HABITAT ASSOCIATION PATTERNS OF AN ENDANGERED LIZARD SPECIES WITH A FOUNDATION PLANT SPECIES IN THE SAN JOAQUIN DESERT OF CALIFORNIA: RADIO TELEMETRY AS AN ECOLOGICAL TOOL.

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A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS OF THE DEGREE OF MASTER OF SCIENCE

GRADUATE PROGRAM IN BIOLOGY

YORK UNIVERSITY

TORONTO, ONTARIO

June 2017

Abstract

Positive facilitation of plant and animal species by dominant vegetation is common in harsh environments such as deserts. Here we tested the hypothesis that desert shrubs facilitate the blunt-nosed leopard lizard (*Gambelia sila*), an endangered species found in the San Joaquin desert of California using radio telemetry. We predicted that lizards are more frequently observed near shrubs due to the positive facilitative benefits shrubs provide. After systematically reviewing the literature on the use of telemetry in deserts, we conducted telemetry habitat surveys of *G. sila* in Carrizo Plain. Thermoregulation and predator avoidance behaviors were performed more frequently at shrubs, indicating that lizards are likely using shrubs as a source of shelter and refuge. Shelter and refuge are two facilitative benefits that shrubs commonly provided to animals, suggesting that shrubs are facilitating lizards in this environment. As a result, shrub restoration would likely have a positive effect on lizard recovery efforts.

Acknowledgements

Thank you first to my advisor Dr. Chris Lortie. Without your guidance none of this would be possible. Thank you for sending me to the desert. Thanks also to Dr. Bridget Stutchbury for her guidance throughout the project. I would like to thank all members of my examining committee, including Dr. Suzanne MacDonald, and Dr. Greg Thiemann for their assistance.

Thanks to everyone at the Bureau of Land Management Central Coast Field Office and the Bakersfield Field Office. Special thanks to Mike Westphal for all you have done. Thank you for introducing me to Carrizo and leopard lizards and all their secrets. Thank you also to Kathleen Sharum and Johna Hurl as well as everyone at Carrizo Plain National Monument for all the assistance you provided. You are lucky to work in such a beautiful place!

A big thanks to Scott Butterfield and everyone at The Nature Conservancy, your assistance and local knowledge was extremely valuable. I would also like to thank Dave Germano and Larry Saslaw for teaching me everything they know about telemetry. I wouldn't have been able to set up such a neat project without you. Thanks to Larry and Anne Saslaw for adopting me for the 2015 season and making sure I ended up with a roof over my head eventually. Thanks to Erin Tennant for your help as well.

Thanks Chase Groninger and Eva Gruber for your help and hard work. 2016 was ten times better than 2015 thanks to you!

Thanks to the entire Lortie Lab. Thanks to Diego Sotomayor for showing me the ropes of the school and the city. Alex Filazzola, thank you for all your help with study design and statistics. I would have been lost without you. Amanda Liczner thank you for your overall advice on my project. Ally Ruttan thanks for your advice as well. I'm glad that the 3 of us survived our grad courses together. Thanks also to our neighbors, the Sapna lab, for their support and for letting me visit whenever I wanted.

Thank you to everyone at Washburn Ranch who made my time on the Carrizo enjoyable and kept me sane. You know who you are! Hope I will get back out to visit you real soon!

Last but not least thanks to my family and friends. Mom and Dad, thank you for your support and for putting up with not hearing from me for months. Mom I’m glad you got to see Carrizo. Jillian, thanks for forgetting where I was when I was out in the field. Tim, glad we got to hang in the desert, let’s do it again! And Marcia Lee, thank you for always being there.

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General Introduction

The blunt-nosed leopard lizard (*Gambelia sila*) is an endangered species, listed both federally and by the state of California (USFWS 1998, Warrick *et al.* 1998, Germano *et al.* 2016). The species was originally listed in 1967 due to habitat loss (Germano et al. 1992). *Gambelia sila* was originally classified with the long-nosed leopard lizard (Gambelia wislizenii) as the same species, then as a subspecies, before being recognized as separate species (Tollestrup 1982, Richmond 2017). The two closely related species are distinguished from each other by the length of their snouts. The blunt-nosed lizard has a shorter, more rounded nose than the long-nosed leopard lizard (Tollestrup 1982, Richmond 2017). The blunt-nosed leopard lizard is endemic to California and is found only in the San Joaquin Desert, California's central valley, and the surrounding hills and smaller valleys (Warrick *et al.* 1998, Germano *et al.* 2016). It is the largest lizard species found in the area, 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). Depending on length and age, lizards can range from about 20 grams to 45 grams (Tollestrup 1982, Germano *et al.* 2016). Blunt-nosed leopard lizards are only active from late March or April through July, spending the fall, winter, and late summer dormant in underground burrows (USFWS 1998, Warrick *et al.* 1998, Germano *et al.* 2016). The species is diurnal and will return to a burrow at night or whenever temperatures are too hot or too cold (Warrick *et al.* 1998, Germano *et al.* 2016). Blunted-nosed leopard lizards are tan or light brown colored with dark spots and lighter bands on their backs (Germano and Williams 2007). During the breeding season (late April-June) females will develop bright red or orange spots or blotches on their sides while the sides of the males will turn salmon or pink (Medica *et al.* 1973, Germano and Williams 2007). This species is insectivorous with most of its diet consisting of grasshopper and beetle species (Germano *et al.* 2007). However, at times it has been observed to eat smaller lizard species such as side blotch lizards (*Uta stansburiana elegans*) (Warrick *et al.* 1998, Germano *et al.* 2007, Germano *et al.* 2016). They are prey for many species including several species of snakes, birds of prey, and mammalian predators such as coyotes (Germano *et al.* 1992, USFWS 1998, Germano *et al.* 2005).

Blunt-nosed leopard lizards are found mainly on semi-arid grassland and scrub habitat within the San Joaquin Desert (USFWS 1998, Warrick *et al.* 1998, Germano *et al.* 2016, Westphal *et al.* 2016). This desert is found in the southern central valley of California (Germano *et al.* 2011). In addition to the blunt-nosed leopard lizard, this area supports many other endangered and threatened species including the San Joaquin kit fox (*Vulpes macrotis mutica*) and the giant kangaroo rat (*Dipodomys ingens*) (Germano *et al.* 2011, Prugh *et al.* 2011). Much of this natural desert habitat no longer exists. It now covers less than 5% of its historic distribution (Germano *et al.* 2011). California's central valley has been highly developed for agriculture and natural resource extraction. Urbanization has also increased in the area (USFWS 1998, Germano *et al.* 2011). This has greatly fragmented the remaining habitat (USFWS 1998, Germano *et al.* 2011). Carrizo Plain National Monument (35.1914° N, 119.7929° W), located in Southeastern San Luis Obispo County, is one of the few remaining large patches of this ecosystem (Germano *et al.* 2011). Today, habitat loss is the main reason for the decline of this species, much as it was when it was originally listed in 1967 (Warrick *et al.* 1998, Germano *et al.* 2016, Westphal *et al.* 2016). Because of this, understanding what habitat features are preferred by these lizards is important so that existing habitat as well as degraded habitat can be restored for their use.

One habitat feature that lizards may benefit from is shrubs, including mormon tea (*Ephedra californica*) and saltbrush (*Atriplex polycarpa*), two common shrubs in the area (Warrick *et al.* 1998, Germano *et al.* 2016). Lizards do not require shrubs for survival and can be found in areas where shrubs are absent. However when shrubs are available, lizard activity is often concentrated around shrubs (Warrick *et al.* 1998, Germano *et al.* 2016). Germano *et al.* (2016) found that blunt-nosed leopard lizard home ranges contained more shrub areas than expected based on the proportion of shrub to open area. Other studies have found similar associations between different lizard species and shrubs, due to the microclimate created by the shrub (Kerr *et al.* 2004, Schaefer *et al.* 2016). Shrubs buffer the extremes of environmental conditions such as temperature, wind, and solar radiation creating a moderate microclimate under their canopy (Kerr *et al.* 2004, Filazzola *et al*. 2014, Lortie *et al*. 2015). Temperature regulation is of utmost importance for poikilotherm such as lizards, and hot, dry environments such as deserts make maintaining body temperature even more important (Huey 1974, Díaz and Cabezas-Díaz 2004, Kerr *et al.* 2004). Many other types of species, especially those living in harsh environments, are positively facilitated by shrub species through direct interactions, such as the shelter from environmental conditions that shrubs provide (Filazzola *et al*. 2014, Lortie *et al*. 2015). Because of this facilitative effect, animal species may seek out shrubs to help them regulate their body temperature when environmental conditions are unfavorable, for example, seeking shrubs in the heat of the day to cool off (Lortie *et al.* 2015, Spiegel *et al.* 2015, Germano *et al.* 2016). In addition to shelter, shrubs provide other benefits to animals, such as refuge from predators. Shrubs can conceal prey animals visually from predators and protect them from attack if spotted (Fields *et al.* 1999, Anderson *et al.* 2010). Shrubs may also have a higher concentration of burrows than open areas, indirectly benefiting small animals by providing additional areas of refuge (Hansen *et al.* 1994, Fields *et al.* 1999, Prugh *et al.* 2011, Filazzola *et al.* 2017). Additional indirect benefits that shrubs may provide to animals include added food resources (insects) that shrubs may attract (Filazzola *et al*. 2014, Lortie *et al*. 2015). Many of these benefits shrubs provide to other species likely apply to leopard lizards as well, as this species is sensitive to temperature, is a source of prey for many predators in the area, uses burrows extensively, and eats insects that may be found around shrubs. However, no study of direct or indirect interactions with shrubs has been conducted for this species (Warrick 1998, Germano *et al.* 2016). However within these net positive interactions, shrubs may have some negative impacts on lizards. Similar to the positive effects they can have on animals, shrubs can have a positive effect on other plants, such as annual grasses, by providing a moderated microclimate. This can lead to dense annual cover around the base of shrubs. Plant cover that is very dense can be negative as it can impact lizards' movements and lead to an increased risk of predation (Germano *et al.* 2016).

When lizards are found in habitat areas without shrubs they will often be concentrated around habitat features that can provide shelter and refuge (Warrick *et al.* 1998, Prugh *et al.* 2011, Germano *et al.* 2016). Blunt-nosed leopard lizards will often use burrows for this purpose. Old kangaroo rat burrows are the type most often used, however lizards will use whatever burrows are available (Prugh *et al.* 2011, Germano *et al.* 2016). In areas without kangaroo rats or other burrowing animals, lizards may dig primitive burrows or bury themselves for shelter (Germano *et al.* 2016). Other sources of shelter and refuge can include everything from natural features such as rocks, the edges of washes, and annual plants, to manmade features such as fence posts and pipelines (Germano *et al.* 2016). Despite the fact that lizards can use manmade features as shelter, too much human disturbance, such a frequent human presence or noise from machinery negatively affects them (Warrick *et al.* 1998, Germano *et al.* 2016).

Objectives

With little of their natural habitat remaining in its original state, the preservation and restoration of the remaining habitat for the blunt-nosed leopard lizard is of utmost importance (USFWS 1998, Warrick *et al.* 1998, Germano *et al.* 2016). The purpose of this thesis was to explore habitat use of the blunt-nosed leopard lizard, with a focus on lizard-shrub facilitative interactions using radio telemetry. Radio telemetry, or radio tracking, is a common survey method for wildlife ecology which consists of a radio transmitter attached to an animal, and a receiver to pick up the signal of the transmitter (Cochran and Lord 1963, Swanson *et al.* 1976, Brand *et al.* 1975, Brugnoli *et al.* 2008). Once the transmitter is attached, the animal can be located repeatedly by searching for the radio frequency the transmitter produces with a receiver. In this way observations can be made for hard to find or elusive animals on a regular basis (Cochran and Lord 1963, Swanson *et al.* 1976, Brugnoli *et al.* 2008). Though other studies have found lizards to associate with shrubs, none have examined how lizards interact with shrubs, if shrubs are in fact facilitating lizards, and if so, what facilitative benefits are drawing lizards to shrubs. To do this, we first explored how our survey method of radio telemetry, a common method for habitat use studies, was utilized in desert environments to study animal species with a systematic review of the literature. No review or study to date has summarized telemetry studies in deserts. Our objective was to determine how telemetry might be used most effectively in similar environments to our study site, which would help guide our study design and deployment of radio transmitters. Next we conducted an in-depth telemetry study of blunt-nosed leopard lizards to determine their habitat use. Our focus in this survey was the interaction of lizards with shrubs, namely mormon tea (*Ephedra californica*), the dominant shrub at our study site. We examined how lizards are using shrubs to determine if facilitation is occurring through any direct or indirect shrub-lizard interactions. To do this, we observed individual lizards 3 times a day for 15 consecutive days. This is a higher survey frequency over similar duration of study compared to the once a day observations of leopard lizard telemetry studies to date. Multiple observations of each individual daily allowed us to compare habitat use and behavior at different times of the day. This is important because behavioral and habitat needs likely vary throughout the day with changing environmental conditions, especially temperature. Habitat type at two spatial scales (mesohabitat and microhabitat), as well as a brief, 1 minute behavioral observation (sunning, cooling, avoiding predators, etc. for a complete list of defined behavior classifications please see Chapter 2, supporting information, table S1), was recorded each time an individual was located. Examining behavior allowed us to determine how lizards were using habitat and by connection what interactions were occurring between them and habitat features such as shrubs. Interactions occur at different scales, so using two habitat scales gave better insight in determining interactions. For example, a lizard may be using a shrub, but when examined at a finer scale, it may be drawn to a burrow under the shrub as opposed to the shrub itself. This would indicate indirect facilitation (the shrub facilitates burrowing mammals, which in turn facilitate lizards) as opposed to direct facilitation. It was our goal that information from this study about how lizards are using different habitat features, such as shrubs, will assist land managers in making habitat management decisions for the conservation of the blunt-nosed leopard lizard.

CITATIONS FOR CHAPTERS SUBMITTED FOR PUBLICATION

This thesis was written as two separate manuscripts, in collaboration with co-authors from the U.S. Bureau of Land Management and The Nature Conservancy that have been submitted to journals for consideration for publication.

