increasing aridity from east to west and provides a useful context for monitoring because changes in populations and communities may occur first and be focused in transition zones where some species approach the limits of their ecological tolerances and where biotic and abiotic factors drive variation in community structure and composition (Barrows et al., 2016). Vegetation in the Arizona Upland subdivision is dominated by short open woodlands and denser thorn-scrub-like associations of leguminous trees such as foothill paloverde (*Parkinsonia microphylla*), ironwood (*Olneya tesota*), and velvet mesquite (*Prosopis velutina*) mixed with cacti, shrubs, perennial grasses, and annual forbs (Brown, 1982). Lower Colorado River desertscrub is dominated by more open associations of shrubs and subshrubs such as creosote bush (*Larrea tridentata*) and bursage (*Ambrosia* sp.), with trees largely restricted to riparian zones along dry streambeds. Riparian areas in both subdivisions are dominated by woodlands of mesquite, catclaw acacia (*Senegalia greggii*), and blue paloverde (*Parkinsonia florida*). Vegetation cover and structural complexity are often greater on rocky slopes and in canyons and riparian zones, and decline from east to west (Bowers, 1980). Typical of the Sonoran Desert, annual precipitation is bimodal and includes a summer monsoon in July–Sept and winter storms that are of greater intensity during the warm phase of ENSO.

We considered five species of lizards that are common in the Sonoran Desert. These focal species have varying life histories and differ broadly in microhabitat, phenology, and other traits (Pianka et al., 1979; Pianka, 1993; Appendix S1). The tiger whiptail (*Aspidoscelis tigris*) and zebra-tailed lizard (*Callisaurus draconoides*) are exclusively terrestrial but differ in foraging mode, whereas the smaller side-blotched lizard (*Uta stansburiana*) is mainly terrestrial but also occurs on arid slopes where it is saxicolous (Pianka 1966). The smaller ornate tree lizard (*Urosaurus ornatus*) and larger desert spiny lizard (*Sceloporus magister*) are mainly arboreal but the later species also exhibits terrestrial habits (Pianka, 1986; Vitt, Van Loben Sels, & Ohmart, 1981). Whereas all species primarily consume arthropods, adults of larger species will consume smaller individuals of small species. In addition, all species are active during the warm season, but

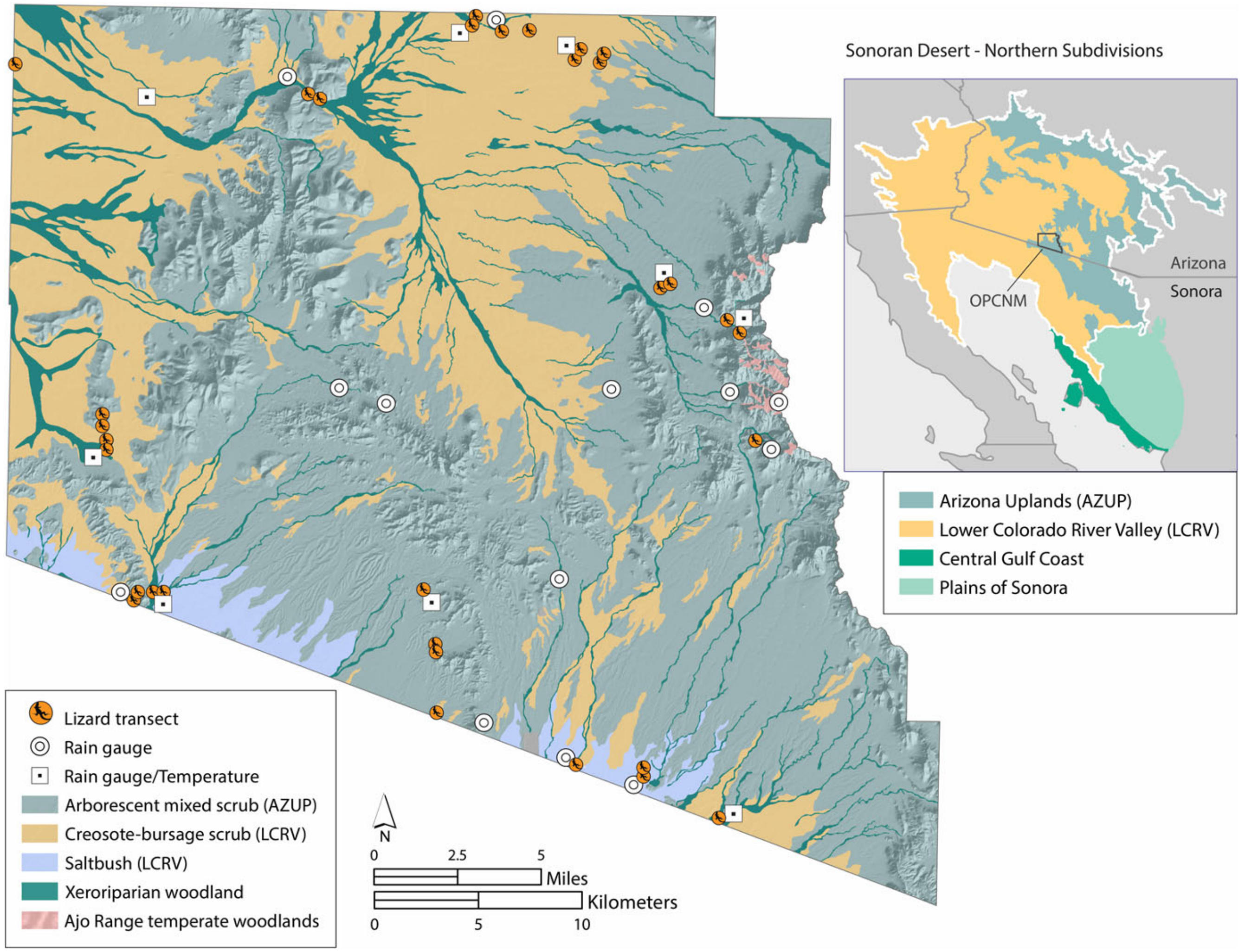

FIGURE 1 Distribution of survey transects for lizards, weather stations, and vegetation communities in Organ Pipe Cactus National Monument. Inset map shows the distribution of four of the six subdivisions of the Sonoran Desert and the transitional nature of the study area

the side-blotched lizard and tree lizard are also active in winter. Breeding by the side-blotched lizard peaks in late winter and spring (Asplund & Lowe, 1964), whereas other species are spring–summer breeders (Appendix S1). In more arid regions west of OPCNM, the side-blotched lizard comprises an increasing proportion of lizard communities, the tree lizard is largely absent except in gallery forest, and other species decrease in abundance (Rosen, 2007; Vitt & Ohmart, 1978).

2.2 | Design

We sampled lizards by repeatedly surveying the same line transects across time. We placed transects across OPCNM to represent gradients in elevation, soils, vegetation, and hydrology (Figure 1). In 1989, we established 19 transects, 100–300 m in length, and increased effort to 26 transects in 1994 and 32 in 2001. Between 1989 and 2013, we surveyed transects during 1, or rarely 2 ($n = 20$) days each spring (5 April–23 June) and summer (12 July–13 October), but not all transects were surveyed each year. To ensure effort coincided with periods of peak above-ground activity of each species, we surveyed during warm calm conditions. During each daily visit, we repeatedly surveyed transects 3–8 times beginning as early as 38 min after local sunrise and continuing as late as 6.8 hr after sunrise.

To survey lizards, one observer slowly walked transects and recorded the time, species, and when known, age class (juvenile, subadult, and adult) of each individual observed from the center line. Transects were initially walked in directions away from the rising sun to augment visibility and only individuals observed within 7.5 m of transects were recorded because initial efforts indicated that most detections were within this distance. We recorded the time and used standard mercury thermometers to measure air (at 1-m above ground) and ground (soil surface in the sun) temperatures at the start and end of each repeated survey. Three experienced observers completed 99.6% of surveys.

We used two general analytical approaches to address our goals. First, to describe the dynamics of populations, we used a modeling approach that explicitly considered the detection process. This approach accounted for the fact that temporal variation in observed lizard counts could be driven by short-term differences in activity levels, variation in detection probability among habitats, as well as changes in true abundance. Second, to assess the influence of climatic flux on populations, we developed a small set of research hypotheses to explain these processes based on the biology of the system, constructed statistical models to represent hypotheses, and used model selection procedures to assess evidence among models.

2.3 | Population dynamics

To estimate population growth rates and abundances, we used *N*-mixture models generalized for open populations (Dail & Madsen, 2011; Royle, 2004). These hierarchical models use spatial and temporal replication in count data to jointly estimate abundance and detection probability, and attribute observation error to the inability to detect all individuals during sampling (Zipkin et al., 2014). We used a simplified version of the Dail-Madsen *N*-mixture model parameterized for exponential population growth described as follows:

$$N_{i1} \sim \text{Poisson}(\gamma) \tag{1}$$

$$N_{it} \sim \text{Poisson}(\lambda, N_{it-1}) \tag{2}$$

$$y_{ijt} \sim \text{Binomial}(N_{it}, p) \tag{3}$$

where N_{it} is abundance at site i during year t, γ is mean initial abundance, λ is the finite rate of increase, y_{ijt} are counts for the j^{th} repeated survey, and p is detection probability. In using this approach, we assumed populations were closed among repeated daily surveys but open between seasons and among years. To model the observation process, we considered the following potential covariates of detection probability: (1) dominant hydrologic regime based on vegetation differences (upland and riparian), (2) topographic formation (rocky slope, bajada, and valley floor) or soil texture (fine sand or silt and coarse pebbles or rocks), (3) vegetation formation (desert shrubland, desert woodland, and xeroriparian woodland), (4) linear and curvilinear (quadratic or x^2) terms for ground or air temperature (for terrestrial and arboreal species, respectively), (5) Julian day, (6) time after sunrise, and (7) monthly precipitation. To estimate parameters, we used the pcountOpen function in the *unmarked* library in R (Fiske & Chandler, 2011; R Development Core Team, 2013). We used Akaike's information criterion adjusted for small sample sizes (AIC$_c$) to select optimal observation models for each species, and then fit process models. We analyzed data for each season separately because populations of some species in each season are the results of reproduction in different years, which made the assumption of closure between seasons unrealistic. We excluded observations of juveniles that had not recruited into the adult or subadult populations, and from transects where each focal species was never detected.

2.4 | Climatic variation and hypotheses

To describe regional climatic variation across time and space, we used data on precipitation (*P*) from 17 weather stations and temperature (*T*) from 9 of those stations located throughout OPCNM (Figure 1). To quantify climatic variation experienced by lizards, we matched each transect with the most similar weather station based on proximity and elevation. Missing values were estimated with linear mixed effects models (LMEM) similar to Equation 4, which included the location and elevation of weather stations as covariates and data from 6 additional stations located at similar positions along the slope gradient to account for cold-air inversions.

To assess temporal trends in *P* and *T*, we used LMEM described as follows:

$$y_{it} = (\beta_0 + b_{0i}) + \beta_1 x_{it} + \varepsilon_{it}, \ \varepsilon_{it} \sim N(0, \sigma^2) \tag{4}$$

where y_{it} is a vector of the climatic attribute of interest, β_0 is an intercept for the population, b_{0i} is a vector of random intercepts for each weather station, β_1 is a trend parameter for a fixed year effect, x_{it} indicates the year of observation, and ε_{it} is an error term that has a normal distribution with a mean of zero and variance σ^2 that measures observation error. To adjust for temporal autocorrelation, we considered various autoregressive moving-average structures (p, q = 0–3) and used restricted maximum likelihood (REML) and AIC$_c$ to determine optimal structures. In all cases, autocorrelation functions confirmed the independence of residuals. We fit models with the *nlme* library in R (Pinheiro, Bates, DebRoy, & Sarkar, 2014).

To assess the influence of climatic attributes on spatiotemporal variation in lizard abundance, we developed four research hypotheses. Local variation in P and T could affect abundance directly through energetic and thermoregulatory constraints, or indirectly by affecting food or heterospecific predators and competitors. In arid environments, P often drives rapid increases in plant biomass, seed production, and insect abundance, which bolsters food availability for small vertebrates, increasing their abundance at short lag times and predator abundance at longer lag times (Beatley, 1969; Holmgren et al., 2006). Thus, the *prey enhancement hypothesis* predicts lizard abundance in year t increase with P in year $\approx t$–1. Similarly, the *predation hypothesis* predicts lizard abundance in year t decreases with P at longer lag times or is highest at moderate P but declines at low and high P. High average maximum daily temperatures (T_{max}) during the warm season could restrict foraging and other lizard activities thereby reducing reproduction or survival, and hence abundance the following year (Kearney et al., 2009; Sinervo et al., 2010). Thus, the *heat stress hypothesis* predicts high T_{max} during the warm season reduces abundance the following year. Low average minimum daily temperatures (T_{min}) could have varying influences on lizards. Low T_{min}, for example, could restrict emergence from winter dormancy, foraging, and ovarian processes in ways that reduce body condition, growth, reproduction, or survival, and hence abundance at lag times of $\approx$1–1.5 years, especially for winter-active species (Asplund & Lowe, 1964). Alternatively, high T_{min} could reduce the quality of low-temperature thermoregulatory refugia and increase energetic costs of maintenance metabolism during dormancy or nocturnal inactivity in ways that diminish energy reserves for reproduction and hence abundance the following year (Zani, 2008; Zani et al., 2012). Thus, these *cold-effects hypotheses* predict decreasing or increasing T_{min} reduces abundance at lag times of $\approx$1–1.5 years. Although extreme low T_{min} could cause freeze mortality and reduce abundance at shorter lag times, reptiles' super-cooling capacity and tendency to overwinter at depths below ground that provide strong thermal buffering suggests this is unlikely (Cowles, 1941; Lowe, Lardner, & Halpern, 1971; but see Tinkle, 1967; Vitt, 1974), which exploratory analyses confirmed.

