



Research Article

Conservation Implications of Spatiotemporal Variation in the Terrestrial Ecology of Western Spadefoots

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ABSTRACT Conservation of species reliant on ephemeral resources can be especially challenging in the face of a changing climate. Western spadefoots (*Spea hammondi*) are small burrowing anurans that breed in ephemeral pools, but adults spend the majority of their lives underground in adjacent terrestrial habitat. Western spadefoots are of conservation concern throughout their range because of habitat loss, but little is known about the activity patterns and ecology of their terrestrial life stage. We conducted a radio-telemetry study of adult western spadefoots at 2 sites in southern California, USA, from December 2018 to November 2019 to characterize their survival, behavior, and movements from breeding through aestivation to refine conservation and management for the species. Western spadefoot survival varied seasonally, with risk of mortality higher in the active season than during aestivation. The probability of movement between successive observations was higher during the winter and spring and when atmospheric moisture was high and soil water content at 10-cm depth was low. The amount of rain between observations had the strongest effect on the probability of movement between observations; for every 20 mm of rainfall between observations, western spadefoots were 2.4 times more likely to move. When movements occurred, movement rates were highest when both relative humidity and soil water content at 10-cm depth were high. The conditions under which western spadefoots were likely active on the surface, likely to have moved, and moved at the highest rates are conditions that reduce the risk of desiccation of surface-active spadefoots. Western spadefoot home range areas varied between study sites and were mostly <1 ha, although 1 individual's home range area was >6 ha. Western spadefoots rapidly dispersed from the breeding pools, and asymptotic distances from the breeding pool were generally reached by June. The asymptotic distance from the breeding pool varied between sites, with the 95th percentile of the posterior predictive distribution reaching 486 m at 1 site and 187 m at the other. Western spadefoots did not select most habitat components disproportionately to their availability, but at Crystal Cove State Park, they avoided most evaluated vegetation types (graminoids, forbs, and shrubs). Spatial variation was evident in most evaluated western spadefoot behaviors; context-dependent behavior suggests that site-specific management is likely necessary for western spadefoots. Furthermore, comparison with an earlier study of western spadefoots at Crystal Cove State Park indicated substantial temporal variation

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in western spadefoot behavior. Therefore, basing management decisions on short-term studies might fail to meet conservation objectives. Better understanding the influences of spatial context and climatic variation on western spadefoot behavior will improve conservation efforts for this species. © 2021 This article is a U.S. Government work and is in the public domain in the USA. The *Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS activity, anuran, California, habitat selection, home range, movement, *Spea hammondi*, survival, western spadefoot.

Many plants and animals rely on ephemeral habitats to complete their life cycles. For example, many rare plants and invertebrates persist as seeds, eggs, or cysts that only sprout or hatch when inundated by seasonal rains filling shallow pools (King et al. 1996, Montrone et al. 2019). Many amphibians also are adapted to breed in ephemeral pools, where a short hydroperiod limits the occurrence and abundance of predators of eggs and larvae (Wilbur 1997). In arid ecosystems, resistant life stages, including seeds, eggs, or aestivating adults, allow ephemeral pool-dependent species to persist during dry periods. The length of droughts must be less than the duration of the desiccation-resistant stages if these species are to persist (Fisher et al. 2018). Even when species persist, however, climate variability might affect hydroperiods or the duration of conditions that allow acquisition of resources for future reproduction or for dispersal and connectivity among ephemeral pools (Montrone et al. 2019). Because of the nature of ephemeral resources, many species that depend on ephemeral habitats also have complex life histories.

Effective conservation of species with complex life histories requires a thorough understanding of the ecological needs of all life stages of the species. For example, conserving freshwater turtles requires maintaining the lakes, rivers, and wetlands in which adults reside and the beaches and uplands where females nest and eggs develop (Reese and Welsh 1997, Rathbun et al. 2002, Gibbons 2003, Riensche et al. 2019). Conversely, many amphibians lay their eggs in aquatic habitats, where larvae develop before metamorphosing into terrestrial adults (Semlitsch 1998, Semlitsch and Jensen 2001, Semlitsch and Bodie 2003, Crawford and Semlitsch 2007). In both of these situations, ensuring species persistence requires that adequate terrestrial habitat and connectivity among aquatic habitats remain to allow exchange of individuals and genes to promote metapopulation dynamics and ensure genetic connectivity (Attum et al. 2008, Semlitsch 2008, Marshall et al. 2009, Muths et al. 2018, Bailey and Muths 2019).

In the case of pool-breeding amphibians, genetic connectivity implies that movement between breeding pools and breeding among individuals from different pools is sufficient to maintain genetic diversity (Frei et al. 2016, Wang and Shaffer 2017, Covarrubias et al. 2021). Demographic connectivity similarly implies that enough individuals move between pools to promote persistence of metapopulations, either through recolonization of breeding pools that become extirpated or through dispersal of individuals from source populations to rescue sink populations

from extirpation (Semlitsch 2008, Muths et al. 2018, Bailey and Muths 2019). In both cases, intervening terrestrial land use and land cover must, at a minimum, allow safe passage of individuals from one breeding pool to another.

