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Diurnal Patterns of Surface Activity of a Desert Roadside Lizard Assemblage Reveal Temporal Niche Partitioning

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ABSTRACT: Desert lizards are ideal animals to study temporal ecological niche partitioning of sympatric taxa. From April–September 2023, we conducted hourly low-speed road transect sampling runs continuously from about dawn to dusk (13 runs), one day each month, to document diurnal surface activity patterns of a roadside assemblage of lizards in the Sonoran Desert of southern Arizona. We obtained 1771 observations of nine heliothermic species during 78 sampling runs. Of six species having ≥20 observations, three exhibited bimodal activity, comprised of a greater mid-morning activity peak, a midday avoidance, and a lesser peak in the late afternoon, whereas the other three species exhibited unimodal activity with late morning peaks. Surface activity among lizards appeared driven by environmental cues more so than intrinsic circadian patterns; activity was greatest when temperature was 31.8 °C, solar irradiance was 433.1 W/m^2, and relative humidity was 43.6%. Our robust methods resolved subtle niche partitioning within a diverse diurnal lizard assemblage. Temporal patterns of surface activity should be considered when designing inventory, monitoring, and research projects.

Keywords: Heliotherm; Ecological niche; Modality; Road ecology; Inventory and monitoring

1. Introduction

Research conducted on desert lizard communities has helped to forge basic ecological principles about coexistence among sympatric species, including the concepts of ecological niches and resource partitioning [1]. Each species has a set of niche penchants that results in multiple taxa coexisting without substantial competition for resources [2–4]. Temporal surface-activity patterns are one of three basal dimensions of ecological niches, along with feeding habits and spatial distribution, although these are not independent of one another or other variables [5–7]. Environmental conditions influence lizard physiology and behavior [8,9], which can vary temporally across daily, seasonal, and long-term periods [10–12].

Temporal aspects of the ecological niche in heliothermic (*i.e.*, sun-basking) lizards are reflected by several behavioral traits, including surface activity and modality. Because these traits are readily observable, desert lizards make ideal models for field ecology studies [1,13,14]. Many heliothermic species in the

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American Southwest tend to have similar activity patterns, but considerable variation can occur because of geographic and environmental factors such as topography, microhabitat complexity, and climate. In general, desert lizards undergo subterranean brumation (*i.e.*, winter dormancy) [15] during cooler winter months, then emerge during spring warm-up, and may remain active into autumn [16]. Populations in relatively cooler deserts (e.g., the Great Basin) tend to have shorter surface activity periods than those in the hotter deserts (e.g., the Mojave) [17]. Some taxa reduce surface activity and may facultatively aestivate during critical activity times because of temperature extremes and drought, or when food resources are lacking [18,19]. Localized weather patterns may also influence temporal surface activity [20,21].

The Sonoran Desert is one of the most biologically diverse deserts in the world [22,23]. Lizard richness in the Sonoran Desert is greatest among the North American deserts, with more than 90 species [24–26]. It is important to evaluate novel data and techniques to resolve a broader understanding of lizard ecology among the Sonoran Desert's breadth of biotic communities, environments, and biodiversity [21]. Road-based studies (*i.e.*, roadside ecology), for example, can be effective at detecting lizards in the American Southwest under suitable conditions [27,28].

Study designs that encompass the nearly entire daily diurnal period during the active season may be informative for refining effective sampling strategies for long-term monitoring goals. For example, an ongoing study at the same site being investigated for roadside ecology and effects of climate change suggested that some species were rare or being undersampled [29]. It is important to determine if adaptive sampling would be warranted to incorporate a more complete representation of the heliothermic lizard assemblage. One way to elucidate on a sampling strategy is to assess taxa for diurnal modality patterns; that is, singular or multiple activity peaks during the day. Robust temporal sampling at finer scales may ensure detection of partitioned activity periods. Surveying across an entire diurnal period may also increase the likelihood of detecting typically under-sampled species [30], and provide resolution into their activity periods and usage of roadside habitats. Because many desert lizards exhibit bimodal surface activity [31–33], determining if mornings or afternoons yield a greater likelihood of detectability for those species could inform more focused monitoring efforts.

Despite much research on desert lizards, there remains a relative dearth of information on temporal surface activity of heliothermic species, especially from anthropogenically disturbed areas, such as roadsides [29]. Our objectives were to (1) investigate temporal patterns of surface activity of a roadside assemblage of lizards in the Sonoran Desert, (2) determine diurnal modality of all commonly encountered lizard species (where $n \geq 20$), and (3) analyze surface activity patterns that may be associated with climatic and environmental influences. Results may also help with applying temporal aspects of adaptive sampling to long-term monitoring projects [34,35]. Understanding surface activity patterns is advantageous for developing climate change models (e.g., [36]) and, hence, conservation strategies for heliothermic lizard species.

2. Materials and Methods

2.1. Study System and Terminology

Our study site was in Saguaro National Park (Tucson Mountain District; SNP), Pima County, Arizona, USA. This region has an annual bimodal rainfall pattern during the winter and summer; the latter is due to the arrival of the North American Monsoon [37]. The vegetation community is the Arizona Upland subdivision of the Sonoran Desert [38]. At a finer scale, it is in the middle bajada, between the upper bajada of the Tucson Mountains proper and the lower bajada of the Avra Valley [29,39]. The middle bajada has a low-gradient slope with a sandy to gravelly substrate overlain by scattered cobbles. The Tucson Mountains are rich in vascular flora, composed of at least 610 species [40]. Based on vegetation transect data along the roadway at the study site [41], there were at least 42 species of perennial shrubs >30 cm high, at a density of 4230 perennial trees and shrubs/ha counted. Overstory plants included ironwood (*Olnea tesota*),

yellow paloverde (*Parkinsonia microphylla*), velvet mesquite (*Neltuma velutina*), and saguaro cactus (*Carnegiea gigantea*). Understory species were numerous, dominated by burro brush (*Hymenoclea salsola*), Engelmann prickly pear (*Opuntia engelmannii*), staghorn cholla (*Cylindropuntia versicolor*), and triangle-leaf bursage (*Ambrosia deltoidea*), among others.