The following is the citation list, including co-authorship from this thesis:

Noble T.J., Lortie C.J. 2017. Finding a clear signal: a systematic review of desert radio telemetry research. Peerj. In Review. Manuscript ID: 17354. (Chapter 1).

Noble T.J., Lortie C.J., Westphal M., Butterfield H.S. 2017. Shrub sweet shrub: habitat association patterns of the blunt-nosed leopard lizard (*Gambelia sila*) in Carrizo Plain National Monument. Manuscript will be submitted to the *Journal of Animal Ecology*. (Chapter 2).

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Chapter 1

Finding a clear signal: a systematic review of desert radio telemetry research.

Summary

Radio telemetry is a common tool to monitor animals in ecosystems. Radio telemetry, or radio tracking, typically uses a tag or collar with a radio transmitter attached to an animal that is monitored by researchers with a receiver. This technique is used for research in many disciplines such as wildlife ecology or conservation biology. Within desert ecosystems, this approach has been used since the 1960s in different research capacities. Desert species often exist at low density and can range widely within a region due to scarce resources, which can make radio telemetry a useful method to use in these environments. Here, we examined the peer-reviewed literature to assess how radio telemetry is used in deserts, what topics and ecological hypotheses are studied in deserts, and methodological similarities between these types of studies. No review to date has summarized telemetry studies in deserts. This information can help guide designs of future studies by summarizing common practices and identifying knowledge gaps or shortcomings in the literature to date. Using the Web of Science with additional search validation on Google Scholar to formally summarize this research, we found 97 studies that fit our criteria. Most primary studies used radio telemetry to examine individual behavior and/or habitat use. The majority of published studies were done in the United States. The most common classes of animal studied were mammals (29.9 % large mammals and 25.8 % small mammals). Most species studied were classified as ‘least concern’ for risk status. VHF radio telemetry devices predominated the technology selected (80.4 %) whilst GPS devices were used in 19.6 % of studies. Radio telemetry devices are an effective tool to survey individual animals and animal

populations in harsh desert environments. However, only about 10% of studies published the associated dataset. We encourage authors using radio telemetry to publish their data when possible and include details of their study area and tracking methods to allow for better replication and data reuse in answering larger ecological questions.

Introduction

Radio telemetry, frequently termed radio tracking, is a common survey method for animal behavior and wildlife ecology studies (Cochran and Lord 1963, Swanson *et al.* 1976, Sokolov 2011). A wildlife radio telemetry system consists of a radio transmitter or other radio telemetry device attached to an animal and a receiver to pick up the signal of the transmitter (Cochran and Lord 1963, Swanson *et al.* 1976, Brand *et al.* 1975, Brugnoli *et al.* 2008). Most often the device is attached using a collar, but other attachment methods such as harnesses, backpacks, or surgical implantation can also be used (Taylor *et al.* 2004, Schorr *et al.* 2011). The animal can then be located by searching for the specific signal of the transmitter using the receiver. Radio telemetry was original developed in the 1960s using Very High Frequency (VHF) transmitters (Cochran and Lord 1963). These early transmitters had a limited range and were usually large and this limited their use to larger animal species (Cochran and Lord 1963, Kaczensky *et al.* 2010, Sokolov 2011). However, even with these limited capabilities, radio telemetry was a useful tool for studying animals. Once the transmitters were attached, rare or elusive animals could be readily located and individuals of a species could be identified and observed repeatedly (Cochran and Lord 1963, Swanson *et al.* 1976, Brugnoli *et al.* 2008). As technology advanced, transmitter size decreased thereby expanding the range of species that could be studied using this method. Today transmitters are small enough that small mammals, birds, and even insects and other arthropods can be effectively tracked (Brand *et al.* 1975, Sokolov 2011, Kays *et al.* 2015). The range of these systems has also increased to the point that animals can be tracked many kilometers away (Meretsky *et al.* 1992, Brugnoli et *al.* 2008, Sokolov 2011). Species that travel long distances, such as the California condor, can now be tracked throughout their range (Meretsky *et al.* 1992, Kays *et al.* 2015). Some radio telemetry systems can even track collared animals automatically through the use of receiving stations within a region (Johansson *et al.* 2011, Kays *et al.* 2015). Technology aside, this is a rapidly evolving research technology and important for both basic science and conservation (Sokolov 2011, Kays *et al.* 2015, Wilson *et al.* 2015).

Though the basic principle of radio telemetry has remained the same, the technology used continues to evolve and this has introduced other research opportunities. Though VHF transmitters are still used in the field, the development of the Global Positioning System (GPS) now provides relatively more accurate tracking for wildlife researchers but typically is more expensive. GPS tracking allows the radio telemetry device to determine the exact position of an animal (Keating *et al.* 1991, Fuller *et al.* 1995, Kaczensky *et al.* 2010, Sivakumar *et al.* 2010). Many systems allow a position to be taken at regular intervals automatically, and this sampling can be used to measure animal movements (Kaczensky *et al.* 2010, Sivakumar *et al.* 2010). Some GPS transmitters will regularly send data directly to researchers (Keating *et al.* 1991, Rodgers 2001). Other systems require that the data be downloaded either by radio transmission or directly when the unit is recovered (Rodgers 2001, Sivakumar *et al.* 2010). GPS units often combine with VHF transmitters to either allow the recorded data to be downloaded or to aid in finding the unit for recovery (Keating *et al.* 1991). Thus, current studies can use either or both technologies depending on specific research needs and budget (Skupien *et al.* 2016).

Both VHF and GPS radio telemetry systems provide location data, and this coupled methodology is often used in studies to determine animal species range and movement (Brugnoli *et al.* 2008, Kaczensky *et al.* 2010, Sivakumar *et al.* 2010). Both daily and long-term movement can be determined by setting the interval appropriately to estimate home range and habitat use (Meretsky *et al.* 1992 Brugnoli *et al.* 2008, Larroque *et al.* 2015). If multiple individuals are tagged in an area, home range overlap and interactions can also be studied (Brugnoli *et al.* 2008, Schorr *et al.* 2011, Long *et al.* 2014). Species can be tracked to determine their interaction with various aspects of their environment including aspects such as available resources and human development (Dyer *et al.* 2001, Brugnoli *et al.* 2008, Johnson *et al.* 2013). Behavior is another topic commonly studied using this method, including individual repeated behavior and time budgets (Swanson *et al.* 1976, Sokolov 2011, Connor *et al.* 2016). In addition to location, radio telemetry devices can be outfitted with additional sensors to record data such as body temperature, motion, and mortality (Taylor *et al.* 2004, Lee *et al.* 2005, Murray 2006, Sokolov 2011). With different protocols and relocation methods, radio telemetry can be used to examine a wide variety of wildlife ecology questions (Allen *et al.* 2013, DeMay 2015).

Radio telemetry is commonly used in desert ecosystems (Meretsky *et al.* 1992, Krausman *et al.* 2004, Bleich *et al.* 2009, Schorr *et al.* 2011, Oppel *et al.* 2015). Desert ecosystems have a high number of endangered and threatened species (Flather *et al.* 1998, Meretsky *et al.* 1992, Germano *et al.* 2011, Schorr *et al.* 2011). These species are often of concern to land managers who may need information on behavior and habitat use (Sokolov 2011, Connor *et al.* 2016). Because resources are scarce, animal that live in these areas are often present at relatively low densities and can have to travel long distances for water or food which can make radio telemetry the most effect means to study these species (Meretsky *et al.* 1992, Schorr *et al.* 2011). In this systematic review, we examined the peer-reviewed literature to assess how radio telemetry was used in deserts. A summary of the general practices of working in these ecosystems with radio telemetry will be useful to researchers planning similar studies. The following objectives were examined herein for desert radio telemetry studies:

1. To determine the method of use for radio telemetry devices used in deserts.
2. To categorize the types of ecological questions and topics examined using radio telemetry.
3. To summarize the frequency that different desert taxa have been studied with radio telemetry and the frequency of the conservation status of study species.
4. To summarize the variety of protocols and designs used.

By better understanding radio telemetry use in desert ecosystems, researchers and land managers can better determine if radio telemetry fits the needs of their study and assess the radio telemetry options available from the published literature. Understand research gaps may also direct where future research is needed. Scientific synthesis of topics and tools is an important mechanism to both summarize and improve future research, and formal systematic reviews provide an excellent indication of the scope of testing and gaps (Lortie 2014). There have been extensive narrative reviews of radio telemetry research in general but none for deserts and no systematic reviews to date. It is our goal that this study will fill this gap in knowledge and provide a useful summary of the field to date.

Methods

We searched the Web of Science (Thomson Reuters) using the terms ‘radio tracking AND desert’, and ‘radio telemetry AND desert’ in October 2016. This search returned a total of 165 studies. Topics unrelated to ecology were excluded such as medical and atmospheric sciences. These studies were then downloaded in full and reviewed to determine if they were relevant to the objectives of this review. Studies were excluded if they did not include radio telemetry, did not take place in an arid or semi-arid environment, were reviews, or did not examine primary research data. This lead to the exclusion of 68 studies thereby retaining 97 papers remaining for further detailed analyses to address objectives. This process was illustrated with a PRISMA report (Fig 1). TJN performed the search strategy. Each paper was then categorized by a set of higher-order ecological hypotheses, and studies that examined multiple hypotheses were also documented (See Supporting information for a list of study classifications). The study species was extracted including the Latin and common names, taxa, and reported species risk status. The number of species examined within each study was also recorded. Sample sizes, year study was performed, animal life stage, attachment method, radio telemetry device type, study duration, and scale of study were recorded. The country and desert were recorded, and geographical coordinates were noted in papers that included them, and these location data were mapped using R (version 3.3.2) to create an evidence map (McKinnon *et al.* 2015). For studies that did not list coordinates, Google Earth was used to map the location of a study and determine its geographic coordinates. The complete dataset can be found on figshare: <https://figshare.com/articles/radiotelemetry_review_full_details_csv/4725499>. Differences in the relative frequency of the major categories of the data extract were compared using Chi-square tests to determine patterns in the use of radio telemetry for the various potential factors. All analyses and graphing were performed using R (version 3.3.2) using the ggplot2 and chisq.test packages. All R code used is provided on GitHub:

<https://cjlortie.github.io/telemetry.review/>.

Results

A total of 97 studies that had been done in deserts using radio telemetry within the research domains of ecology, conservation, wildlife biology, and environmental studies was retained for this review. The studies were located in desert environments throughout the world; however, there were clusters of studies. The largest proportion of studies was in the United States (36 %, n = 35), Australia (16.5 %, n = 16), and South Africa (7.2 %, n = 7) (Fig 2). The main ecological purpose of these studies was individual behavior and habitat use with 39.2 % and 37.1 % respectively (Fig 3, Chi-square test, $\chi 2 = 82.814$, $p < 0.001$). Slightly over a third of the studies examined only one hypothesis (39.2 %), but the majority examined 2 or 3 (59.8%). Amongst those that studied more than one, behavior (40.7 %), habitat use (28.8 %) and thermoregulation (10.2 %) were the most common secondary ecological question examined. The most common target taxa studied were large and small mammals (small mammals were classified as any mammal under 30 cm in length and less than 10 kgs, while large mammals were classified as any mammal larger than that) (29.9 % and 25.8 % respectively), followed by birds (21.6 %) and reptiles (20.6 %) (Fig 3). Species studied did change slightly through time with mammals and birds making up the earlier studies. A wider variety of taxa made up later studies (post-2010), including mammals, birds, reptiles, and amphibians. Most studies focused on only one species (87.6 %). Most species studied were classified as 'least concern' for risk status by the International Union for Conservation of Nature (IUCN) (70 %, n = 64) followed by species classified as vulnerable (20.6%, n = 20). Endangered and threatened species were also studied in a smaller proportion of studies.

The number of individuals sampled varied among studies. Hypotheses examining demographics and distribution had higher mean sample sizes compared to other study types in the review (One-way ANOVA, F = 3.2941, p <0.01) (Fig 4). Most studies utilized vhf radio telemetry devices (80.4 %, n = 78, Chi-square test, $\chi2 = 35.887$, p > 0.001). GPS devices were used in 19.6 % of studies (n = 19). The GPS devices were used exclusively in studies that examined behavior and habitat use (Fig 5, Chi-square test, $\chi2 = 35.9$, $p = 0.0001$). GPS and VHF devices were used for similar purposes for these types of studies. The majority of GPS studies took place after 2004. Most studies were local in scale, i.e. at the scale of several square kilometers (79.4 %, n = 77). Duration of studies also varied. Studies examining demographics and distribution had a longer average duration.

Discussion

Radio telemetry is a common method used for ecology and wildlife biology studies in most ecosystems globally including desert environments (Bleich *et al.* 2009, Sokolov 2011, O'Mara *et al.* 2014, Oppel *et al.* 2015). The majority of the studies we reviewed examined animal behavior and habitat by using detailed, individual observations. This included both studies that used VHF transmitters as well, as those that used GPS transmitters, indicating that both types can be a relatively precise research instrument in deserts (Swanson *et al.* 1976, Sokolov 2011, Kays *et al.* 2015). The most common classes of animal studied were large and small mammals suggesting that both highly mobile organisms, and those with a more localized range within a desert region can be examined using these technologies and survey techniques. The exact protocol and study design used varied based on the scientific purpose and on studies species. Only around 10% of the studies examined made the associated dataset availably. This summary of desert telemetry studies can help to guide the design of similar studies. Future studies of desert telemetry could be improved by making data open access to increase replication and data reuse to answer ecological questions.

