**Combining facilitation theory with radio telemetry to assess the benefits of desert shrubs to vertebrate ectotherms**

**Other options**

**A population-level analysis of lizard-shrub association patterns in a desert ecosystem using telemetry.**

**Or**

**A test of a desert shrub species foundational role for an endangered leopard lizard using telemetry.**

**Etc – think over and cook up a more representative title.**

**A test of desert shrub facilitation through telemetry analyses of an endangered lizard species.**

**Author names**

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**Abstract**

Shrubs can play a key role in the structure of desert communities and function as foundation species. Describing the relationships among shrubs and other species, including vertebrates, is important for preserving and restoring desert habitat. - vague Prior efforts based on movement ecology to characterize the importance of a shrubs to the endangered blunt-nosed leopard lizard, *Gambelia sila*, obtained ambiguous results. - cut Ecological facilitation has been well developed in the context of of shrub-plant interactions but less well studied for plant-animal intearctions. Here, we use movement ecology methods, i.e. telemetry, to measure the association between lizards and *Ephedra californica*, a dominant shrub species in the Carrizo National Monument, to infer whether there was evidence for facilitation. hypothesis???? We propose that??? We scored microhabitat attributes and behavior to identify proximate drivers of lizard preference for ‘shrub’ vs ‘open.’ Clunky – I would just say we measured relocations of lizards at two scales – shrub-open and at a finer resolution. Home-range sizes were also calculated and correlated with shrub densities at each relocation instances for every individual lizard. We also assessed home range size and within-home-range shrub density to assess the relationship of individual shrub use to shrub availability confusing be more direct. Local shrub density measures….. state finding etc.. We obtained strong evidence that *E. californica* provided essential services to *G. sila* by showing that lizard use of shrubs is correlated with time of day, thermoregulatory behavior and predator avoidance, but not with shrub availability. Reword - Our study suggests that shrubs be considered as a component of high-quality habitat for *G. sila* when making decisions about habitat preservation or restoration, and provides a methodological model for assessing similar relationships for other desert species at risk. OK

**Introduction**

I like a general topic sentence first without citations – Deserts are…? The conversion and loss of desert habitat is a global biodiversity crisis requiring immediate intervention including conservation of remaining undisturbed habitat and restoration of degraded desert (Hannah et al. 1995, Hoekstra et al. 2005, Kefi 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 ecology of desert ectotherms (Sears et al 2016). Shelter in the form of shrubs can also facilitate ectotherm populations in the face of climate change by providing refuges (Adolph 1990, Angilletta 2009, Kearney, Shine and Porter 2009, Sinervo et al 2010, Sears and Angilletta 2015, Sears et al 2016). Shrub restoration projects have been proposed and even initiated in at-risk deserts to benefit sensitive species (C. Fiehler, California Department of Fish and Wildlife, pers. comm; L. Peppel, Wildlands Conservancy, pers. comm., C. Hauser, California Natural Lands Management) even though the presumed benefits of shrub restoration to the specific ectotherms targeted for conservation are still subject to debate (Germano and Rathbun 2016). The applied question that we address here is what benefits do shrubs provide to ectotherms of conservation interest but we do not test this – we do measure ‘benefits’ ie mechanisms – we measure only association patterns., and how do we confirm and describe these potential benefits? – we do not test this. We test the applied hypothesis here that shrubs are important to lizards through the relative frequency of association in the choices by the animals… etc. or something like that.

Topic sentence first. Ecological interactions are important to the maintenance of desert ectotherms (Norbury 2001) – just said that above.. Ecological facilitation theory which seeks to identify benefits of one organism to another, provides a roadmap for describing and predicting the interaction of shrubs with other organisms within their communities clunky (Filazzola and Lortie 2014, Filazzolaet al. 2017). Using facilitation theory, Filazzola et al (2017a) extended the exploration of the beneficial interactions of desert shrubs to vertebrates by incorporating one species of lizard. However, their measures of association (feces detection, trap cameras) were correlative and indirect measures of animal presence. Radio telemetry is a well-tested conservation tool that allows the longitudinal tracking of individual animals throughout their daily behavioral cycles and promotes the field observation of key behaviors (McGowan et al 2017). We used radio telemetry study to test and refine our understanding of the interaction of shrub with lizard but also measure shrub-open and finer-scale environmental through classification of each relocation. conclusion sentence -…. This is an innovation of shrub-animal facilitation studies and movement ecology studies because…?

We developed our study within the same system used by Filazzola et al (2017a and 2017b) and Lortie et al. (2017). : the co-occurrence of California jointfir *Ephedra californica* with the blunt-nosed leopard lizard *Gambelia sila*. Both species are important ecological and conservation components of the San Joaquin Desert (Germano et al. 2011, Lortie et al 2017). The San Joaquin Desert supports one of the highest concentrations of threatened and endangered species in the continental United States, including the federally endangered *G. sila* as well as other endangered species such as the San Joaquin kit fox (*Vulpes macrotis mutica*) and giant kangaroo rat (*Dipodomys ingens*) (USFWS 1998, Germano et al 2011). Much of this area has been converted to agriculture or developed for industry such as oil extraction and solar energy, with natural desert habitat only covering 5% of its former extent (Germano et al 1992, USFWS 1998, Germano et al 2011, Stewart et al 2017). What natural habitat remains is fragmented, with only a few large patches still intact, such as the Carrizo Plain, Panoche Valley, and Pixley National Wildlife Refuge (USFWS 1998, Germano et al 2011). CUT – not Intro – move to methods and have a Species and site description section.