Safe passage between breeding pools is not enough, however, for amphibians that make extensive use of uplands. In these cases, the terrestrial resources required by adult amphibians must remain intact around breeding ponds. The idea of core terrestrial habitat for amphibians has been described in the literature (Semlitsch 1998, Semlitsch and Jensen 2001, Semlitsch and Bodie 2003) and can encompass substantial upland area. For example, the distance from the pool shoreline necessary to protect 90% of California tiger salamanders (*Ambystoma californiense*) at Jepson Prairie, California, USA, was nearly 1,500 m (Searcy et al. 2013). Terrestrial habitat requirements for many amphibians, however, remain poorly understood. Maintaining both connectivity among breeding pools and sufficient upland resources around breeding pools are necessary for conserving pool-breeding amphibian populations.

Western spadefoots (*Spea hammondi*) are small, nocturnal, burrowing anurans. The adults spend the majority of their lives burrowed in terrestrial habitat, primarily emerging during rain events to feed and breed. Western spadefoots historically bred in vernal pools but now take advantage of any seasonal water body, such as road ruts, cattle ponds, and created pools because vernal pools are limited (Morey and Reznick 2004). Pools must persist for a minimum of 30 days for western spadefoot larvae to complete development (Morey and Reznick 2004). In southern California >80% of western spadefoot habitat has been lost to development (Jennings and Hayes 1994) and suitable habitat in northern California has been significantly reduced (Fisher and Shaffer 1996, Rose et al. 2020), prompting review for federal listing by the United States Fish and Wildlife Service (U.S. Fish and Wildlife Service 2020) and listing as a Species of Special Concern by the California Department of Fish and Wildlife (California Natural Diversity Database 2021). Despite the importance of terrestrial habitat in western spadefoot life history, how and where adults and juveniles use that habitat is poorly understood. The only past telemetry study of western spadefoots was conducted during a particularly dry winter (2012–2013), and western spadefoot movement was highly correlated to rainfall events (Baumberger et al. 2019). Additional data on the spatial ecology of adults is necessary for a more comprehensive understanding of their terrestrial

habitat use in a variety of environmental conditions (Thomson et al. 2016) to ensure protection of breeding sites and adequate terrestrial habitat to support adults.

Our goal was to examine western spadefoot terrestrial habitat use and movements during their breeding and aestivation periods. Our objectives were to estimate survival rates for adult western spadefoots, relate western spadefoot surface activity and movement to environmental cues, measure how far adults disperse from breeding pools, and model selection of different components of the terrestrial environment by western spadefoot adults. We hypothesized that western spadefoot movement frequency and rate would be positively related to precipitation, humidity, and soil moisture and that western spadefoots would select locations that facilitated burrow construction or use (i.e., areas with less soil compaction or with more existing burrows). We evaluated these hypotheses and described survival and maximum distance from breeding pools at 2 sites, 1 coastal and 1 inland, to assess regional differences in western spadefoot terrestrial ecology.

STUDY AREA

We studied western spadefoots at Crystal Cove State Park (i.e., Crystal Cove) and Limestone Canyon Regional Park (i.e., Limestone Canyon), 2 natural reserves in Orange County in southern California from December 2018 through November 2019 (Fig. 1). The study locations have a Mediterranean climate, with warm, dry summers (May–Sep) and mild, wet winters (Dec–Mar). The backcountry of Crystal Cove starts at sea level and rises to 315 m at the highest point, encompassing 970 ha of wilderness area open only to hiking, biking, and equestrian use. It is one of the few remaining parcels of coastal sage scrub in Orange County and is dominated by California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum fasciculatum*), non-native annual grasses, and black mustard (*Brassica nigra*). The Limestone Canyon site is approximately 20 km inland from Crystal Cove; its 1,618 ha are only open to the public for docent-led programs. The elevation ranges from 251 m to 539 m. The study area in Limestone Canyon is dominated by black mustard and non-native annual grasses, whereas nearby slopes were dominated by California sagebrush, chamise (*Adenostoma fasciculatum*), and California lilac (*Ceanothus* spp.). The dominant fauna at both sites included desert cottontail (*Sylvilagus audubonii*), western fence lizard (*Sceloporus occidentalis*), and California quail (*Callipepla californica*), which support populations of red-tailed hawks (*Buteo jamaicensis*), southern Pacific rattlesnakes (*Crotalus oreganus helleri*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Crystal Cove received 42.3 cm of rain between December 2018 and September 2019 and had an average temperature of 13°C (range = 0.66–28.8°C) from December 2018 to April 2019 (the breeding season). Limestone Canyon received 58.5 cm of rain between December 2018 and September 2019, and the average temperature was 12.5°C (range = –1.38–31.2°C) between December and April. We recorded successful breeding at both sites.

METHODS

Field Methods

We encircled 2 known breeding pools, 1 at each study site, with a drift fence interrupted at 5–7-m intervals with 16 pitfall traps. We placed the drift fence 10 m from the high water mark at each vernal pool. To determine direction of travel, we inserted a thin piece of plywood (extending to the bottom of the bucket) into each bucket along the axis of the silt fence (Figs. S1–S3, available in Supporting Information). We sampled pitfall traps during and for 5 days after rain events predicted to result in >6 mm precipitation and closed them with a lid when not in use. We also conducted nocturnal visual encounter surveys for adult western spadefoots at other known pool locations in Crystal Cove because this technique works well to detect this species (U.S. Geological Survey 2006, Richmond et al. 2016).