Contemporary radio telemetry technologies can be applied to a wide-range of taxa however our review found mammals to be the primary species studied in deserts (Kays *et al.* 2015). This is a pattern that is common with many types of studies because mammals are often the most prominent species for researchers to study in an environment (Small 2011). This is important to note as animals vary in their sensitivity to environmental change (McKinney 2008) and by instrumenting mostly mammals we are potentially skewing our understanding of how species respond to change or use desert ecosystems (Small 2011). Admittedly, the feasibility of attaching collars to a study species is an important consideration, as attached device cannot exceed a certain percentage of the animal's mass, usually 5-10%, to minimize the effect they have on animal behavior and survival (Cochran and Lord 1963, Kaczensky *et al.* 2010, Sokolov 2011). With advances in radio telemetry technology, devices can now be made smaller allowing them to be used on small mammals, birds, reptiles, and arthropods (Brand *et al.* 1975, Sokolov 2011). Consequently, radio telemetry should be explored as a tool for many taxa in desert ecosystems to better shape our understanding of animal responses to change and to broaden available data for future syntheses including species distribution models (Rice *et al.* 2013) and habitat use estimates (Christ *et al.* 2008).

Radio telemetry is a useful tool for conservation biologists because the behavior and habitat use data needed to make management decisions for species can be collected in effectively designed surveys. Deserts have a high number of threatened and endangered species (Flather *et al.* 1998, Meretsky *et al.* 1992, Germano *et al.* 2011), but the majority of studies reviewed did not focus on species threatened in some way. Radio telemetry can also provide larger-scale pattern data relevant to management and is commonly used to study species of concern in many other ecosystems such as forests and grasslands (Burgess *et al.* 2009, Sokolov 2011, Connor *et al.* 2016). Importantly, the classification of a species as endangered does not guarantee that the study will be best served by the use of radio telemetry because other aspects of the species besides behavior or habitat may need to be studied. Acquiring permits to instrument listed species can also be a challenge in many jurisdictions. Some desert species are also locally threatened rather than globally threatened (Phelan *et al.* 2005). In addition these are species who are not uncommon on a global level, but may have local populations or subspecies which are threatened (Wells *et al.* 2010). The bighorn sheep (*Ovis canadensis*) is a species that lives in the desert, and it is a species of concern in certain areas but classified by the IUCN as 'least concern'

(Bleich *et al.* 2010, Wells *et al.* 2010). Global risk status thus does not necessarily include these locally threatened populations (Wells *et al.* 2010). Radio telemetry is less invasive than many survey methods, such as mark-recapture surveys, but it does involve some handling and the attachment of a device the animal is not accustomed to (Bird *et al.* 2014, Habib *et al.* 2014). This may lead to fewer radio telemetry studies being permitted by land managers (Habib *et al.* 2014). Identifying the most relevant data for conservation of species is an important first step. However in deserts, the relatively low frequency of study of listed species suggests that additional research on a variety of animals would benefit the assessment of general ecosystem-level priorities and impacts.

Sample sizes are a critical issue in many domains of animal research. Often sample sizes in animal-focused studies are relatively lower than other domains of research such as plant ecology for instance (Elzinga et al. 2001). Animal studies present unique challenges because of their mobility, and data at larger scales are often needed. Some animals do have relatively small or restricted distribution patterns with a research region of interest or conservation (Meretsky *et al.* 1992, Krementz *et al.* 2012, Liminana *et al.* 2012), and for desert research, different ecological research topics both assume and sometimes need different levels of sampling and replication. A demographic survey will require a much higher sample size than a relatively more limited study of body temperature because demographic studies by definition will need to get a representative sample of the population (Elzinga *et al.* 2001, Robinson *et al.* 2016). As would be expected there was some variation in sample size of studies examining the same ecological hypothesis. This is likely due to the differences between species and the differences in radio telemetry device required for each species as well as simple variation in study design (Taylor *et al.* 2004, Brugnoli *et al.* 2008, Schorr *et al.* 2011). Additionally the collection of radio telemetry data can be time consuming which can limit the number of animals that can be feasible tracked The commonness of a species, ease of capture, and the cost and/or ease of deployment for the device used also play a part in the extent of animals sampled (Sokolov 2011).

Radio telemetry studies can be a wealth of information for researchers in any environment, however we observed several missed opportunities among the desert radio telemetry studies reviewed. Home range sizes are an example of potential measures available if more data is reported. Home range calculations were reported for many studies, usually calculated using the Minimum Convex Polygon method (MCP), though other methods such as Least Convex Hull or kernel density estimators were used either alone or in combination with MCP. However, several studies did not report home range size where it could have been calculated using the available data. Including these data would also allow for comparisons of home range area between radio telemetry studies of related species and increase the potential that the data from an individual study will be reusable (Schorr *et al.* 2011). Desert animal studies should include estimates of spatial extent of study and estimate total population sizes for the study area whenever possible because the ability to connect different studies would be useful for examining larger conservation issues (Goldingay 2015, Lopez-Lopez 2016). Another missed opportunity is the availability of data from these studies. Only around 10% of the papers reviewed made their data available to other researchers. Publishing data is important because it supports data reuse and makes large scale ecological research possible, a plus for conservation (Campbell *et al.* 2015, Lopez-Lopez 2016). Radio telemetry data can be published on tracking specific databases such as Movebank or Zoatrack, or on more general databases such as figshare (Dwyer *et al.* 2015, Wikelski and Kays 2017). The major benefit of radio telemetry is its ability to provide detailed datasets for wildlife conservation and management (Kays *et al.* 2015). By ensuring that radio telemetry studies are used to their full potential, we can provide land managers and biologist with the information they need to ensure the survival of desert species.

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Figures

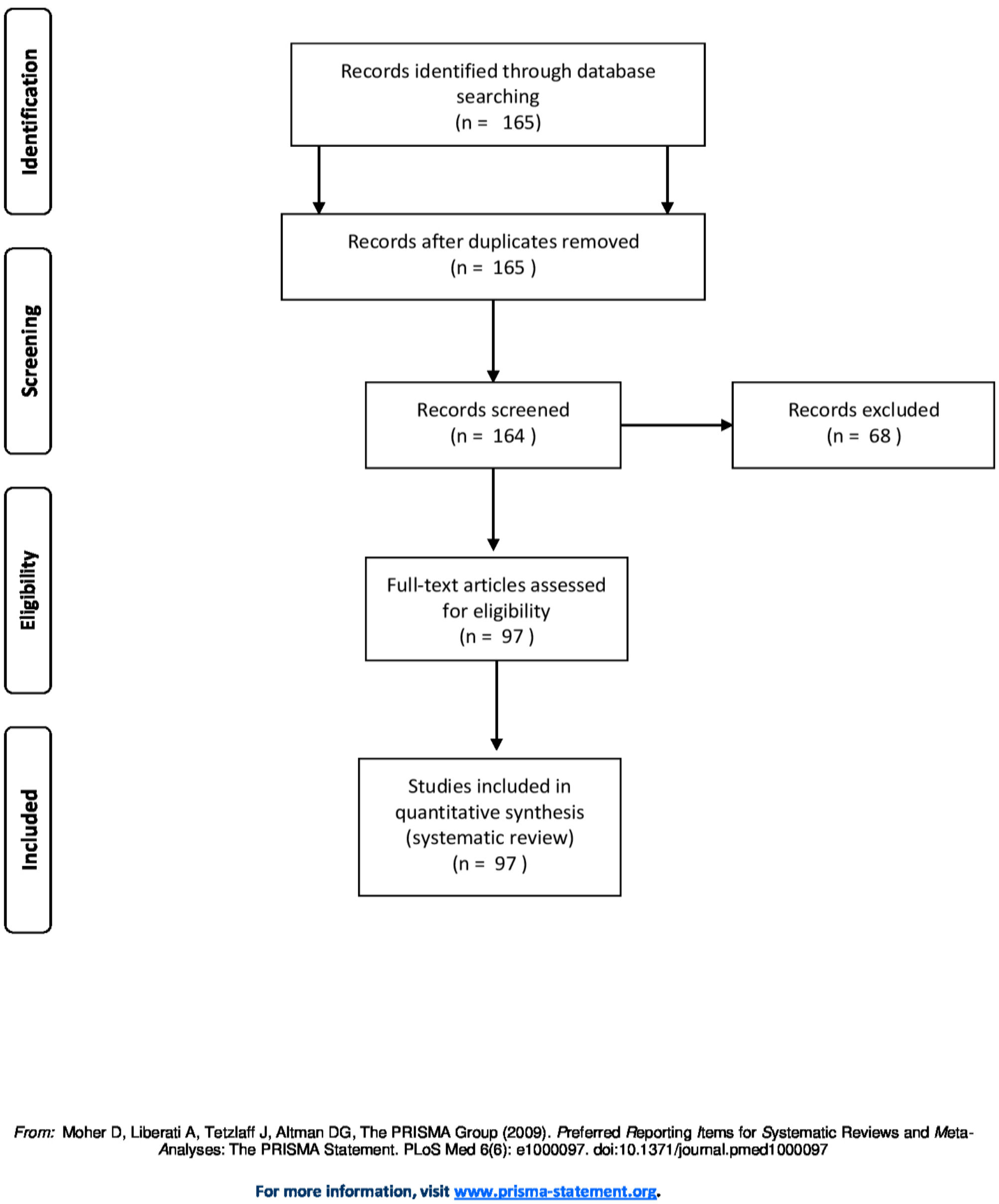

Figure 1: PRISMA Flow Diagram for the identification of studies included in this review.

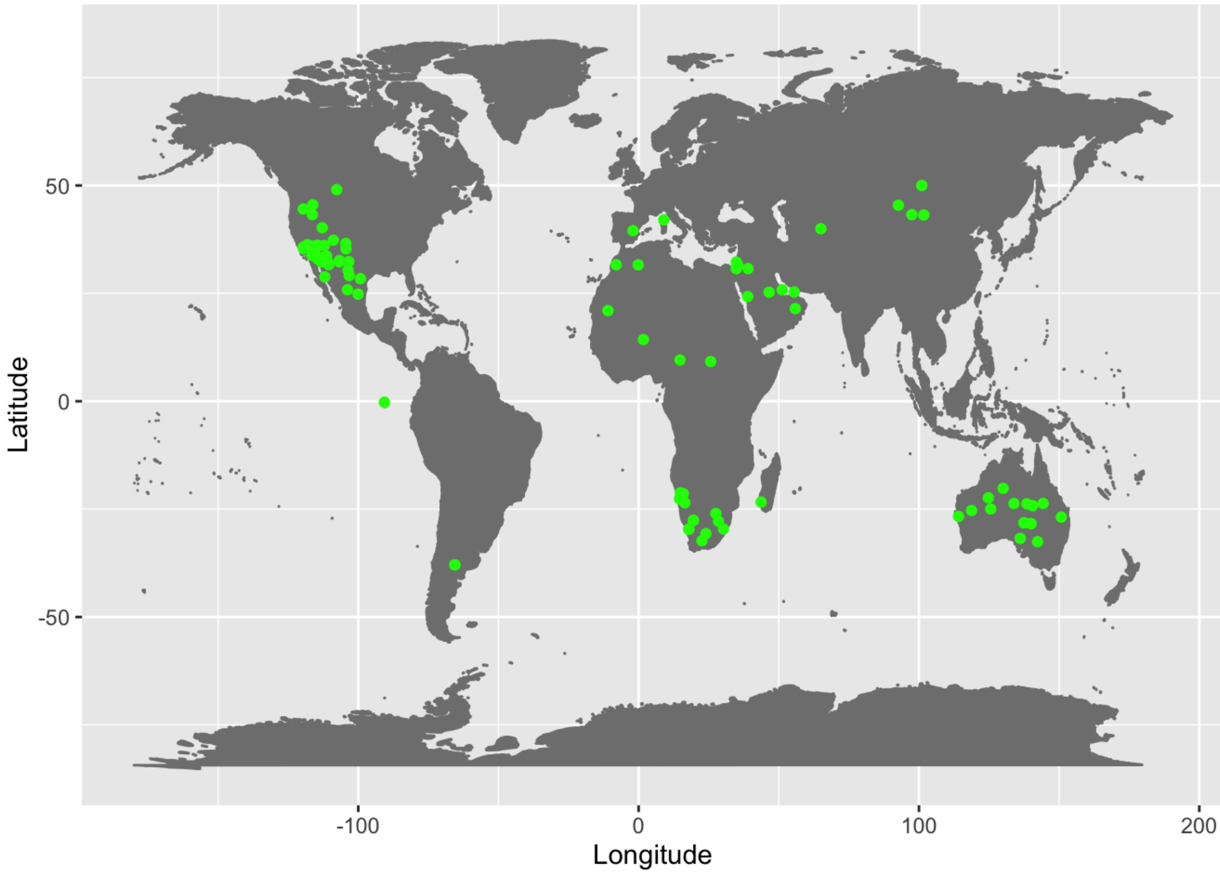

Figure 2: A map of the world showing the global distribution of studies examined in this review. Most studies were in the United States (36 %, n = 35), Australia (16.5 %, n = 16), and South Africa (7.2 %, n = 7).