In this study, we examined the relationship between blunt-nosed leopard lizard and shrubs in Carrizo Plain National Monument, the largest remaining remnant of San Joaquin Desert habitat (Fig. 1) why??? I think you need a hypothesis or at least objective. The mesohabitat scale captured the broad dichotomy of whether lizards were or were not in proximity to a shrub.- either need to define now or CUT from intro.. also it is coming out of nowhere – this is a prediction. I would move the meso micro to Methods. BUT if you set up prediction in the Intro, then you need to define them – your call. To explore why lizards might be choosing one mesohabitat over the other, we scored a microhabitat association by choosing from an identical set of possible microhabitat associations within each mesohabitat. We also included a behavioral observation from a list of predefined behaviors in each instance. Clunky and repetitive Our rationale for including behavioral data was that they might provide further insights into the proximate drivers of any shrub x lizard association we observed.??? CUT…. Or state as prediction Because habitat use of desert lizards varies over the course of their daily activity cycle we took multiple observations for each lizard each day. We calculated the home ranges of individual lizards to test for consistency of patch size (Hirzel and LeLay 2008) and for the purposes of comparing our study with previous radiotelemetry studies of *G. sila* (Germano and Rathbun 2016) as well as to assess the availability of shrub habitat to each lizard and to test the interaction of shrub density with individual shrub use. This paragraph needs work for flow, organization, and clarity. I prefer hypothesis and predictions that you test. However, you can also state an objective and what you will test. You are kind of doing the latter but it is hard to follow.

**Methods**

*Study site***.--** The study was done on the Elkhorn Plain within Carrizo Plain National Monument (San Luis Obispo County, California, USA, 35.1914° N, 119.7929° W). 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, Gurney et al. 2015). The dominant shrubs on the Elkhorn Plain are California jointfir (*Ephedra californica*) and saltbrush (*Atriplex polycarpa*) (Stout et al. 2013). *Ephedra* *californica* was the dominant shrub at our study site with only a few *Atriplex polycarpa* found in adjacent areas. *G. sila* had been found in the area during surveys by our research team in previous years as well as being documented by historical studies (Germano et al. 2007).

*Study species* .— *Ephedra californica*, a basal gymnosperm in the Gnetophyta division, is a large, slow-growing woody shrub restricted to arid environments in western North America (citation). 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). *Gambelia sila* is a state and federally listed endangered species found in the San Joaquin Desert of California (Germano et al. 1992, USFWS 1998, Warrick et al. 1998, Germano et al. 2016). *G. sila* is a relatively large lizard compared to other temperate New World lizards, with males ranging from 89 to 119 mm and females ranging from 86 to 112 mm (Tollestrup 1982, Warrick et al. 1998, Germano et al. 2016). *G. sila* are diurnal and mainly insectivorous though they may eat smaller lizard species such as side-blotched lizards (*Uta stansburiana elegans*) on occasion (Warrick et al. 1998, Germano et al. 2007, Germano et al. 2016). *G. sila* is also prey for many species including snakes, bird of prey and coyotes (Germano et al. 1992, USFWS 1998, Germano et al. 2005). Though *G. sila* can bury themselves and will occasionally dig primitive burrows, they mostly utilize abandoned burrows of other animals such as kangaroo rats (Fields et al. 1994, Grillet et al. 2010, Prugh et al. 2011). Adult *G. sila* are inactive in burrows for much of the year, emerging only from late March or April through July (USFWS 1998, Warrick et al. 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 et al. 1998, Germano et al. 2016).

*Experimental design*.-- *G. sila* individuals were located during foot and vehicle surveys and captured using a pole and noose made of either dental floss or surgical thread. The sex of each lizard was determined, and its snout to vent length (SVL) and mass were measured. *G. sila* were collared following the method of Germano et al. (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. *G. 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, parts of the collar catching on plants or causing abrasions on the lizard, and any deviation from normal lizard behaviors. *G. 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.

Lizards 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). Additionally, date and time, meso- and microhabitat, and behavior were recorded for each observation of a lizard. Mesohabitat was categorized as whether a lizard was within 0.5 meters of a shrub (shrub) or not (open) (henceforth, the “shrub association zone”). Good. Microhabitat was also recorded as the fine-scale habitat where the lizard was observed. These microhabitats including the following categories: in a burrow, within the annual grassland, in the road, in a shrub, within a bare patch, or in a wash). A brief behavior observation was taken for one minute at the same time (see supporting information Appendix A for behavior classifications). Behavior observations were brief to ensure that there would be adequate time to observe all animals 3 times daily. 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. See below, but I think you need to have a figure for microhabitat too? And show differences by behavior in a plot? We have them. I know you were trying for clean, streamlined story but I think if you mention here, you have to present. OR cut altogether and keep it really simple – ie the black and white boxplot… then done. Cut all mention of behavioural observation? Your call. I just think this halfway story will not be great with referees.

*Analyses*.-- All analyses were conducted in R (version 3.3.2). Meso- and microhabitat were analyzed using a generalized linear model (Bolker et al. 2009) with the multcomp package (Hothorn et al. 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 et al. 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 and with Zoatrack ( XX ). All R code used for this project can be found at https://cjlortie.github.io/Carrizo.telemetry.

Shrub density BIG IDEA here – really we should have shrub density for each and every relocation and test using those data… that would be really cool to know. However, that would involve 1000 look-ups. Do you trust Eva to do this very rapidly for us. I think just like ALL the data-model issues, this would be good to have. was calculated from aerial photographs within each lizard’s MCP and dividing that number by the area in square meters of the MCP (source for photographs, google maps?, and perhaps state year of imagery used just in case shrubs have changed since then?). Shrub association zones were calculated by measuring a large number of randomly chosen shrubs in the study area, taking two perpendicular diameter measurements in meters, and assigning an average radius to each shrub, to which we added the 0.5m association criterion described above. We calculated the area of each shrub association zone using the formula r2 and then took the average of the sample. We then multiplied this standard 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. This is for Fig 3 right? If so, maybe just state simply at end These calculates allowed us to regress shrub density by a weighted association measure.

**Results**

*Summary.—* The study took place in July 2016.  We tracked 29 lizards for 24 days, and we relocated lizards 3 times a day cut or move to methods.  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.