We measured mass and length (snout-vent length; SVL) of all western spadefoots and characterized their age (juvenile or adult) and sex. We permanently marked adult western spadefoots (>40 mm SVL) with an 8-mm passive integrated transponder (PIT) tag inserted subcutaneously on the lower right side of the animal, just above the hind leg. We retained 26 adult western spadefoots (18 from Crystal Cove; 8 from Limestone Canyon) whose mass was >24 g for intracoelomic surgical implantation of a 1.1–1.2-g radio-transmitter (model A2455, Advanced Telemetry Systems, Isanti, MN, USA). Transmitter mass was always ≤5% of the spadefoot's mass (Goldberg et al. 2002). We transferred selected western spadefoots to a veterinary hospital, where veterinarians performed surgery under aseptic conditions following Gray et al. (2005) and Long et al. (2010). We anesthetized western spadefoots by immersion in 0.4 g of tricaine methanesulfonate (Tricaine-S, Western Chemical, Ferndale, WA, USA) dissolved in 500 ml of water buffered with 1 g of sodium bicarbonate. We made a 10-mm incision on the side of the abdomen with a sterile scalpel, and opened the coelomic cavity with surgical scissors. We then placed a sterilized transmitter in the coelomic cavity along the muscle wall. We sutured the abdominal wall and skin, and covered the sutures with surgical glue to seal the incision. We revived animals with distilled water and held them for observation overnight before releasing them at their capture site.

We tracked western spadefoots at both sites twice a week from December 2018 to May 2019, then once a week during June and July 2019. From August to November 2019, the tracking decreased to once a month as the western spadefoots aestivated. Tracking increased to once a week in December 2019 following the first significant rain event of the winter. Only 4 of the tracking sessions took place at night to conduct welfare checks on the spadefoots. During each tracking session, we tracked western spadefoots to their exact burrow location or their location on the surface. To evaluate habitat selection for western spadefoots, we placed a 1-m × 1-m polyvinyl chloride square at each burrow location with the western spadefoot burrow at the center and recorded several habitat variables within the square,

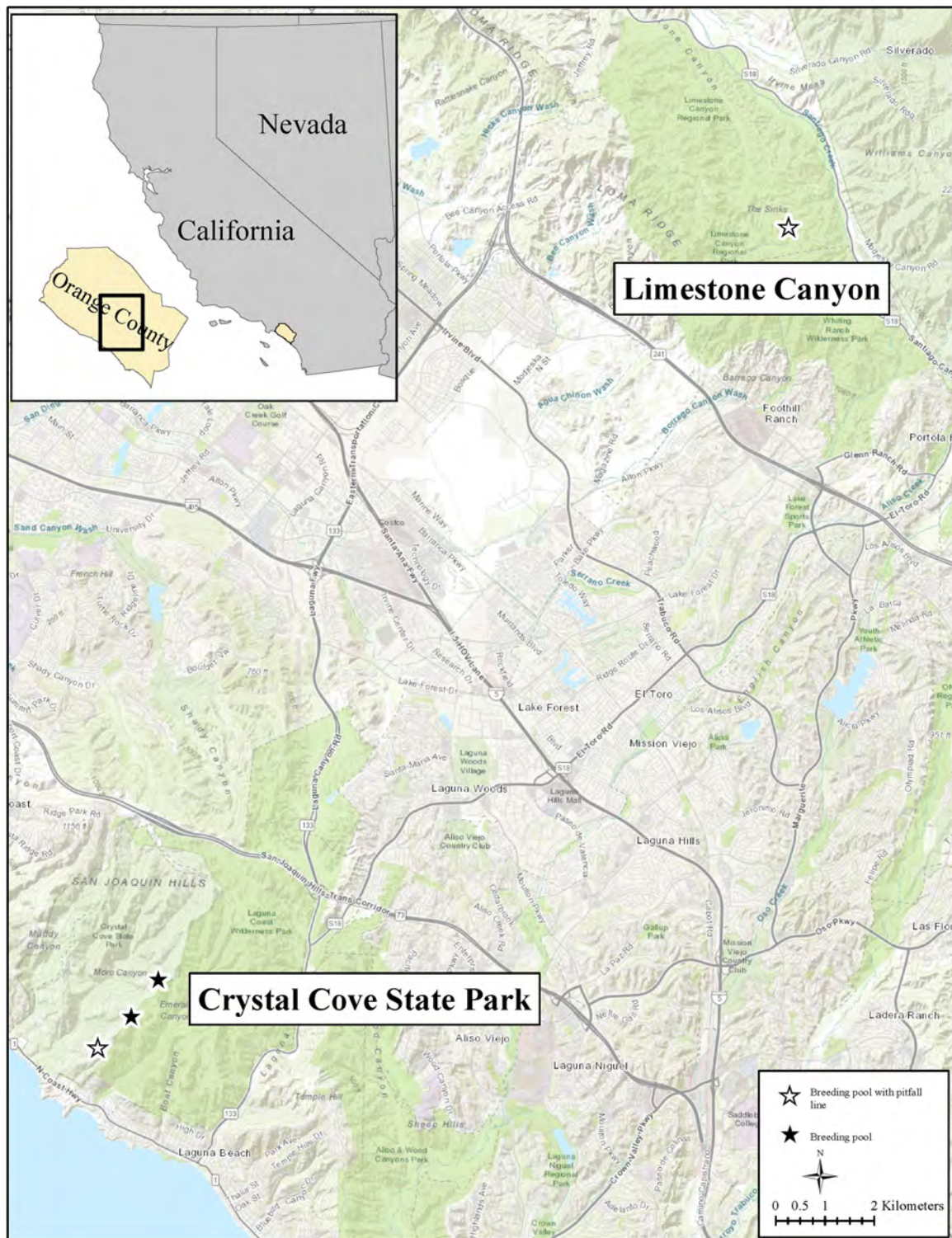


Figure 1. Overview of western spadefoot telemetry sites in southern California, USA, 2018–2019.

