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A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard

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Summary

1. Preservation of desert ecosystems is a worldwide conservation priority. Shrubs can play a key role in the structure of desert communities, and can function as foundation species. Understanding desert shrub ecology is therefore an important task in desert conservation. A useful model for the function of shrubs in deserts is ecological facilitation, which explores benefits that shrubs confer on their community. Facilitation has been well developed in the context of shrub-plant interactions but less well studied for plant-animal interactions.

2. We used radiotelemetry to test the hypothesis that a dominant desert shrub facilitates one species of diurnal lizard. We hypothesized that the blunt-nosed leopard lizard *Gambelia sila* would spend some part of its daily activity cycle associated with California jointfir *Ephedra californica*, and that lizard association with shrubs would increase during the afternoon peak temperature period. We relocated lizards three times daily for 24 days and scored whether lizards were within 0.5 meters of a shrub, which we used as an indicator of shrub association. For each relocation we also scored lizard association with a set of predefined microhabitat features. We also scored lizard behavior according to a set of predefined behavioral traits. We constructed home ranges following the minimum convex polygon method and generated estimates of shrub density and relative shrub area within each home range polygon.

3. We obtained 1190 datapoints from a sample of 27 lizards. We found that lizards were associated with open sites significantly more often than with shrubs but were associated with shrubs more than predicted by percent shrub area within their home ranges. Lizards were associated significantly more often under shrubs during the afternoon peak temperature period, and lizards were observed cooling under shrubs significantly more often. The frequency of association of individual lizards with shrubs was not correlated with the density of shrubs within their home range.

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4. *Synthesis and Applications*. Shrubs can be considered as a component of high-quality habitat for ectothermic desert vertebrates for the purposes of restoration and management. Furthermore, radiotelemetry provides a novel methodological approach for assessing shrub-animal facilitative interactions within desert communities.

Keywords: *Gambelia sila*, *Ephedra californica*, San Joaquin Desert, plant-animal interactions, endangered species, thermoregulatory behavior, ectotherm

Introduction

Deserts are highly distinct ecosystems that contribute significantly to global biodiversity and global ecosystem function. The conversion and loss of desert habitat is therefore a global biodiversity crisis requiring immediate intervention, including conservation of remaining undisturbed habitat and restoration of degraded desert (Hannah et al. 1995, Cook et al. 2004, Hoekstra et al. 2005, Kéfi et al. 2007, Mouat et al. 2008, Bachelet et al. 2016, Westphal et al. 2016). Identifying the drivers of ecological health in desert communities will be a crucial component of such interventions. Shrubs can maintain the diversity of desert plant communities (Flores & Jurado 2003) and are predicted to play significant roles in the thermal ecology of desert ectotherms (Sears et al 2016, Basson et al. 2017). Shrubs can also facilitate ectotherm populations in the face of climate change (Adolph 1990, Kearney, Shine and Porter 2009, Sinervo et al 2010, Sears and Angilletta 2015, Sears et al 2016).

Ecological facilitation theory provides a roadmap for describing and predicting the beneficial interactions of shrubs with other organisms within their communities (Bruno et al. 2003, Mcintire & Fajardo 2014, Filazzola and Lortie 2014, Bulleri et al 2016, Filazzola et al. 2017). Using facilitation theory, Filazzola et al (2017) extended the exploration of the beneficial interactions between desert shrubs and vertebrates, and found that one species of shrub provided facilitative benefits to a target species of lizard. We sought to confirm and add depth to their findings using radiotelemetry tracking of the same target species. . Radio telemetry is a well-tested and powerful tool that allows the longitudinal tracking of individual animals throughout their daily behavioral cycles (McGowan et al 2017) and enables the direct observation of habitat interactions and behaviors. We used radio telemetry study to test and refine our understanding of the beneficial interaction of shrubs with lizards. To our knowledge, incorporating radiotelemetry into a facilitation study is a novel use of the method.

We sought to test the hypothesis that shrubs facilitated lizards by providing thermoregulatory opportunity. We predicted that lizards would associate with shrubs for a meaningful proportion of their daily activity cycle; that shrub association would increase in the afternoon when daytime temperatures peak (Filazzola, Sotomayor, and Lortie, 2017); and that lizard association with shrubs would be correlated with thermoregulatory behaviors. The results of our study confirm the application of radiotelemetry to ecological facilitation studies and the application of such studies to the description of beneficial interactions between shrubs and vertebrate ectotherms.