*Home range.—* Home range sizes were calculated for the 27 fully-tracked lizards. 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 (check journal for style. Might need: GLM< test-stat, then p-value) 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. Got ya on this – checked model. With gender x time class model, you get mesohabitat and gender significant with no significant interaction terms. So that means more time in open and differences between genders in frequency of relocations. You do indeed lose the time.class factor as significant. The thing is, as we discussed, gender uses a different data model – ie lizards. Using the + gender model – you can conclude open more than shrub and females more than males relocated. Does not get to the root of test. So, could be a good call to leave as is. However, see repo – IF we add gender to the pop data model, time.class is still significant etc. SO that is the best model. You have a MUCH bigger decision to make here – how much complexity. Right now, it alludes to all this complexity, and we do not really present it.

SO I see two choices.

1. Keep complexity – just present more of the results. Need to a plot for behavior, gender, and something about HR data. SO basically add more data viz, add VERY clear hypothesis and predictions so the reader can navigate complexity.
2. Cut complexity, go really simple and shoot for fast pub. CUT gender, cut behavior, and basically just present what you present here. The boxplot, regression, but also add a nice home range figure. Done. Cut meso-micro too. This will make this a lower-tier PONE paper though. Or some version of a lower-tier J of Animal Ecology paper.

HOWEVER – to do #2 really well and not raise eyebrows – ie with referees and it becomes ONLY a population level study of both shrubs and lizards we WOULD dump HR analyses. We would then need a shrub density estimate for every relocation. 1100 data points more. Eva? Then we do not need home range at all for a super simple paper.

OTHER IDEA – it is SOOO clear that you, Mike, could write an individual-level paper in your sleep. Basically, a Germano-Warrick better paper. CUT most ecology and do all the stuff you are keen to do. I do not care what paper we have as first Carrizo paper, I just want one in print. There are two papers here – and we are borrowing from one or the other no matter what we write UNLESS we go REALLY simple on each.

SS (super simple) cut: shrub density at every relocation, frequency of association of lizards, time of data. Nice little ecology paper.

SS cut #2: individual paper, SVL, mass, gender as predictors, microscale data only, what lizards were doing behavior, and home range data. VERY nice individual paper.

NOTE \_ the real Achilles heel, I actually do not believe that this exists for papers, there is NEVER a perfect experiment or set of stats, is a ‘habitat occupancy model’ – referees may ask for this. THIS is at the landscape-level and on my TODO list but not now for me. However, that is the third paper I want to save for later when we have three-years data. SOOO powerful.

So, an ‘Ecology’ paper would have a 3-section Result section…. Ideally three years data to be safe. I would not want to do do all this work and then referees say well, ecology changes year-to-year SO Much in deserts that you need more years. The ‘individual-level’ data are not as sensitive. The three sections to this GOLD paper are:

1. landscape; shrub density for home ranges (large scale matching large scale). Plus percent shrub-open for whole site and each relocation.
2. Population level: frequency, shrub open, and density by shrubs by density of lizards and HR.
3. Individual level: TRAITS and fine-scale measures – micro, size of animals, gender etc.

I think THAT is the paper we write with the three-year data because NO ONE can criticize us on being robust, covering all bases, or having sampled enough. SOOO – the decision is what to do with 1-2 shorter papers. Choice 1-2 above.

*Mesohabitat:—* The frequency of lizard observation differed significantly between mesohabitat 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. Frequency of observations between different times of day was significantly different at the mesohabitat scale (Figure X, Table 1, p < 0.01). Observations of lizards within open mesohabitat did not differ between different times of day. Observations at shrub mesohabitat differed significantly between morning and afternoon with lizards being found more frequently at shrubs in the afternoon (Figure, Table 1, p = 0.0252) KEY findings for this ‘simple’ paper so I think you need a plot.. yes, solid. Key findings. Intact with or without gender if we are doing a population-level analysis. SEE new stats using the pop-data model. Perfect.

*Microhabitat:--* Fine-scale observation patterns at the microhabitat scale were similar to the patterns at the mesohabitat scale. The frequency of observations differed significantly between microhabitat types (Table 2, p < 0.0001), with lizards found at burrow microhabitat significantly more than any other type (Table 2, p < 0.0001).  The frequency of observations at shrub microhabitat was also significantly greater than any other microhabitat types besides burrows (Table 2, p < 0.0001). OK – I love this scale stuff. More complexity though. ALSO, you need to tie into Introduction with Hypothesis and Predictions – ie why measure at two scales? The reader is left wondering why this is here. It confirm the shrub finding above at meso scale so that is really important. I think that is why you keep it in, just need to have it be a prediction at the start of ms.

Lizards were observed at shrub microhabitat more frequently than in annuals, bare patches, washes, and roads. Observation frequency also differed significantly between different times for microhabitat (FIGURE, Table 2, p < 0.0001 –what is the p-value for? The main effect in model or the post hoc test. Typically, if you cite a stats table you do not also need here in parentheses too. However, check your target journal). Lizard observations at shrub microhabitat differed between morning and afternoon, with more shrub observations occurring in the afternoon (Table S2, p = 0.0003).  Night refugia accounted for about 12% of the total number of observations of lizards at shrubs.

*Behavior:—*Behavior observations differed significantly between microhabitat types (Table 3, p < 0.0001). Lizards were observed cooling under shrubs significantly more than other habitat types (Figure, Table 3, p <0.0001). Lizards were also observed avoiding predators under shrubs more frequently than at other microhabitat types (Table 3, p < 0.0001). Super findings for pop-level paper.. 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 (Table 3, p < 0.001) e.g. lizards were more frequently observed sunning in the morning in both mesohabitat types compared to the afternoon (Table 3, p < 0.001) and more often burrowing and avoiding predators in the afternoon.   NEED a figure or cut… does this help our story?

*Shrub use as 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. KEY finding keep – BECAUSE this suggests that the 25% of time found at shrubs not due to random chance or just loads of shrubs within region. SUPER Important. Good addition Mike.

SIMPLE paper.

Map, relocation frequency shrub-open, keep time.class, CUT gender and CUT behavior, then shrub density with a home range figure too. GOOD paper. Need to write a punchy style paper.

OR keep what you have here, but just present it a bit more – show more of the data in plots. Then good.