Terminology in community-ecology papers is often not standardized [42,43]. Here, we define a community of lizards as all species present within a given geographic area [43]. Our use of the term assemblage refers only to those heliothermic species that are detectable from the roadway. Our use of the term surface activity refers to periods when lizards are above ground and not asleep. We estimated the developmental age-class of lizards to be either Young-of-Year (YoY) or hatched in previous years (>YoY); these two lumped age classes were useful in understanding annual reproductive success. In this way, subjective terms such as immature, juvenile, and subadult (which could be YoY or >YoY or both) were avoided. The known lizard community in the immediate area of SNP consists of 14 species [29], of which 12 are considered obligate heliotherms. Our sampling design spanned across the general active season of most species to incorporate seasonal changes [21].

2.2. Surveys and Data Collection

Once monthly, April–September 2023, we used low-speed road transects (LSRT) [27,44] to conduct hourly replicated survey runs (single vehicle surveys from the start to end of route) across the daylight period starting each hour, 06:00–18:00. We selected survey days that were conducive to heliothermic lizard surface activity (forecasted non-raining, midday sun) and when personnel were available. The LSRT technique involves driving at very slow speeds (3–8 kph) while visually scanning for lizards on the roadway and road-edge topography; lizards seen in the adjacent visibility-limited uplands were recorded. Details of survey design are described elsewhere [27,44]. There were 1–2 observers per vehicle. The survey route was along a 3.7 km stretch of Golden Gate Road, which is a non-paved, native-materials road with a conspicuous berm on each side and some xeroriparian features that crossed the roadway. When lizards were encountered, surveyors recorded species, developmental age class, and road-associated topographic feature (e.g., berm, road surface, wash crossing) when first detected. We used binoculars from stopped vehicles to aid in identification and classification. All surveyors were biologists trained by the senior author in local species identification and methods before conducting their own survey runs; individual lizards that could not be reliably identified to species were entered as "unknowns". Surveys always proceeded in a westward direction. We staggered drivers to ensure continuous coverage at the start of each hour; drivers usually conducted two to four runs per survey day. The transect runs were not temporally constrained to be completed in exactly one hour, as this would have compromised the ability to detect lizards along the entire stretch, which was always surveyed from start to finish at each run (see [27]).

Because climate and weather can influence when lizards are surface active [6,12,45], we also obtained weather data from a nearby (<3 km) weather station. Those data were recorded every five minutes and consisted of ambient air temperature (°C), barometric pressure (mm), dewpoint (°C), precipitation (cm), relative humidity (%), solar irradiance (W/m^2), and wind speed (m/s). We pooled weather data into hourly bins (12 measurements/h) and calculated means for all metrics except precipitation, which was summed. Reliable cloud cover variables were not available in a meaningful way, so this factor was not assessed.

2.3. Statistical Analyses

We performed all the following analyses in the program R v. 4.5.3 [46]. For the temporal assessment, we evaluated daytime surface activity distributions bounded within the diurnal period (06:00–18:00 h). After testing assumptions of normality with Shapiro-Wilk and Levene's tests, we used non-parametric statistical frameworks to test for modality and quantified emergence patterns for datasets containing all

lizards (Objective 1) and separately for species with at least 20 observations (Objective 2). Because field data were recorded as aggregated hourly counts, we implemented a data-replication framework to reconstruct continuous time-vectors based on hourly bin midpoints by using the rep() function without interpolation. This approach avoids artificial oversampling or inflating degrees of freedom. To evaluate diurnal modality and cross-validate temporal distributions, we utilized a multi-metric approach: Hartigan's dip test for unimodality [47] via the *diptest* package [48] and the non-parametric bootstrap critical bandwidth test (hereafter, "Bootstrap") via the *multimode* package [49]; we also calculated Sarle's Bimodality Coefficient (BC) [50], where values exceeding 0.556 denote a bimodal distribution. For species exhibiting cryptic or facultative bimodality, this multi-test approach allowed us to reconcile minor visual afternoon surges against formal statistical classifications of unimodality [51]. For taxa with at least 20 observations, we compared cumulative surface activity distributions (*i.e.*, diurnal temporal niche partitioning) using non-parametric Two-Sample Bootstrapped Kolmogorov-Smirnov tests via the *Matching* package [52], utilizing 1000 bootstrap shuffles to resolve structural ties inherent to binned data.

To understand extrinsic associations that may influence surface activity, here, as the abundance of lizards observed per hour, 06:00–18:00, we conducted a generalized additive mixed model (GAMM) with a negative binomial distribution in the *mgcv* package [53,54]. We chose a GAMM due to anticipated nonlinear effects of weather covariates on ectothermic lizards [28,55–57]. We included the hour period (factor) and the environmental predictors obtained from the weather station, except dewpoint, which was highly correlated with humidity. To account for confounding effects [58], we set month and observers as random effects using random intercept smooths and included survey duration as an offset term [28]. We used the *REML* option and implemented automatic smooth term selection by adding a double penalty to the null space of each spline, which penalizes uninformative environmental covariates entirely out of the model by shrinking their effective degrees of freedom to zero [59]. To ensure adequate k (*i.e.*, maximum degrees of freedom dimensionality) per smoothed covariate, we used the k.check() function [60]. Lastly, we used the *gratia* package [61] to inspect model diagnostics, evaluating model fit and residual assumptions through simulated deviations via the appraise() function.

Because air temperature, solar irradiance, and relative humidity were important in earlier analyses, we used Kruskal-Wallis tests to assess interspecific variation among focal taxa (≥20 observations). We used Dunn's tests in the *rstatix* package [62] for pairwise posthoc comparisons with the Benjamini-Yekutieli correction for false discovery rates. Statistical significance for all tests was evaluated at an alpha level of 0.05.

3. Results

3.1. General Findings

We completed a total of 78 hourly LSRT runs. Combined runs from nine surveyors added up to 94.7 vehicle-hours, covering a total of 288.6 km of roadway. Mean run duration was 80.9 min (SD ± 19.2). There were no significant differences in survey duration among surveyors ($F_{(8, 66)} = 1.43$, $p = 0.199$).