Materials and Methods

Study site.-- The study was conducted on the Elkhorn Plain within Carrizo Plain National Monument (San Luis Obispo County, California, USA, 35.1914° N, 119.7929° W) (Fig, 1) within the San Joaquin Desert ecosystem (Germano et al 2011). Average annual precipitation within the Monument ranges from 15 cm in the southeast to 25 cm in the northwest (Hijmans et al. 2005). The Elkhorn Plain is located within the Monument on an elevated plain separated from the main valley floor of the Carrizo Plain by the San Andreas Fault (Germano et al. 1994). The area has been heavily invaded by non-native annual grasses including *Bromus madritensis, Erodium cicutarium*, and *Hordeum murinum* (Schiffman 1994, Stout et al. 2014, Gurney et al. 2015) but still provides habitat for endemic keystone species such as the giant kangaroo rat *Dipodomys ingens* (Bean et al. 2014). California jointfir, *Ephedra californica* was the dominant shrub at our study site. The blunt-nosed leopard lizard, *Gambelia sila*, was well documented on the study (Germano, Smith and Tabor, 2007).

Study species .— *E. californica*, a basal gymnosperm in the Gnetophyta division, is a large, slow-growing woody shrub restricted to arid environments in western North America (Sawyer, Keeler-Wolf & Evens 2009). Although the genus has a worldwide distribution and is represented by over a dozen species in the desert southwest of North America, *E. californica* is the only species that occurs in the San Joaquin Valley, where it is locally considered rare and sensitive (Sawyer, Keeler-Wolf & Evens 2009) and has been documented to be a foundation species in the San Joaquin desert community (Hawbecker 1951, Lortie et al. 2017, Lortie, Filazzola & Westphal 2017). *Gambelia sila* is a state and federally listed endangered species endemic to the San Joaquin Valley and restricted to San Joaquin Desert habitat (Germano & Williams 1992, U.S. Fish and Wildlife Service 1998, Warrick, Kato, & Rose 1998, Germano et al. 2011, Germano & Rathbun 2016). *Gambelia sila* are diurnal and mainly insectivorous though they may eat smaller lizard species on occasion (Warrick et al. 1998, Germano, Smith & Tabor, 2007). Though *G. sila* can bury themselves and will occasionally dig primitive burrows, they mostly utilize abandoned burrows of other animals such as *D. ingens* (Fields, Coffin & Gosz 1999, Prugh et al. 2012). Adult *G. sila* are inactive in burrows for much of the year, emerging only from late March or April through July (U.S. Fish and Wildlife Service 1998, Warrick, Kato, & Rose 1998, Germano et al. 2016). During the active season, *G. sila* will also spend the night underground in burrows and may return to a burrow during the day if the temperature becomes too hot or cold (Warrick, Kato, and Rose 1998, Germano and Rathbun 2016).

Experimental design.-- *Gambelia sila* individuals were located during foot and vehicle surveys and captured using a pole and noose. Individuals were collared following the method of Germano & Rathbun (2016). VHF radio transmitters (Holohil model BD-2, frequency 151-152 MHz, battery life 8-16 weeks, Holohil Systems Ltd., Carp, ON, Canada) were attached to a small beaded chain collar using jewelry wire and epoxy, and the collars were then fastened around the lizard's neck. *Gambelia sila* were kept overnight to ensure the collar was fitted correctly and did not irritate or harm the animal, and then were then released at their capture site. Collars weighed 1.6-2.2 grams (depending on the size of chain needed for the lizard's neck), and we ensured that the weight of the collar did not exceed between 5% and 10% of the body mass of the individual.

In the first two days following release, all captured *G. sila* individuals were relocated (i.e. repeatedly sighted using radio telemetry) several times between to ensure that the lizards were successfully adjusting to the collars and that impacts to their behavior and survival were minimal. We looked for any negative effects the collar had on the lizards, such as impacts on movement or any other deviation from normal lizard behaviors. *Gambelia sila* were then formally surveyed for 24 consecutive days. Surveys were conducted on each lizard 3 times a day. Two of these daily surveys were conducted during daylight hours, when lizards were typically active above ground. One survey was conducted before noon and one was conducted after noon. The third survey was conducted during the night when lizards are inactive below ground. The 'night survey' was conducted before 7:30 AM or after 7:30 PM on each day.