**Discussion**

Shrubs are foundation species in many ecosystems because of the facilitative benefits such as shelter, refuge, and food resources, they provide to both plant and animal species **(**Filazzola et al. 2014, Lortie et al. 2015). Restate Hypothesis here then state main finding. Our observation of increased association of *G. sila* with shrubs in the afternoon, and the types of lizard behaviors that were observed significantly more at shrubs, are consistent with thermoregulatory behavior of other lizards (Vickers et al 2016) and suggest that shrubs facilitate *G. sila* by providing thermoregulatory shelter and a refuge from depredation. Then work through each prediction here and just state simply what it means – for me – means that implication is that there is more than one mechanism of facilitation by shrubs for lizards, that population-level trends support the need for a heterogeneous landscape, and that telemetry can be used to infer association patterns and suggest important mechanisms for restoration and management. I like strong first paragraphs in a Discussion.

We saw interactions of *E. californica* and *G. sila* to be chiefly mediated by thermoregulatory and predator-avoidance behaviors, but *E. californica* may provide other benefits to lizards through indirect interactions due to the shrub’s positive effect on many other species such as burrowing mammals (Hansen et al. 1994, Fields et al. 1999, Prugh et al. 2011, Filazzola et al. 2017). CUT or work into a paraggraph

Scale is important in ecology because relevant processes can function at many scales simultaneously, and patterns can vary in magnitude and sign at local versus landscape levels and may mediate important climatic interactions with organisms (Schneider 2001, Chave 2013). In particular, documenting variation in microhabitat use (cite a result) is important because climate effects at this scale may have disproportionate effects on a species’ persistence (Pincebourde et al 2016). Our observations of significant variation in microhabitat use suggests that microhabitat variation can be a driver of habitat quality and in particular of thermoregulatory opportunity for *G. sila*. CUT.

You did not introduce direct versus indirect facilitation in the Introduction. I would not frame this way. I would likely have this paragraph by about mechanisms of facilitation. Very nice finding at pop-level that deserves discussion.Direct facilitation of *G. sila* by shrubs was also detected at both scales. Shrubs were used by *G. sila* significantly more than all remaining mesohabitat and microhabitat categories except burrows. Shrubs can buffer the extremes of 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. a dispersed) will affect lizard thermoregulatory behavior and can be crucial to an ectotherm’s thermoregulatory efficiency (Sears et al 2016, Basson et al 2017). Shelter against temperature changes is 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). Overall, lizards were located over 75% of their time near a shrub or burrow. These patterns suggest the importance to *G. sila* of having some form of shelter and/or refuge within close proximity (Huey 1974, Díaz and Cabezas-Díaz 2004, Anderson et al. 2010). The advantage of having a quick escape from predators as well as easy access to shade may cause *G. sila* to concentrate in areas where cover is available, whether this is in the form of burrows alone or in combination with shrubs. Our observation that shrub use did not vary as response to shrub availability 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. OK – this is a mechanism paragraph – end with a nice statement of implication of shrub providing important mechanisms of facilitation that may not be present without shrubs.

Discussion (my suggestion)

Para 1. Nice big picture hypothesis restate, state whether each prediction was supported, then end with big implications.

Para 2. Mechanisms of facilitation

Para 3. Gender and behavior links to existing lit (optional paragraph)./

Para 4. Strength of telemetry study to infer facilitation through association patterns. Then link to previous studies and compare. Then end with statement that a novel way to understand plant-animal interactions.

One previous radio telemetry study of *G. sila* addressed the subject of shrub use. Germano and Rathbun (2016) found a marginally significant effect suggesting that a larger than expected area of *G. sila* home ranges were occupied by shrubs, suggesting to them a potential positive interaction between shrubs and *G. sila*. Their estimates of home range were somewhat larger than our estimates: for males they estimated 6.915 ha, averaged over the 2 years of their study, vs. 5.14 ha in our single-year study, and for females they estimated 3.17 ha, vs. 1.87 ha in our study. However, the general similarity between estimates suggests that the two systems are generally comparable. In our study, we did not see a general correlation between shrub use by individual lizards and shrub density within home ranges, suggesting that a home range-based approach to assessing the benefit of shrubs to lizard may not reveal a strong effect, even if the benefit is substantial. By approaching the question from the perspective of shrub facilitation, however, we were able to obtain strong evidence for a positive interaction between shrubs and lizards based on direct observations of those interactions at multiple habitat scales and of the behaviors exhibited by lizards within each habitat scale. This paragraph needs work.

Topic sentence? Is this anew paragraph or a continuation of same idea from above? Germano and Rathbun (2016) conclude their discussion of *G. sila* shrub use by citing personal observation that robust *G. sila* populations exist in landscapes that do not contain shrubs, and stating that restoration of *G. sila* habitat may be adequate without a shrub component. Given the variation that we observed in lizard habitat use within one population, it 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 et al. 2014). More to the point, where population-scale variation exists in an individual lizard’s predisposition to use shrubs, it would be reasonable to propose that shrubs be made available so that those lizards within a given population that are predisposed to associating with shrubs will have shrubs with which to associate. The net effect is 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, heterogeneous habitats are becoming increasingly recognized as important to achieve individual-scale thermoregulatory optimization for lizards (Basson et al 2016, Sear et al 2016). OK so this is a how different paragraph?? OK but needs some work for flow. End with an implication.