Baseline weather data for survey days (Table S1) generally corresponded to typical regional conditions experienced during lizard activity season from April through September, except that precipitation, dewpoint, and relative humidity during May were higher than seasonally normal due to some pre-monsoonal storms. Weather conditions for lizard observations by hour are included in a supplemental file (Table S2).

We obtained 1771 lizard observations (6.1 lizards/km) from at least nine species; 19 lizards fled before identification could be obtained; six species yielded ≥20 observations (Table 1). Most encounters ($n = 1767$, 96.4% of observations) were associated with the road prism, especially berms ($n = 1367$, 77.6%) and similar anthropogenic features (water diversions and road debris piles; $n = 147$, 19.8%). Edge habitat (1–3 m past berm crest) accounted for 6.8% of the detections ($n = 121$). Only 3.8% ($n = 68$) of the observations were on the surface of the roadway. A total of 3.6% of detections ($n = 64$) were not considered to be road-

associated (either in arroyos or upland habitat beyond the edge). We did not encounter any lizard roadkill during this study.

Table 1. Observations of lizards detected (n = 1771) during low-speed road transects (LSRT). Observations occurred during continuous hourly transect runs starting from 06:00 to 18:00 per monthly survey.

Species (n)	Apr	May	Jun	Jul	Aug	Sep
Aspidoscelis tigris (Tiger Whiptail, n = 102)	14	22	13	17	13	23
Callisaurus draconoides (Zebra-tailed Lizard, n = 824)	98	209	100	143	118	156
Crotaphytus nebrius (Sonoran Collared Lizard, n = 1)	--	1	--	--	--	--
Dipsosaurus dorsalis (Desert Iguana, n = 274)	10	61	25	22	66	90
Gambelia wislizenii (Long-nosed Leopard Lizard, n = 20)	2	7	3	2	4	2
Phrynosoma solare (Regal Horned Lizard, n = 9)	--	2	--	1	2	4
Sceloporus magister (Desert Spiny Lizard, n = 218)	24	56	29	19	33	57
Urosaurus ornatus (Ornate Tree Lizard, n = 3)	--	--	--	--	--	3
Uta stansburiana (Common Side-blotched Lizard, n = 301)	15	16	11	64	88	107
Unknown lizard (n = 19)	3	2	5	1	7	1
Total	166	376	186	269	331	443

3.2. Diurnal Modality and Species Temporality

Cumulatively, surface activity among the lizard assemblage was strongly bimodal (Hartigan's dip test: D = 0.07, p < 0.001; Bootstrap test: p < 0.001). There was a greater peak in surface activity around 08:00–09:00 and a lesser peak around 16:00 (Figure 1G), supported by a high assemblage-wide bimodality coefficient (BC = 0.616). Three species exhibited bimodal diurnal activities: *Callisaurus draconoides* (Zebra-tailed Lizard; BC = 0.607, dip: p < 0.001, Bootstrap: p = 0.008), *Sceloporus magister* (Desert Spiny Lizard; BC = 0.798, dip: p < 0.001, Bootstrap: p < 0.001), and *Uta stansburiana* (Common Side-blotched Lizard; BC = 0.844, dip: p < 0.001, Bootstrap: p < 0.001; Figure 1). However, both *Dipsosaurus dorsalis* (Desert Iguana; BC = 0.444, Bootstrap p = 0.430) and *Gambelia wislizenii* (Long-nosed Leopard Lizard; BC = 0.465, Bootstrap p = 0.964) revealed steady unimodal activity periods (Figure 1). Although *Aspidoscelis tigris* (Tiger Whiptail) visually displayed a minor late afternoon surge (Figure 1A), it was formally classified as unimodal (BC = 0.524; Bootstrap test: p = 0.214). Pairwise comparisons demonstrated extensive temporal niche partitioning across the diurnal window. Non-parametric distribution testing confirmed that *A. tigris* diverged significantly from the system's strongest bimodal anchor, *U. stansburiana* (Two-Sample Bootstrapped K-S test: D = 0.2528, p < 0.001). Except for indistinguishable overlap of *S. magister* and *U. stansburiana*, interspecific temporal distributions differed across the community (K-S tests: p < 0.05; Table 2). That is, the differing temporal activity distributions revealed subtle but clear temporal niche partitioning among the lizard assemblage.

Table 2. Pairwise comparison of diurnal surface activity orientation among lizard species ($n \geq 20$). Values below the dash are Two-Sample Bootstrapped Kolmogorov-Smirnov test statistics (D) calculated via 1000 bootstrap shuffles to resolve binned ties. Respective exact p-values are displayed above dashes.

	ASTI	CADR	DIDO	GAWI	SCMA	UTST
ASTI	—	0.045	0.151	0.315	<0.001	<0.001
CADR	0.145	—	<0.001	0.210	<0.001	<0.001
DIDO	0.132	0.151	—	0.032	<0.001	<0.001
GAWI	0.190	0.240	0.280	—	0.037	0.018
SCMA	0.254	0.292	0.365	0.287	—	0.845
UTST	0.253	0.313	0.384	0.318	0.055	—

Abbreviations: *Aspidoscelis tigris* (ASTI), *Callisaurus draconoides* (CADR), *Dipsosaurus dorsalis* (DIDO), *Gambelia wislizenii* (GAWI), *Sceloporus magister* (SCMA), *Uta stansburiana* (UTST).