including vegetation type (graminoid, forb, shrub, tree, leaf litter, and duff) and percent cover, soil compaction and moisture, and slope and aspect (Figs. S4–S5, available in Supporting Information). We measured soil compaction using a soil compaction meter (Lang Penetrometer, Gulf Shores, AL, USA), taking 3 measurements from left to right across the top of the 1-m square and then averaging the results. We measured soil moisture by burying the plate

of a soil acidity and moisture tester (model HB-2, Kelway Instruments, Wycoff, NJ, USA) ≥ 5 cm from the soil surface. We recorded the same measurements at randomly selected points located at a bearing of 1–360 degrees and a distance of 3–25 m from the spadefoot burrow location to characterize the available habitat. This research abided by the stipulations of California Department of Fish and Wildlife Scientific Collecting Permit SC838 and followed

United States Geological Survey Institutional Animal Care and Use Committee protocol WERC 2014-01.

We installed 2 HOBO micro stations (H21-USB, Onset Computer Corporation, Bourne, MA, USA) approximately 15 m from the high water mark on 2 sides of each pitfall pool. One station at each site recorded precipitation, and the other recorded air temperature and relative humidity. Each of the stations recorded data from 3 soil moisture meters (10HS-S-SMD-M005, Onset Computer Corporation) placed 10 cm, 50 cm, and 1 m underground. We programmed the stations to record data hourly for the duration of the project. Data used in this study are available as a United States Geological Survey data release (Rochester et al. 2021; <https://doi.org/10.5066/P912W368>).

Analytical Methods

We examined the survival, spatial ecology, and habitat selection of western spadefoots using several different models analyzed in a Bayesian framework. We estimated survival rates of adult western spadefoots using time-to-event (survival) analysis of radio-telemetry data (Williams et al. 2002). Our survival analysis accommodated staggered entry, interval censoring, and right truncation (Halstead et al. 2019). Because we expected the risk of mortality to vary with surface activity, we used a piecewise constant hazard (i.e., daily risk of mortality) that treated the risk of mortality from the time of release until the end of April (the estimated active season) as constant, with the remainder of the study period having a different, but also constant, risk of mortality (Halstead et al. 2019). To this baseline hazard model, we evaluated the effects of site (binary: 0 = Crystal Cove, 1 = Limestone Canyon), sex (binary: 0 = female, 1 = male), and mass (continuous) on the risk of mortality. We standardized mass to zero mean and unit variance. We selected variables from the full model using indicator variables (Kuo and Mallick 1998, Hooten and Hobbs 2015), and accounted for prior sensitivity in model selection (Link and Barker 2010) by using hierarchical shrinkage priors on model coefficients (Kruschke 2015). We selected variables with a higher posterior than prior probability for inclusion in a best model, and we based inference on this model. We selected priors at both stages of model fitting to be uninformative, with priors for the initial full model as follows: Uniform(min. = -20, max. = 20) on the baseline hazard, hierarchical coefficients distributed as $\mathcal{t}(\text{location}=0, \text{scale}=\sigma_\beta, \text{df}=1)$, where σ_β was distributed as half-Cauchy (scale = 1), and indicator variables distributed as Bernoulli ($p=0.5$) (Code S1, available in Supporting Information). Priors for the best model were the same, except that coefficients were not hierarchical and were distributed as Gaussian($\bar{x}=0$, SD = 10) and the model did not include indicator variables. We analyzed the survival models using Bayesian inference with Markov chain Monte Carlo (MCMC) simulation. We ran the models on 5 independent chains of 20,000 iterations each after an adaptation period of 1,000 iterations and a burn-in period of 1,000 iterations by calling JAGS (version 4.3.0; Plummer 2003) from R

(version 3.6.1; R Core Team 2020) using the package *runjags* (Denwood 2016).

We examined the probability western spadefoots were visible on the surface (i.e., surface activity) at the time of observation using a hierarchical binomial model with a logit link function. Each individual's baseline probability of surface activity varied according to a logit-normal distribution centered on the population mean probability of being visible. We examined the effects of site, sex, mass, date (circular), time of day (circular), wind (binary: 0 = none or light, 1 = moderate or strong), cloud cover (binary: 0 = clear or partly cloudy, 1 = mostly cloudy or overcast), and air temperature (continuous) on the probability of surface activity. We converted circular variables to radians and used the sine and cosine as predictors for these variables (Pewsey et al. 2013). For circular variables, we placed the same indicator variable on the coefficients for both the sine and cosine transformation of the variable. We selected variables with a higher posterior than prior probability for inclusion in a best model, and we based inference on this model. We selected priors at both stages of model fitting to be uninformative, with priors for the initial full model as above for survival, with differences as follows: mean probability of being surface active distributed as $\text{beta}(\alpha=1, \beta=1)$ and the standard deviation of the logit-normal random intercept for individuals distributed as half-Cauchy(1) (Code S2, available in Supporting Information). As for the survival analysis, priors for the best model were the same as for the full model, except that coefficients were distributed as Gaussian (0, 2) and the model did not include indicator variables.