Despite similarities among species, interspecific differences in breeding phenology, age of maturity, and other traits should influence the seasonal periods and lag times of associations between abundances and P or T. Thus, in developing models to represent hypotheses, we first evaluated the effects of weather during different seasonal periods and over a small set of likely lag times, which we based on the biology of each species (Appendix S1). For the *prey enhancement hypothesis*, we considered P during the prior fall (Sept–Oct of prior year; P_{fall}), cool season (Nov 2 years prior to Apr of prior year; P_{cs}), warm season (May–Oct of prior year; P_{ws}), and annually ($P_{cs} + P_{ws} = P_{year}$), and for the *predation hypothesis* we averaged values of P_{year} from the prior 2–4 years ($P_{year\text{-}234}$). For the *heat stress hypothesis*, we considered T_{max} during Apr–May, Apr–Jun, Jul–Aug, and Jul–Sept of the prior year and Sept 2-years prior because they could influence activity, reproduction, or recruitment (Appendix S1). For the *cold-effects hypotheses*, we considered T_{min} during Nov–Mar, Mar–May, May–Jul, and annually (Nov–Oct) at lag times of $\approx$1 or 1–1.5 years. Finally, because the side-blotched lizard is largely an annual species, we lagged weather factors an additional time step when assessing associations with spring abundance.

To evaluate support for our hypotheses, we developed statistical models to represent hypotheses and used an information-theoretic approach based on AIC$_c$ and AIC$_c$ weights (w_i; e.g., probability a model is the best approximating model) to assess support among models (Burnham & Anderson, 2002). Models within $\approx$2 ΔAIC$_c$ units were considered competitive except when they included uninformative parameters. As a general strategy, we first compared models that included only single related weather factors linked to each hypothesis at the lag times and seasonal periods noted above. In assessing these preliminary models, we considered each factor on the untransformed and logarithmic scales, quadratic terms for T_{min} and $P_{year\text{-}234}$ to assess curvilinear associations, and used models with the lowest AIC$_c$ to represent hypotheses. Second, we considered models that included combinations of hypotheses, after first assessing pair-wise correlations between factors linked to each hypothesis, which were low in all cases ($|r|$ = .04–.40; Appendix S2). Finally, we refined the top-ranked model for each species by assessing the effects of including, excluding, or changing terms.

To fit models, we used LMEM similar to Equation 4 and fit P and T as fixed effects. We fit transect and year as crossed random intercepts, which REML and AIC$_c$ confirmed was optimal, used autocorrelation functions to confirm independence of residuals, and fit models with the *lme4* library in R (Bates, Maechler, Bolker, & Walker, 2015). As response variables, we used log-transformed transect- and season-specific estimates of abundances from our best N-mixture models that were corrected for variation in detection probability. To assess relative effect magnitudes of factors linked to each hypothesis, we computed standardized (e.g., z-scored) regression coefficients for a full model that included factors linked to all four hypotheses for each focal species. Because observed associations between abundances and P or T could be driven by coincidentally co-occurring long-term trends (Grosbois et al., 2008), we further evaluated effect magnitudes with residual regressions of detrended variables. We excluded one high-elevation transect where most focal species were rare because estimates of T were outliers.

3 | RESULTS

3.1 | Effort and observations

Over 25 years, we completed 2,847 surveys in spring and 2,701 surveys in summer, and detected 14,305 individuals of the five focal species (Table 1). Each year, we surveyed an average of 23.5 ± 1.5

TABLE 1 Trends in abundance of five focal species of diurnal lizards in Organ Pipe Cactus National Monument over 25 years (1989–2013). Abundances were measured along line transects 3–8 times per day during 1 or 2 days in both spring and summer of each year at up to 32 transects per year. Counts were modeled with hierarchical *N*-mixture models that explicitly accounted for variation in detection probability. Estimates of finite rate of population growth (λ) are intercepts from a Poisson process model. Total percent population change (Δ%) was estimated across all 24 time steps assuming exponential population growth

		Sample size			Population change				
Species	**Season**	**Sites**	**Surveys**	**Encounters**	λ	*SE*	*Z*	*P*	Δ%
Tiger whiptail	Spring	32	2,847	2,360	0.959	1.012	3.55	<.001	−64
	Summer	32	2,701	3,310	0.995	1.012	0.42	.68	−11
Zebra-tailed lizard	Spring	29	2,556	858	0.963	1.019	2.01	.044	−60
	Summer	27	2,353	623	0.979	1.018	1.15	.25	−40
Side-blotched lizard	Spring	32	2,847	1,046	1.037	1.012	3.11	.002	237
	Summer	32	2,701	2,960	1.045	1.104	4.37	<.001	285
Tree lizard	Spring	26	2,249	1,623	0.995	1.015	0.33	.74	−10
	Summer	24	2,031	1,144	1.032	1.012	2.11	.035	211
Desert spiny lizard	Spring	20	1,835	182	1.008	1.018	0.446	.66	121
	Summer	19	1,662	199	0.991	1.020	0.445	.66	−19

(±*SE*) transects in spring and 23.3 ± 1.5 in summer. Across all years, we visited each of the 32 transects over an average of 18.2–18.4 ± 0.7 years.

All eight potential covariates of detection probability were associated with the observation process of at least one species, but temperature effects were often greatest and consistently curvilinear (Table S3, Figs. S3, S4). Detection probability of tiger whiptail and side-blotched lizard peaked sharply at moderate temperatures, whereas that of the ornate tree lizard and zebra-tailed lizard peaked at lower and higher temperatures, respectively (Fig. S3). Detection probability often increased with precipitation in spring but not during the summer monsoon, and the influence of Julian day varied widely among species and seasons.

3.2 | Population dynamics

Abundance dynamics and population growth rates varied among species but were often similar between seasons for a given species and also among species with similar life-history traits (Table 1, Figure 2). Among terrestrial species, abundance of a winter–spring breeder increased across time while that of two spring–summer breeders declined. In contrast, there was no evidence of systematic declines of arboreal species (Table 1). Specifically, abundances of the side-blotched lizard increased markedly by an estimated 237%–285% over time, while the larger tiger whiptail and zebra-tailed lizard declined by an estimated 60%–64% based on spring surveys (Table 1). Although there was much less evidence of declines during summer (Table 1), after year 2000 population growth rates of both the tiger whiptail and zebra-tailed lizard were negative in virtually all years in both seasons (Figure 2). Among arboreal species, there was some evidence that abundance of the tree lizard increased (Table 1), whereas abundance of the more terrestrial desert spiny lizard generally decreased after year 2000 (Figure 2). More generally, abundances of most species were relatively high between 1999 and 2001, and again between 2006 and 2008.

Abundance dynamics among similar and dissimilar species were often correlated in expected directions. For example, both terrestrial warm-season breeders displayed similar dynamics in both seasons (r = .55–.69, $p \leq .004$, $n = 25$; for correlations among annual abundance estimates), with similar patterns for both arboreal species in spring ($r = .80$, $p < .001$) but not summer ($r = .01$, $p \geq .96$). Dynamics of the terrestrial, winter–spring breeding side-blotched lizard, however, were negatively correlated with that of larger terrestrial, warm-season breeding tiger whiptail in spring ($r = -0.67$, $p < .001$), and positively correlated with dynamics of the arboreal tree lizard in spring ($r = .39$, $p = .057$) and especially summer ($r = .71$, $p < .001$).

3.3 | Climatic variation

Precipitation (*P*) during all seasonal periods declined across the study period, but declines in cool-season *P* occurred at a rate >2 times greater than that during the monsoon-influenced warm season (Table 2, Figure 3). Mean maximum temperature ($T_{\max}$) during the warm season increased across time, especially in late summer (Figure 4), but there was little evidence $T_{\min}$ increased (Table 2). Cyclical temporal changes in cool-season $T_{\min}$, and to a lesser extent mean annual *P* during the prior 2–4 years, suggested the influence of global climate patterns (e.g., ENSO).

Associations between local spatiotemporal variation in abundances and both *P* and *T* were often strong, with evidence for the combined influence of factors linked to all four hypotheses highest for three of five focal species (Table 3). As predicted by the *prey enhancement hypothesis*, abundances of all species increased with precipitation at short lag times (Table 3), but associations were relatively weak for the side-blotched lizard (Table 4). Abundance of the

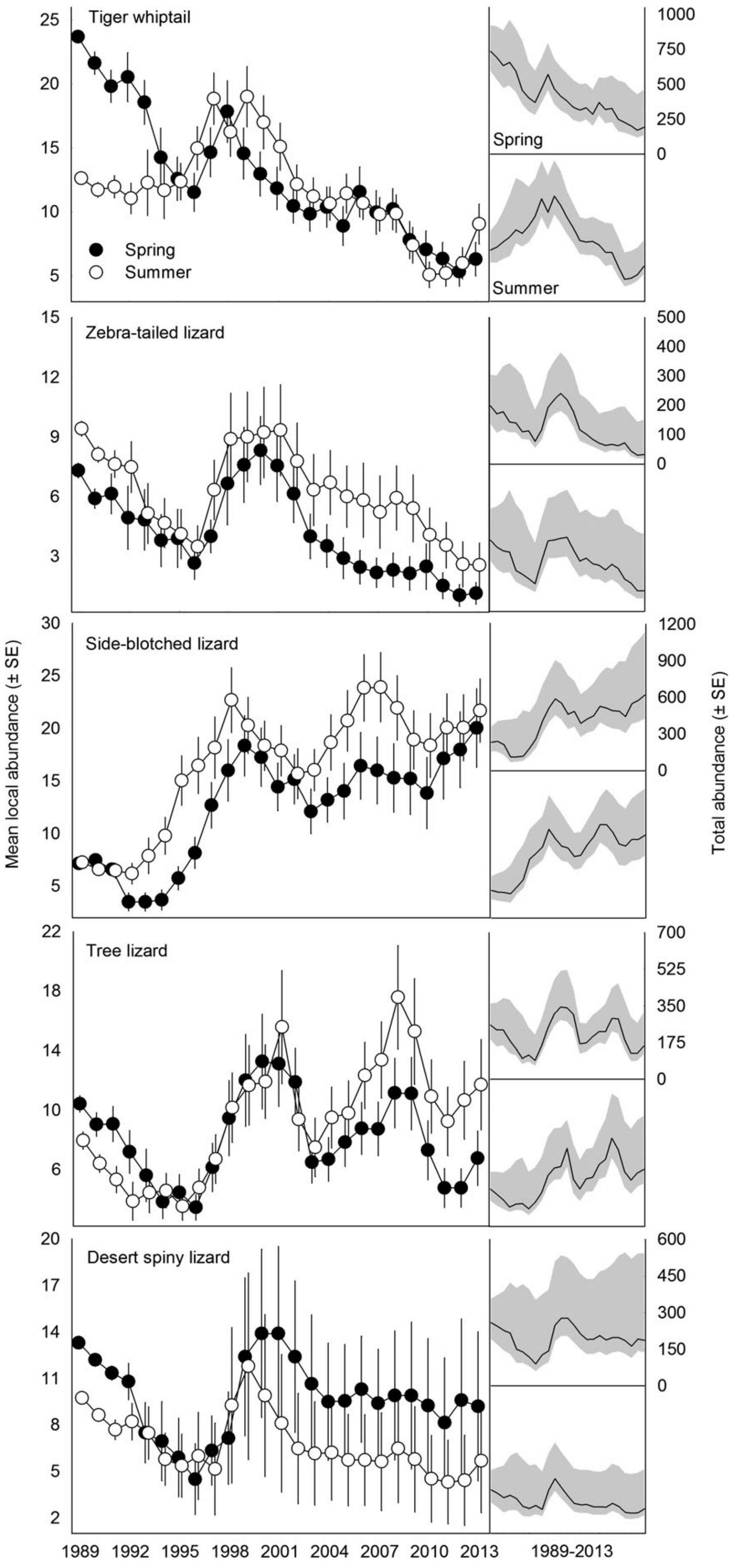

FIGURE 2 Temporal variation in local and regional abundances of five species of lizards in spring and summer over 25 years in Organ Pipe Cactus National Monument (1989–2013). Estimates are from *N*-mixture models and are adjusted for variation in detection probability

TABLE 2 Trends in precipitation and temperature factors considered when assessing the influence of climatic variation on lizards in Organ Pipe Cactus National Monument (OPCNM) over 25 years (1989–2013). Parameter estimates (β) and standard errors (*SE*) are based on linear mixed effects models with a fixed year effect, random station effect, and autoregressive moving-average covariance structures (p, q = 0–3). Temperature (°C) was measured at 9 stations and precipitation (mm) was measured at 17 stations across time throughout OPCNM