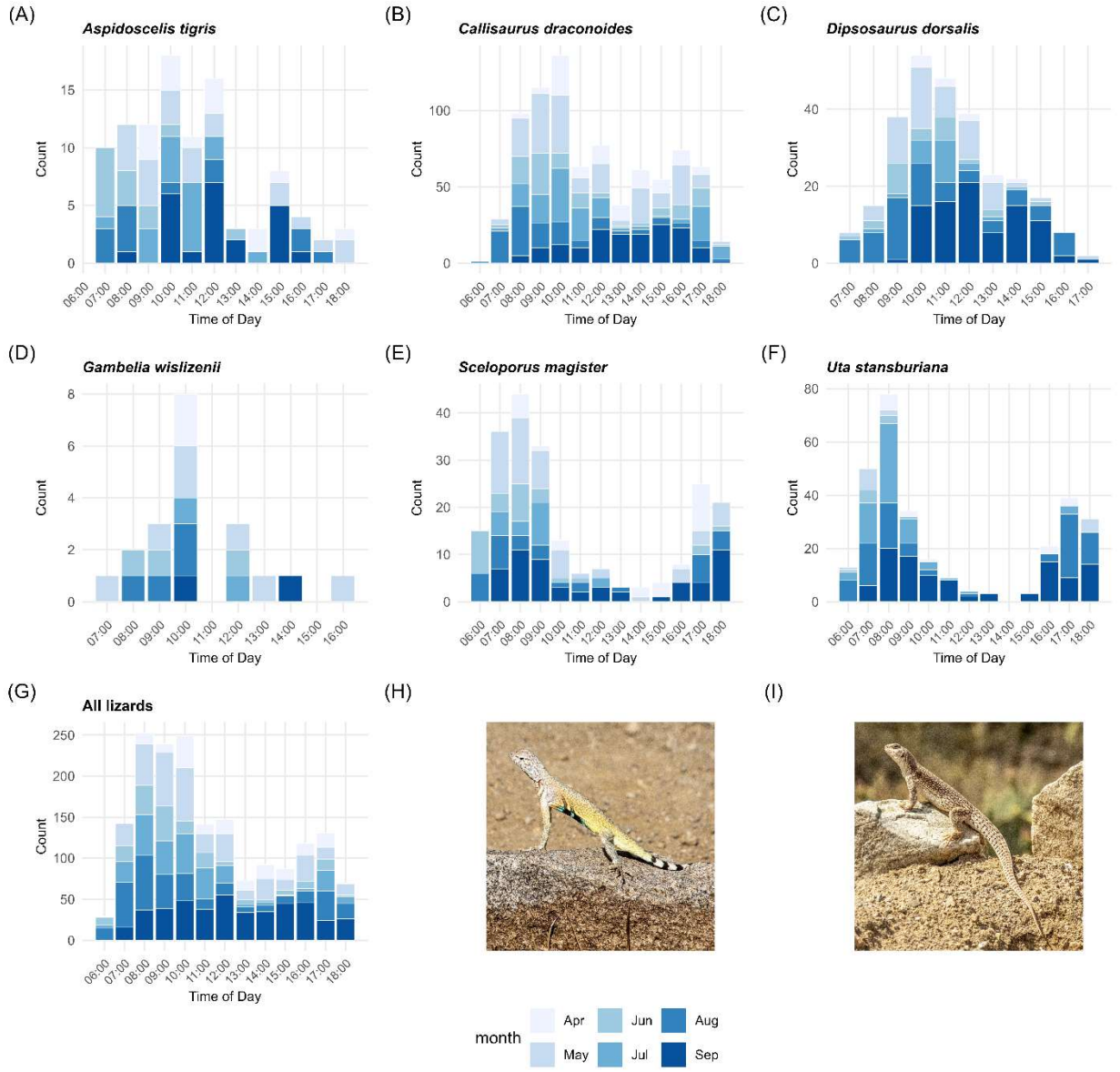


Figure 1. Activity modality for diurnal roadside lizard assemblage in the Sonoran Desert of southern Arizona. Surveys began each hour, 06:00–18:00. Data reflect counts per hourly period (vertical bins) by month (blue gradients) for six commonly encountered ($n \geq 20$) species of heliothermic lizards (**A**–**F**) and total encountered lizards (**G**). Representatives of modality for species basking along the roadway: *Callisaurus draconoides*, having an overall bimodal distribution (**H**), and *Dipsosaurus dorsalis*, a unimodal species (**I**). Photographs (**H**,**I**): CC-BY-4.0, LLCJ.

Temporal species richness ranged from zero to seven species during specific runs (Table 3). The hour with the lowest mean number of species detected was around 06:00, and the highest were around 10:00 and 09:00, respectively. The afternoon peaks in diversity, albeit lower than mornings, were: 16:00 and 17:00. The doldrums for species diversity detection occurred during the afternoon from 13:00 to 15:00.

Table 3. Number of lizard species detected during the 78 hourly LSRT surveys.

Hour	6	7	8	9	10	11	12	13	14	15	16	17	18
April	0	0	3	4	6	3	3	2	4	3	3	3	1
May	1	5	5	6	5	4	5	3	4	3	5	4	4
June	2	5	6	6	4	4	3	3	2	2	1	2	2
July	1	5	4	5	5	3	6	2	2	1	1	2	1
August	3	5	7	5	7	3	4	3	2	2	4	4	3

September	0	3	4	5	7	6	5	5	3	5	6	4	3
Mean	1.17	3.83	4.83	5.17	5.67	3.83	4.33	3.00	2.83	2.67	3.33	3.17	2.33
SD	1.17	2.04	1.47	0.75	1.21	1.17	1.21	1.10	0.98	1.37	2.07	0.98	1.21

Over the course of the season, the observed developmental age-class distribution changed, which varied by species (Figure 2). The earliest month of appearance for YoY was in June for *U. stansburiana.* The YoY was the predominant age class for this species from June through September and accounted for 79.4% of its observations (239/301); this is consistent with the reported low survivorship for individuals >12 months of age [63]. Conversely, for *C. draconoides*, only four of 824 encounters (0.5%) were of YoY. Hatchling *C. draconoides* have been reported to appear between July and November across their range [31], and the long-term monitoring project suggests YoY for this species often appear in the latter portion of this range (October and November), at least during spring-drought years. The YoY for other species primarily appeared in late July or early August through September (Figure 2), coinciding with the monsoonal green-up and increases in food availability.