Gambelia sila were relocated using a 3-element Yagi antenna and Model R-100 telemetry receiver (Communications Specialists, Inc., Orange, CA, USA). Once found, a location was taken for each lizard using a Garmin 64st GPS unit (Garmin Ltd., Olathe, KS, USA) and a laser range-finder (Bushnell Outdoor Products, Overland Park, KS, USA). Habitat was categorized as whether a lizard was within 0.5 meters of a shrub (shrub) or not (open) (henceforth, the "shrub association zone"), and behavior was scored from a suite of predetermined behavioral syndromes (Table S1). Disturbance from the observer to the lizard was kept to a minimum for each observation to avoid influencing behavior and habitat selection. At the completion of the study all collars were removed from the lizards.

Analyses.-- Analyses were conducted in R (version 3.3.2). Habitat association was analyzed using a generalized linear model (Bolker et al. 2009) with the multcomp package (Hothorn, Bretz & Westfall

2008). Behavioral data were analyzed with a multinomial logistic regression using the nnet package that accounts for the multiple levels of nominal outcomes of the observations (Venables and Ripley 2002). Home range size was calculated using a 95% Minimum Convex Polygon (MCP) estimation (Mohr 1947) using the adehabitatHR package (Calenge 2006). MCPs were visualized in two dimensions in R.

Shrub density was calculated by visually counting individual shrubs within each lizard's MCP using aerial photographs (**Google Earth**, image taken December 20, 2016, accessed November 2017) and dividing that number by the area in square meters of the MCP. We calculated a standardized measure of shrub association zone area using on-the-ground measurements of a large number of randomly chosen shrubs in the study area, from which we calculated an average radius for each shrub following the method of Filazzola et al. (2017) and to which we added the 0.5m association criterion described above. We calculated the area of each shrub association zone using the formula **πr2** and then took the average across the sample. We multiplied this standardized shrub association zone area by the number of shrubs counted in each MCP to obtain an estimate of the percent area of an MCP subsumed by shrub association zones.

R code used for this project can be found at https://cjlortie.github.io/Carrizo.telemetry.

Results

A total of 27 lizards were relocated more than 5 instances cumulatively either in the AM or the PM across the sampling period. On a given day, the median total number of relocations was 22 with a maximum of 27 and a minimum of 1 relocation. There were a total of 1190 relocations and MCPs generally did not overlap (Fig 1). Mean female MCP area was 1.87 ha +/- 0.53 se. Mean male MCP area was 5.14 ha +/- 2.15 se. The difference in MCP area between males and females was not significant (Pr < Chi 0.095920). Gender was initially included as a factor in all other analyses but no relevant effects were significant (not reported), therefore gender was subsequently removed from the remaining analyses.

Habitat:-- The frequency of lizard observation differed significantly between habitat types (Fig. 2, Table 1, $p < 0.01$). Lizards were observed in the open on an average of 18.8 days and in shrubs an average of 10.5 days. Shrub association frequencies of individual lizards ranged from 0 to 0.63 with a mean of 0.23 +/- 0.035 se (Table S2). Observations of lizards within open habitat did not differ between different times of day, but observations of lizards associating with shrubs differed significantly between morning and afternoon with lizards being found more frequently at shrubs in the afternoon (Table 1, $p = 0.0252$).

Behavior:—Behavior differed significantly between habitat types (Fig. 2, Table 2, $p < 0.0001$). Lizards were observed cooling under shrubs significantly more than other habitat types (Fig. 2, Table 2, $p < 0.0001$). Lizards were also observed avoiding predators under shrubs more frequently than at other microhabitat types (Table 3, $p < 0.0001$). The predators that lizards were observed avoiding in this study were all aerial predators (either ravens or raptor species). Burrowing and interacting occurred significantly less often under shrubs (p < 0.,0001). Other types of behavior such as sunning, hunting, or active observation did not differ significantly between habitat types. Observed behavior also differed significantly between different times of day e.g. lizards were more frequently observed sunning in the morning in both habitat types compared to the afternoon and more often burrowing and avoiding predators in the afternoon (Fig. 2, Table 2, $p < 0.001$).

Shrub use as a function of shrub density and area.-- Shrub use by individual lizards did not vary significantly as a function of shrub density within that lizard's home range (Fig 3.) Percent of MCP areas subsumed by shrub association zones ranged from 1% to 15% with an average of 5% of total surface area, and frequency of shrub use by lizards was significantly higher than predicted by the percent of MCP area subsumed by shrubs ($Z = -4.714$ from a Wilcoxon Signed ranks test, $p < 0.001$).