Factor (units) Period	ARMA structure (p, q)	Trend			
		β	*SE*	*t*	*P*
Precipitation (mm)					
Annual (Nov 2 years prior–Oct 1 year prior)	2,2	−3.69	.46	−7.96	<.001
Warm season (prior May–Oct)	3,2	−1.21	.28	−4.36	<.001
Cool season (Nov 2 years prior–Apr 1 year prior)	2,2	−2.70	.47	−5.75	<.001
Annual (mean, 2–4 years prior)	0,2	−4.30	.40	−10.69	<.001
Temperature – mean maximum (°C)					
Spring (prior Apr–Jun)	3,2	0.029	.011	2.69	.008
Summer (prior Jul–Aug)	2,0	0.021	.011	1.85	.066
Late summer (prior Sept)	3,1	0.040	.013	2.99	.003
Temperature – mean minimum (°C)					
Annual (Nov 2 years prior–Oct 1 year prior)	3,1	0.017	.012	1.35	.178
Winter (Nov 2 years prior–Mar 1 year prior)	2,2	−0.006	.012	−0.52	.604
Early breeding season (prior Mar–May)	3,2	0.009	.008	1.09	.278
Breeding season (prior May–Jul)	1,1	0.037	.021	1.76	.080

tree lizard, for example, increased by an estimated 0.14 ± 0.06% with each 1 mm increase in warm-season *P*, with similar associations for the tiger whiptail and zebra-tailed lizard. Associations for other species, however, were with cool-season or fall *P* (Table 4). As predicted by the *predation hypothesis*, abundances of the tiger whiptail and tree lizard increased up to moderate levels of *P* at a 2- to 4-year lag time, but declined markedly thereafter (Figure 5). In contrast, but also as predicted, abundance of smaller side-blotched lizard decreased linearly and markedly with increasing *P* at this longer lag time (Figure 5). Associations between abundances and *P* at both short and long lag times persisted and sometimes increased in significance based on detrended estimates (Table 4). Thus, variation in abundances that remained after removing linear time effects was explained by variation in *P*, and associations were not driven by co-occurring temporal trends. Where significant, *P* at long lag times had greater relative effects than *P* at short lag times (based on standardized regression coefficients), but effect magnitudes declined in one case based on detrended estimates (Table 4).

As predicted by the *heat stress hypothesis*, abundances of the zebra-tailed lizard and especially tree lizard declined with increasing T_{max} during prior warm seasons (Table 4). Contrary to predictions, however, other species showed the opposite pattern. As predicted by the *cold-effects hypotheses*, abundances of four species declined markedly with increasing T_{min}, with similar patterns for desert spiny lizard from low to moderate T_{min} (Table 4). Associations between abundances and T_{min} were strongest during winter for the side-blotched lizard and tree lizard or just prior or during the breeding season for the tiger whiptail and zebra-tailed lizard. Associations with T_{min} were greater than that for T_{max} for three species but lower for the tree lizard and zebra-tailed lizard. Importantly, associations between abundances and *T* largely remained significant and relative effect magnitudes remained similar after detrending data (Table 4).

4 | DISCUSSION

We documented marked and divergent long-term changes in abundances of five common species of diurnal lizards in the Sonoran Desert over 25 years. Given the warming and drying trends we observed over the study period, simple expectations might be that all species would decline, or that species with high temperature preferences (T_b) and adaptations to cope with extreme aridity might fare best. Few patterns, however, matched these expectations. Although the species most associated with aridlands increased markedly despite low T_b (side-blotched lizard), species with high T_b generally declined, whereas other species with lower T_b that are associated with more mesic environments, largely remained stable. Thus, abundance dynamics were variable and explicable based largely on differences in microhabitat use, breeding phenology, and other species' traits. In general, species that increased or remained stable are arboreal and thus mainly shade dwelling, or breed during winter or spring, which are traits that tend to insulate individuals from abiotic extremes. In contrast, species that declined use more open microhabitats on the ground and breed mainly during summer, which are traits that augment exposure to abiotic extremes. Such trait-mediated responses to climatic variation have been reported for other taxa (e.g., Diamond, Frame, Martin, & Buckley, 2011; Lavergne, Molina, & Debussche, 2006), are consistent with the anticipated influence of climate change on ectotherms (Kearney

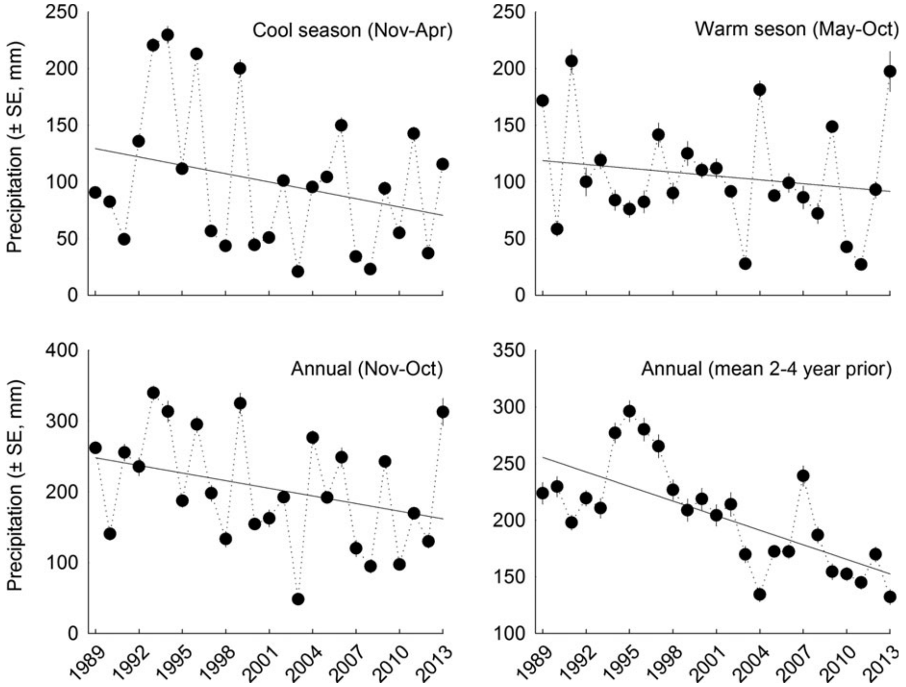

FIGURE 3 Temporal variation in precipitation during four time periods considered when assessing the influence of climatic variation on lizard populations over 25 years in Organ Pipe Cactus National Monument (1989–2013). Estimates are from 17 weather stations located throughout the monument. Trend estimates are based on linear mixed effects models with autoregressive moving-average structures to adjust for temporal autocorrelation. Parameter estimates and significance levels are summarized in Table 2

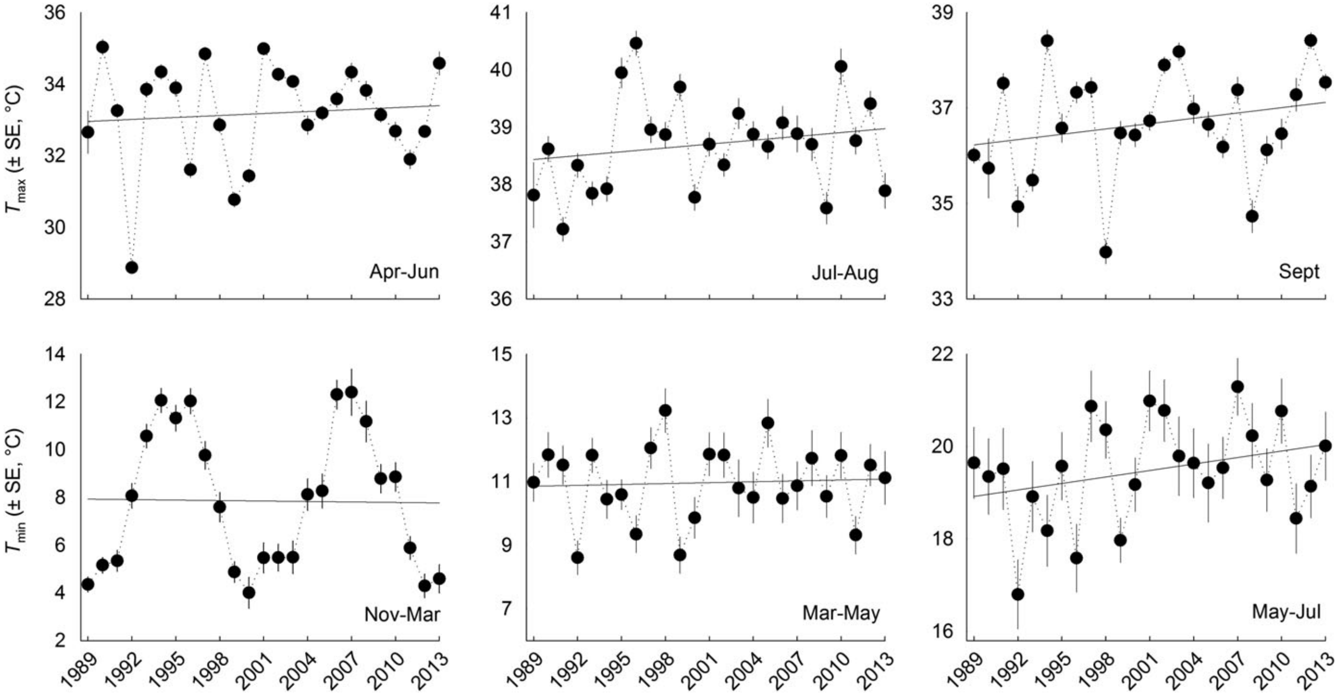

FIGURE 4 Temporal variation in mean maximum (T_{max}) and mean minimum (T_{min}) daily temperature during various time periods considered when assessing the influence of climatic variation on lizard populations over 25 years in Organ Pipe Cactus National Monument (1989–2013). Estimates are from at 9 weather stations located throughout the monument. Trend estimates are based on linear mixed effects models with autoregressive moving-average structures. Parameter estimates and significance levels are summarized in Table 2

et al., 2009; Huey et al., 2012; Huey and Tewksbury, 2010; Sinervo et al., 2010), but had not been described over the long term in aridlands.

Spatiotemporal changes in abundances were highly associated with climatic variation but the influence of different climatic attributes varied, sometimes in novel ways. Despite the increasingly

TABLE 3 Rankings of hypothesized models that explained the influence of weather on spatiotemporal variation in abundance (ln no.) of five species of diurnal lizards in Organ Pipe Cactus National Monument over a 25-year period (1989–2013). *K* represents the number of model parameters, ΔAIC_c is the change in AIC between each model and the best approximating model, and AIC_c weights (w_i) are probabilities each model is the best approximating model in each model set. Only models within 6 ΔAICc points are shown; other models are in Table S4. Variables representing each hypothesis are in Table 4

Species model	*K*	ΔAICc	w_i
Tiger whiptail			
Prey + predation + warm stress + cold effects	9	0.00	1.000
Prey + predation + cold effects	8	3.26	0.196
Zebra-tailed lizard			
Prey + warm stress + cold effects	7	0.00	1.000
Prey + cold effects	6	2.42	0.298
Prey + predation + warm stress + cold effects	9	3.60	0.165
Warm stress + cold effects	6	3.84	0.146
Side-blotched lizard			
Prey + predation + warm stress + cold effects	8	0.00	1.000
Predation + warm stress + cold effects	7	1.59	0.451
Prey + predation + cold effects	7	4.31	0.116
Predation + cold effects	6	5.91	0.052
Tree lizard			
Prey + predation + warm stress + cold effects	9	0.00	1.000
Predation + warm stress + cold effects	8	2.41	0.299
Prey + predation + warm stress	8	5.22	0.074
Desert spiny lizard			
Prey + warm stress + cold effects	8	0.00	1.000
Warm stress + cold effects	7	1.18	0.555
Prey + predation + warm stress + cold effects	9	1.55	0.461
Predation + warm stress + cold effects	8	2.29	0.318
Cold effects	6	2.98	0.226
Prey + cold effects	7	3.18	0.204
Predation + cold effects	7	3.71	0.156
Prey + predation + cold effects	8	4.29	0.117

extreme environment we considered and global threats to ectotherms posed by climate warming (Kearney, 2013; Sinervo et al., 2010), abundances were often weakly and sometimes positively associated with daily maximum air temperatures (T_{max}) during the warm season. In contrast, abundances of all species declined, often markedly, with increasing daily minimum air temperatures (T_{min}) in either the cool or warm season, which to our knowledge has not been reported for ectotherms. As commonly found in populations of small desert consumers, however, abundances increased with precipitation (*P*) at short lag times (Lima, Ernest, Brown, Belgrano, & Stenseth, 2008; Lima et al., 2002; Whitford & Creusere, 1977) due likely to bottom-up processes that augment food resources (Holmgren et al., 2006; Rosenzweig, 1968), but these associations were often relatively weak. At longer lag times, however, abundances often declined after periods of high *P* likely due to the top-down effects of predators and other biotic processes. Thus, whereas some patterns we observed are consistent with the anticipated influence of climatic flux on desert ectotherms, our results suggest a complexity of direct and indirect effects driven by various biotic and abiotic factors (Ockendon et al., 2014).