**Immediate Management Applications**

*G. sila*’s close association with shrubs indicates that positive interactions between shrub and lizards can be beneficial to lizards (Warrick et al. 1998, Lortie et al. 2015, Filazzola et al. 2017). Whether or not landscapes contain shrubs, and how those shrubs are distributed over the landscape (eg clumped vs. dispersed) is expected to affect a lizard’s thermoregulatory efficiency, and therefore its ecological resilience (Sears et al 2016). Indeed, behavioral differences in *G. sila* in shrubbed vs. unshrubbed landscapes were observed by Tollestrup (1979). Given the observed heterogeneity of use of shrubs from the present study, it seems reasonable to conclude that making shrubs available to those lizards who are predisposed to use shrubs will increase the overall resilience of the population to disturbance, including disturbance from climate change. In our study, lizards used shrubs significantly more for behaviors such as thermoregulation and predator avoidance over other habitat types. Body temperature regulation is of particular importance to the survival of ectotherms such as lizards (Huey 1974, Díaz and Cabezas-Díaz 2004, Kerr et al. 2004). With climate change predicted to have a high impact on the San Joaquin Desert, this activity could potentially take up even more time due to increased temperature stress on lizards (Vickers 2011, Westphal et al. 2016, Filazzola et al. 2017). The presence of shrubs, whether naturally occurring or planted, could benefit lizards by providing additional sources of shelter and refuge (Kerr et al. 2004, Lortie et al. 2015, Filazzola et al. 2017). Shrubs can also benefit other burrow-dwelling species, such as kangaroo rats (Hawbecker 1951, Prugh et al. 2011, Lortie et al. 2015). Higher densities of burrows are found under shrubs compared to open areas (Hansen et al. 1994, Filazzola et al. 2017). Burrows are often used by lizards for shelter and refuge (Hansen et al. 1994, Grillet et al. 2010), so the increased abundance of these burrowing animals could increase the number of burrows available to *G. sila* (Steffen and Anderson 2006, Prugh et al. 2011, Filazzola et al. 2017). We therefore recommend that *E. californica* and other shrubs should be taken into account as part of the effort to recover *G. sila*. Our findings are likely applicable to other lizard species and small animals that face similar environmental conditions.

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**Tables**

**Table 1**: Generalized linear model for mesohabitat, with degrees of freedom, deviance, and p-values. Check JAE or whatever journal you select to ensure the table matches what they require. I have not seen this format before. Typically, you state test statistic too.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Generalized linear model |  |  |  |  |  |
| Factor | Df | Deviance | P-value |  |  |
| mesohabitat | 1 | 88.33 | < 0.0001 |  |  |
| Time class | 1 | 2.901 | 0.1 |  |  |
| mesohabitat: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**: Generalized linear model for microhabitat with degrees of freedom, deviance, and p-values. For the least square means post hoc for microhabitat:time class see Supporting information.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Generalized Linear Model |  |  |  |  |  |
| Factor | Df | Deviance | P-value |  |  |
| microhabitat | 5 | 1044.1 | < 0.0001 |  |  |
| time class | 1 | 0.5 | > 0.5 |  |  |
| microhabitat:time.class | 5 | 55.26 | < 0.0001 |  |  |
|  |  |  |  |  |  |
|  |  |  |  |  |  |
| Microhabitat Post Hoc, Least squared means |  |  |  |  |  |
| contrast | estimate | SE | df | z.ratio | p.value |
| annuals-bare | 0.3377215 | 0.179633 | NA | 1.88 | 0.4145 |
| annuals-burrow | -1.95300636 | 0.131068 | NA | -14.901 | <.0001 |
| annuals-road | 0.50298261 | 0.218936 | NA | 2.297 | 0.195 |
| annuals-shrub | -1.06739262 | 0.144933 | NA | -7.365 | <.0001 |
| annuals-wash | 0.24454864 | 0.166362 | NA | 1.47 | 0.6836 |
| bare-burrow | -2.29072786 | 0.134072 | NA | -17.086 | <.0001 |
| bare-road | 0.16526112 | 0.220747 | NA | 0.749 | 0.9757 |
| bare-shrub | -1.40511412 | 0.147655 | NA | -9.516 | <.0001 |
| bare-wash | -0.09317285 | 0.168739 | NA | -0.552 | 0.9939 |
| burrow-road | 2.45598898 | 0.183412 | NA | 13.391 | <.0001 |
| burrow-shrub | 0.88561374 | 0.081932 | NA | 10.809 | <.0001 |
| burrow-wash | 2.19755501 | 0.115688 | NA | 18.996 | <.0001 |
| road-shrub | -1.57037523 | 0.193563 | NA | -8.113 | <.0001 |
| road-wash | -0.25843397 | 0.210089 | NA | -1.23 | 0.8222 |
| shrub-wash | 1.31194127 | 0.131188 | NA | 10 | <.0001 |

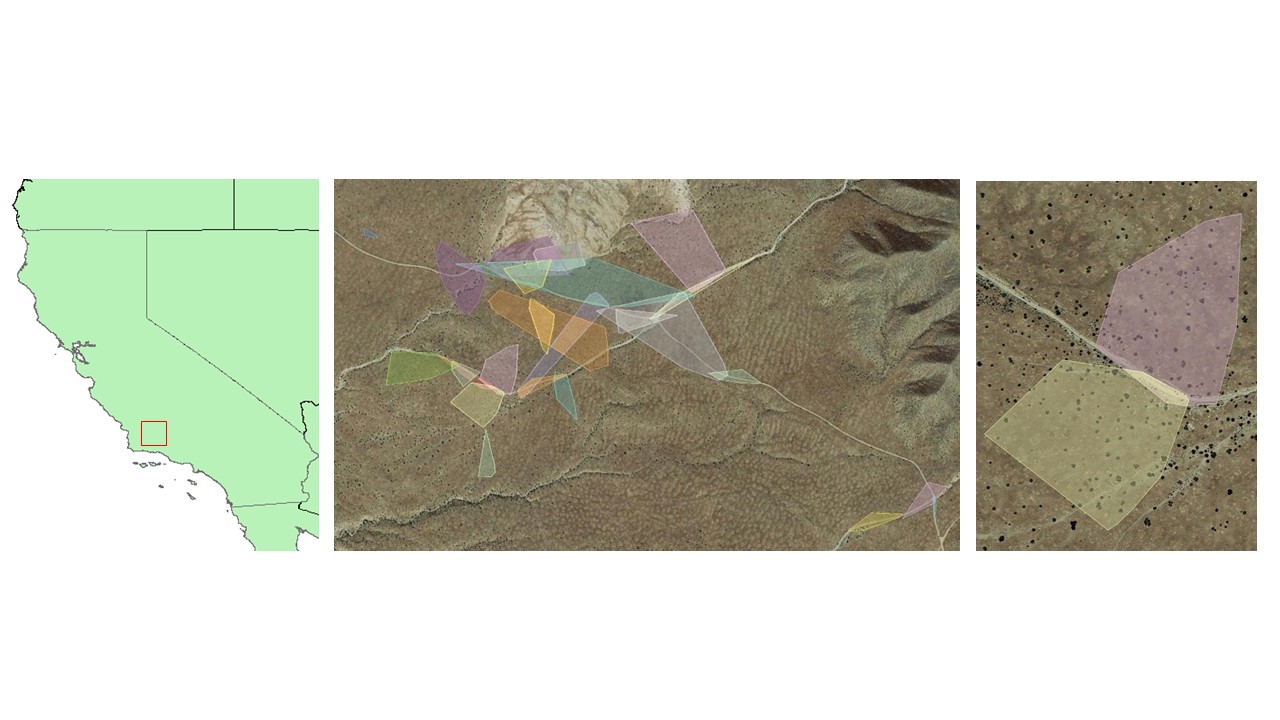
**Table 3**: Multinomial logistic regression for behavior observations.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  | | |  | | |
|  | | mesohabitatshrub | | | 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 |