Discussion

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Shrubs are foundation species in many ecosystems due to the facilitative benefits that they provide to both plant and animal species (Filazzola & Lortie 2014, Lortie, Filazzola & Sotomayor 2015). We hypothesized that *E. californica* facilitates *G. sila* by providing thermoregulatory benefits. Our finding that *G. sila* was associated with *E. california* an average of 10 out of 24 days, and that individual lizards were associated with shrubs more than predicted by shrub area within their home ranges, support our hypothesis. Our hypothesis is also supported by the observed significant shift towards shrub association in the afternoon during peak daytime temperatures. Our observation that shrub use was not correlated with shrub desnity suggests that lizards are actively choosing shrubs over open habitats rather than as a consequence of shrubs being more densely distributed in their home ranges. The observed association of *G. sila* with shrubs is consistent with results of studies of thermoregulatory behavior of lizards (Sears et al. 2016, Vickers et al 2016, Basson et al. 2017) and suggest that shrubs facilitate *G. sila* by providing shade. Shrubs can buffer the extremes of multiple environmental conditions such as temperature, wind, and solar radiation, creating a moderate microclimate under their canopy (Kerr et al. 2004, Pugnaire 2010). At the landscape scale, the presence of shrubs and their pattern of distribution (i.e. clumped vs. dispersed) will affect lizard thermoregulatory behavior and can be crucial to an ectotherm's thermoregulatory efficiency (Sears et al 2016, Basson et al 2017). Sources of shade are particularly important for ectotherms, which must maintain body temperature through behavior (Huey 1974, Huey and Slatkin 1976, Díaz and Cabezas-Díaz 2004, Kerr et al. 2004). Visual concealment from predators and physical protection is also important (Fields et al. 1999, Anderson et al. 2010, Filazzola et al. 2017). Shrubs may therefore provide important mechanisms of facilitation for *G. sila*. Our results suggest an important mechanism (shrub restoration) for the management of desert ectotherms such as *G. sila*, and provide support for radiotelemetry as a viable method for studying ecological facilitation.

Shrub use by *G. sila* was addressed in one previous paper that also used radiotelemetry. Germano & Rathbun (2016) employed *post hoc* tests to answer the question of whether shrubs are important components of *G. sila* habitat. One test depended on an assumption based on Schoepf et al 2015 that home ranges were resource-based (ie shrub-limited) and would thus be smaller in the presence of high quality habitat (= shrubs), while another test sought to bound the amount of shrub habitat present in lizard home ranges away from a null expectation. The authors found no effect of shrubs on home range size but did find more shrubs present within lizard home ranges than predicted. Our *a priori* approach (ie taking direct observations of association with shrubs) provided evidence that lizards actively seek out shrubs rather than randomly encountering them during their daily activity. The lack of a correlation between individual shrub use and shrub density suggests that a threshold presence of shrubs may be sufficient to provide thermoregulatory opportunity, therefore a strong correlation between absolute number of shrubs within a home range and home range size would not be predicted. This conclusion is further supported by the Germano and Rathbun's (2106) result that home ranges tended to include more shrub habitat than predicted by the study-site wide prediction, i.e. it is likely beneficial that SOME shrubs be available within the daily activity theater of individual lizards. Our results therefore confirm and are consistent with the results from Germano & Rathbun (2016). Germano and Rathbun (2016) also provide a caveat against overestimating the importance of shrubs to *G. sila* by noting that *G. sila* occurs in places that lack shrubs. Given the variation that we observed in lizard shrub association within one population, is not surprising that entire populations can persist in relatively shrubless areas. Although heritability of thermoregulatory response in lizards is still undescribed, heritable variation in propensity to use shrubs would predispose a population to adapt either to the presence of shrubs or the absence of shrubs (Logan, Cox & Calsbeek 2014). More to the point, where population-scale variation exists in the predisposition to use shrubs, such as we found in this study, it would be reasonable to propose that shrubs be made available to those lizards that are predisposed to associated with shrubs. The net effect would be to optimize the habitat available for that population. Such optimization may be crucial to impart population resilience to climate change (Sinervo et al 2010, Sears et al 2016). Additionally, structured and/or heterogeneous habitats are becoming increasingly recognized as important to achieve individual-scale thermoregulatory optimization for lizards (Clusella-Trullas & Chown 2014, Basson et al 2016, Sears et al 2016).