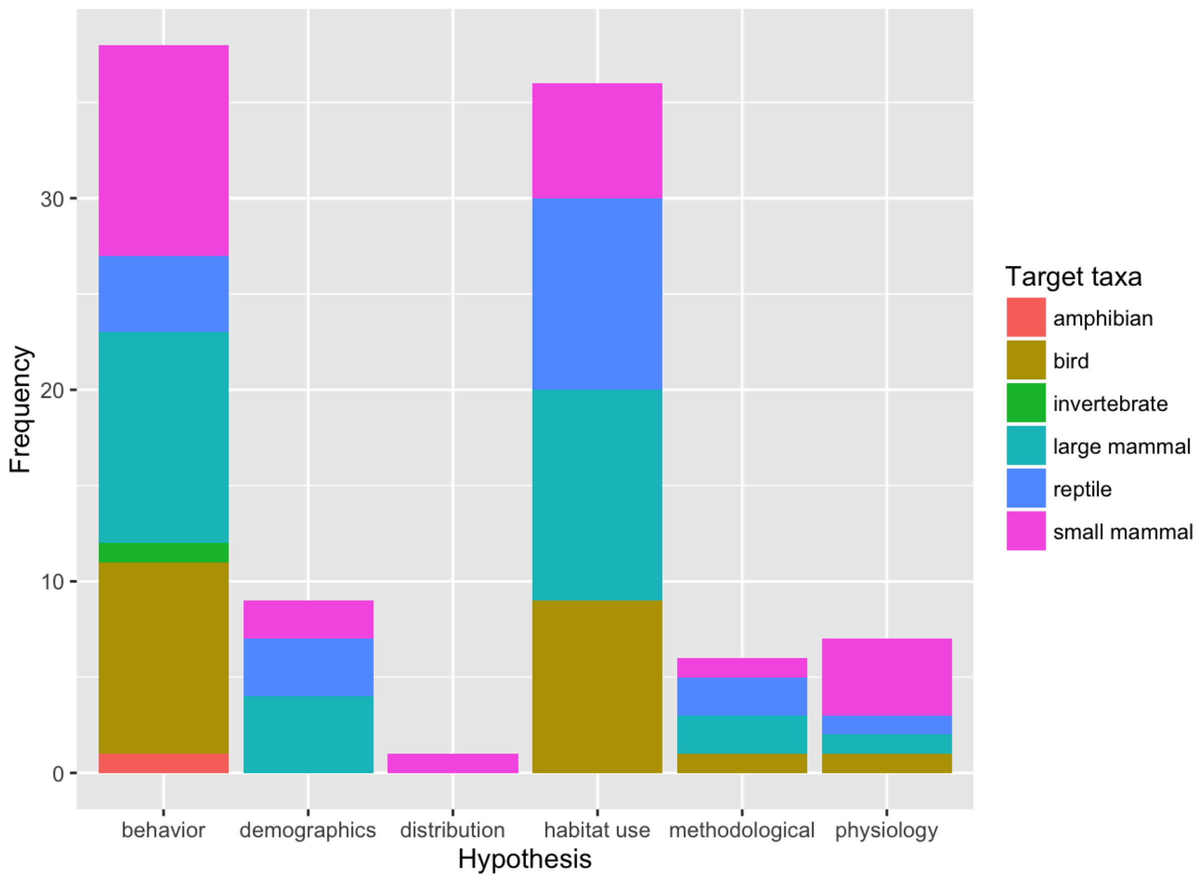

Figure 3: The frequency of the primary ecological purpose examined by each study with the frequency of taxa studied in each. The main ecological purpose of these studies were behavior and habitat use with 39.2 % and 37.1 % respectively. The most common classes of animal studied were large and small mammals (29.9 % and 25.8 % respectively), followed by birds (21.6 %) and reptiles (20.6 %).

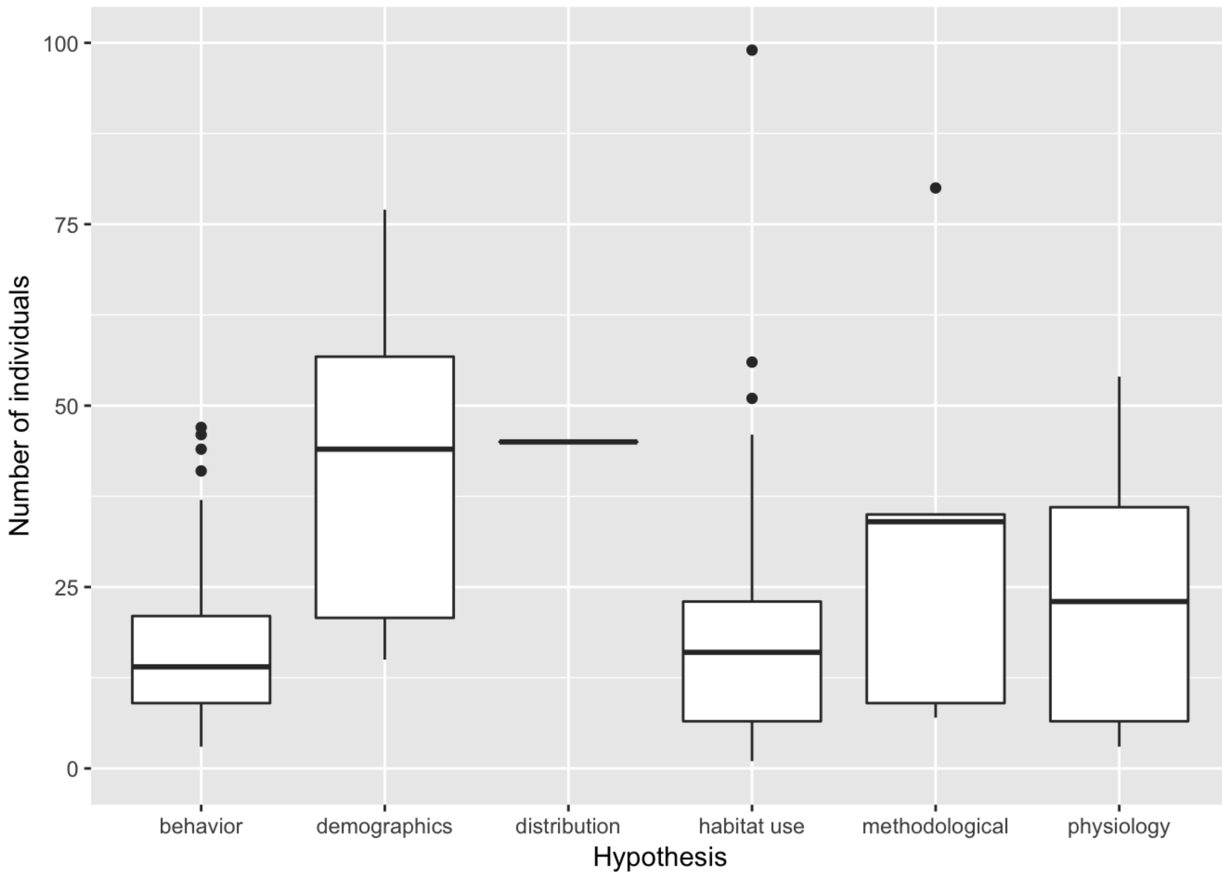

Figure 4: Sample size of studies by ecological purpose examined. Hypotheses examining demographics and distribution had a higher mean sample sizes than studies examining other topics.

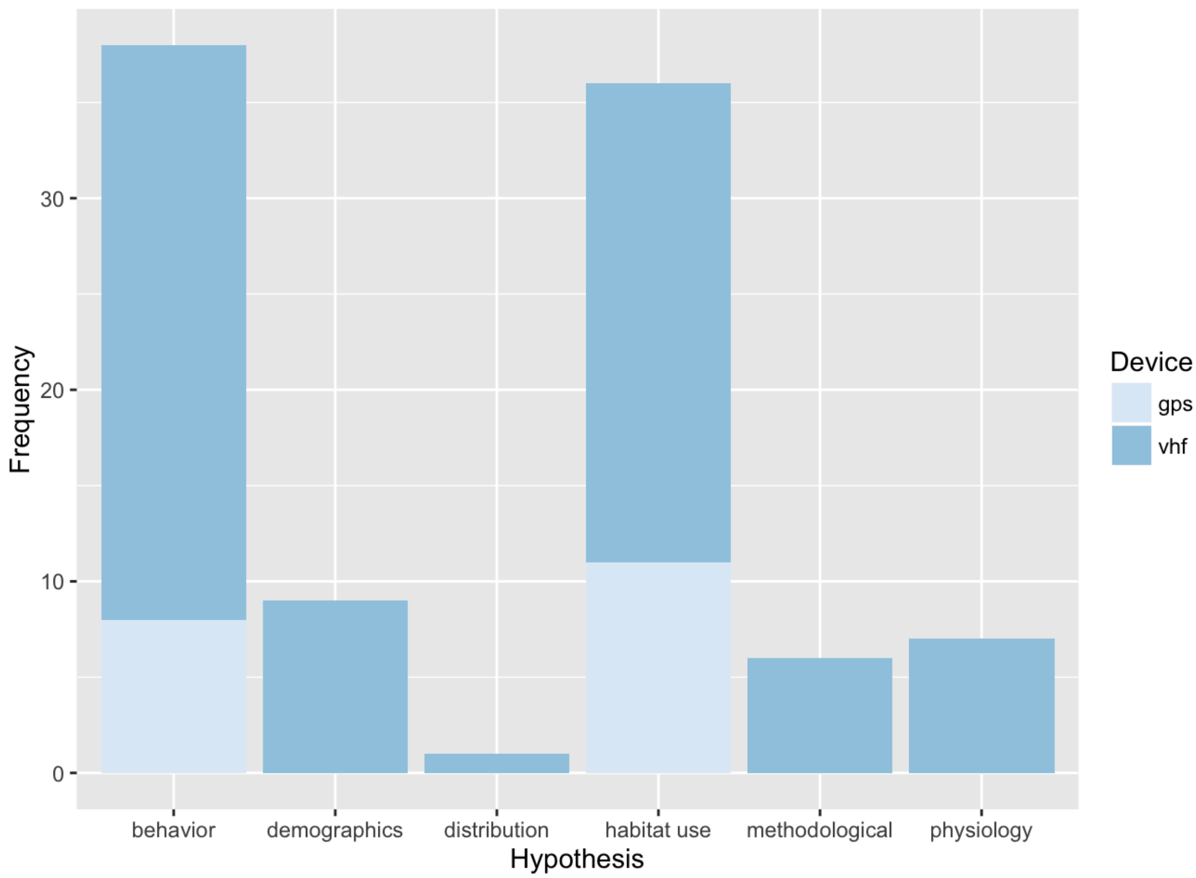

Figure 5: Frequency ecological purpose studied with frequency of radio telemetry device used. Most studies utilized VHF radio telemetry devices (80.4 %). GPS devices were used in 19.6 % of studies (n = 19). The GPS devices were used exclusively in studies that examined behavior and habitat use. Among studies that examined these two topics, GPS and VHF transmitters were used in similar ways.

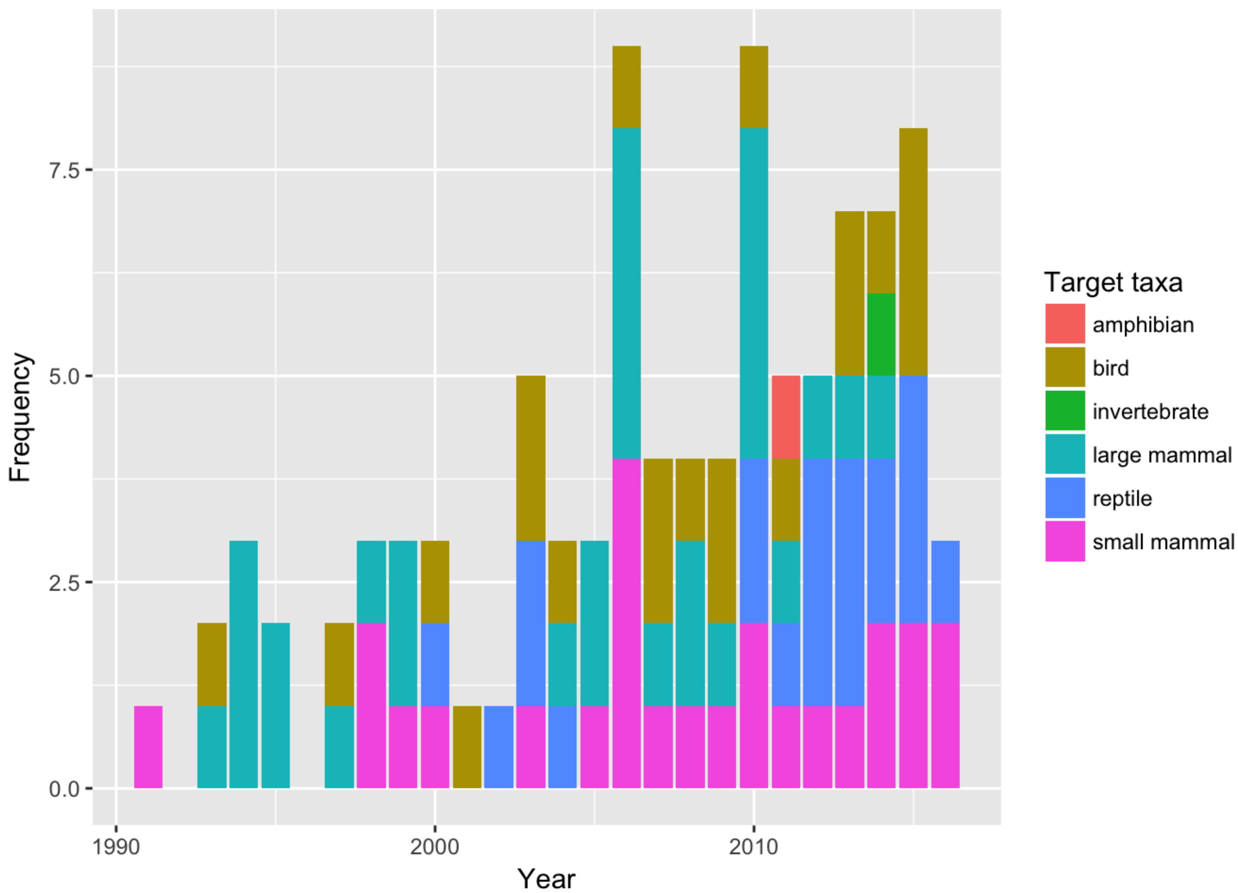

Figure 6: Frequency of telemetry studies conducted by year with frequency of taxa studied in each year. Number of studies conducted in each year increased through time, and a wider variety of taxa was studied in later years.