We examined the probability western spadefoots moved between observations using the same model structure as for the probability of surface activity but with different predictor variables. For this model, we examined the effects of site, sex, mass, date, total rainfall between observations (continuous), mean relative humidity between observations (continuous), and mean soil water content at 10-cm depth between observations (continuous). We used soil water content at 10 cm because although the moisture content at the 3 depths was correlated, soil moisture at 10 cm was the most variable and we hypothesized it would be most likely to affect spadefoot behavior during and following the active season (as opposed to ending aestivation). We used the same variable selection procedure and priors for the probability of movement as for the probability of surface activity analysis (Code S2).

For the analysis of western spadefoot movement rate, we used a hierarchical lognormal model with an identity link function. We considered only intervals during which movement occurred in this analysis, the variable selection procedure was identical to the analyses of surface activity and movement probabilities, and we considered the same predictor variables as for the probability of movement. We also selected priors for the movement analysis to be uninformative: mean movement rate was distributed as Gaussian (0, 10), and we gave mean coefficients for the best model the same priors (Code S3, available in Supporting Information).

We used nonlinear regression based on an asymptotic Michaelis-Menten function (Hobbs and Hooten 2015) and an overdispersed Poisson error distribution to phenomenologically evaluate the distance western spadefoots moved from the breeding pool as a function of days since release. We considered only terrestrial locations and those after the western spadefoot had moved to avoid counting single locations multiple times in the analysis. The variable selection procedure was the same as for the previous models, and we considered effects of site, sex, and mass on asymptotic distance from the breeding pool and the half-maximum parameter, which describes the rate at which western spadefoots disperse from the breeding pool. To account for statistical noise and individual variation in behavior, we included an overdispersion parameter and individual random effects, respectively, for the asymptotic distance from the pool and the half-maximum parameter. We selected priors for this analysis to be uninformative: the log-scale intercept and coefficients for the asymptotic distance from the breeding pool and half-maximum parameter were distributed as Gaussian(0, 10) and standard deviations for overdispersion and individual variation in the intercept for log(asymptotic distance from pool) were distributed as half-Cauchy(1) (Code S4, available in Supporting Information).

We analyzed all of the above hierarchical models using Bayesian inference and MCMC techniques. We ran the models for probability of surface activity, probability of movement, and movement rate on 5 independent chains of 20,000 iterations each after an adaptation period of 1,000 iterations and a burn-in period of 9,000 iterations by calling JAGS from R using the package jagsUI (Kellner 2019). We ran the Poisson Michaelis-Menten model for distance from pool on 5 independent chains of 2 million iterations each after an adaptation period of 1,000 iterations and a burn-in period of 999,000 iterations and thinned the output by a factor of 100. Inference for all models was based on 100,000 samples from the posterior distribution, and the smallest effective sample size for a monitored parameter in the best models was 806. We assessed convergence by visually examining trace plots and with the partial scale reduction factor (Gelman and Rubin 1992); we did not observe evidence for lack of convergence.

We used 2 methods to estimate home range area of western spadefoots. We used 95% minimum convex polygons (MCPs) so comparisons could be made to previous studies. We also used kernel density estimates (KDEs) at the 50% isopleth level to estimate core areas and at the 95% isopleth level to estimate home ranges using the R package adehabitatHR (Calenge 2006). Kernel density estimates allow finer resolution and quantification of areas of more and less intense use than MCPs. Because bandwidth selection algorithms for KDEs often result in oversmoothed, excessively large home ranges for herpetofauna, we manually adjusted the bandwidth for each western spadefoot until the 95% KDE was equal in area to the 95% MCP (Row and Blouin-Demers 2006). We used only western spadefoots with >20 observations for home range analysis. We plotted home ranges and evaluated whether site, sex, or mass

affected home range area using a lognormal model with an identity link. The model fitting procedure, including variable selection and priors, were as above for the movement rate analysis.

We evaluated habitat associations of western spadefoots by comparing observations of habitat components used by western spadefoots with paired observations of habitat components available to western spadefoots at nearby locations using the differences parameterization of hierarchical case-control logistic regression models (Keating and Cherry 2004, Duchesne et al. 2010, Halstead and Kleeman 2017). Briefly, this model uses the differences between used and available habitat components as predictor variables and does not contain an intercept. We allowed selection to vary among individuals with individual selection of habitat components varying around the population mean as Gaussian($\mu_{\beta,k}$, $\sigma_{\beta,k}$), where $\mu_{\beta,k}$ is the population mean response to habitat component k . Because western spadefoots frequently did not move between observations, we added further hierarchical structure to account for multiple observations of the western spadefoot in the same location. Thus, we allowed selection for each series of observations in which a western spadefoot remained in the same location to vary around the individual mean coefficient as Gaussian($\beta_{i,k}$, $\sigma_{i,k}$), where $\beta_{i,k}$ is the individual-specific coefficient for habitat component k (Halstead et al. 2016). We gave mean coefficients for this model Gaussian(0, 2) priors and all standard deviations for the model half-Cauchy(1) priors (Code S5, available in Supporting Information). We analyzed each site separately using Bayesian inference and MCMC techniques. We ran each habitat selection model on 5 independent chains of 2 million iterations each after an adaptation period of 1,000 iterations and a burn-in period of 99,000 iterations by calling JAGS from R using the package jagsUI (Kellner 2019). We thinned output by a factor of 100 and based inference on 100,000 samples from the posterior distribution. The smallest effective sample size at the population level of the model was 81, with all other effective sample sizes >100. We assessed convergence by visually examining trace plots and with the partial scale reduction factor (Gelman and Rubin 1992); we did not observe evidence for lack of convergence. Unless otherwise indicated, we present results as posterior median (95% symmetrical credible interval).