Conclusions

Our results document the benefits of shrubs to vertebrate ectotherms in desert communities, including endangered species such as *G. sila*, thus providing guidance for land managers evaluating habitat preservation and restoration designs. We also advance methodology by demonstrating the utility of combining ecological facilitation theory with radiotelemetry. It should be noted that our study was not intended to test the hypothesis that *G. sila* require shrubs per se. Rather, we designed our study to ask whether shrubs provide benefits to *G. sila,* and found evidence to support our hypothesis. In our view this subtle divergence in focus and outcome demonstrates the power of taking an ecological facilitation approach to community interactions.

Author's Contributions

MFW, CL and CB acquired funding for the project; MW, CJL, SB and TN conceived the study; TN and MW collected the data; CL, TN and MW analysed the data; MW and TN led the writing of the manuscript. Noble participated in design, fieldwork and writing. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

Data are available at https://cjlortie.github.io/Carrizo.telemetry

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Tables

Table 1: Generalized linear model for habitat associated with relocated *G. sila*, with degrees of freedom, deviance, and p-values.

Generalized linear model					
Factor	Df	Deviance	P-value		
habitat	1	88.33	< 0.0001		
Time class	1	2.901	0.1		
habitat:time.class	1	5.281	0.01		
Post Hoc, least squared means					
contrast	estimate	SE	df	z.ratio	p.value
open,AM-shrub,AM	0.769229	0.102934	NA	7.473	<.0001
open,AM-open,PM	-0.01848	0.067966	NA	-0.272	0.993
open,AM-shrub,PM	0.44597	0.085189	NA	5.235	<.0001
shrub,AM-open,PM	-0.78771	0.102727	NA	-7.668	<.0001
shrub,AM-shrub,PM	-0.32326	0.11485	NA	-2.815	0.0252
open,PM-shrub,PM	0.464446	0.084938	NA	5.468	<.0001

Table 2: Multinomial logistic regression for observations of *G. sila* behaviors associated with shrubs.

	shrub		Time.class	
Factor	z	P-value	z	P-value
avoiding.predators	6.61E+01	<0.0001	4.60E+07	<0.0001
burrowing	-1.88E+07	<0.0001	2.71E+01	<0.0001
cooling	8.80E+00	<0.0001	1.65E+00	9.91E-02
hunting	8.27E-01	0.4084232	-1.94E+00	5.23E-02
interacting	-1.74E+01	<0.0001	-8.19E-01	4.13E-01
observing	1.14E+00	0.2534383	-8.04E-01	4.21E-01
sunning	6.02E-01	0.5468632	-6.51E+00	7.67E-11

Figures

Figure 1: Left: location of *G. sila* radiotelemetry study. Top left: Location of study area within California. Top right: aerial photograph of study site overlain with sample home ranges calculated using a 95% minimum convex polygon (MCP) estimate, for each individual. Bottom: Aerial image depicting all home ranges of lizards in the study. Different individuals are indicated by different colors.