4.1 | Effects of maximum daily air temperatures (T_{max})

By limiting activity to avoid lethally high environmental temperatures, rising breeding season temperatures linked to climate change are expected to drive pervasive declines in populations of diurnal lizards (Huey et al., 2009; Sinervo et al., 2010). Nonetheless, associations we observed between abundances and T_{max} varied widely among species and were sometimes positive or focused in seasons other than mid-summer, suggesting the influence of climate warming on lizards may be more complex than previously envisioned. Abundances of the tiger whiptail and desert spiny lizard, for example, increased with rising T_{max} during spring, suggesting warmer early spring conditions promote foraging activity and reproduction. Collectively, the direction and timing of associations between abundances and T_{max} varied with habitat use, foraging behavior, and other species' traits. Only the most arboreal species, the tree lizard, showed the expected strong negative association between abundance and T_{max} during the breeding season (Sinervo et al., 2010), which coincides with peak temperatures of mid-summer. Despite these patterns and low T_b, abundance of the tree lizard did not decline over time. This species' highly arboreal life style may limit access to subterranean thermal refugia commonly used by terrestrial species to avoid extreme heat, thereby augmenting susceptibility to T_{max}. The widely foraging tiger whiptail, however, may be able to avoid risks associated with T_{max} by moving from open microhabitats to cooler, shade-moderated thermal environments under trees, shrubs, and leaf litter (Ryan et al., 2015). In contrast, the sit-and-wait foraging strategy of the zebra-tailed lizard, which involves fast running on open ground, offers fewer options to compensate for rising operative environmental temperatures (T_e) via shade utilization, thus explaining observed negative associations with T_{max}. However, both of these species declined. Thus, observed associations between abundances and T_{max} may not be directly linked to the dynamics of some focal populations in expected ways.

Absences of the anticipated effects of T_{max} may be due to the ways different microhabitats modulate T_e experienced by individuals (Sears & Angilletta, 2015). For example, variation in T_{max} is likely highly correlated with T_e in the shaded woodland environments occupied by the tree lizard, thus explaining marked negative associations we observed. For terrestrial species, however, T_{max} may not effectively quantify T_e because it is strongly linked to substrate (vs. air) temperatures, which are determined largely by solar insolation. Such relationships could explain a lack of predicted associations, and

TABLE 4 Estimated effects of precipitation (*P*, mm) and temperature (*T*, °C) on spatiotemporal variation in abundance (ln no.) and time-detrended abundance of five species of lizards in Organ Pipe Cactus National Monument over 25 years (1989–2013). Parameter estimates (β) and standard errors (*SE*) are from linear mixed effects models with crossed random intercepts for transect and year. Effect forms note where log (ln) or quadratic (^2) terms fit better than linear terms, and sample sizes note the number of transects, seasons, and years for which data were available. Unstandardized parameter estimates are on the original scale, whereas standardized estimates are for *z*-scored factors and thus illustrate relative effect magnitudes. Detrended models show effects after removing linear time effects from local abundance and weather data. Weather factors were measured at 9–17 stations across the monument. *T*-values ≥2 are indicative of statistically significant relationships

Species (sample size)		Local abundance					Detrended local abundance				
		Unstandardized		Standardized			Unstandardized		Standardized		
Hypotheses	Factor (period; form)	β	*SE*	β	*SE*	*t*	β	*SE*	β	*SE*	*t*
Tiger whiptail (1140)											
Prey enhancement	P_{ws} (May–Oct 1-year lag; ln)	0.183	0.050	0.111	0.030	3.63	0.181	0.044	0.109	0.026	4.14
Predation	P_{year} (annual 2–4 years lag; ^2)	−2.29E-05	4.96E-06	−0.578	0.125	−4.62	−3.20E-05	6.10E-06	−0.119	0.023	−5.24
Warm stress	T_{max} (Apr–May 1-year lag)	0.067	0.029	0.104	0.045	2.31	0.064	0.026	0.075	0.036	2.11
Cold effects	T_{min} (Mar–May 1-year lag)	−0.096	0.025	−0.210	0.054	−3.91	−0.072	0.022	−0.156	0.048	−3.29
Zebra-tailed lizard (1026)											
Prey enhancement	P_{ws} (May–Oct 1-year lag; ln)	0.169	0.069	0.102	0.042	2.45	0.146	0.066	0.088	0.039	2.23
Predation	P_{year} (annual 2–4 years lag; ^2)	−1.43E-06	6.62E-06	−0.036	0.168	−0.22	−4.17E-06	8.50E-06	−0.015	0.031	−0.49
Warm stress	T_{max} (Sept 2-year lag)	−0.085	0.038	−0.114	0.051	−2.22	−0.066	0.036	−0.086	0.047	−1.84
Cold effects	T_{min} (May–Jul 1-year lag)	−0.108	0.030	−0.229	0.065	−3.54	−0.080	0.029	−0.167	0.061	−2.73
Side-blotched lizard (1140)											
Prey enhancement	P_{fall} (Sept–Oct 1-year lag)	0.002	0.001	0.072	0.038	1.91	0.002	0.001	0.068	0.036	1.88
Predation	P_{year} (annual 2–4 years lag)	−0.50	0.17	−0.138	0.048	−2.89	−0.193	0.186	−0.044	0.043	−1.04
Warm stress	T_{max} (Jul–Sept 1–2 years lag; ln)	3.30	1.30	0.079	0.031	2.55	2.999	1.292	0.071	0.031	2.32
Cold effects	T_{min} (Nov–Mar 0–2 years lag)	−0.047	0.015	−0.158	0.050	−3.16	−0.041	0.014	−0.136	0.046	−2.97
Tree lizard (890)											
Prey enhancement	P_{ws} (May–Oct 1-year lag)	1.37E-03	6.46E-04	0.082	0.039	2.12	1.41E-03	6.28E-04	0.085	0.038	2.25
Predation	P_{year} (annual 2–4 years lag; ^2)	−3.01E-05	6.20E-06	−0.78	0.16	−4.86	−2.42E-05	7.62E-06	−0.094	0.029	−3.18
Warm stress	T_{max} (Jul–Aug 1-year lag; ln)	−7.00	2.10	−0.181	0.054	−3.34	−8.89	2.00	−0.229	0.051	−4.44
Cold effects	T_{min} (Nov–Mar 1–2 years lag; ln)	−0.39	0.14	−0.164	0.061	−2.70	−0.30	0.13	−0.125	0.055	−2.27
Desert spiny lizard (743)											
Prey enhancement	P_{cs} (Nov–Apr 1–2 years lag)	0.002	0.001	0.150	0.090	1.69	0.046	0.021	0.146	0.068	2.15
Predation	P_{year} (annual 2–4 years lag; ln)	0.20	0.27	0.053	0.073	0.73	−0.46	0.27	−0.098	0.057	−1.72
Warm stress	T_{max} (Apr–May 1 year lag; ln)	3.82	1.74	0.187	0.084	2.20	0.076	0.039	0.111	0.064	1.75
Cold effects	T_{min} (Nov–Mar 1–2 years lag; ^2)	0.011	0.004	0.56	0.19	2.96	0.012	0.004	0.132	0.039	3.40

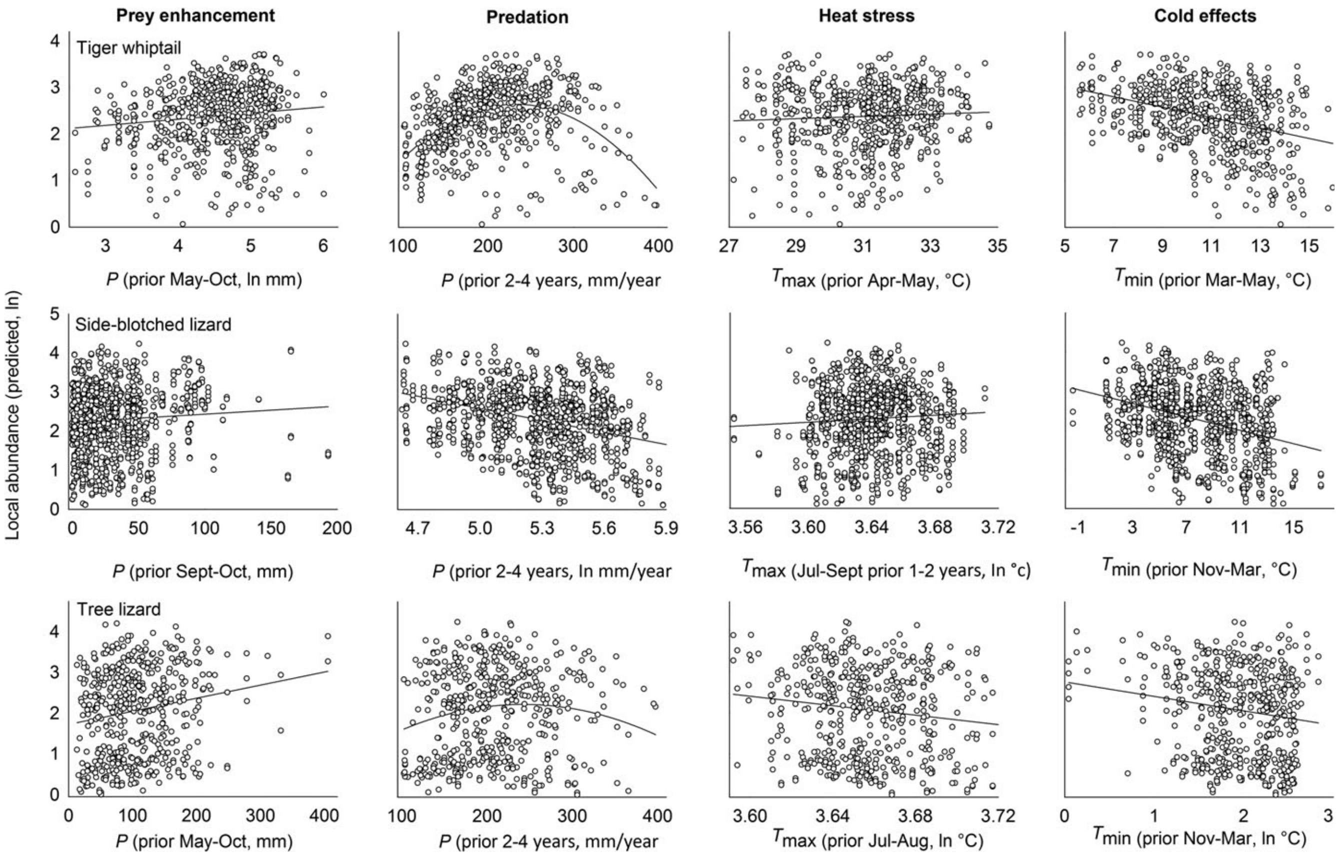

FIGURE 5 Associations between lizard abundance and weather factors linked to four hypotheses that explained the influence of precipitation (*P*, mm) and temperature (*T*, °C) on spatiotemporal variation in lizard abundance in Organ Pipe Cactus National Monument over 25 years (1989–2013). Associations are shown for three species of lizards that exemplify differences in life-history traits: the terrestrial, spring–summer breeding tiger whiptail; smaller, terrestrial, winter–spring breeding side-blotched lizard; and the arboreal ornate tree lizard. Estimates are from linear mixed effects models with crossed random intercepts for transect and year. Parameter estimates are summarized in Table 4

suggest the importance of shade and need for more focused studies that integrate monitoring T_e among various microhabitats (Dzialowski, 2005).

The influence of *T* or *P* on abundances, and more generally, differences in dynamics among species may also be driven by the direct effects of climate on vegetation. In aridlands, most diurnal lizards use shade provided by vegetation to sustain activity and avoid risks of lethal temperatures (Cowles & Bogert, 1944; Huey, 1982). Thus, higher levels of recent drought-induced mortality of smaller plants such as shrubs and subshrubs (McAuliffe & Hamerlynck, 2010), which provide important sources of shade for terrestrial lizards, may explain declines in the tiger whiptail and other similar species. In contrast, over the same period in our region, larger deep-rooted trees declined at lower rates and hence generally persisted (McAuliffe & Hamerlynck, 2010), possibly explaining greater stability of arboreal populations. Because the tree lizard in our region is at the margins of its geographic range and already near tolerance limits, expected increases in mortality of long-lived trees linked to climate change (Ackerly, Cornwell, Weiss, Flint, & Flint, 2015) suggest future declines are likely. If such indirect effects mediated by vegetation are operating, they could influence the lag times and seasonal periods of associations between abundances and *T* or *P*, and drive a complexity of patterns.

Given the intricacy of ways T_{max} and other climatic attributes can influence populations and their habitats, we recognize that identifying the drivers of various associations is challenging. For the side-blotched lizard, for example, abundance increased with T_{max} during mid to late summer, when most individuals are nonreproducing subadults, and when terrestrial habits and low T_b constrain activity to cooler morning hours. Such facts make observed associations difficult to explain physiologically and suggest the importance of biotic interactions.