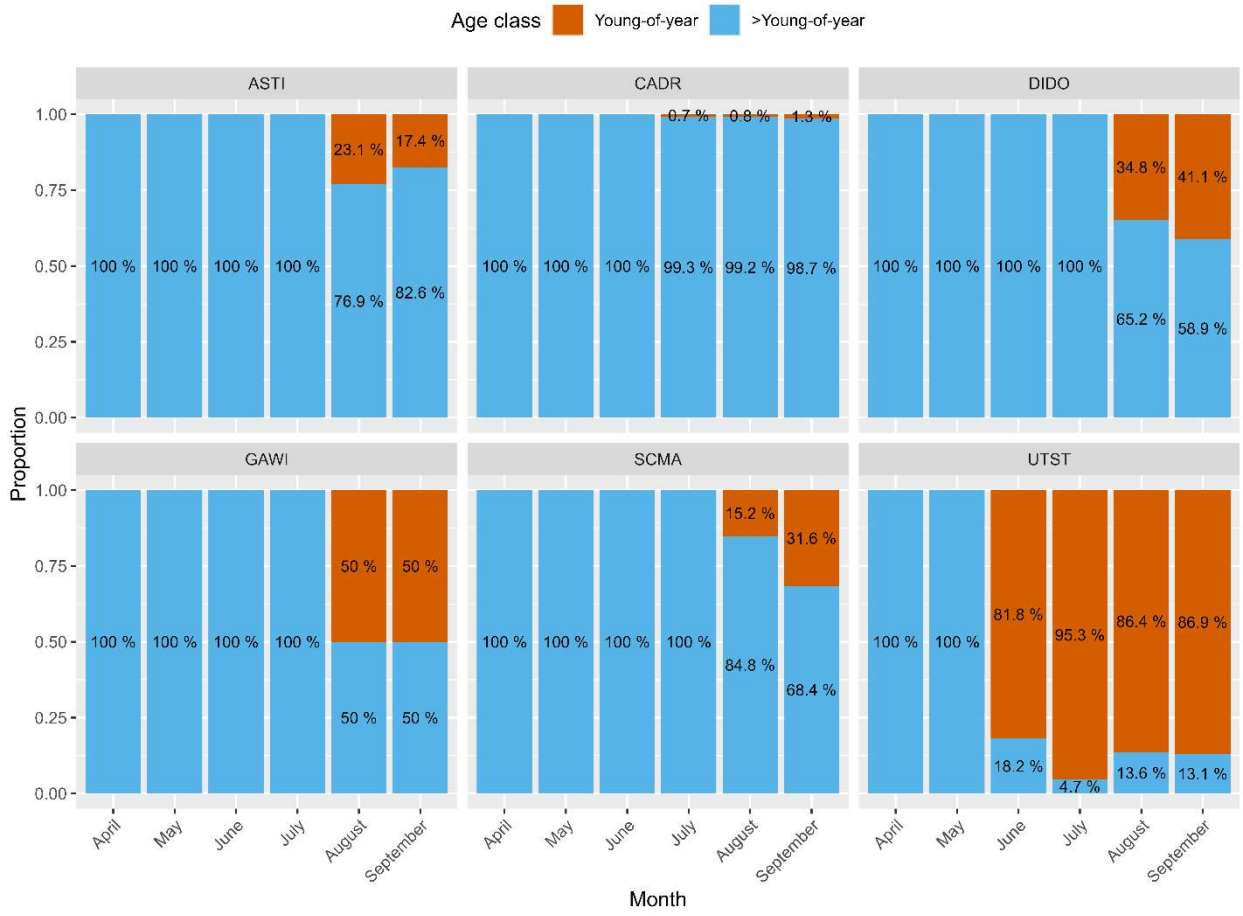


Figure 2. Distribution of young-of-year (YoY, orange) and >YoY (blue) lizards by month during this study. Abbreviations: *Aspidoscelis tigris* (ASTI), *Callisaurus draconoides* (CADR), *Dipsosaurus dorsalis* (DIDO), *Gambelia wislizenii* (GAWI), *Sceloporus magister* (SCMA), *Uta stansburiana* (UTST).

3.3. Relationship of Weather and Surface Activity

The GAMM that best explained diurnal lizard abundance per hour included air temperature, solar irradiance, relative humidity, and barometric pressure (deviance explained = 80.5%, Adjusted R^2 = 0.814; Table 4). Air temperature (*edf* = 3.10, $p < 0.001$), humidity (*edf* = 2.89, $p < 0.001$), and solar irradiance (*edf* = 3.32, $p < 0.001$) had nonlinear additive effects on the abundance of lizards per hour, after accounting for

random effects (Figure 3). Barometric pressure also retained a weaker, near-linear significant relationship (*edf* = 1.78, $p = 0.011$), while wind speed had no measurable impact and was automatically dropped by the model's regularization penalty (*edf* = 0.002, $p = 0.344$). Among the random structures, baseline variation across months was negligible (*edf* = 0.67, $p = 0.265$), whereas individual observer biases (*edf* = 5.57, $p < 0.001$) justified its inclusion to isolate search efficiency variance. Initial model variants included hour period as a fixed categorical factor; however, Akaike Information Criterion (AIC) comparisons optimized for additive models [54] demonstrated that including categorical hours inflated degrees of freedom without improving fit (ΔAIC = 6.56), and it was subsequently omitted.

Table 4. Generalized additive mixed model (GAMM) summary of environmental predictors of diurnal lizard abundance by hour ($n = 75$). The model uses a negative binomial error distribution (*theta* = 11.88) and a log link function under a restricted maximum likelihood frameworks. Predictors are smoothed "s()" or random effect with random intercept smooths "RE()"; survey duration was included as an offset term. Effective degrees of freedom (*edf*) proxy for nonlinearity in GAMMs; values = 1 are linear, values approaching 0 are uninformative, and values > 1 are increasingly nonlinear.