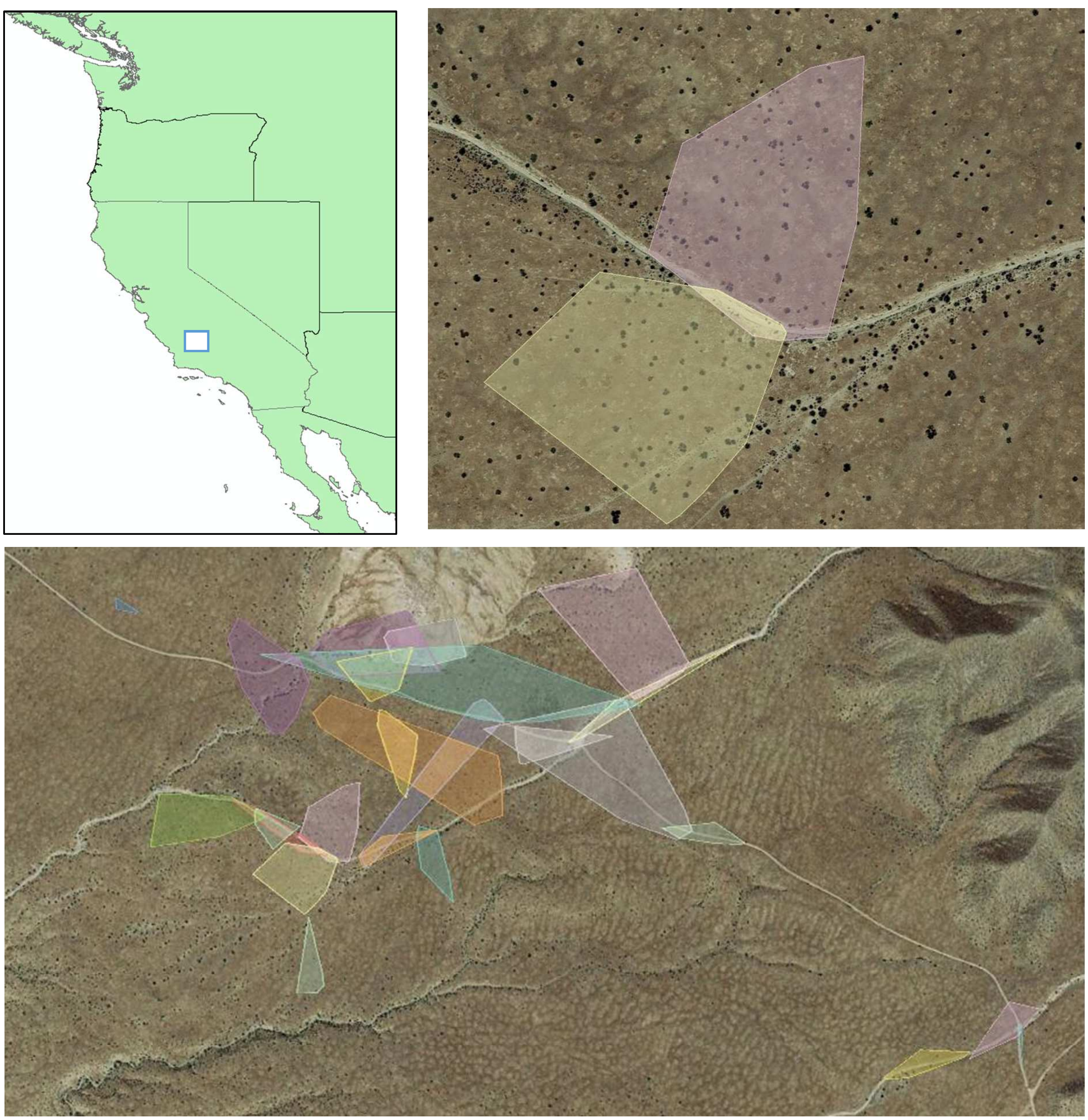


Figure 2: Plot of *G. sila* behaviors with respect to habitat and time. Lizards engaged significantly more often in cooling behaviors when under shrubs during afternoon temperature peak.