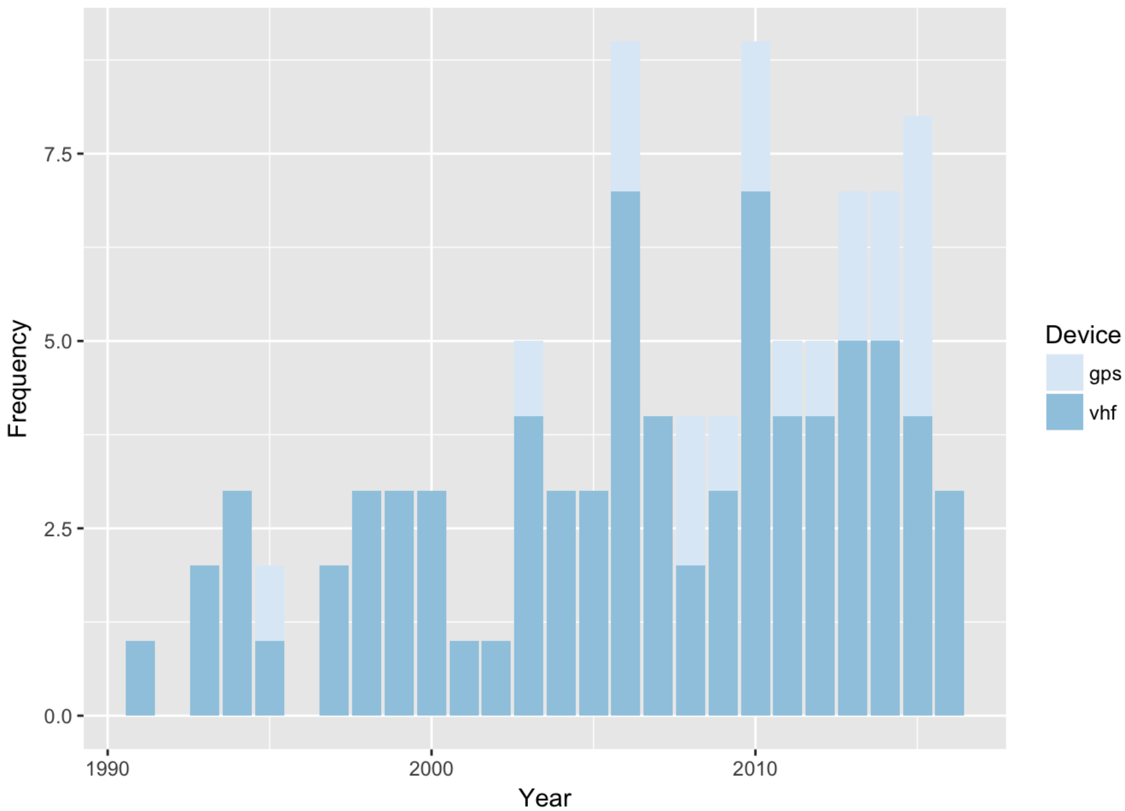

Figure 7: Frequency of telemetry studies conducted by year with frequency of device type used shown. Number of studies conducted per year increased through time with more GPS studies being conducted in later years.

Supporting Information

Table S1: Explanation for the classification system used to categorize ecological hypothesis or topics for this review.

Ecological Hypothesis or Topic	Explanation
Behavior	Any study examing animal behavior or activity, such as time-budgeting.
Demographic	Examination of the dynamics and makeup of an animal population
Distribution	Any study looking at a species distribution across a landscape or habitat.
Habitat Use	Studies that examine how animals are using habitat or what type of habitat they were using.
Methodological	Exploration of new methods or techniques
Physiology	Any study dealing with animal physiology such as body temperature

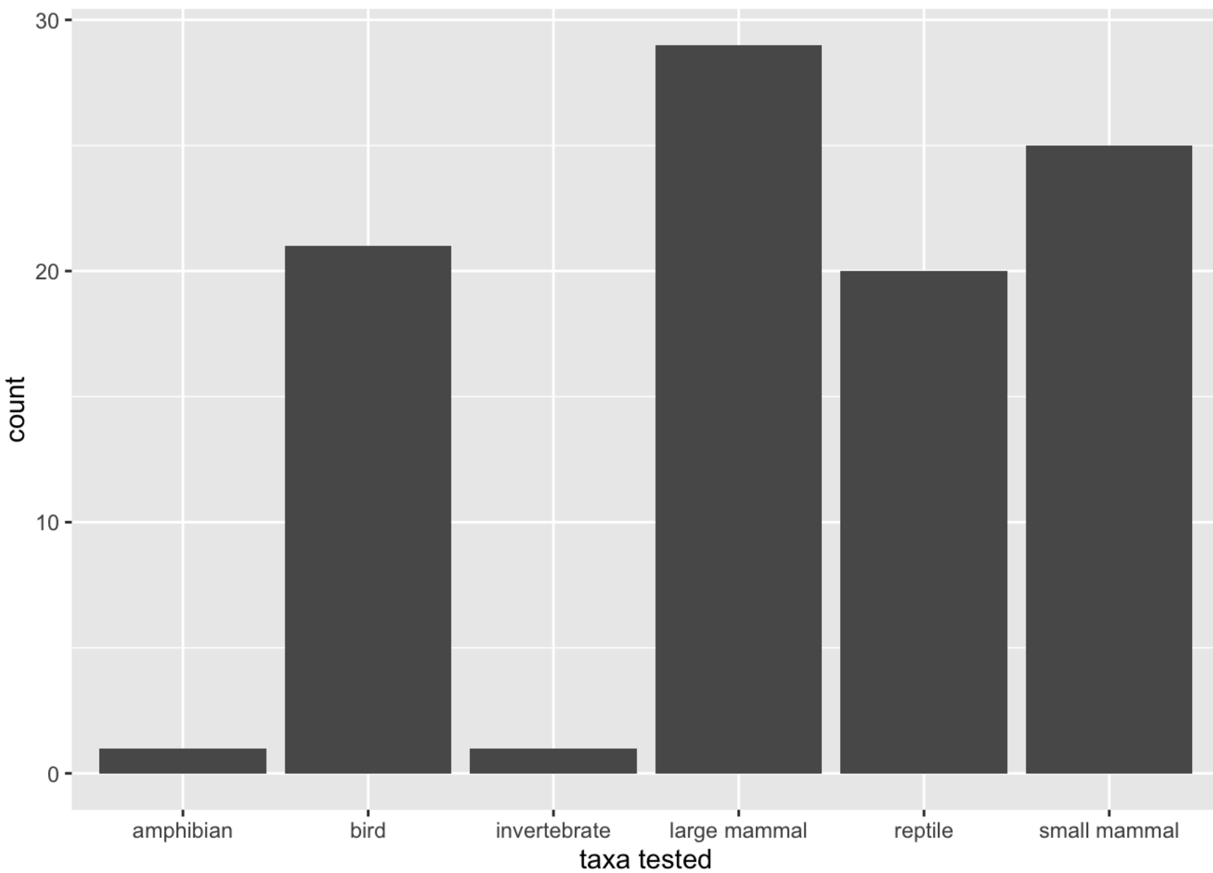

Figure S1: Figure showing the frequency of each type of target taxa for the 97 reviewed studies.

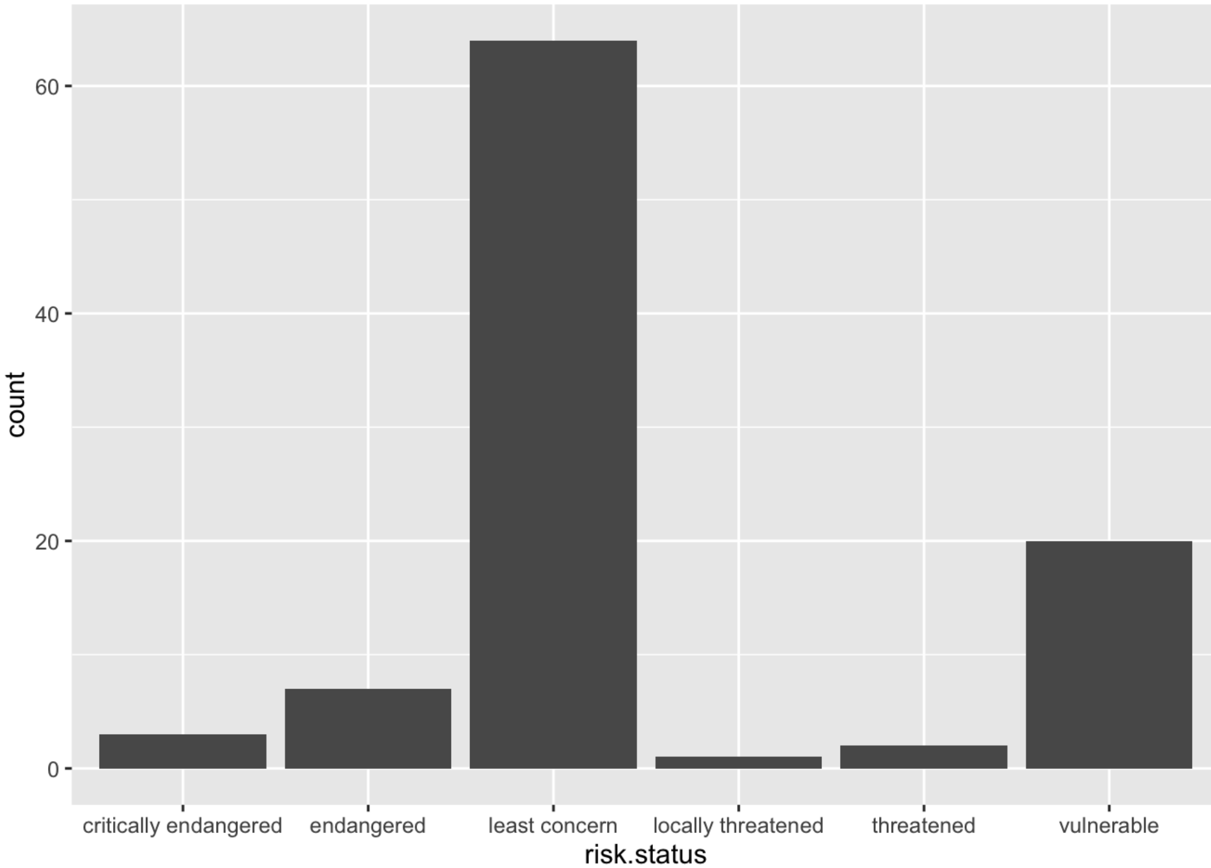

Figure S2: Figure showing the frequency of the assessed IUCN risk status of the target species for the 97 reviewed studies.

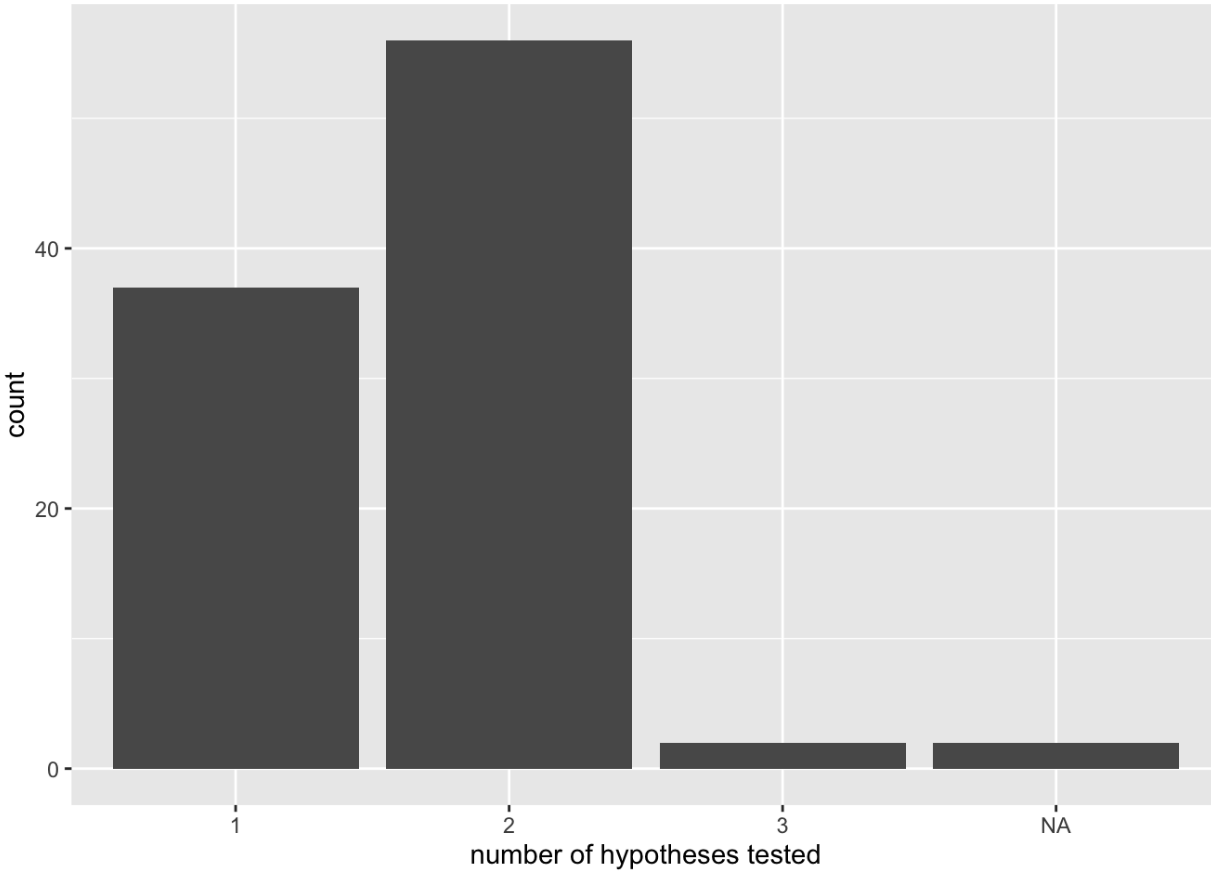

Figure S3: Frequency bar chart of the number of hypothesis examined for the 97 studies.