Predictor Variable	*edf*	*df*	*Chi.sqX*^{2}	*p*-Value
s(Temperature)	3.100	4	89.556	<0.001
s(Solar Irradiance)	3.323	9	30.799	<0.001
s(Relative Humidity)	2.888	9	44.865	<0.001
s(Barometric Pressure)	1.778	9	9.150	0.011
s(Wind)	0.002	4	0.002	0.344
RE(Month)	0.668	5	0.876	0.265
RE(Observer)	5.570	8	23.260	<0.001

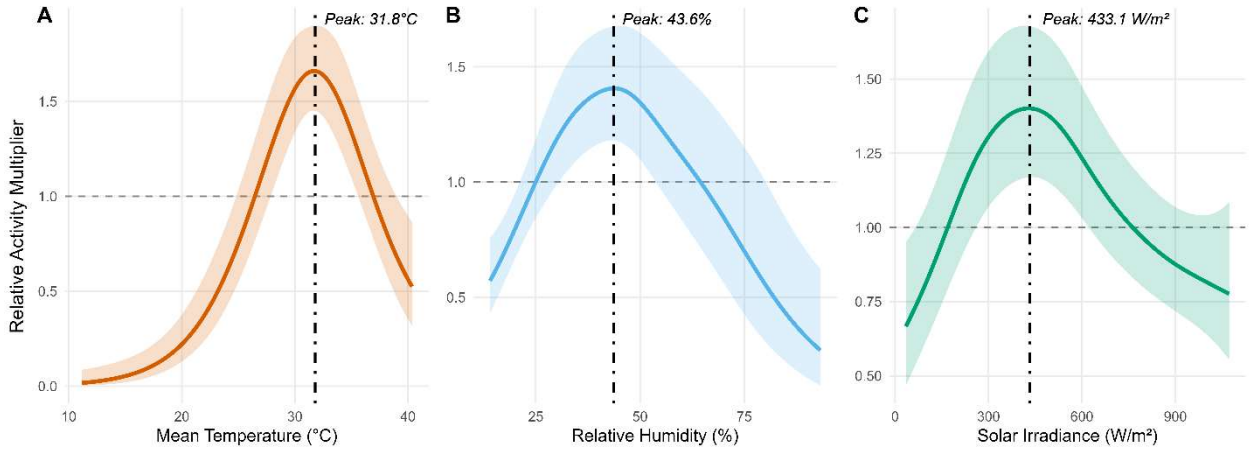


Figure 3. Relationship between environmental conditions and activity by diurnal heliothermic lizards observed during LSRT surveys. Relative Activity Modifier shows activity increases (values > 1) or decreases (values < 1) relative to the baseline average (value = 1), after accounting for other covariates, for mean air temperature (**A**), relative humidity (**B**), and solar irradiance (**C**).

Continuous threshold analysis of the partial effect curves revealed that lizard surface activity exceeded baseline expectations (Relative Activity Multiplier > 1.0) when ambient temperatures were between 26.5–36.8 °C (peaking at 31.8 °C) and when relative humidity was between 25.2–64.4% (peaking at 43.6%; Figure 3). Heliothermic activity appeared bound by solar radiation, rising above baseline averages at 170.9 W/m^2 and maximizing at an optimal intensity of 433.1 W/m^2 before falling back to baseline levels at 758.2 W/m^2 as radiant heat approached thermal limits. This corroborates our findings that peak lizard surface activity near the roadway occurs sufficiently after sunrise and wanes prior to sunset (Figure 1G).

For taxa with ≥20 observations, there were species differences related to air temperature ($H = 115.5$, *df* = 5, $p < 0.001$), mean humidity ($H = 226.3$, *df* = 5, $p < 0.001$), and solar irradiance ($H = 424.9$, *df* = 5, $p < 0.001$; Figure 4). Post-hoc pairwise Dunn's tests with Benjamini-Yekutieli correction revealed distinct

climatic guilds across the community (Table S3). *Sceloporus magister* occupied lower temperatures than all peers except *G. wislizenii* ($p \leq 0.133$). For hydric and solar metrics, *D. dorsalis* split away as a strict hot-dry, high-exposure outgroup, tracking lower relative humidity ($p < 0.001$) and higher solar irradiance loads ($p \leq 0.037$) than all other taxa. Conversely, *U. stansburiana* occupied the lowest solar exposure extreme of the radiant spectrum ($p < 0.001$). Demonstrating strong climatic alignment, *A. tigris* and *C. draconoides* shared statistically identical relative humidity and solar irradiance profiles across all pairwise metrics ($p = 1.00$).