RESULTS

We caught 32 adults at Crystal Cove and 35 adults at Limestone Canyon between 6 December 2018 and 19 February 2019 (Table S1, available in Supporting Information). The mean mass for adult western spadefoots at Crystal Cove was 23.5 g (range = 12–37.5 g). The animals at Limestone Canyon tended to be smaller with a mean mass of 18.9 g (range = 8–29.25 g). Eighteen of the adult western spadefoots at Crystal Cove were >24 g; of those, 7 were female and 11 were male. At Limestone Canyon, 8 of the adult western spadefoots were >24 g; of those, 4 were female and 4 were male. We radio-tracked western spadefoots for mean of 222 days (range = 25–348 days).

Table 1. Posterior inclusion probabilities of variables for models of western spadefoot movement and behavior in southern California, USA, 2018–2019. All variables had a prior inclusion probability of 0.5; asterisks (*) indicate variables that had a higher posterior than prior probability and were included in the best-fit model. Site, wind, and cloud cover variables were binary; precipitation, relative humidity, and soil water content variables were aggregated for the period between observations. Date and time of day were treated as circular variables, with a common indicator for the sine and cosine terms. All other continuous variables were standardized to mean = 0, standard deviation = 1 for analysis. Blanks indicate that the variable wasn't considered in the model for that response.

Response	Predictor variable										
	Site	Sex	Mass	Date	Time of day	Air temperature	Wind	Cloud cover	Precipitation (sum)	Relative humidity (mean)	Soil water content (mean at 10 cm)
Survival	0.445	0.470	0.366								
<i>P</i> (visible)	0.899*	0.325	0.225	0.929*	>0.999*	0.963*	0.380	0.320	0.918*	0.925*	0.998*
<i>P</i> (moved)	0.362	0.278	0.397	>0.999*					0.201	>0.999*	0.902*
Movement rate	0.881*	0.282	0.220	0.240							
Asymptotic distance from pool	0.691*	0.027	0.022								
Half-maximum parameter for distance from pool	0.499	0.499	0.499								
Home range area	0.500*	0.359	0.302								

Eleven of the 26 western spadefoots in Orange County with transmitters died during the course of the study; 6 died at Crystal Cove and 5 at Limestone Canyon. One of the spadefoots at Crystal Cove was eaten by a southern Pacific rattlesnake, and 2 of the western spadefoots at Limestone Canyon were likely eaten by birds of prey (based on where we found the transmitters). Three western spadefoots were victims of unknown predators (we found only the transmitter). Four western spadefoots died of unknown causes during the course of the study. One western spadefoot died in a pitfall bucket, where it presumably drowned. We censored this spadefoot at the time we last observed it alive for the survival analysis.

The survival analysis indicated that the risk of mortality for adult western spadefoots in our study varied seasonally but was not affected by site, sex, or mass (Table 1). The median daily risk of mortality for adult western spadefoots during the active season was 0.0027 (95% credible interval = 0.0011–0.0056) and the daily risk of mortality during aestivation was 0.0011 (0.00022–0.0029). We estimated the annual probability of survival for western spadefoots to be 0.51 (0.30–0.72; Fig. 2).

Western spadefoots were unlikely to be observed on the surface, yet the probability of surface activity varied with conditions. Site, date, time of day, and air temperature all were related to the probability of surface activity (Table 1). The probability of surface activity at Limestone Canyon (median = 0.12 [95% credible interval = 0.037–0.28]) was 3.4 (1.5–7.7) times higher than the probability of surface activity at Crystal Cove (0.038 [0.014–0.084]; Fig. 3), though the tracking period for most western spadefoots at Limestone Canyon occurred during the seasonal peak of surface activity, whereas the tracking period for most western spadefoots at Crystal Cove continued through the drier summer and autumn months (Table S2, available in Supporting Information). The seasonal peak in surface activity occurred in the winter (Dec–Jan; Fig. 3), and the daily peak in surface activity occurred during the night, from about 2100–2300 (Fig. 3). Surface activity declined with increasing temperature; spadefoots were 0.49 (0.30–0.77) times as likely to be surface active with a 6°C (1 SD) increase in air temperature (Fig. 3).

Like surface activity, the probability western spadefoots moved between observations varied with conditions. Date, total rainfall, mean relative humidity, and soil water content at 10-cm depth were related to the probability a western spadefoot moved between observations (Table 1). The probability of movement peaked in March but was relatively high from January through April (Fig. 4). Precipitation was strongly and positively related to the probability of movement; for every 14-mm (1 SD) increase in rainfall between observations, western spadefoots were 1.3 (1.1–1.5) times more likely to move (Fig. 4). Higher humidity also was positively related to the probability of movement but to a lesser extent. For every 13% (1 SD) absolute increase in relative humidity, western spadefoots were 1.3 (1.1–1.5) times more likely to move (Fig. 4). Soil water content at 10 cm was negatively related to the probability of movement, with probability of movement decreasing by a factor