4.2 | Effects of minimum daily air temperatures (T_{min})

Studies of the influence of climate change on ectotherms focus on $T_{max,}$ whereas potential threats posed by rising T_{min} have been largely ignored. We hypothesized extreme values of T_{min} could reduce lizard abundances by restricting, or possibly enhancing activity or emergence from winter dormancy, or by degrading low-temperature thermal refugia in ways that augment costs of maintenance metabolism during periods of seasonal dormancy or nocturnal inactivity. We found marked and consistently negative associations between abundances and rising T_{min} for all five focal species. Despite the relative novelty of these patterns, core aspects of lizard behavior and thermal biology suggest a mechanism we proposed is plausible. Rising T_{min} and T_e can increase energetic costs of maintenance metabolism if inactive, nonforaging individuals experience physiologically costly body temperatures (Brischoux, Dupoué, Lourdais, & Angelier, 2016; Clarke & Zani, 2012; Patterson & Davies, 1978; Zani, 2008; Zani et al., 2012). In ectotherms, metabolic activity rises exponentially with temperature and consumes energy important for growth, reproduction, and other processes, thereby requiring additional activity and risk to acquire lost energy (Adolph & Porter, 1993; Bennett & Dawson, 1976; Huey & Slatkin, 1976). Metabolic and water-loss costs of high T_{min} may be especially large for small juveniles with low fat stores and high surface-to-volume ratios (Walker, Stuart-Fox, & Kearney, 2015), although other processes may be involved. Thermal physiological constraints outside the breeding season, for example, can influence developmental processes in the reproductive cycle and elsewhere (Mendez De La Cruz, Morán, Ríos, & Ibargüengoytía, 2015). Although additional study is needed to understand mechanisms by which T_{min} influences populations, patterns we observed suggest T_{min} was more important than T_{max} in driving past dynamics. Whereas versatile behavioral repertoires combined with sufficient microhabitat diversity may buffer lizards from ambient T_{max} during day, less behavioral plasticity during cool-season dormancy, and nocturnal inactivity could constrain compensating for deleterious metabolic costs of rising T_{min}. Regardless, patterns we observed have grave implications for aridland ectotherms because rising T_{min} is among the strongest documented trends linked to both regional and global climate change, especially during cooler months (Easterling et al., 1997, 2000; Weiss & Overpeck, 2005) that correspond to the timing of some associations we observed. More broadly, rising nighttime temperatures can have unexpected negative effects on other taxa such as plants via increased water loss that could interact with CO_2 concentrations (Yamori, Hikosaka, & Way, 2014; Zeppel, Lewis, Phillips, & Tissue, 2014), which may be especially pronounced in aridlands (Bronson, English, Dettman, & Williams, 2011; Williams, Hultine, & Dettman, 2014).

Interestingly, biphasic, sinusoidal temporal fluxes in T_{min} during the study period were somewhat similar to temporal changes in abundances of some lizard populations. We presume such patterns are linked to ENSO that influences both cool-season *P* and T_{min}, which were significantly but relatively weakly correlated. Despite expected relationships between abundances and cool-season *P* driven by its influence on food availability (Anderson, 1994; Whitford & Creusere, 1977), we only observed strong associations with T_{min}. Thus, the effect of cool-season *P* may be masked, possibly by biotic interactions with species that benefit from wet winters. We suspect observed associations with T_{min} were driven by a complexity of biological processes interacting with both global climate phenomenon and the local weather patterns they create.

4.3 | Precipitation (*P*)

In arid, resource-limited environments, the positive bottom-up effects of *P* on populations of small vertebrates have been observed nearly worldwide (Holmgren et al., 2006; Lima et al., 2002; Whitford & Creusere, 1977). In these systems, *P* drives rapid increases in plant biomass, seed production, and insect abundance, creating resource pulses that directly bolster food availability for small consumers, thus augmenting reproductive output and subsequently abundances at lag times of ≈0.5–1.5 years depending on their life history (Anderson, 1994; Beatley, 1969; Dunham, 1980; Jaksic, 2001; Lima et al., 2002, 2008). Predator populations respond indirectly to these resource pulses at longer lag times of typically two or more years (Dennis & Otten, 2000; Jaksic, Jimenez, Castro, & Feinsinger, 1992; Letnic, Tamayo, & Dickman, 2005; Lima et al., 2002). More locally in the Sonoran Desert, increases in reproductive output and abundance of snakes, raptors, and other lizard predators after periods of high *P* match these patterns and are consistent with the lag times we used as a proxy for the hypothesized influence of predation (Flesch, 2014; Flesch et al., 2015; Rosen, 2000).

Accordingly, we found that abundances of all species increased with *P* at short lag times, although the strength, timing, and seasonal periods of associations varied among species likely due to differences in breeding phenology and perhaps age to maturity. Associations for the side-blotched lizard were relatively weak and with fall *P*, which likely augments resources at times of peak reproduction in winter and spring when energy demands are high. At a more arid site in the Mohave Desert, however, Turner, Medica, Bridges, and Jenrich (1982) found stronger positive associations between abundance of the side-blotched lizard and winter *P*. In contrast, but consistent with their breeding phenology, associations for larger spring–summer breeders were strongest during the warm season indicating the importance of the summer monsoon. Both of these species also showed strong correlations in abundance dynamics, as did the two smaller, early maturing species. However, during an extreme drought culminating in 2002, dynamics of smaller species varied somewhat with very low abundance of the side-blotched lizard in spring increasing the summer following its winter–spring breeding period, with similar but more delayed responses by the summer breeding tree lizard. Thus, shifting patterns of fall, winter, and summer *P* under future climates may differentially influence species based on their breeding phenology.

At longer lag times that we hypothesize are linked to variation in predator populations, abundances of three lizard species were significantly higher at moderate *P* and declined markedly at lower and higher *P*. Abundance of the side-blotched lizard, however, declined linearly and markedly with increasing long-term *P*. This pattern is consistent with strong documented effects of predation on the side-blotched lizard by larger lizard species, including those considered here, and by other small predators that can depress population sizes

(Turner et al., 1982). In addition, limited defenses (Sinervo & Doughty, 1996; Tinkle, 1967), and a diverse predator community in our region (Rosen, 2007) likely augment sensitivity of the side-blotched lizard to predation.

Despite evidence for the prey enhancement and predation hypotheses, we caution that the complexity of the influence of P at different lag times does not entirely differentiate bottom-up from top-down processes, and that observed associations may be driven by other processes. For example, many lizard-eating snakes in our region respond rapidly to rainfall by increasing foraging activity, which likely augments predation pressure on lizards long before resource-mediated increases in snake abundance occur (George, Thompson, & Faaborg, 2015). Moreover, P can affect bottom-up resource pulses at longer lag times than we considered (Barrows, 2012; Barrows & Allen, 2009). Such processes may partly mask the effects of P at short lag times and explain higher effect magnitudes of P at longer lag times. Thus, increases in lizard abundance from low to moderate levels of long-term P are likely driven by both prey enhancement and low predation pressure at times when populations are small and hence growing in a density-independent manner. Conversely, declining abundance from moderate to high levels of long-term P are likely driven by mounting predation pressure, and by endogenous density-dependent feedbacks and other processes.

Interspecific competition may also contribute to observed associations between abundances and P, and more generally, to differences in dynamics among species. Experimental studies of lizards in continental aridlands, however, generally suggest small (Cuellar, 1993; Price, LaPointe, & Atmar, 1993) or fluctuating (Dunham, 1980) influences of competition during periods of resource scarcity. For the side-blotched lizard, however, strong linear declines in abundance with increasing long-term P may be attributable to reduced competitive interactions with larger terrestrial species that declined and contributed to the nearly threefold increase in abundance we observed over time. Regardless, the relative contribution of top-down, bottom-up, and endogenous processes in driving dynamics we observed is not entirely clear based on our results.

4.4 | Population dynamics, climate, and species' traits

Patterns we observed suggest a diversity of factors that influence the exposure and sensitivity of individuals to climatic variation and interactions with other species drove dynamics. Such factors include intrinsic, trait-mediated responses to climatic flux, as well as extrinsic, biotic, and environmental drivers such as predation, food availability, and vegetation resources linked to the quantity and quality of microhabitats. Intrinsic factors that influence individual exposure and sensitivity to a changing environment include microhabitat use, thermal physiology, reproductive phenology, time to maturity, and the ability to evade predatory and competitive interactions with other species. Arboreal species, for example, that occupy shaded and thus thermally buffered habitats created by large trees, which are less susceptible to drought, showed no evidence of decline despite an increasingly extreme environment and observed negative associations with warm-season $T_{\max}$. In contrast, two dominant terrestrial spring–summer breeders with high $T_{b,}$ activity times focused during the heat of day, and that depend on shade provided by smaller shrubs and subshrubs, which are more vulnerable to drought (McAuliffe & Hamerlynck, 2010), declined likely due to the influence of an increasingly harsh environment on vegetation and food resources. Marked increases in a third terrestrial species that has low T_b and avoids the heat of summer by breeding in winter and spring, and by focusing activity during cool early mornings (Asplund & Lowe, 1964; Pianka, 1986; Tinkle, 1967), suggest phenological and physiological traits that reduce exposure to abiotic extremes drove these dynamics. Because this later species, the side-blotched lizard, is smaller and highly susceptible to predation, including that by larger, more dominant terrestrial species that declined (Turner et al., 1982), biotic interactions likely also contributed substantially to dynamics. Such a broad array of responses to climatic flux that include both the direct and indirect effects of climate on habitat resources and biotic interactions will continue to drive a complexity of patterns in the future (Huey et al., 2012; Kearney et al., 2009; Ockendon et al., 2014). Identifying the mechanisms and relative roles of various processes in driving these dynamics, and devising management strategies focused on the most threatening processes will require additional study.

Broad changes in the lizard assemblage we studied reflect complex community-wide responses to climatic variation that over time trended toward conditions expected to be more frequent in the future. Declines in some terrestrial species we observed are consistent with global trends for other reptile populations that have been attributed to climate change (Reading et al., 2010; Sinervo et al., 2010). These changes are also consistent with similar trends for many other taxa in this and other arid regions of western North America (Barrows, 2006; Zylstra et al., 2013; Flesch, 2014; Lovich et al., 2014; Cruz-McDonnell & Wolf, 2015), and have broad implications for conservation and management in aridlands worldwide. However, we found a range of dynamics that included declines in ecologically dominant species that are adapted to aridity, fluctuations without systematic trend of species associated with more mesic environments that occur near the limits of their range boundaries, and major increases in one species that is dominant in increasingly arid regions to the west of our study area. Whereas some associations between abundances and climatic flux that we observed were expected and widely known in aridlands (e.g., positive effects of P on food resources), others were unexpected (e.g., small or positive effects of increasing $T_{\max}$) or novel (e.g., universally negative effect of increasing $T_{\min}$). Past dynamics together with anticipated increases in temperature and drought (Cook et al., 2015; Garfin et al., 2013; Seager et al., 2007) will have large, complex effects on this and other communities of aridland ectotherms.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supporting Information

Appendix S1. Phenology of climatic effects on five focal species of lizards.

We synthesized the ecological literature and our field data on the five focal species of lizards in our analysis (Table S1) and used this information to develop hypotheses for the effects of climatic variation on abundances. In general, hypotheses are diagrammed in Fig. S1, and the resulting variables we employed as predicted effects are in Table S2. Here we provide details of the logic employed in representing each research hypothesis. All five species of lizards were represented similarly, but for one with divergent life history the application of climate variables was slightly modified as described below.