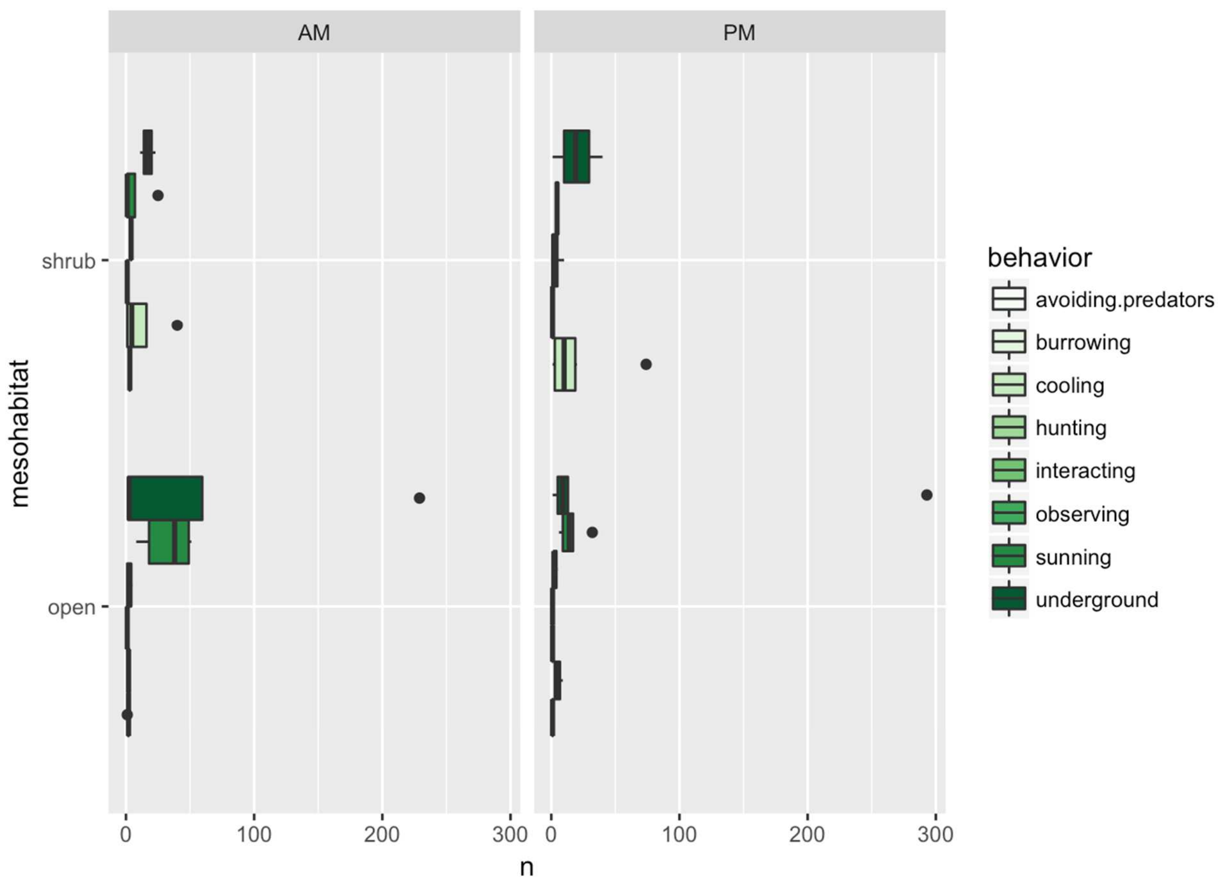
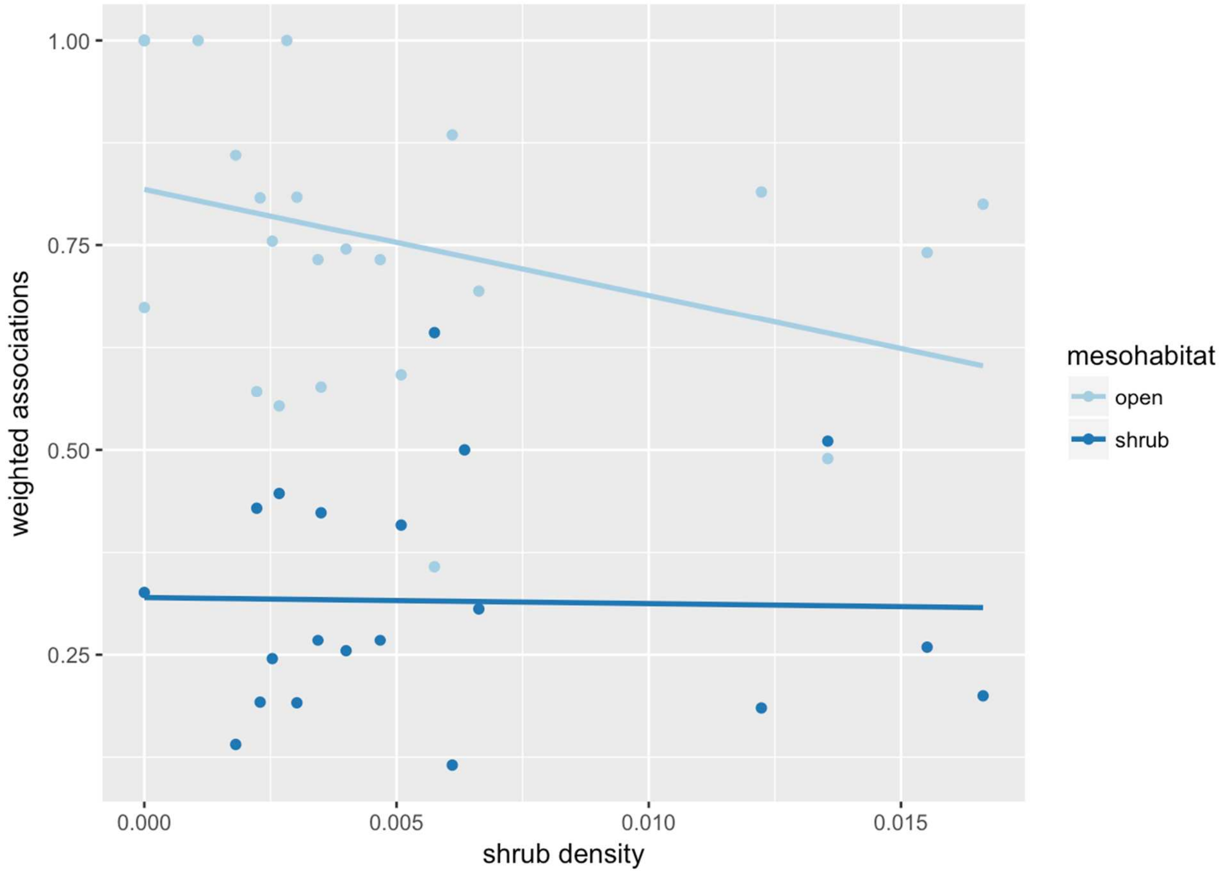