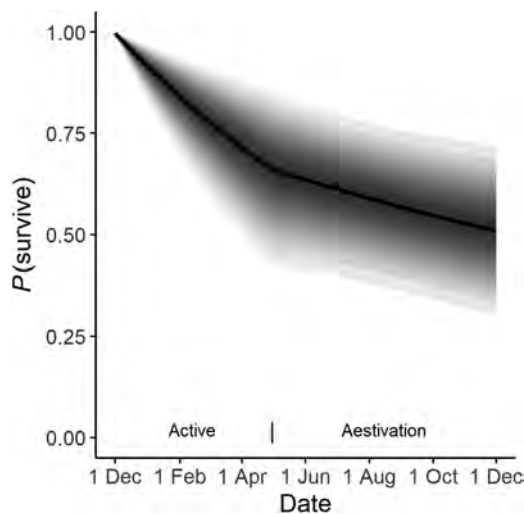


Figure 2. Cumulative survival curve for adult western spadefoots in southern California, USA, 2018–2019, based on a piecewise constant hazard model that allowed different daily risk of mortality in the active season (1 Dec–30 Apr) and aestivation (1 May–30 Nov). The line represents the posterior median, and shading represents the posterior distribution in 2.5 percentile bands, with the outermost shading representing 95% credible intervals.

of 0.52 (0.40–0.68) with an increase of 0.09 (1 SD) in soil water content at 10-cm depth (Fig. 4).

The movement rate of western spadefoots varied by site and with conditions between observations (Table 1). Mean movement rate at Limestone Canyon (1.9 [1.3–2.7] m/day) was 0.52 (0.35–0.80) times that of Crystal Cove (3.6 [3.0–4.4] m/day; Fig. 5). Relative humidity was positively related to movement rate, with movement rate increasing 1.4 (1.3–1.6) times with a 13% absolute increase in relative humidity (Fig. 5). Soil water content also was positively related to movement rate, with a 0.09 increase in soil water content at 10-cm depth increasing movement rate 1.3 (1.1–1.4) times (Fig. 5).

The asymptotic distance western spadefoots were found from pools varied by site, but the half-maximum parameter did not change with the variables we examined (Table 1; Figs. 6 and 7). The mean asymptotic distance of western spadefoots from the breeding pool at Crystal Cove (139 [94–200] m) was 3.61 (1.81–7.92) times the mean asymptotic distance of western spadefoots from the breeding pool at Limestone Canyon (39 [18–72] m). The 0.95 quantile of the posterior predictive distribution for distance from the breeding pool at 180 days post-release was 486 m at Crystal Cove and 187 m at Limestone Canyon (Fig. 8). On average, western spadefoots dispersed half their asymptotic distance from the breeding pool within 8 (5–12) days of release. The maximum observed distance from the breeding pool was 601 m (Table S2).

Home ranges of western spadefoots were relatively small, with a mean 95% home range area of 0.52 ha (SD = 1.2 ha; range = 0.0067–6.1 ha; Table S2). Home range area was potentially related to site but not sex or mass (Table 1). Mean home range area at Crystal Cove (0.20 [0.091–0.44] ha) was 3.6 (0.69–19) times larger than at Limestone

Canyon (0.056 [0.013–0.24] ha (Figs. S6–S11, available in Supporting Information).

Patterns of habitat selection by western spadefoots varied by site (Fig. 9). At Limestone Canyon, none of the examined habitat components were statistically selected or avoided, although a tendency existed for bare ground, forbs, and shrubs to be used more than they were available (Fig. 9). In contrast, graminoids, forbs, and shrubs were all avoided by western spadefoots at Crystal Cove. With a 10% increase in graminoid cover, the probability of use by a spadefoot decreased by 88% (23–98%; Fig. 9). The same increase in forb and shrub cover decreased the probability of use by western spadefoots by 93% (63–99%) and 95% (79–99%), respectively (Fig. 9).

DISCUSSION

Western spadefoots spend the majority of the year, and the majority of their adult lives, in terrestrial environments. Therefore, understanding the terrestrial ecology of western spadefoots is essential for their conservation. We found that western spadefoot terrestrial ecology varies substantially between a coastal and an inland site, with profound implications for establishing best management practices for conservation design. Further, comparison with a previous study at 1 of our sites (Baumberger et al. 2019) indicates substantial temporal variation in western spadefoot terrestrial ecology. Together, this spatial and temporal variation in ecology suggests that conserving western spadefoots and other species reliant on increasingly stochastic ephemeral resources will likely require innovative approaches to maintain metapopulation dynamics consistent with persistence in a changing landscape (Searcy et al. 2011, 2013).

Our findings provide an interesting comparison to an intensive, multi-year study of the terrestrial ecology of eastern spadefoots (*Scaphiopus holbrookii*) in Florida, USA (Pearson 1955, 1957). Eastern spadefoot surface activity varied over the year with emergence from burrows more likely in spring and fall than in summer and winter (Pearson 1955), whereas western spadefoot surface activity in southern California was most likely in winter. The difference in seasonal activity in eastern and western spadefoots might be a function of the very different climates in Florida and California (humid subtropical with a May–October rainy season in Florida vs. Mediterranean with dry summers in California). Rainfall, relative humidity, and temperature were positively associated with eastern spadefoot surface activity (Pearson 1955); we also found a positive association of movement with rainfall and relative humidity for western spadefoots but a negative association of surface activity with air temperature. In both eastern and western spadefoots, daily activity peaked after nightfall and before midnight; we had too few observations in the pre-dawn hours to corroborate Pearson's (1955) finding of a secondary peak in activity before dawn. The home ranges of eastern spadefoots were much smaller than those of the western spadefoots in our study, with a mean home range area of 10 m² (range = 0.7–83 m²; Pearson 1955). These home range estimates, however, do not include movements