To avoid excessive complexity beyond established specifics and precision of knowledge of autecology and demographics (see Table S1), we treated the following four species identically:

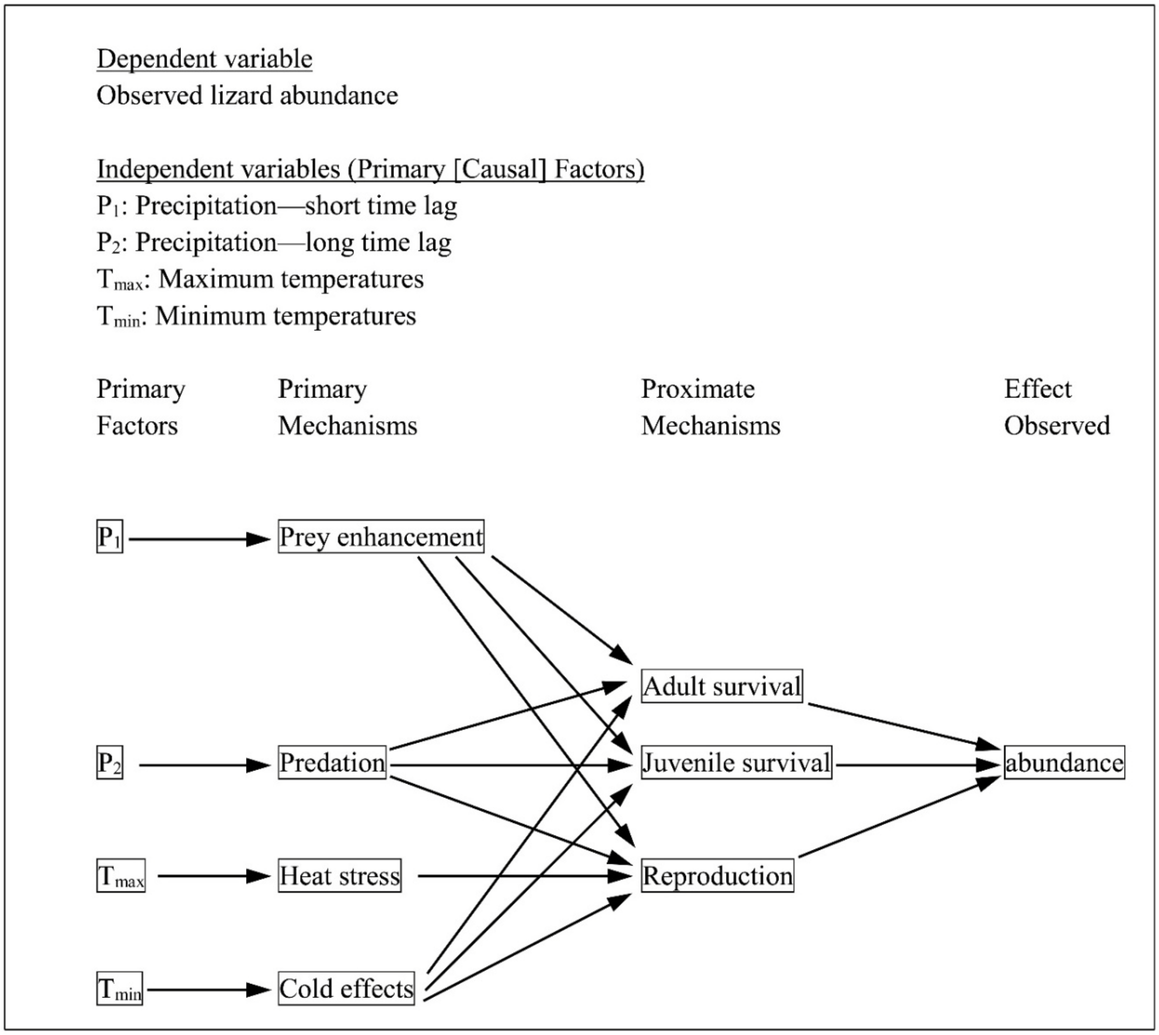

Figure S1. Diagrammatic representation of mechanistic connections of climate and weather variables to ecological hypotheses tested

Table S1. Ecological characteristic for five focal species of lizards we considered in the Sonoran Desert. Items shown in parentheses are subsidiary aspects of niche or phenology.

English name	Zebra-tailed lizard	Desert spiny lizard	Ornate tree lizard	Side-blotched lizard	Tiger whiptail
Scientific name	*Callisaurus draconoides*	*Sceloporus magister*	*Urosaurus ornatus*	*Uta stansburiana*	*Aspidoscelis tigris*
Family	Phrynosomatidae	Phrynosomatidae	Phrynosomatidae	Phrynosomatidae	Teiidae
Principal macrohabitat [1]	flats, bajadas, canyon bottoms	bajadas and flats	ubiquitous	ubiquitous	bajadas, flats, arid slopes
Lifestyle - microhabitat [1]	terrestrial	arboreal (terrestrial)	arboreal (saxicolous)	terrestrial, saxicolous	terrestrial
Egg-laying season [2]	(Apr) May-Aug (Sept)	May-Aug	(May) June-Aug (Sept)	Mar-May (Jun-Aug)	(Apr) May-Aug (Sept)
♀ Age (YR) at 1st reproduction [2]	1	1-1.5 (2)	(≈0.9) 1	(≈0.7) 1	1-1.5 (2)
T_b or T_{pref} [3]	39.08	35.03	35.85	36.23	40.14
Clutch frequency [4]	2	1-2	2-4	3-6	2-3
Mean clutch size [4]	4.6	7.8	6.9	4.2	2.6
Diet [4]	arthropods	arthropods (small lizards)	arthropods	arthropods	arthropods (small lizards)
Predominant foraging behavior	sit-wait	sit-wait	sit-wait	sit-wait	active forager
General life history type	iteroparous, multi-clutched	iteroparous, multi-clutched	≈ annual, multi-clutched	annual, multi-clutched	iteroparous, multi-clutched

[1] at OPCNM, [2] from literature and unpublished OPCNM field data, [3] estimated for OPCNM from literature, [4] from literature

The zebra-tailed lizard, desert spiny lizard, ornate tree lizard, and tiger whiptail all breed during the warm season (late April – early September), mature at $\approx$1 -1.5 years of age, and populations have approximately similar proportions of older adults and recruiting sub-adults from reproduction corresponding to predicted time-lagged effects of $\approx$1 year. A fifth species, the common side-blotched lizard, breeds earlier (February-May, with limited breeding through August), matures earlier ($\leq$1 year of age), and has nearly annual population turnover throughout its range. Thus it is expected to show different time-lag effects, especially between spring and summer seasons. Differences in climate-based ecological hypotheses linked to this species are described below.

We represented the prey enhancement hypothesis using precipitation variables at short time lags (Table S2). This hypothesis predicts increases in precipitation augment arthropod activity and primary productivity, which increases arthropod productivity and thus yields rapid increases in prey availability. Increased food resources are assumed to translate into increased reproductive output of lizards at time lags dependent on reproductive phenology and time to maturity. For the four similar species, summer rainfall leads to enhanced hatchling production, and based on our observations, many of these hatchlings are large enough to be counted the following spring and all are large enough by the following summer. The same logic applies to winter rainfall, as well as annual rainfall as defined in Table S2, thus indicating an approximately 1-year lag time relating precipitation to observed abundance changes in lizards. For fall precipitation, we assume that increased rainfall results primarily in increased juvenile growth and survival, and hence we also based our predictions on a 1-year lag time. The same applies to the positive effects of fall precipitation on adult survival, although we suspect this effect and other similar ones are likely small.

The predation hypothesis assumes the strongest effect of increased long-term precipitation (>1-year time lag) results from increases in predator populations. These changes are caused by increased reproduction of predators in response to greater resource abundance, which results from bottom-up processes such as those identified by the prey enhancement hypothesis but at longer time lags. Although predator activity may also increase immediately (or at least at short time-lags, implying a <1-year time lag) in response to precipitation, we assumed this effect was small enough so that precipitation time lags linked to prey enhancement and predation variables could be separated. Although other factors such as intra- and interspecific competition may also operate at longer time lags in response to long-term precipitation, our predation hypothesis assumes these processes are weaker than predation. Further discussion of these issues is in the main text. We also considered 2-3-year time lags for precipitation linked to the predation hypotheses but this yielded somewhat weaker associations and is not presented in the results.

We represented high temperatures based on daily thermal maxima ($T_{\max}$; Table S2). As with $T_{\min}$, we found no associations with abundances at short lag times that would suggest direct mortality from overheating as an important factor in lizard population change, and we therefore focused on likely effects of $T_{\max}$ on activity and thence reproductive output as described by Sinervo et al. (2010) and others. Sinervo et al. (2010) highlighted the potential importance of $T_{\max}$ during the breeding season on restricting activity and we therefore partitioned our examination of this factor into several variables representing effects of spring and summer breeding and of high temperatures just after the breeding season (late summer and fall) on reproductive output and resulting abundances in subsequent breeding seasons. Thus, we considered T_{max} at time lags of 1 and 2 years (Table S2).

We represented cold-effects hypotheses with four daily minimum temperature variables (T_{min}; Table S2). We assumed that high T_{min} increased resting metabolism, reducing stored energy and subsequent reproductive output, and following the logic for precipitation variables, operated at a 1-year time lag. We initially suspected that low winter temperatures might cause freeze mortality, resulting in a negative effect on populations at lag times of <1 year, but discarded this hypothesis after exploratory analyses indicated no associations. Thus it appears that overwinter freezing mortality is not important to lizard population changes in our system; nor did we find evidence that overwinter starvation of adults and larger juveniles was an important factor in population change, which would also have appeared as a <1-year time lagged effect. We tested for cold effects in other seasons following the same logic as above for winter thermal minima. We tested variables for minimum warm-season temperature effects in the pre-breeding and breeding periods (Table S2, T_{minS} and T_{minBS}) to correspond with findings in the literature (Sinervo et al. 2010).

Slight modifications to time lags for various variables were needed to reflect the winter-spring breeding peak and high population turnover of the side-blotched lizard. These traits result in differences in reproductive output at different time lags for populations surveyed in summer versus spring. In summer, most observed individuals are subadults and small adults from the immediately preceding winter-spring breeding season (time-lag = 0 for some variables) whereas in spring all observed individuals are adults, predominantly those from the previous winter-spring plus a few older survivors (thus, time-lag = 1 for most models). We thus lagged weather factors an additional time step when assessing associations with spring abundance.

Table S2. Names and definitions of weather factors considered when assessing hypotheses for the effects of climatic variation on population dynamics of diurnal lizards in Organ Pipe Cactus National Monument over 25 years (1989-2013)..

Factor	Code	Time Period	Definition	Hypotheses
Precipitation	P_{ws}	Warm season	May through Oct of prior year	Prey enhancement
Precipitation	P_{cs}	Cool season	Nov 2 years prior through April of prior year	Prey enhancement
Precipitation	P_{fall}	Fall	Sept and Oct of prior year	Prey enhancement
Precipitation	P_{yr}	Annual	Sum of P_{cs} and P_{ws}	Prey enhancement
Precipitation	P_{yr234}	Annual	Mean P_{yr} 2-4 years prior	Predation
Temperature	T_{minW}	Cold season	1-2 years prior Nov to 0-1 year prior Mar	Cold effects
Temperature	T_{minA}	Annual	1-2 years prior Nov to 0-1 years prior Oct	Cold effects
Temperature	T_{minS}	Emergence, pre-breeding, breeding season	0-1 year prior Mar-May	Cold effects
Temperature	T_{minBS}	Breeding season	0-1 year prior May-Jul	Cold effects
Temperature	T_{maxSp}	Spring	prior April-May	Heat stress
Temperature	T_{maxSp}	Spring-early summer	prior April-June	Heat stress
Temperature	T_{maxSu}	Summer	prior July-August	Heat stress
Temperature	T_{maxFall}	Late summer	2-yr prior Sept.	Heat stress
Temperature	T_{maxSpSu}	Spring-summer	prior April-Sept	Heat stress
Temperature	$T_{\mathrm{maxSu\text{-}Sept}}$	Mid-late summer	2-yr prior July-Sept.	Heat stress

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Appendix S2. Correlations among climatic attributes linked to our four hypotheses.

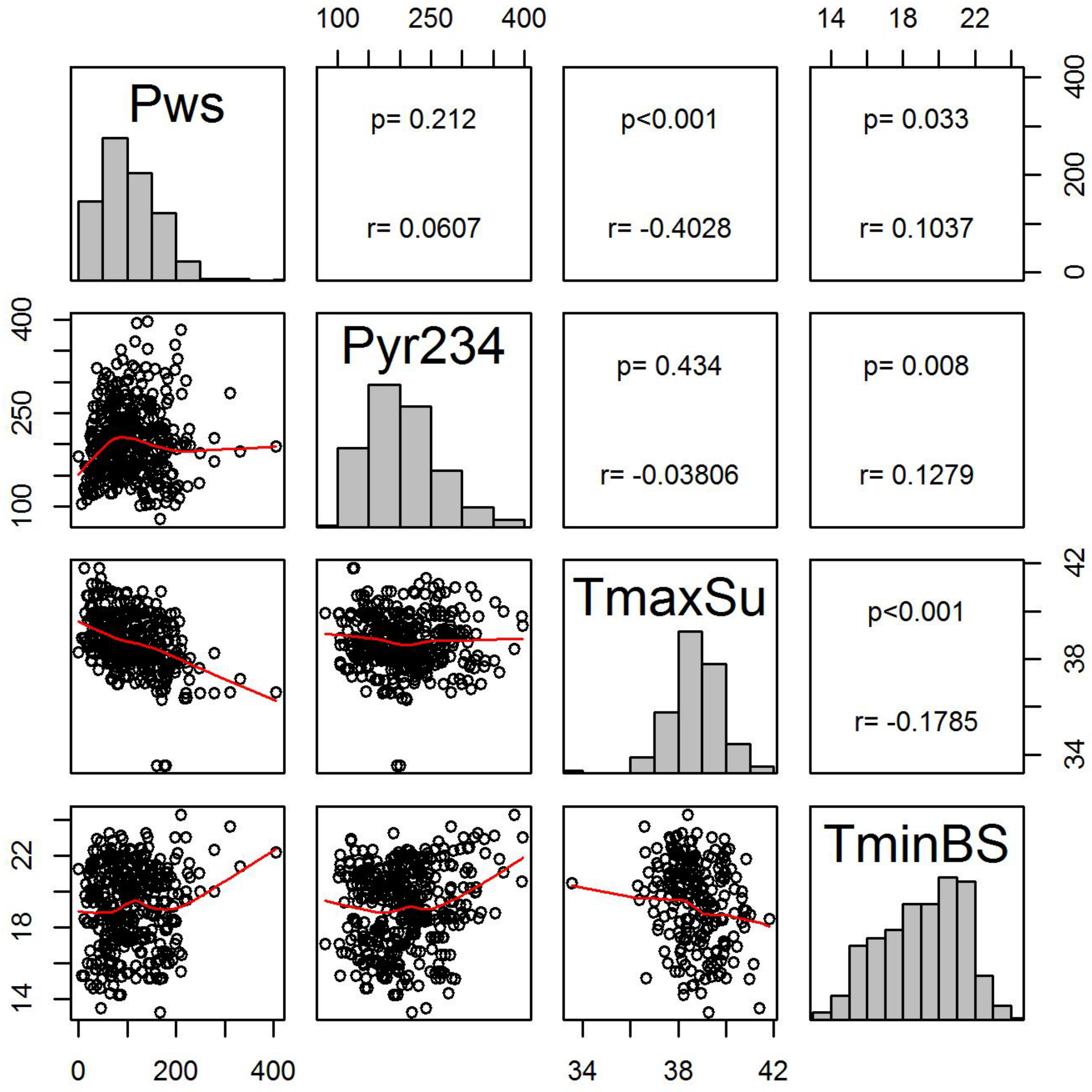

Figure S2A. Correlations between warm-season climatic attributes linked to each of our four hypotheses. Names and definitions of factors are in Table S2.