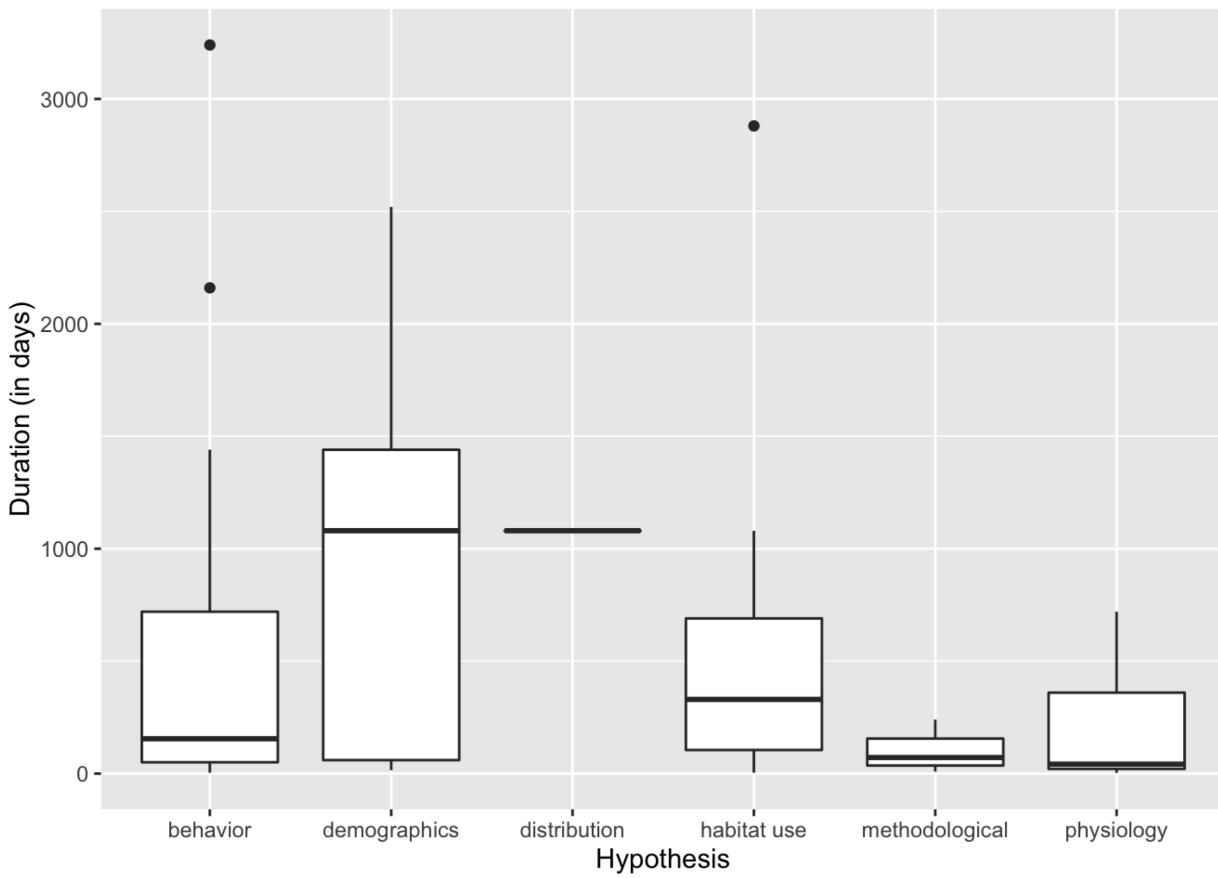

Figure S4: Frequency histogram for the duration of study by the hypothesis tested.

Chapter 2

Shrub sweet shrub: habitat association patterns of the blunt-nosed leopard lizard (*Gambelia sila*) in Carrizo Plain National Monument.

Summary

Animal interactions with dominant or foundation plant species are an important component of many ecosystems including deserts. The blunt-nosed leopard lizard (*Gambelia sila*) is an endangered species found in the San Joaquin Desert of California. This species is found mainly on semi-arid grassland habitat where the dominant plant species are most often shrubs such as mormon tea (*Ephedra californica*). Here, we examine habitat association by *G. sila* to determine whether these lizards are positively influenced by shrubs through facilitation. We compare the use of shrubs relative to other habitat types to examine whether lizards are potentially facilitated by shrubs. We examine potential facilitation through both direct interactions, such as shelter and refuge provided by the shrub, and indirect interactions, such as an increase shelter from burrows dug by small mammals that can be associated with shrubs. We located and observed 31 *G. sila* individuals using radio telemetry, 3 times a day, for 15 consecutive days in summer 2016 at the Carrizo Plain National Monument, California. Observing individuals multiple times a day as opposed to the once daily observation typical in *G. sila* studies allows us to observe and compare locations and behaviors at different times of the day, when environmental conditions and physiological needs can be very different. We found *G. sila* most frequently at burrows compared to other habitat types with 58.4% of observations of lizards occurring at or in a burrow. Shrubs were the second most common habitat type individuals were observed at, with lizards being observed significantly more at shrubs than all habitat types besides burrows.

Thermoregulation and predator avoidance behaviors were observed under shrubs significantly more compared to other habitat types. Shrubs were also used by *G. sila* more frequently in the afternoon, when temperatures are typically at their highest, compared with the morning when temperatures are typically lower. These findings do not necessarily suggest that *G. sila* require shrubs to persist within a region. However, the behavior types observed under shrubs and the daily timing of increased shrub use indicates that the services shrubs provide such as shelter from heat and refuge from predators may directly benefit lizards in many instances. Desert shrubs also positively influence many other species of animals such as small mammals that provide necessary burrow habitats for lizards, suggesting that shrubs indirectly facilitate lizards. This indicates that facilitation of *G. sila* by shrubs is facultative. This association between lizards and shrubs is an important indicator of potential ecological interaction that may be useful for blunt-nosed leopard lizard management.

Introduction

Habitat loss and fragmentation is a pressing issue in desert ecosystems worldwide (Hannah et al. 1995, Hoekstra et al. 2005, Kefi et al. 2007, Germano et al 2011). Desert habitat is increasingly being developed for industry, agriculture and urban development (Hoekstra et al. 2005, Germano et al 2011). Climate change further increases the risk to desert environments and species where in many places environmental conditions are predicted to become more extreme with higher temperatures and less rain. This will likely increase the environmental stress on many species (Mouat et al. 2008, Bachelet et al. 2016, Westphal et al. 2016). One at-risk desert is the San Joaquin Desert (Germano et al. 2011). The San Joaquin Desert supports one of the highest concentrations of threatened and endangered species in the continental United States, including species such as the San Joaquin kit fox (*Vulpes macrotis mutica*), giant kangaroo rat (*Dipodomys ingens*), and blunt-nosed leopard lizard (*Gambelia sila*) (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). Most of the remaining natural habitat is small and 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). In addition, increased drought is predicted for this part of California, further increasing stress on the species that live here (Cook et al. 2004, Griffin et al. 2014, Bachelet et al. 2016). One habitat feature that can help species survive harsh environmental conditions is shrubs. Shrubs are a foundation species in deserts as they are the dominant vegetation form and have a strong influence on the community structure due to the habitat they provide. Shrubs can provide facilitative, or positive effects to other species by providing benefits such as shelter and refuge

(Filazzola et al. 2014, Lortie et al. 2015, Filazzola et al. 2017). In addition to direct benefits such as shelter and refuge, shrubs can also provide benefits to other species indirectly by facilitating beneficial intermediate species. These intermediate species can include insects, which can provide additional food, annual plants, which can provide additional shelter or food, or small mammals, which can provide additional shelter through the creation of burrows (Filazzola et al. 2014, Lortie et al. 2015). Ecological facilitation is rapidly becoming embedded in many ecological theories, and it is also relevant for conservationists because animal taxa are also likely influenced by positive and negative interactions with plants at relatively fine scales (Bruno et al. 2003, McIntire et al. 2014, Bulleri et al. 2016). With many desert species experiencing increasing environmental stress in desert ecosystems due to climate change, the role of shrubs as foundation species may increase in importance. Because of this, there is a need to know to what extent and how species use shrubs as shelter and refuge and what interaction pathways are influencing behavior and habitat use the most. Understanding how shrub-animal interactions are occurring in deserts may allow land managers to apply facilitative shrub benefits as a part of the restoration plan for threatened and endangered desert species.

Many studies have examined the positive effect of shrubs on other plants (Filazzola et al. 2014,) and on small mammals (Hansen et al. 1994, Fields et al. 1999, Prugh et al. 2011, Lortie et al. 2015) but fewer studies have focused on reptiles, such as the blunt-nosed leopard lizard (*Gambelia sila*). *G. sila* is a federally listed endangered species found mainly in semi-arid grassland habitat within the San Joaquin Desert of California (USFWS 1998, Warrick et al. 1998, Germano et al. 2016). Though *G. sila* can also be found in areas without shrubs, when shrubs are present, lizard activity will often be concentrated around the shrubs (Warrick et al. 1998, Germano et al. 2016). It is likely that benefits from shrubs extend to *G. sila* as well, as lizards are sensitive to temperature (Germano et al. 2016), use burrows from small mammals (Prugh et al. 2011), and consume invertebrates that can be concentrated near desert shrubs (Ruttan et al. 2016). Thus there is an opportunity to test whether shrubs act as a foundation species and what facilitative benefits they provide to *G. sila*.

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. We using radio telemetry to survey lizards, which allowed for repeat observation of multiple individuals at a high survey intensity of 3 times a day. We recorded the frequency of observation of *G. sila* at different habitat types with an emphasis on shrub versus open habitat, but also included a brief behavior observation in each instance. The inclusion of a behavior observation with habitat type is important as the two are closely linked and have not been studied in great detail. Though other studies have found lizards to associate with shrubs, none have examined how lizards interact with shrubs, if shrubs are in fact facilitating lizards, and if so, what facilitative benefits draw lizards to shrubs. We tested the hypothesis that shrubs facilitate *G. sila* by providing habitat associated with their specific behavioral and physiological needs. The following predictions were tested in this specific desert ecosystem: (i) lizards are found more frequently under shrubs in the afternoon for thermoregulation compared to shrub observations in the morning (shelter function), (ii) behaviors linked to predator avoidance, such as hiding in shrubs and running to shrubs when predators are present, are more frequent under shrubs compared to open area (refuge function), (iii) lizard hunting behaviors, such as stalking and observation of insects, are less frequent under shrubs because shrubs typically facilitate annual plants and the resulting dense vegetation can interfere with lizard movement and visibility. The final prediction is important because one habitat type is likely not ideal for all behavioral needs of a species. The multiple direct and indirect interactions between lizards and shrubs means that there may be some negative interactions within a net positive effect, such as the negative impact of increased annual growth around shrubs on hunting by lizards despite the overall benefit of shelter shrubs provides. It is our goal that this information on shrub facilitation can be useful when managing habitat for the conservation of *G. sila*.

Methods

Study site

We conducted our telemetry study along Elkhorn Plain within Carrizo Plain National Monument (San Luis Obispo County, California, USA, 35.1914° N, 119.7929° W). The Monument is the largest remaining patch of San Joaquin Desert ecosystem in California and supports many endangered and threatened species such as the San Joaquin kit fox (*Vulpes macrotis mutica*), giant kangaroo rat (*Dipodomys ingens*), and blunt-nosed leopard lizard (*Gambelia sila*) (USFWS 1998, Germano et al 2011). Because of this it is the largest remaining piece of blunt-nosed leopard lizard habitat and likely supports the largest population of these lizards (USFWS 1998, 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 the following species: *Bromus madritensis, Erodium cicutarium*, and *Hordeum murinum* (Schiffman 1994, Gurney et al. 2015). The dominant shrubs are mormon tea (*Ephedra californica*) and saltbrush (*Atriplex polycarpa*) (Stout et al. 2013). Ephedra was the dominant shrub at the study site with only a few saltbrush found in the immediate area. *G. sila* had been found in the area during surveys by our research team in previous years as well as being documented by previous studies in the area (German et al. 2007).

Study species

The blunt-nosed leopard lizard 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). This species is a relatively large species of lizard 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). They are diurnal and mainly insectivorous though they may eat smaller lizard species such as side blotch lizards (*Uta stansburiana elegans*) on occasion (Warrick et al. 1998, Germano et al. 2007, Germano et al. 2016). Blunt-nosed leopard lizards are also prey for many species including snakes, bird of prey and coyotes (Germano et al. 1992, USFWS 1998, Germano et al. 2005). Though leopard lizards can bury themselves and will occasionally dig primitive burrows, they mostly utilize abandoned burrows of other animals and have been found to be closely associated with burrowing mammals such as kangaroo rats (Fields et al. 1994, Grillet et al. 2010, Prugh et al. 2011). Blunt-nosed leopard lizards 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). Lizards 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). When leopard lizards first emerge in the spring, they are tan or light brown colored with dark spots and lighter bands on their backs, but during the breeding season (late April-June), females develop bright red or orange spots or blotches on their sides while the sides of males will turn salmon or pink (Medica et al. 1973, Germano and Williams 2007).

Experimental design

The study area was visually surveyed for lizards to capture on May 19th, June 2nd, and June 17th, 2016. Surveys were done by walking the area in a back and forth grid pattern. This was supplemented with vehicle surveys done by slowly driving the 2 km section of road that ran through the site. When a lizard was spotted, it was captured using a pole and noose made of either dental floss or surgical thread. In total, 31 lizards were captured for this study. The sex of each lizard was determined, and its snout to vent length (SVL) and mass were measured. Lizards 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. Lizards were kept overnight to ensure the collar was fitted correctly and did not irritate or harm the animal, and they 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.

Following release of the final captured lizards on June 18th, 2016, all lizards were relocated (i.e. repeatedly sighted using telemetry) several times between June 18th and June 20th 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. The lizards were then formally surveyed for 15 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. This survey was conducted before 7:30 AM or after 7:30 PM on each day.

Lizards were located 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). In addition, date and time, meso and microhabitat, and behavior were recorded for each observation. Mesohabitat was categorized as a determination of whether a lizard was within 0.5 meters of a shrub (shrub) or not (open). Microhabitat was recorded as the habitat where the lizard was observed at an even finer spatial scale (burrow, annuals, road, in shrub, bare patch, or 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. During the course of the survey, a few collared individuals were depredated or the signal from their radio was lost. These collars were recovered if possible. Lizards were recaptured between July 11th and July 18th at the end of the survey and collars were removed.