Figure 3: Plots of shrub density on the weighted *G. sila* associations with shrubs.



Supporting Information

Table S1: Behavior classification table for lizard observations.

Classification	Observed behavior
avoiding predators	Moving (most often running) away from predators
burrowing	Actively digging a burrow, or burying itself. This classification was only used if the lizards was actively creating its own burrow, it was not used if a pre-existing burrow was utilized.
cooling	Lizard moving into, or remaining still in shade. Lizard would typically sit upright in shade with front legs extended and rear toes pointed up and off the ground. Occasionally the tail would be lifted off the ground as well.
hunting	Actively stalking or attempting to catch prey. Usually comprised of a slow stalking of an insect and then a sudden burst of speed.
interacting	Interacting with another lizard including either genders of the same species as well as members of other lizard species such as whiptail lizards (*Aspidocelis tigrinum*).
observing	Actively observing environment (eg moving head or body to track motion).
underground	Lizard underground, behavior could not be otherwise be determined.
sunning	Lizard in sun, not moving. Most often either low to ground, with lower body touching ground or sitting upright with head and shoulders up and rear toes pointed out. Eyes often closed or squinted.

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Table S2. Frequencies of shrub association of individual lizard, density of shrubs within individual home ranges, and percent of area of individual Minimum Convex Polygons (MCP) subsumed by shrub association zones for radiotracked *Gambelia sila* on Elkhorn Plain in 2016.

Lizard ID	Total obs.	Shrub obs.	Shrub association frequency	MCP area m^2	Number of shrubs	Shrub density	Shrub assoc area m^2	% Shrub assoc area within MCP
180	59	0	0.000	7509	8	0.001	73.491	0.010
320	5	0	0.000	2	0	0.000	0.000	0.000
360	5	0	0.000	8	0	0.000	0.000	0.000
500	50	0	0.000	803	0	0.000	0.000	0.000
900	9	0	0.000	354	1	0.003	9.186	0.026
939	12	0	0.000	9	0	0.000	0.000	0.000
780	55	5	0.091	8190	50	0.006	459.318	0.056
220	56	7	0.125	57400	104	0.002	955.381	0.017
740	31	4	0.129	5636	7	0.001	64.304	0.011
919	47	8	0.170	40998	124	0.003	1139.108	0.028
381	17	3	0.176	5533	92	0.017	845.144	0.153
439	55	10	0.182	3597	44	0.012	404.200	0.112
760	52	10	0.192	4356	10	0.002	91.864	0.021
660	50	11	0.220	5500	22	0.004	202.100	0.037
960	54	12	0.222	18920	48	0.003	440.945	0.023
520	53	12	0.226	4120	5	0.001	45.932	0.011
820	55	14	0.255	3802	59	0.016	541.995	0.143
840	55	14	0.255	10693	50	0.005	459.318	0.043
240	57	15	0.263	21786	75	0.003	688.976	0.032
979	50	16	0.320	13723	91	0.007	835.958	0.061
0	46	15	0.326	20331	88	0.004	808.399	0.040
800	28	11	0.393	7136	25	0.004	229.659	0.032
540	50	20	0.400	15908	81	0.005	744.095	0.047
420	50	21	0.420	4488	10	0.002	91.864	0.020
680	56	24	0.429	51618	138	0.003	1267.717	0.025
860	51	25	0.490	12759	81	0.006	744.095	0.058
460	50	26	0.520	3838	52	0.014	477.690	0.124
717	56	36	0.643	39292	226	0.006	2076.116	0.053