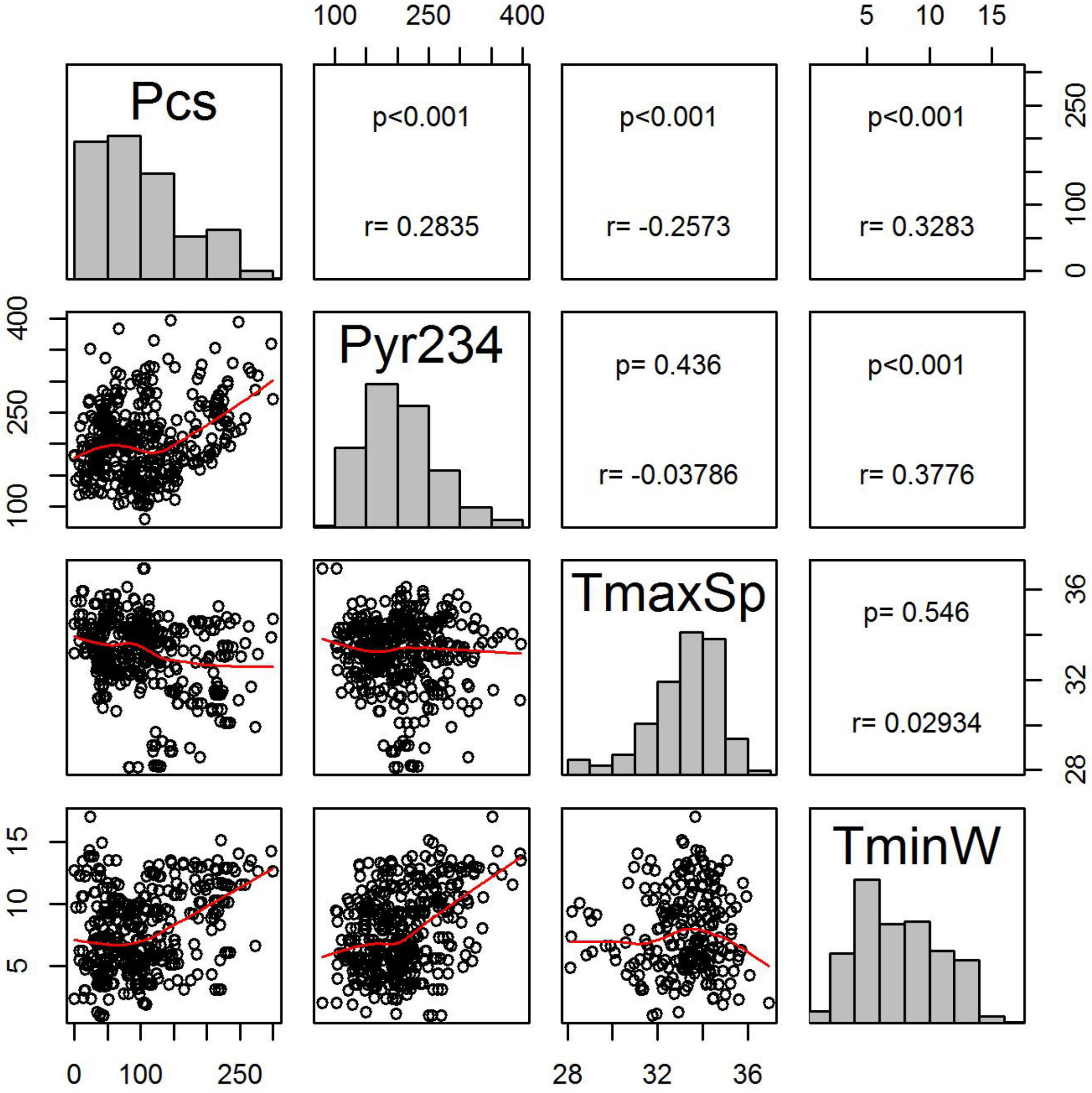

Figure S2B. Correlations between cool-season climatic attributes linked to each of our four hypotheses. Names and definitions of factors are in Table S2.

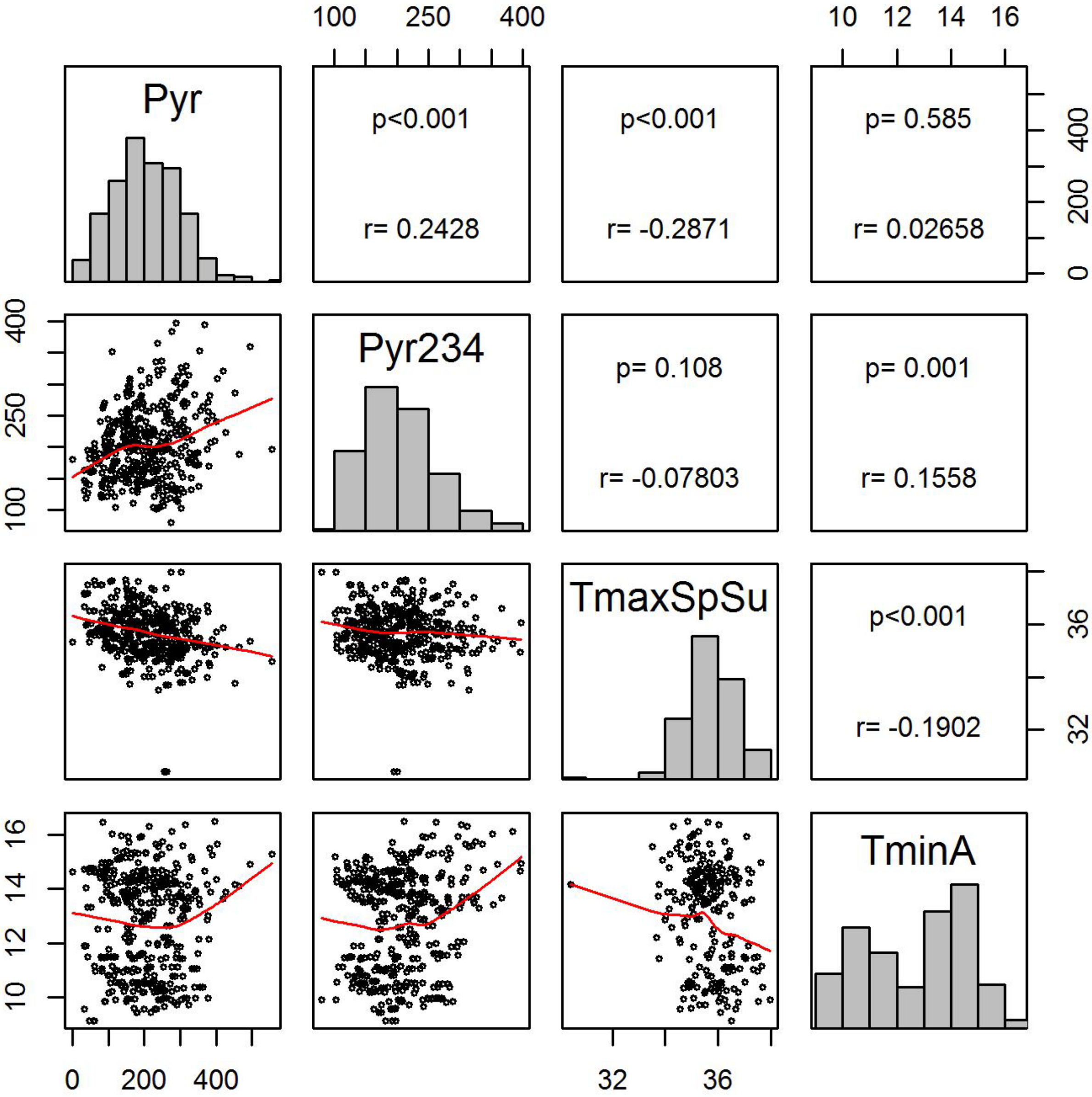

Figure S2C. Correlations between annual climatic attributes linked to each of four hypotheses. Names and definitions of factors are in Table S2.

Table S3. Binomial detection models for five species of lizards in Organ Pipe Cactus National Monument over 25 years (1989-2013). Each species was surveyed along line transects 3-8 times per day in both spring and summer of each year at up to 32 sites per year. Count data from these repeated daily surveys were modeled with hierarchical *N*-mixture models that explicitly considered variation in detection probability.

Species - season Factor	Estimate	SE	*Z*	*P*
Western whiptail - spring				
Intercept	-2.55	0.19	-13.79	<0.0001
Temperature	-0.051	0.072	-0.71	0.077
Temperature^2	-0.25	0.038	-6.58	<0.0001
Time after sunrise	0.10	0.075	1.36	0.18
Time after sunrise^2	-0.15	0.034	-4.29	<0.0001
Precipitation	0.11	0.025	4.43	<0.0001
Day of year	-0.12	0.030	-4.02	<0.0001
Rocky slope	-1.25	0.20	-6.29	<0.0001
Valley floor	0.24	0.14	1.69	0.091
Western whiptail - summer				
Intercept	-2.17	0.17	-12.42	<0.0001
Temperature	-0.10	0.057	-1.70	0.089
Temperature^2	-0.31	0.031	-10.22	<0.0001
Time after sunrise	0.35	0.056	6.31	<0.0001
Time after sunrise^2	-0.068	0.026	-2.51	0.012
Precipitation	-0.072	0.025	-2.93	0.0034
Rocky slope	-0.90	0.20	-4.41	<0.0001
Valley floor	0.26	0.156	1.69	0.091
Side-blotched lizard - spring				
Intercept	-3.57	0.22	-16.26	<0.0001
Temperature	-0.63	0.12	-5.42	<0.0001
Temperature^2	-0.22	0.037	-5.84	<0.0001
Precipitation	0.12	0.032	3.68	0.0002
Day of year	-0.20	0.042	-4.69	<0.0001
Desert shrubland	0.56	0.22	2.51	0.012
Xeroriparian woodland	0.17	0.23	0.74	0.46

Soil fine	-0.52	0.18	-2.89	0.0039
Side-blotched lizard - summer				
Intercept	-2.41	0.15	-16.26	<0.0001
Temperature	-0.52	0.070	-7.44	<0.0001
Temperature^2	-0.33	0.035	-9.48	<0.0001
Time after sunrise	-0.32	0.075	-4.32	<0.0001
Time after sunrise^2	0.072	0.035	2.01	0.045
Day of year	0.026	0.049	0.54	0.59
Day of year^2	-0.18	0.034	-5.37	<0.0001
Soil fine	-0.48	0.15	-3.21	0.0013
Zebra-tailed lizard - spring				
Intercept	-2.35	0.22	-10.48	<0.0001
Temperature	0.71	0.057	12.40	<0.0001
Temperature^2	-0.64	0.059	-10.71	<0.0001
Precipitation	0.23	0.047	4.95	<0.0001
Rocky slope	-1.30	0.30	-4.30	<0.0001
Valley floor	-0.77	0.30	-2.57	0.010
Desert shrubland	-0.53	0.39	-1.38	0.17
Xeroriparian woodland	0.82	0.30	2.72	0.0066
Zebra-tailed lizard - summer				
Intercept	-2.68	0.18	-14.72	<0.0001
Temperature	0.36	0.054	6.77	<0.0001
Temperature^2	-0.42	0.054	-7.72	<0.0001
Day of year	-0.17	0.058	-2.87	0.0041
Rocky slope	-1.15	0.37	-3.10	0.0020
Valley floor	-0.30	0.19	-1.54	0.12
Tree lizard - spring				
Intercept	-3.12	0.20	-15.46	<0.0001
Temperature	-0.29	0.050	-5.94	<0.0001
Temperature^2	-0.068	0.021	-3.28	0.0011
Time after sunrise	-0.34	0.046	-7.25	<0.0001
Time after sunrise^2	-0.13	0.030	-4.50	<0.0001
Precipitation	0.13	0.026	4.88	<0.0001
Desert shrubland	-0.022	0.26	-0.08	0.93
Xeroriparian woodland	0.83	0.20	4.09	<0.0001
Tree lizard - summer				