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). Behavior observed was analyzed with a multinomial logistic regression using the nnet package which accounts for the multiple levels of nominal outcomes of the behavior observations (Venables et al. 2002). All locations of collared individuals were mapped using the leaflet package (Graul 2016). Home range size was calculated using a 95% Minimum Convex Polygon (MCP) estimation (Mohr 1947) using the adehabitatHR package (Calenge 2006). All R code used for this project can be found at <https://cjlortie.github.io/Carrizo.telemetry/>.

Results

A total of 31 lizards was tracked, comprising 14 females, 15 males, and 2 lizards of undetermined sex. The lizards of unknown sex were likely younger individuals without fully developed sex characteristics. Home range sizes were calculated for 28 of the lizards. Of the 3 lizards where home range was not calculated, two were found dead in the first few days of the study and the other had a malfunctioning collar, and the signal was lost. The mean home range size was 10790 m^2. Home range size varied from 0.5 m^2 (this was an individual that had gone dormant for the summer and did not move or emerge from its burrow during the study) to 38600 m^2. The total area occupied was 1.7145 km^2 based on relocation data from all collared individuals. As we sampled during only a portion of the time that lizards are active during the year (15 days) this is likely an underestimate of home range sizes for this species.

The frequency of lizard observation differed significantly between mesohabitat types (Table 1, $p < 0.01$). Lizards were observed more frequently at open mesohabitat (73.7 % of observations) than at shrub mesohabitat (26.3%). Frequency of observation between different times of day was also significantly different for mesohabitat (Table 1, $p < 0.01$). Observations of lizards at open mesohabitat did not differ between different times of day, however, observations at shrub mesohabitat did differ significantly between morning and afternoon. Lizards were found more frequently at shrubs in the afternoon than in the morning (Table 1, $p = 0.0252$). 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 (58.4% of observations, Table 2, $p < 0.0001$). The frequency of observations at shrub microhabitat was also significantly greater than any other microhabitat types besides burrows

(15.9% of observations, Table 2, $p < 0.0001$). Lizards were observed at shrubs more frequently than annuals, bare patches, washes, and roads. Observation frequency also differed significantly between different times for microhabitat (Table 2, $p < 0.0001$). Lizard observations at shrub microhabitat differed between morning and afternoon, with more shrub observations occurring in the afternoon (Table S2, $p = 0.0003$).

Behavior observations differed significantly between habitat types (Table 3, $p < 0.0001$). Lizards were observed cooling or thermoregulating under shrubs significantly more than other habitat types (Table 3, $p <0.0001$). Lizards were also observed avoiding predators under shrubs more frequently than other habitat types (Table 3, $p < 0.0001$). The predators lizards were observed avoiding in this study were all aerial predators (either ravens or raptor species). Other types of behavior such as running, hunting, or active observation by lizards did not differ significantly between habitat types. Observed behavior also differed significantly between different times of day with some behaviors being observed more frequently at certain times of day (Table 3, $p < 0.001$). Lizards were more frequently observed sunning in the morning in both mesohabitat types compared to the afternoon (Table 3, $p < 0.001$).

Discussion

Shrubs are a 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). Although shrubs were not the habitat that was used most frequently by lizards, the timing of increased observations at shrubs in the afternoon and the types of behaviors that were observed significantly more at shrubs suggest that that shrubs do facilitate lizards. This observation pattern supports the general hypothesis that shrubs provide facilitative benefits for animals in deserts. Lizards were located more frequently under shrubs in the afternoon compared to the morning. This is likely due to lizards seeking out the shade that shrubs provide during the hottest part of the day for thermoregulation purposes, supporting the role of shrubs as a source of shelter (Kerr et al. 2004, Pugnaire 2010). Shrubs are well documented as a source of refuge for many prey animals and this likely extends to lizards (Anderson et al. 2010, Filazzola et al. 2017). Predator avoidance behaviors, such as hiding in shrubs when predators were nearby and moving to shrubs when threatened, were more frequently observed under shrubs. Avian predators, such as ravens and hawks flying overhead were the predator that the lizard were observed reacting to. The lizard would usually look up upon the approach of the bird and then quickly move towards shelter. Observations of lizard hunting behaviors were not significantly different between habitat types. This may be due to the opportunistic nature of leopard lizard hunting behavior. Lizards will hunt prey when and where it is present, rather than seeking out a specific habitat for hunting (Pietruszka et al. 1981, Germano et al. 2007). Hunting near shrubs may also not have a large impact on hunting success. Despite the indication that shrubs are important for thermoregulation and predator avoidance, these are only the benefits provided through direct interactions. Shrubs likely provide other benefits to lizards through indirect interactions due to their 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). Lizards were observed in burrows more frequently than in any other type of habitat and these burrows are most often created by other animal species. The benefits to burrowing mammals shrubs provide and the resulting increased burrow density under shrubs likely translate to benefits for lizards (Prugh et al. 2011, Filazzola et al. 2017). The frequency of observation in the open suggest that *G. sila* populations do not require shrubs to persist within a region. However the ways that lizards use shrubs indicates that shrub presence likely has a positive effect on lizard populations due to the benefits lizard receive through direct and indirect shrub interactions.

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 (Schneider 2001, Chave 2013). We did not sample on a continuum that varied to this extent but did examine mesohabitat versus microhabitat scales relevant to a desert lizard. We found close correspondence between the two scales tested with lizards being found most frequently at a certain habitat types. Burrows were one habitat type that lizards were observed at frequently. Burrows are important habitat features for this species providing shelter against environmental conditions and a refuge from predators (Grillet et al. 2010, Germano et al. 2016, Prugh et al. 2011). Both leopard lizards as well as other desert creatures tend to be closely associated with burrows (Hansen et al. 1994, Milne and Bull et al. 2000, Grillet et al. 2010, Prugh et al. 2011). Lizards will return to a burrow every night and spend late July through March dormant underground (USFWS 1998, Warrick et al. 1998, Germano et al. 2016).

Direct facilitation by shrubs was also detected at both scales because shrubs were used significantly more than all remaining mesohabitat and microhabitat categories. Shrubs 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). Shelter against temperature changes is particularly important for poikilotherms such as reptiles, which must maintain body temperature through behavior (Huey 1974, Díaz and Cabezas-Díaz 2004, Kerr et al. 2004). The refuge against predators shrubs provide, including 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 demonstrate the importance of having some form of shelter and/or refuge accessible for lizards (Huey 1974, Díaz and Cabezas-Díaz 2004, Anderson et al. 2010). The advantage of having a quick escape from predators and easy access to shade may cause lizards to concentrate in areas where cover is available, whether this is in the form of burrows alone or in combination with shrubs as with this study site (Germano et al. 2016). In addition to directly facilitating lizards, shrubs facilitate many animal species including kangaroo rats and other burrowing mammals (Hansen et al. 1994, Fields et al. 1999, Prugh et al. 2011). An increased number of burrows is often found under shrubs compared to open habitat (Filazzola et al. 2017). Lizards have been associated with animals whose burrows they utilize, such as kangaroo rats, so the benefits shrubs provided to burrowing mammals likely extends to lizards (Fields et al. 1994, Grillet et al. 2010, Prugh et al. 2011). Because of this, indirect facilitation of lizard by shrubs through the intermediate species of kangaroo rats and other burrowing mammals is likely. These findings suggest that shrubs are foundation species for animals in deserts both because of direct benefits they provided, as well as the influences shrubs have on the microhabitat through their effects on annual plants and other animal species (Filazzola et al. 2014, Lortie et al. 2015).

Animal behavior patterns are an important indication of shrub facilitation because plant and animal interaction can provide a wide variety of functions for animals (Lortie et al. 2015). Different behavior types can indicate that an animal is using a shrub for a different purpose, for example hunting near a shrub could indicate that an animal is using the shrubs for the food resources associated with it, while cooling itself in the shade could indicate that the animal is using the shrub as a source of shelter from environmental conditions. Observations of behavior supported the specific use of shrubs as shelter and refuge. Shrubs are the largest sources of shade on the landscape, and it is thus likely that lizards will seek out shrubs in order to cool down when necessary. This supports the potential role that shrubs can play in providing a thermoregulation function or shelter for other taxa (Kerr et al. 2004, Filazzola et al. 2017). Furthermore, shrubs were used more often in the afternoon when temperature is typically at its hottest and the need for thermoregulation greatest suggesting that shrubs are an important source of shelter from environmental conditions. Similarly, behavior observations support shrubs as a source of refuge because lizards sought out shrubs when predators (in this study mainly avian predators) were present (Lortie et al. 2015). Other behavior types where lizards were expected to select against shrub for open habitat did not show a significant difference. For example lizards were expected to be observed sunning more in open habitat types but did not show a difference between shrub and open habitat. Having a shrub nearby for a quick escape may outweigh any negative effect it has on the efficiency of a behavior (Huey 1974, Díaz and Cabezas-Díaz 2004, Anderson et al. 2010). Other behaviors may be determined on a more opportunistic basis rather than by habitat type, such as hunting. Lizards are opportunistic hunters, so they may attempt to capture any insect, regardless of where they come across it, rather than seeking out open areas to hunt (Pietruszka et al. 1981, Germano et al. 2007). Shrubs do not appear to have an impact on hunting success, provide additional hunting opportunities or provided preferred prey. Overall, shrubs likely provide facilitative benefits to lizards, and though these functions can be provided by other habitat features, shrubs may potentially act as a foundational species for lizards (Warrick et al. 1998, Prugh et al. 2011, Germano et al. 2016).

Management Implications

Although lizards can survive in areas without shrubs, their close association with shrubs when possible indicates that positive interactions between shrub and lizards are likely important to lizards (Warrick et al. 1998, Lortie et al. 2015, Filazzola et al. 2017). 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 poikilotherms such as lizards (Huey 1974, Díaz and Cabezas-Díaz 2004, Kerr et al. 2004). With climate change predicted to have a high impact on this area, 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 burrow density (Prugh et al. 2011). This would provide additional benefits to lizards due to the increased shelter and refuge available (Steffen et al. 2006, Filazzola et al. 2017). Because of this shrubs should be taken into account as part of blunt-nosed leopard lizards species recovery efforts whether shrubs are present or shrub restoration and/or addition is being considered for the site (Filazzola et al. 2017). These findings are likely applicable to other lizard species and small animals that face similar environmental conditions. By including shrubs as an aspect of the blunt-nosed leopard lizard recovery plan, land managers can help to ensure quality habitat is available for leopard lizards and ensure their survival into the future.

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Tables

Table 1: Generalized linear model for mesohabitat, with degrees of freedom, deviance, and p-values.

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 Mode					
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

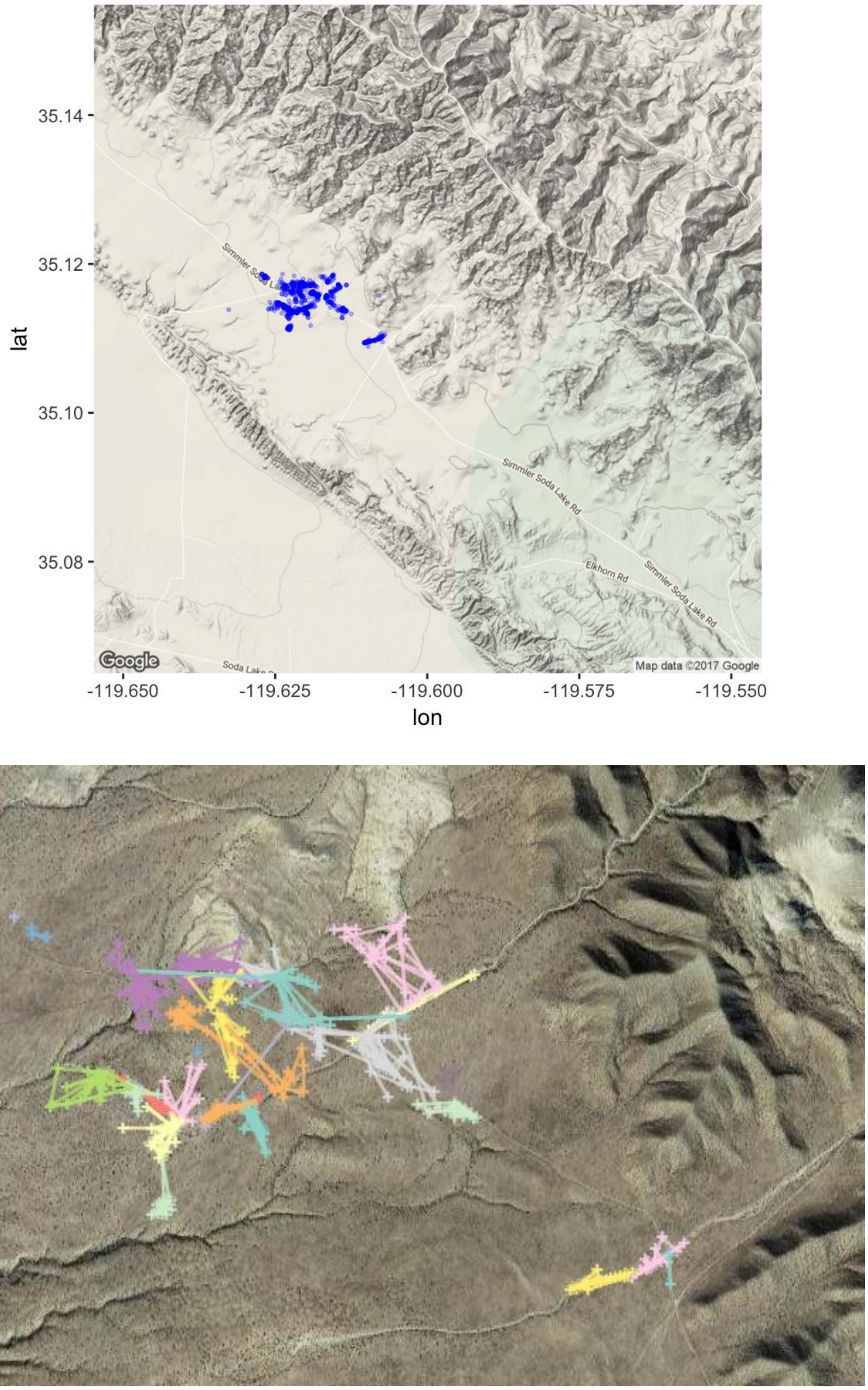

Figure 8: Map showing observed location and movement of all lizard observations at the study site. The first map groups all observations, the second shows individual lizards by color.