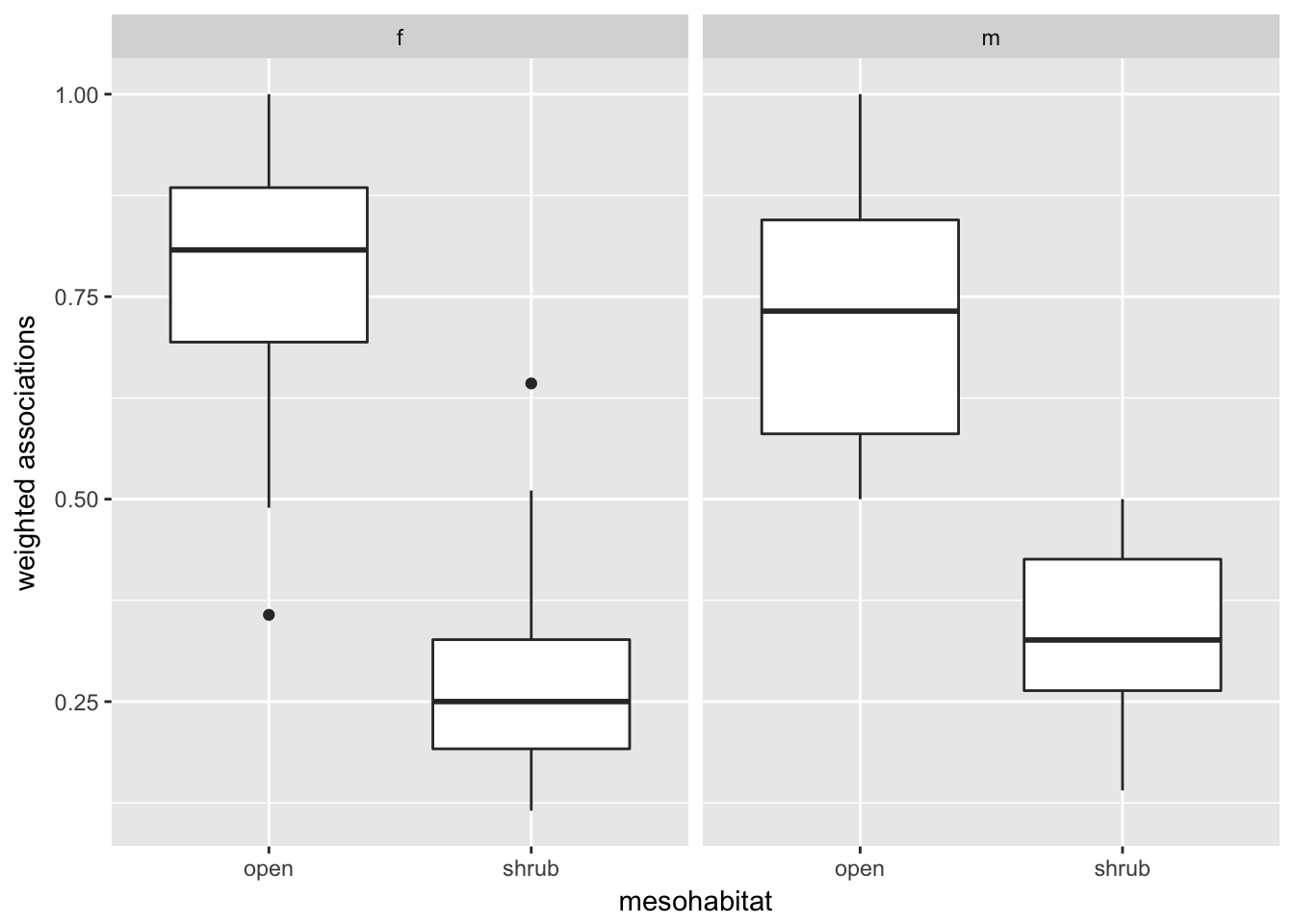
**Figures**

**Figure 1:** Left: location of study. Middle: aerial photograph of study site overlain with home ranges calculated using a 95% minimum convex polygon (MCP) estimate, for each individual. Different individuals are indicated by different colors. Right: Two example MCPs showing the presence of shrubs.

This figure is not that pretty.