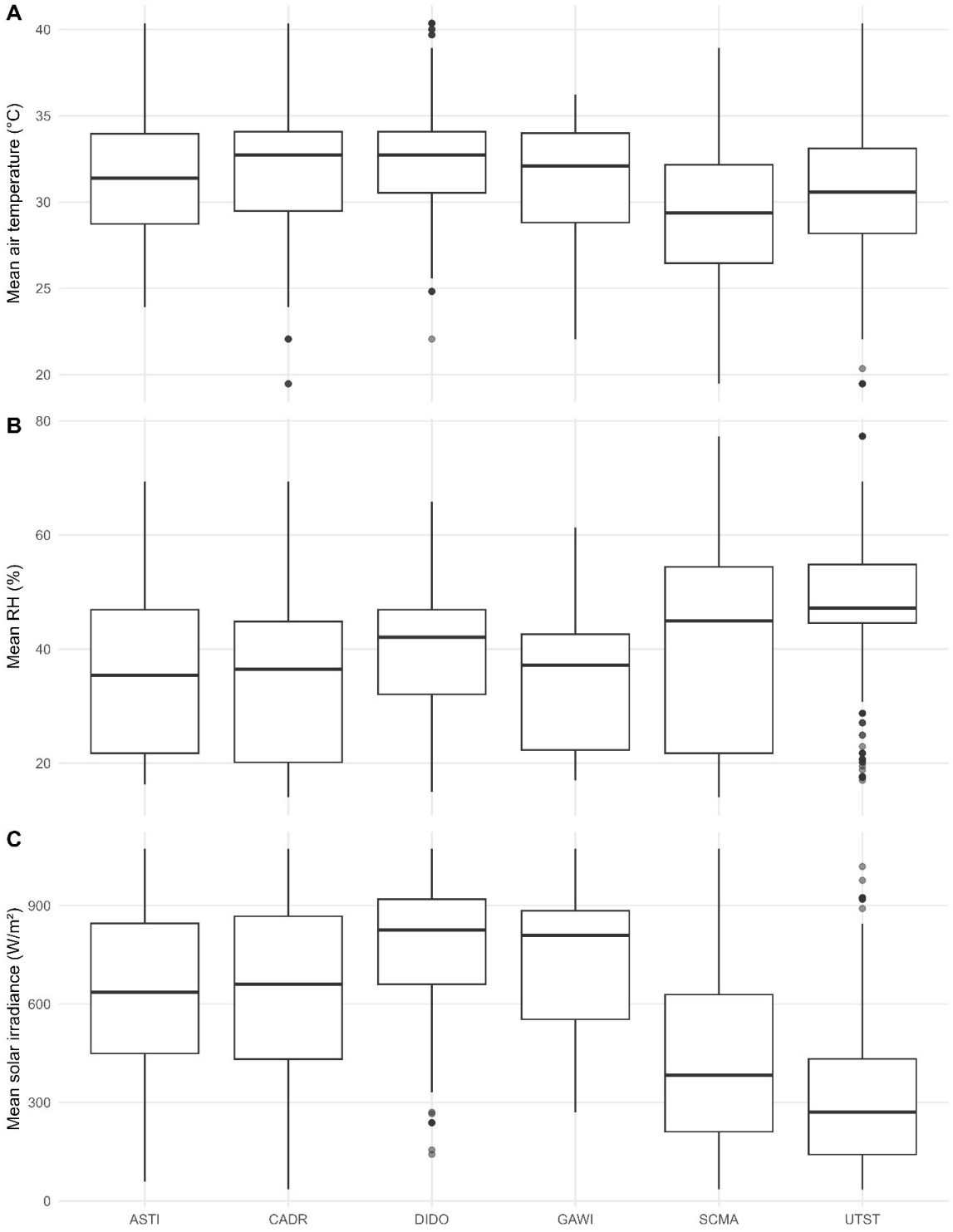


Figure 4. Distributions of mean, SD, and spread for air temperature (**A**), relative humidity (**B**), and solar irradiance (**C**) for the six diurnal lizards having ≥20 observations. Abbreviations: *Aspidoscelis tigris* (ASTI), *Callisaurus draconoides* (CADR), *Dipsosaurus dorsalis* (DIDO), *Gambelia wislizenii* (GAWI), *Sceloporus magister* (SCMA), *Uta stansburiana* (UTST).

4. Discussion

4.1. Overview

This study showed utility in ecology and ethology by using modality testing and additive modeling to explore heliothermic desert lizard activity under a new light. Through continuously replicated transects across the full diurnal period of each survey day, repeated across the active period of most species, we generated information that helps resolve our understanding of desert lizard surface activity and temporal niche partitioning. Crucially, our modeling selection framework demonstrates that real-time environmental covariates render rigid, categorical time-of-day structures redundant. Sonoran Desert lizards appear to operate as opportunistic, real-time thermoregulators tracking a shifting climate rather than adhering to immutable internal circadian schedules.

4.2. Use of an Anthropogenically Disturbed Ecosystem and Temporal Niche Partitioning

The study reported here, and a long-term monitoring study at the same site [29], are atypical of most other surface-activity research because they specifically address a roadside assemblage of heliotherms, rather than an upland community of lizards. However, researchers at this site [27] noted some species-specific differences in relative abundance of roadside *vs*. upland detections at the SNP site. Lizards at this site may use roadside berms and similar structures for various natural history needs, such as refuge, territorial display, and thermoregulation, although uses may differ by species [29].

The observed patterns of surface activity and modality at the roadside can likely be explained by a complex interplay of foraging strategies, thermal preferentia, mobility, social behaviors, and responses to anthropogenic disturbances. Despite biotic and climatic variation across the North American deserts, each species in the roadside assemblage had diurnal activity times during hot weather similar to most other studies in hot deserts (*i.e.*, Chihuahuan, Mojave, and Sonoran), suggesting some specific behaviors are innate. Almost all species differed in daily activity times in our study, showing their appearance at the roadside was partially staggered. However, we did not assume that roadside appearance was positively correlated with emergence times or surface activity in the adjacent uplands. For example, radio-tracked *G. wislizenii* at the study site emerge early and are typically surface active for nearly the entire day, yet individuals only tend to appear on the roadside during the late morning [64].

4.3. Surface Activity Patterns and Diurnal Modality

There was a distinct pattern of bimodal surface activity for total lizards in the morning and late afternoon. However, this may be an artifact of the skewed sample size of certain bimodal taxa. Deconstructing this aggregate profile may expose fundamentally diverge solutions across the environmental landscape [65]. At a finer scale, for example, our results reveal two temporal pulses of species-group activity along the roadway in the morning (Figure 1). This largely reflects the findings of others for surface appearance time after sunrise [6]. The first pulse of roadside surface activity is the early morning appearance of *S. magister* and *U. stansburiana*, which have a morning peak from ca. 07:00 to 09:00. These two species have among the lowest mean field body temperatures (T_b) of the heliothermic lizard communities of the Sonoran, Mojave, and Chihuahuan deserts [1,66,67]. Our pairwise assessment supports the idea that they share highly synchronized daily activity curves; these phrynosomatids may avoid competition through fine-scale microhabitat partitioning [68]. *Urosaurus ornatus* may also be part of the early morning shift because of its low T_b [1], but the species is uncommonly detected in the Tucson Mountains [69].

The next spike in surface activity is in the late morning, when *A. tigris*, *C. draconoides*, *D. dorsalis*, and *G. wislizenii* appear on the roadside, between about 09:00 and 11:00, which is consistent with other research [6,67,70]. These species tend to have higher T_b than the first group of species to appear on the

surface [1,65], but differ behaviorally: *C. draconoides* being more stationary, whereas *A. tigris* continuously paces the landscape, albeit the latter may exhibit general avoidance of the roadway [27]. As the day heats up, the herbivorous *D. dorsalis* leverages thermal tolerances to maximize digestion [71], whereas predatory *G. wislizenii* exploits bimodal prey that may be thermally trapped or sluggish in shaded refuges [70]. Combined, these two pulses of species groups in the morning constitute the greater peak of surface activity of total lizards throughout the day.