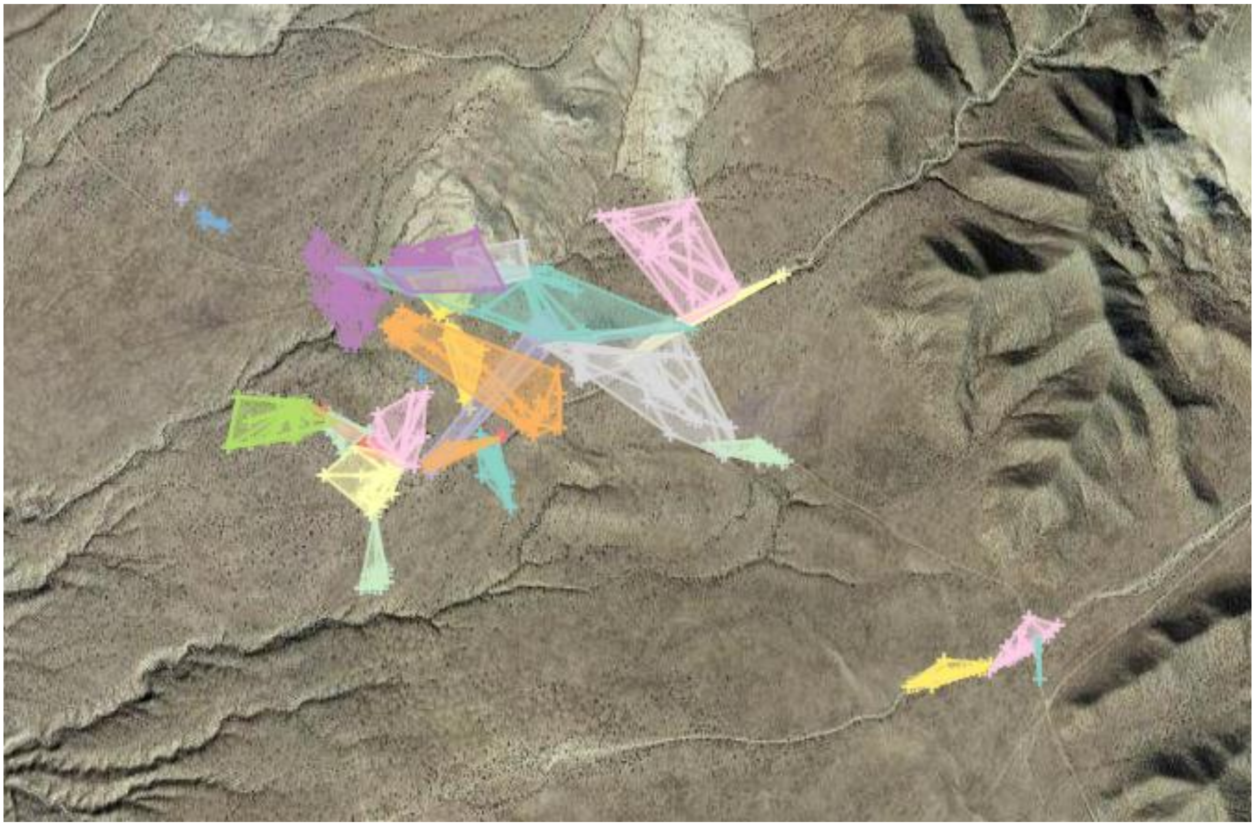

Figure 9: Map showing home range, calculated using a 95% minimum convex polygon estimate, for each individual. The mean home range size was 10790 m^2. Different individuals are indicated by different colors.

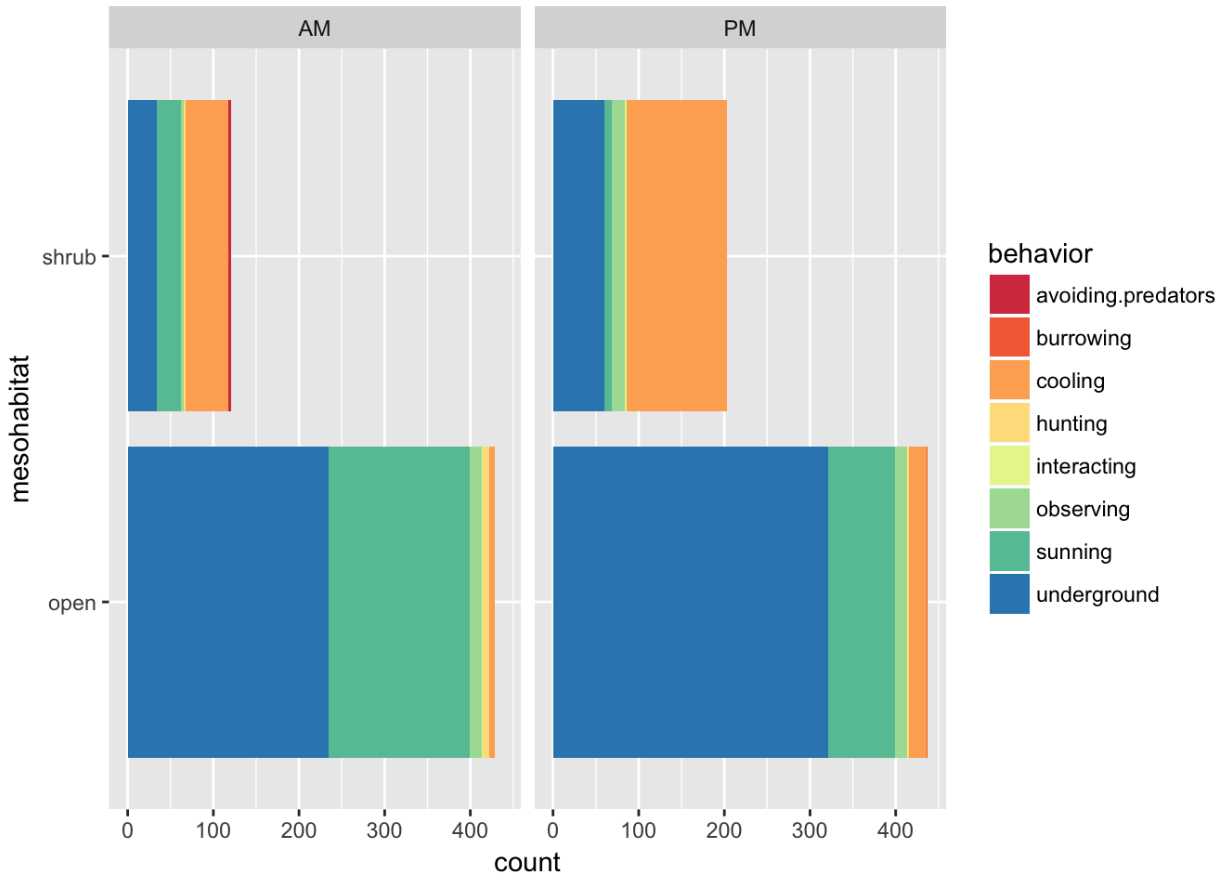

Figure 10: Graph showing the frequency of observation by mesohabitat type and time (AM or PM). Behavior observed is also indicated by color.

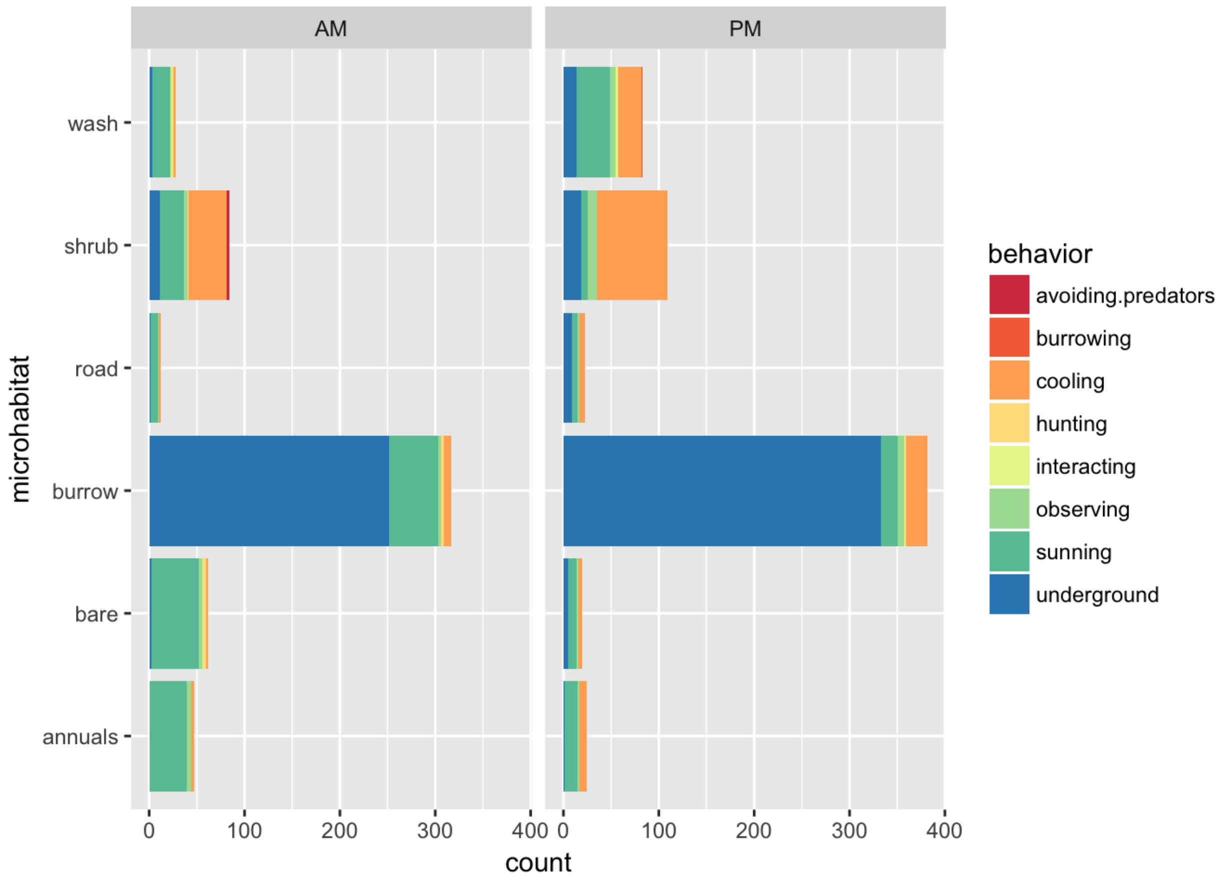

Figure 11: Graph showing the frequency of observation by microhabitat type and time (AM or PM). Behavior observed is also indicated by color.

Supporting Information

Table S2: 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 S3: 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

Summary and Conclusions

For this study, we examined habitat use of blunt-nosed leopard lizard in Carrizo Plain National Monument, the largest remaining area of San Joaquin desert habitat (Germano *et al.* 2011). First we explored the literature to determine how telemetry is used in desert ecosystem studies of animals (Chapter 1). We then examined lizard habitat use with a focus on the lizards' use of shrubs, specifically mormon tea (*Ephedra californica*), the dominant shrub found at our study site (Stout *et al.* 2013) (chapter 2). We found that radio telemetry was most commonly used to study behavior and habitat use. Mammals were the type of species most frequently examined by these studies followed by birds and reptiles. The majority of study species were not endangered or threatened, with only a third of the studies examining a species that was classified as endangered in some way (chapter 1).

After completing our systematic review we used the information to design our telemetry survey. We examined leopard lizard habitat association at 2 scales with a focus on lizard-shrub interactions throughout different periods of the day. We observed patterns of behavior and timing of shrub use that suggest that shrubs are an important feature in this desert ecosystem and likely facilitate leopard lizards. Lizards used shrubs more frequently in the hotter afternoon compared with the morning. Certain behaviors, namely thermoregulation and predator avoidance, also were observed more frequently at shrubs than open areas. This indicates that although lizards are using shrubs less frequently than open areas, shrub presence may be beneficial to lizards at certain times (Lortie *et al*. 2015, Filazzola *et al*. 2017). These shrub-lizard interactions indicate that facilitation of lizards by shrubs is likely occurring. As *G. sila* is endangered, this information is important as shrub facilitation may be able to be applied to management and recovery efforts for this species (chapter 2).

Despite the fact that lizards can find shelter and refuge from other sources, the direct benefits shrubs provide through facilitation likely make them important to lizards (Warrick et al. 1998, Lortie et al. 2015, Filazzola et al. 2017). In addition, shrubs can further facilitate lizards indirectly through benefits to burrowing species, such as kangaroo rats (Prugh et al. 2011, Lortie et al. 2015). Lizards often use abandon burrows for shelter and refuge along with shrubs (Hansen et al. 1994, Grillet et al. 2010). The increased abundance of burrowing animals due to shrubs can increases overall burrow density and make more shelter available to lizards (Prugh et al. 2011). We found evidence suggesting facultative, as opposed to obligate, facilitation, but this supports the role of shrubs as a foundation species for lizards, as well as many other animal species in deserts. As the dominant vegetation, shrubs provide the largest source of shade in the area, providing a moderate microclimate many plant and animal species. With climate change predicted to increase temperatures and drought for this area, this microclimate will likely become increasingly important for many species. As poikilotherms, leopard lizards will be severely affected by increased thermal stress, making shelter from environmental conditions even more important (Westphal et al. 2016, Filazzola et al. 2017). As such, the importance of shrubs to animal species, especially lizards, is likely to increase. This makes shrubs a potential mitigating factor when considering management choices in the face of climate change. Shrubs should be considered when assessing lizard habitat, whether shrubs are naturally occurring or planted (Filazzola et al. 2017). Considering shrubs and shrub condition as part of the blunt-nosed leopard lizard recovery plan will help ensure that quality habitat is available for this species.

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