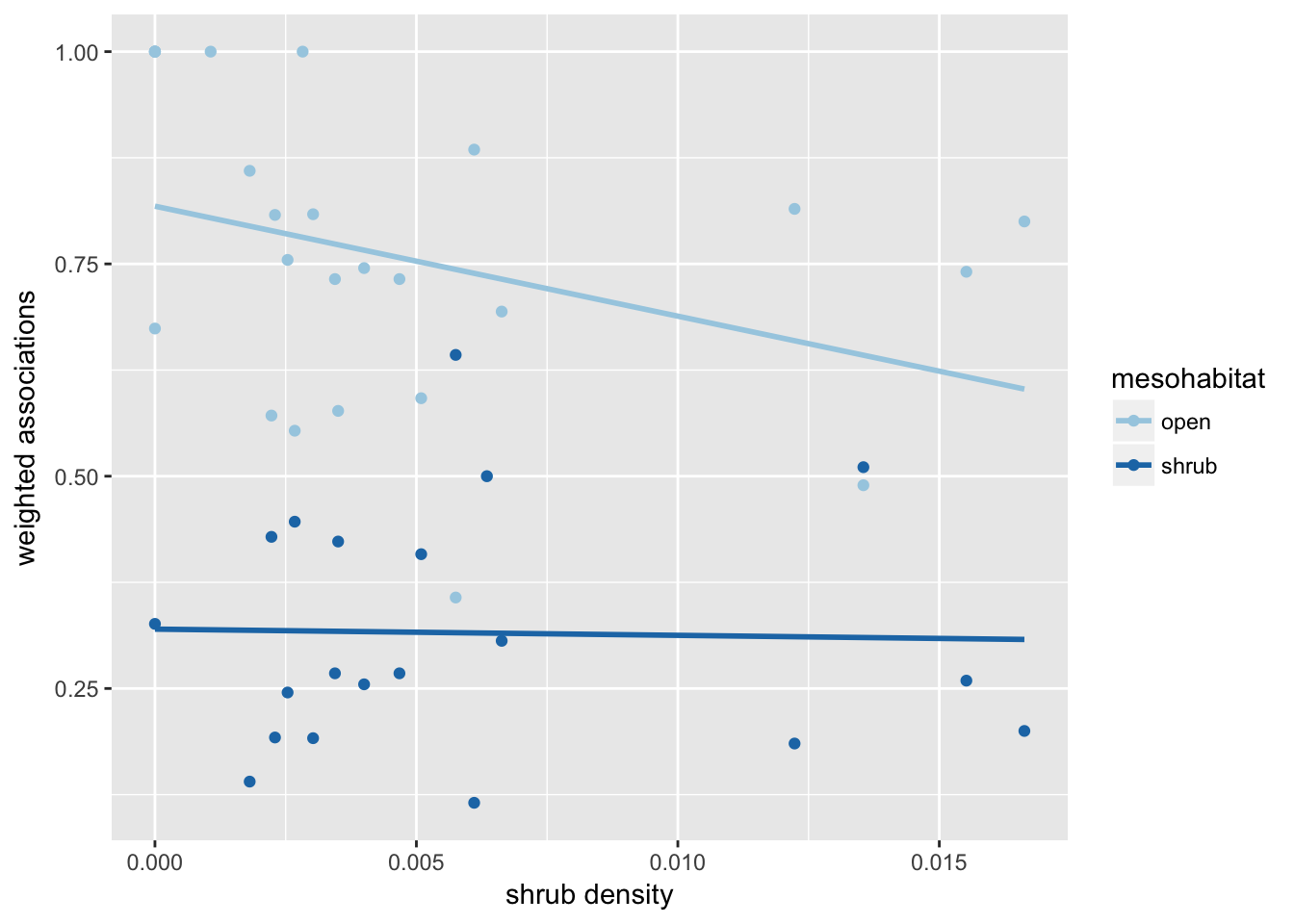


**Figure 2**: Boxplot showing the frequency of observation by mesohabitat type and gender.



if you present microhabitat, you should also have a figure?

**Figure 3:** Plots of shrub density on the weighted lizard 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, in this study aerial predators such as ravens and raptor species were the only predators observed. The lizard would typically look up as the predator flew overhead or nearby then move quickly towards some form of refuge, such as shrub, annuals or burrow. |
| burrowing | Actively digging a burrow, or burying itself. This behavior occurred more often towards the end of the season where some lizards were found in shallow spiral burrows after becoming dormant. 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. Shade could be from any source including shrubs, rocks, burrow mounds, annuals or manmade objects such as fence posts. 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 for the ambush. |
| interacting | Interacting with another lizard including both members of the same species and members of other lizard species such as whiptail lizards. Usually as part of mating or territory displays. Included pushups, mating, and chasing another lizard. |
| observing | Actively observing environment. Usually from vantage point such as burrow mound, open area or from branches of shrub. Occasional head turning. |
| 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. |