Intercept	-3.18	0.23	-14.11	<0.0001
Temperature	-0.76	0.071	-10.64	<0.0001
Temperature^2	-0.11	0.026	-4.43	<0.0001
Time after sunrise	0.033	0.058	0.57	0.57
Time after sunrise^2	-0.12	0.033	-3.66	0.0003
Day of year	-0.38	0.052	-7.38	<0.0001
Day of year^2	0.11	0.039	2.97	0.0030
Rocky slope	1.36	0.31	4.45	<0.0001
Valley floor	-0.074	0.23	-0.32	0.75
Desert spiny lizard - spring				
Intercept	-6.06	0.41	-14.81	<0.0001
Time after sunrise	-0.42	0.096	-4.40	<0.0001
Time after sunrise^2	-0.23	0.094	-2.42	0.016
Soil fine	1.47	0.39	3.81	0.0001
Desert spiny lizard - summer				
Intercept	-5.69	0.42	-13.50	<0.0001
Time after sunrise	-0.32	0.075	-4.25	<0.0001
Soil fine	1.35	0.40	3.37	0.0008

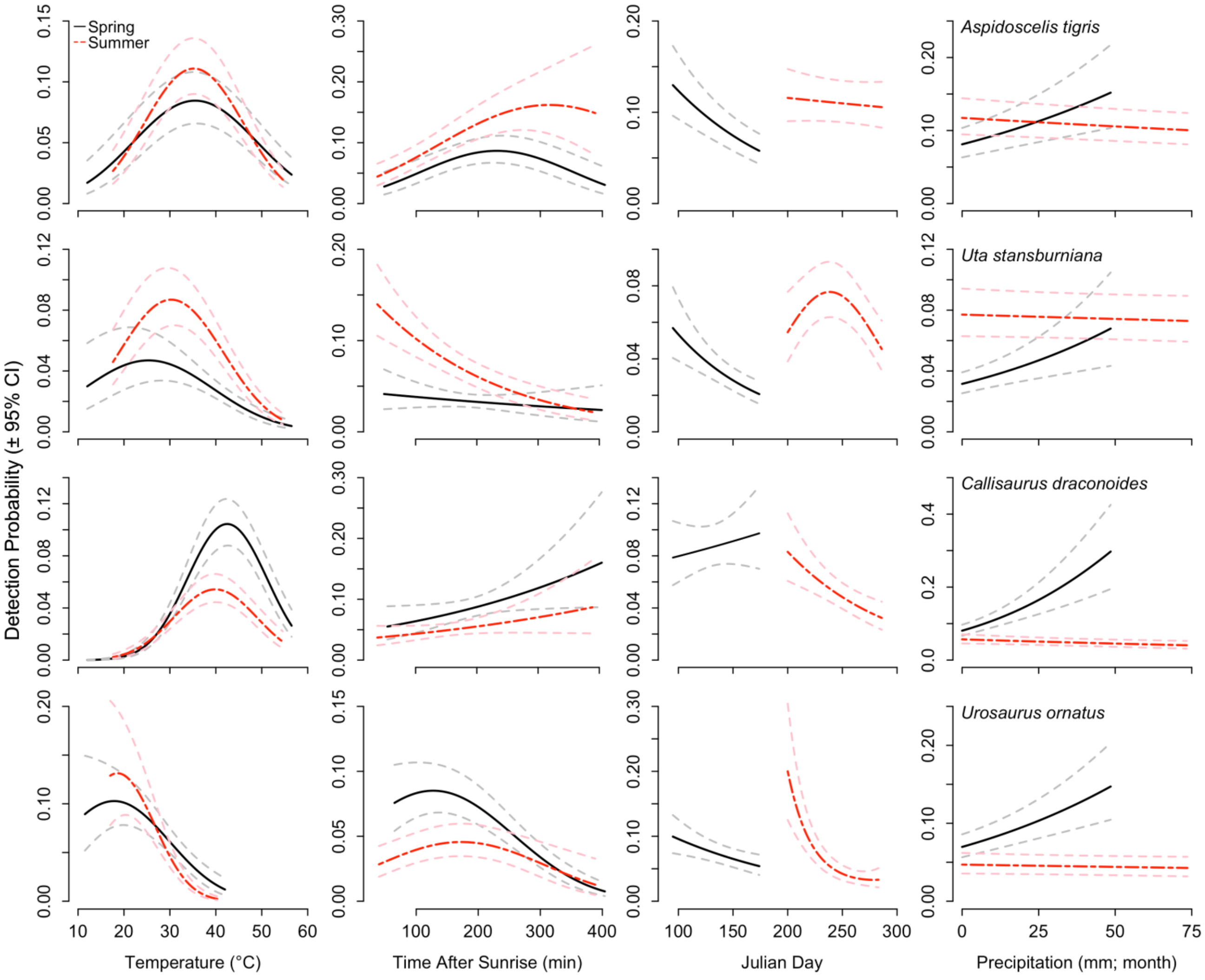

Figure S3. Effects of temperature, precipitation, and temporal factors on detection probability of four species of lizards in Organ Pipe Cactus National Monument, 1989-2013. Estimates are from binomial detection models summarized in Table S3

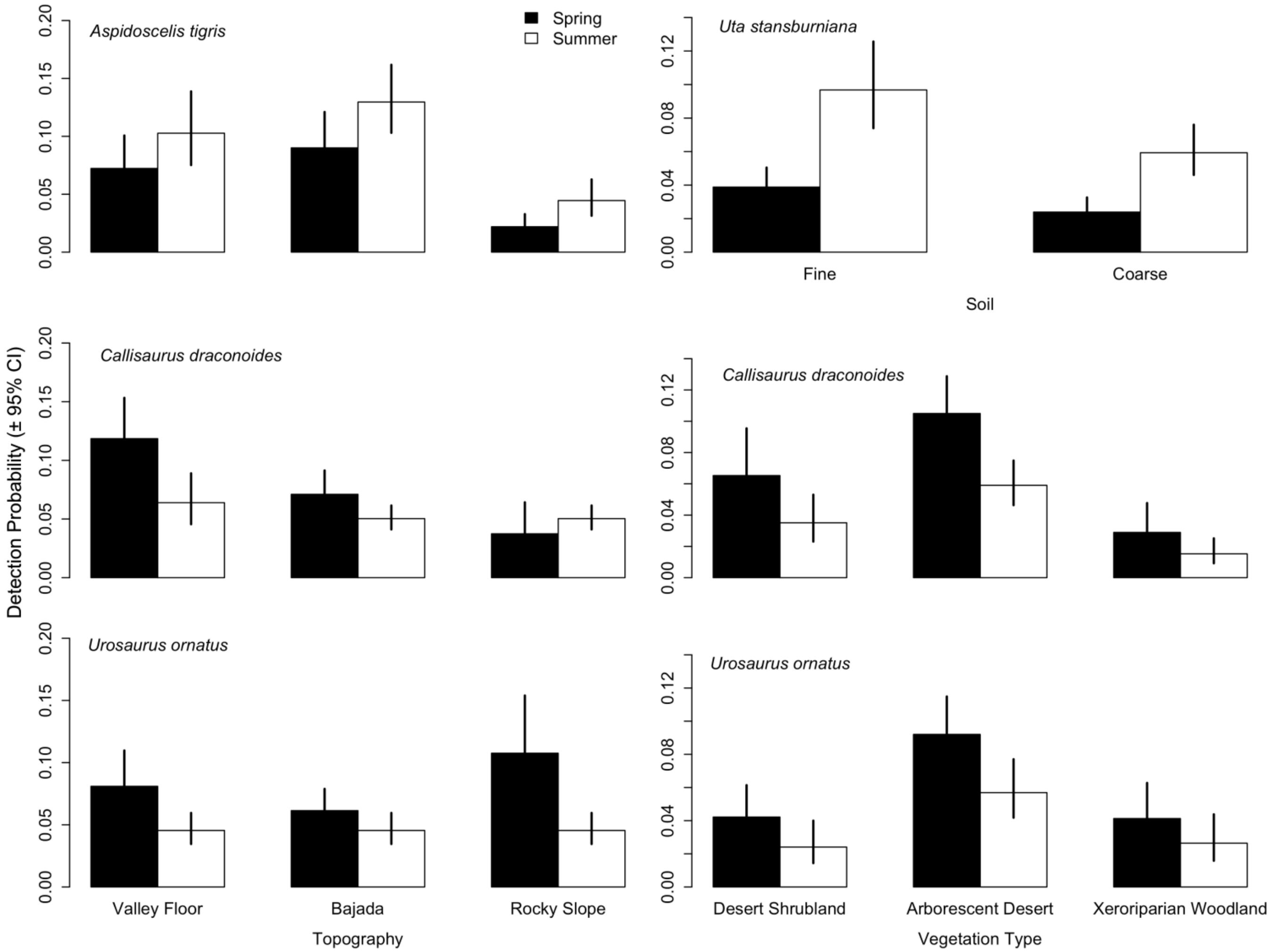

Figure S4. Effects of categorical covariates on detection probability of four species of diurnal lizards in Organ Pipe Cactus National Monument, 1989-2013. Estimates are from binomial detection models summarized in Table S3.

Table S4. Rankings of hypothesized models that explained the influence of local weather on spatiotemporal variation in abundance (ln no.) of five species of diurnal lizards in Organ Pipe Cactus National Monument over a 25-year period (1989-2013). *K* represents the number of model parameters, ΔAIC_c is the change in AIC between each model and the best approximating model, and AIC_c weights (w_i) are probabilities each model is the best approximating model in each model set. Variables representing each hypothesis are in Table 4.

Species Hypothesis	*K*	ΔAICc	w_i
Western whiptail			
Prey + predation + warm stress + cold effects	9	0.00	1.000
Prey + predation + cold effects	8	4.23	0.120
Predation + warm stress + cold effects	8	4.57	0.100
Predation + cold effects	7	8.09	0.020
Prey + predation + warm stress	8	9.93	0.010
Prey + predation	7	11.67	0.000
Prey + warm stress + cold effects	7	12.96	0.000
Prey + cold effects	6	17.66	0.000
Predation	6	17.99	0.000
Cold effects + warm stress	6	19.76	0.000
Prey + warm stress	6	22.06	0.000
Cold effects	5	23.99	0.000
Prey	5	25.72	0.000
Warm stress	5	31.00	0.000
Null	4	34.37	0.000
Side-blotched lizard			
Prey + predation + warm stress + cold effects	8	0.00	1.000
Predation + warm stress + cold effects	7	1.59	0.451
Prey + predation + cold effects	7	4.31	0.116
Predation + cold effects	6	5.91	0.052
Prey + warm stress + cold effects	7	6.07	0.048
Prey + predation + warm stress	7	7.88	0.019
Cold effects + warm stress	6	8.01	0.018

Prey + cold effects	6	9.59	0.008
Cold effects	5	11.48	0.003
Prey + predation	6	12.60	0.002
Predation	5	15.10	0.001
Prey + warm stress	6	16.02	0.000
Warm stress	5	18.86	0.000
Prey	5	19.67	0.000
Null	4	22.44	0.000
Zebra-tailed lizard			
Prey + warm stress + cold effects	8	0.00	1.000
Prey + cold effects	7	1.84	0.399
Cold effects + warm stress	7	3.40	0.183
Prey + predation + warm stress + cold effects	10	3.68	0.159
Cold effects	6	5.22	0.073
Prey + predation + cold effects	9	5.70	0.058
Predation + warm stress + cold effects	9	7.06	0.029
Predation + cold effects	8	9.00	0.011
Prey + warm stress	6	10.38	0.006
Warm stress	5	12.67	0.002
Prey + predation + warm stress	8	13.13	0.001
Prey	5	14.45	0.001
Null	4	16.71	0.000
Prey + predation	7	17.66	0.000
Predation	6	20.13	0.000
Tree lizard			
Prey + predation + warm stress + cold effects	9	0.00	1.000
Predation + warm stress + cold effects	8	2.41	0.299
Prey + predation + warm stress	8	5.22	0.074
Prey + predation + cold effects	8	8.72	0.013
Predation + cold effects	7	13.18	0.001
Prey + predation	7	15.26	0.000
Predation	6	22.09	0.000
Prey + warm stress + cold effects	7	22.67	0.000
Cold effects + warm stress	6	23.88	0.000
Prey + warm stress	6	25.95	0.000
Warm stress	5	28.47	0.000
Prey + cold effects	6	34.53	0.000

Cold effects	5	38.24	0.000
Prey	5	39.25	0.000
Null	4	45.14	0.000
Desert spiny lizard			
Prey + warm stress + cold effects	8	0.00	1.000
Cold effects + warm stress	7	1.09	0.579
Prey + predation + warm stress + cold effects	9	1.54	0.463
Predation + warm stress + cold effects	8	2.21	0.332
Cold effects	6	2.87	0.238
Prey + cold effects	7	3.07	0.216
Predation + cold effects	7	3.60	0.165
Prey + predation + cold effects	8	4.18	0.124
Prey + warm stress	6	7.57	0.023
Prey + predation + warm stress	7	8.22	0.016
Warm stress	5	8.43	0.015
Predation	5	8.97	0.011
Null	4	9.81	0.007
Prey + predation	6	9.91	0.007
Prey	5	9.98	0.007