After the heat-of-day doldrums, when extreme ambient temperatures drive a coordinated community evacuation into thermal refugia, a lesser peak of activity occurs in the late afternoon, when all common species except *D. dorsalis* and *G. wislizenii* may likely be encountered again under appropriate conditions. This constitutes the lesser mode of surface activity for those species. None of the species showed greater surface activity during the afternoon pulse, and diversity was lower in the afternoon than in the morning (Table 3). It may appear counterintuitive that different species that maintain high and low T_b appear at roughly the same time in the afternoon, but this is likely explained by thermoregulatory behavior and weather conditions. Notably, T_b does not necessarily reflect ambient temperature at the time of encounter [1]. Here, *C. draconoides* was found slightly earlier than *S. magister* and *U. stansburiana* in the late afternoon. Another factor allowing coexistence among thermally diverse species in the late afternoon is weather and long shadows or cloud cover (e.g., thermoregulatory response to shade [72]).

Our additive modeling framework contextualizes these shifts by isolating environmental threshold windows where relative community activity scales significantly above baseline expectations. Air temperature sets boundary conditions of surface activity, whereas solar irradiance triggers thermoregulatory behaviors [6,71]. Lastly, hydric stress limits activity, capturing a structural suppression of emergence during hyper-arid extremes to prevent vital evaporative water loss [73]. During the spring, the ambient conditions in the afternoon are often hot and dry. During the monsoon, some afternoons may also be hot and sunny, while other days may have air temperatures moderated by cloud cover or rainstorms. Relative humidity and dew point are highest during the monsoon and during periods of rain. Our model results suggest that high humidity, such as during monsoonal storms, may disrupt solar availability and thermal gradients for effective heliothermy. Although our observations would suggest lizards are responding to the weather changes concomitant with the arrival of the North American Monsoon, further research is warranted to examine seasonal and microclimatic trends.

4.4. Comparison with Similar Studies on Heliothermic Lizard Assemblages

Our findings of diurnal modality were generally consistent with similar research in the hot deserts. Ecological studies of *C. draconoides* [31,74,75], *S. magister* [67,76–78], and *U. stansburiana* [32,67,79] showed these species to have bimodality during hot periods. While *A. tigris* has historically been classified as bimodal [80,81], our analytical framework isolated a cryptic statistically unimodal profile that challenges traditional classifications. Even desert lizards that exhibit diurnal bimodality tend to have unimodal activity during cooler times, as in March and April [1,31]. Common in the literature, the activity peak of temporal bimodality is usually greatest in the morning, as in our study, although there are exceptions. *Dipsosaurus dorsalis* exhibits unimodality starting in the late morning in our study and in other studies [71,78,82]. Our observations also suggest general morning unimodality in *G. wislizenii*, but because of our relatively small sample size and because of mixed reports of modality in the literature [17,67,83], we believe more extensive research on the species is required to assess modality and surface activity.

4.5. Method Utility for Future Research

The LSRT method [27] and exhaustive diurnal coverage were effective for this study at SNP. Most species expected in the community were found to use the roadside environment to some degree, supporting

the efficacy of the study design at observing ecological activity patterns. By accounting for random observer biases, the modeling approach isolated biological signals from searcher efficiency. The results of the study intimated that the first pulse of the morning species group was being undersampled in the long-term monitoring study at the same site [29], so adaptive sampling is warranted. The utility of sampling during the afternoon pulse of activity is unclear, as the mornings had the highest species diversity and surface activity, but further research into the lesser afternoon peak at a seasonal scale would help elucidate afternoon activity.

Because of the ability to capture robust data, we recommend that other researchers and managers consider multiple full-day pilot inventories to identify temporal hot spots if resources are limited. This will help to maximize data for all species in the assemblage. However, LSRT and repeated surveys may be best suited to roads that are low-speed, low-traffic volume, constructed from native materials, and have roadside microhabitat structure (e.g., berms and boulders [16]). Testing this method on a diversity of road types may prove important in understanding limitations. Most of the literature on reptiles and roadways focuses on road-caused mortality (see [84]), but there is less focus on how the roadside can be targeted for inventory and monitoring [85], or as amenable habitat. As species must adapt to ever-changing environmental conditions, it is critical to maximize the impact of effective strategies for monitoring these changes.

5. Conclusions

In summary, we utilized an effective monitoring strategy to investigate surface activity patterns among an assemblage of lizards that included six common desert species. By conducting repeated hourly transect runs during daylight hours, we were able to isolate subtle yet significant differences in surface activity timing and modalities among heliothermic species. Additionally, we analyzed specific environmental variables that influenced activity patterns. While there were some intrinsic species-specific activity patterns, environmental factors such as temperature, relative humidity, and solar irradiance served as zeitgebers (extrinsic environmental cues that affect the circadian rhythm). These are mechanisms of the temporal niche resulting in sympatry among related and ecologically similar taxa. Our research also validates that, under certain circumstances, the roadside of non-paved, native materials roads may serve as amendable anthropogenic lizard habitat, rather than merely a biological sink. These fundamental findings are important to consider when determining strategies for inventory, monitoring, research, and conservation, in a global environment where climate change, habitat loss/conversion, and other anthropogenic disturbances affect populations of heliotherms.

Supplementary Materials

The following supporting information can be found at: https://www.sciepublish.com/article/pii/1317, Table S1: Weather conditions during survey days by month. Conditions were seasonally typical, except for May, due to some early pre-monsoonal storms; Table S2: Weather conditions during survey days by hour; conditions change throughout the course of the day; Table S3: Interspecific environmental relationships resulting from Dunn's multiple comparison tests.

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Author Contributions

Conceptualization, L.L.C.J.; Methodology, L.L.C.J.; Software B.R.B. and L.L.C.J.; Validation, all authors; Formal Analysis, B.R.B.; Investigation, all authors; Resources, all authors; Data Curation, B.R.B. and L.L.C.J.; Writing—Original Draft Preparation, L.L.C.J. and B.R.B.; Writing—Review and Editing, all authors; Visualization, L.L.C.J. and B.R.B.; Supervision, L.L.C.J.; Project Administration, L.L.C.J.; Funding Acquisition, not applicable.

Ethics Statement

Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

These data are proprietary until adequate time has elapsed for formal analyses of all aspects of the broader Bajada Lizard Study can be completed. Although data are owned by the Principal Investigator (L.L.C.J.) as a third party, studies done on Saguaro National Park holdings will be shared with the National Park System upon completion of the Bajada Lizard Study, a long-term monitoring project. Special requests for data sharing can be directed to L.L.C.J.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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