**Table S2**: Least means squares post hoc test for microhabitat:time class.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| contrast | estimate | SE | df | z.ratio | p.value |
| annuals,AM-bare,AM | 0.31079988 | 0.193404 | NA | 1.607 | 0.907 |
| annuals,AM-burrow,AM | -1.72643262 | 0.156305 | NA | -11.045 | <.0001 |
| annuals,AM-road,AM | 1.1420974 | 0.323435 | NA | 3.531 | 0.0212 |
| annuals,AM-shrub,AM | -0.39834764 | 0.182157 | NA | -2.187 | 0.5593 |
| annuals,AM-wash,AM | 0.85441533 | 0.238728 | NA | 3.579 | 0.0179 |
| annuals,AM-annuals,PM | 0.67209377 | 0.250885 | NA | 2.679 | 0.2367 |
| annuals,AM-bare,PM | 1.03673688 | 0.266977 | NA | 3.883 | 0.0058 |
| annuals,AM-burrow,PM | -1.50748634 | 0.154578 | NA | -9.752 | <.0001 |
| annuals,AM-road,PM | 0.5359616 | 0.258324 | NA | 2.075 | 0.641 |
| annuals,AM-shrub,PM | -1.06434383 | 0.174502 | NA | -6.099 | <.0001 |
| annuals,AM-wash,PM | 0.30677573 | 0.182551 | NA | 1.68 | 0.8774 |
| bare,AM-burrow,AM | -2.0372325 | 0.138864 | NA | -14.671 | <.0001 |
| bare,AM-road,AM | 0.83129752 | 0.315376 | NA | 2.636 | 0.2594 |
| bare,AM-shrub,AM | -0.70914752 | 0.167432 | NA | -4.235 | 0.0014 |
| bare,AM-wash,AM | 0.54361545 | 0.22769 | NA | 2.388 | 0.4145 |
| bare,AM-annuals,PM | 0.36129389 | 0.240407 | NA | 1.503 | 0.9403 |
| bare,AM-bare,PM | 0.725937 | 0.257155 | NA | 2.823 | 0.1702 |
| bare,AM-burrow,PM | -1.81828622 | 0.136917 | NA | -13.28 | <.0001 |
| bare,AM-road,PM | 0.22516172 | 0.24816 | NA | 0.907 | 0.9991 |
| bare,AM-shrub,PM | -1.37514371 | 0.159069 | NA | -8.645 | <.0001 |
| bare,AM-wash,PM | -0.00402415 | 0.16786 | NA | -0.024 | 1 |
| burrow,AM-road,AM | 2.86853002 | 0.294088 | NA | 9.754 | <.0001 |
| burrow,AM-shrub,AM | 1.32808498 | 0.122716 | NA | 10.822 | <.0001 |
| burrow,AM-wash,AM | 2.58084794 | 0.197152 | NA | 13.091 | <.0001 |
| burrow,AM-annuals,PM | 2.39852639 | 0.21171 | NA | 11.329 | <.0001 |
| burrow,AM-bare,PM | 2.7631695 | 0.230553 | NA | 11.985 | <.0001 |
| burrow,AM-burrow,PM | 0.21894627 | 0.075975 | NA | 2.882 | 0.1473 |
| burrow,AM-road,PM | 2.26239421 | 0.220475 | NA | 10.261 | <.0001 |
| burrow,AM-shrub,PM | 0.66208878 | 0.111036 | NA | 5.963 | <.0001 |
| burrow,AM-wash,PM | 2.03320835 | 0.1233 | NA | 16.49 | <.0001 |
| road,AM-shrub,AM | -1.54044504 | 0.308607 | NA | -4.992 | <.0001 |
| road,AM-wash,AM | -0.28768207 | 0.345033 | NA | -0.834 | 0.9996 |
| road,AM-annuals,PM | -0.47000363 | 0.353553 | NA | -1.329 | 0.9754 |
| road,AM-bare,PM | -0.10536052 | 0.365148 | NA | -0.289 | 1 |
| road,AM-burrow,PM | -2.64958374 | 0.293174 | NA | -9.038 | <.0001 |
| road,AM-road,PM | -0.6061358 | 0.35887 | NA | -1.689 | 0.8737 |
| road,AM-shrub,PM | -2.20644123 | 0.304151 | NA | -7.254 | <.0001 |
| road,AM-wash,PM | -0.83532167 | 0.308839 | NA | -2.705 | 0.2236 |
| shrub,AM-wash,AM | 1.25276297 | 0.218218 | NA | 5.741 | <.0001 |
| shrub,AM-annuals,PM | 1.07044141 | 0.231455 | NA | 4.625 | 0.0002 |
| shrub,AM-bare,PM | 1.43508453 | 0.248807 | NA | 5.768 | <.0001 |
| shrub,AM-burrow,PM | -1.1091387 | 0.120509 | NA | -9.204 | <.0001 |
| shrub,AM-road,PM | 0.93430924 | 0.239498 | NA | 3.901 | 0.0054 |
| shrub,AM-shrub,PM | -0.66599619 | 0.145186 | NA | -4.587 | 0.0003 |
| shrub,AM-wash,PM | 0.70512337 | 0.154767 | NA | 4.556 | 0.0003 |
| wash,AM-annuals,PM | -0.18232156 | 0.278174 | NA | -0.655 | 1 |
| wash,AM-bare,PM | 0.18232156 | 0.29277 | NA | 0.623 | 1 |
| wash,AM-burrow,PM | -2.36190167 | 0.195786 | NA | -12.064 | <.0001 |
| wash,AM-road,PM | -0.31845373 | 0.284901 | NA | -1.118 | 0.994 |
| wash,AM-shrub,PM | -1.91875916 | 0.211869 | NA | -9.056 | <.0001 |
| wash,AM-wash,PM | -0.5476396 | 0.218546 | NA | -2.506 | 0.336 |
| annuals,PM-bare,PM | 0.36464311 | 0.302765 | NA | 1.204 | 0.9888 |
| annuals,PM-burrow,PM | -2.17958011 | 0.210439 | NA | -10.357 | <.0001 |
| annuals,PM-road,PM | -0.13613217 | 0.295163 | NA | -0.461 | 1 |
| annuals,PM-shrub,PM | -1.7364376 | 0.225479 | NA | -7.701 | <.0001 |
| annuals,PM-wash,PM | -0.36531804 | 0.231765 | NA | -1.576 | 0.9179 |
| bare,PM-burrow,PM | -2.54422323 | 0.229385 | NA | -11.091 | <.0001 |
| bare,PM-road,PM | -0.50077529 | 0.308957 | NA | -1.621 | 0.9018 |
| bare,PM-shrub,PM | -2.10108072 | 0.243258 | NA | -8.637 | <.0001 |
| bare,PM-wash,PM | -0.72996115 | 0.249095 | NA | -2.93 | 0.1301 |
| burrow,PM-road,PM | 2.04344794 | 0.219254 | NA | 9.32 | <.0001 |
| burrow,PM-shrub,PM | 0.44314251 | 0.108591 | NA | 4.081 | 0.0026 |
| burrow,PM-wash,PM | 1.81426207 | 0.121103 | NA | 14.981 | <.0001 |
| road,PM-shrub,PM | -1.60030543 | 0.233728 | NA | -6.847 | <.0001 |
| road,PM-wash,PM | -0.22918587 | 0.239797 | NA | -0.956 | 0.9985 |
| shrub,PM-wash,PM | 1.37111956 | 0.145679 | NA | 9.412 | <.0001 |