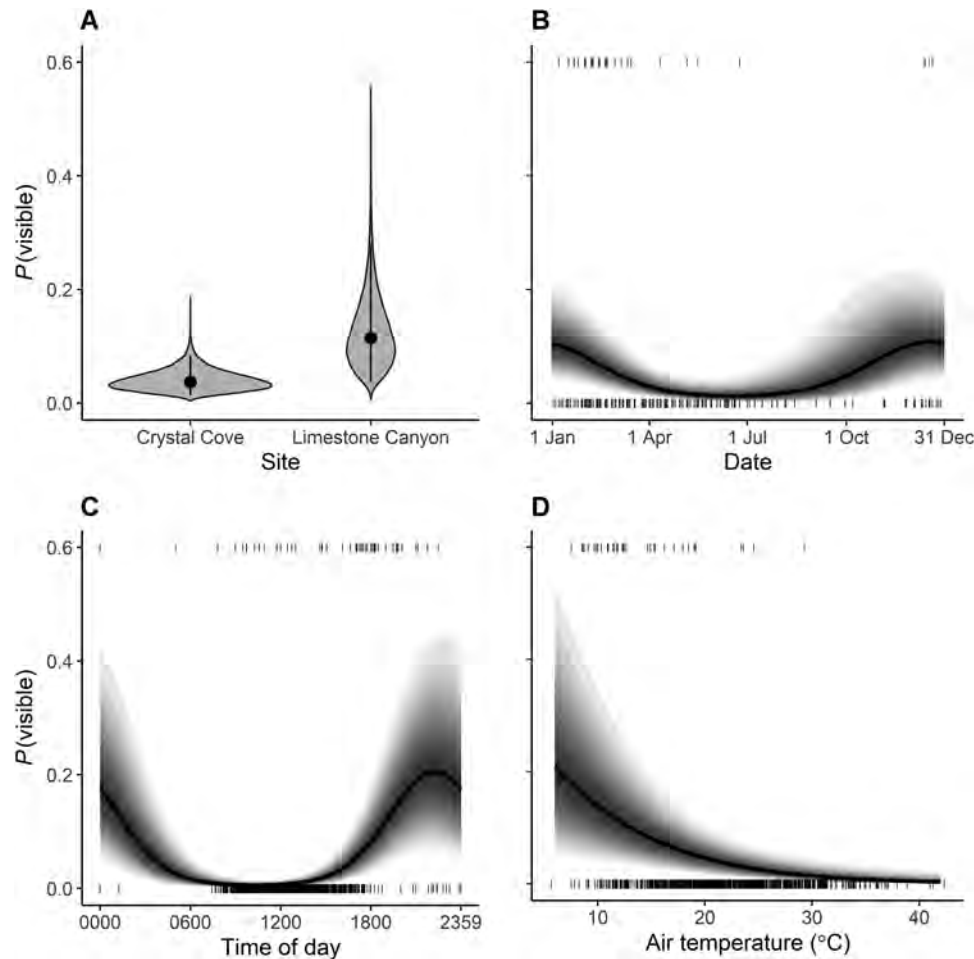


Figure 3. Probability western spadefoots were visible on the surface at the time of observation based on A) site, B) date, C) time of day, and D) air temperature in southern California, USA, 2018–2019. In A, shaded areas represent the posterior distribution, points represent posterior medians, and vertical lines represent 95% credible intervals. In frames B–D, the black lines represent posterior medians, and shading represents the posterior distribution in 2.5 percentile bands, with the outermost shading representing 95% credible intervals. Ticks represent observed values, with bottom ticks indicating not visible and top ticks indicating visible. Each plot holds the other variables at their mean values. Plots B–D represent probabilities at Crystal Cove State Park (Crystal Cove).

to and from breeding pools, whereas our estimates include these movements. Perhaps most striking was Pearson's (1955, 1957) observation that eastern spadefoots returned to the same burrows after foraging or breeding, sometimes for years; our telemetry data did not include individuals tracked for multiple years, so it is unclear if burrow use is equally consistent over time in western spadefoots. Although statistical methods and technological advances have improved our ability to answer difficult ecological questions for secretive species, Pearson's (1955, 1957) study demonstrates that volumes can be learned about natural history through careful observation.

The distance that western spadefoots move from breeding pools is a key metric for western spadefoot conservation. Distance from the breeding pool indicates how much terrestrial habitat around a breeding pool might be used by western spadefoots, and provides a direct link to the effective reserve sizes needed to preserve western spadefoot populations. Western spadefoot distances from the breeding pool generally increased rapidly through time, reaching half their asymptotes within 1–2

weeks of release and nearing their asymptote by about June. The mean asymptotic distance to the breeding pool was greater at Crystal Cove than at Limestone Canyon, suggesting that site characteristics, such as humidity, vegetation structure, topography, or other variables, might affect how western spadefoots use the landscape surrounding breeding pools.

The need for core terrestrial habitats around amphibian breeding sites is documented (Semlitsch 1998, Semlitsch and Jensen 2001, Semlitsch and Bodie 2003, Harper et al. 2008, Searcy et al. 2013), as are the negative consequences of roads separating adult habitat from breeding pools (Becker et al. 2007, Brehme et al. 2018). Ensuring that enough terrestrial habitat exists to provide the life cycle needs for western spadefoots is best measured by the predictive distribution of distance from breeding pools. The 95th percentile of the posterior predictive distribution for western spadefoot asymptotic distance from the breeding pool was 486 m at Crystal Cove. This predicted value encompassed the maximum distance from the breeding pool of all but 1 of the spadefoots at the site. The 95th percentile of the posterior

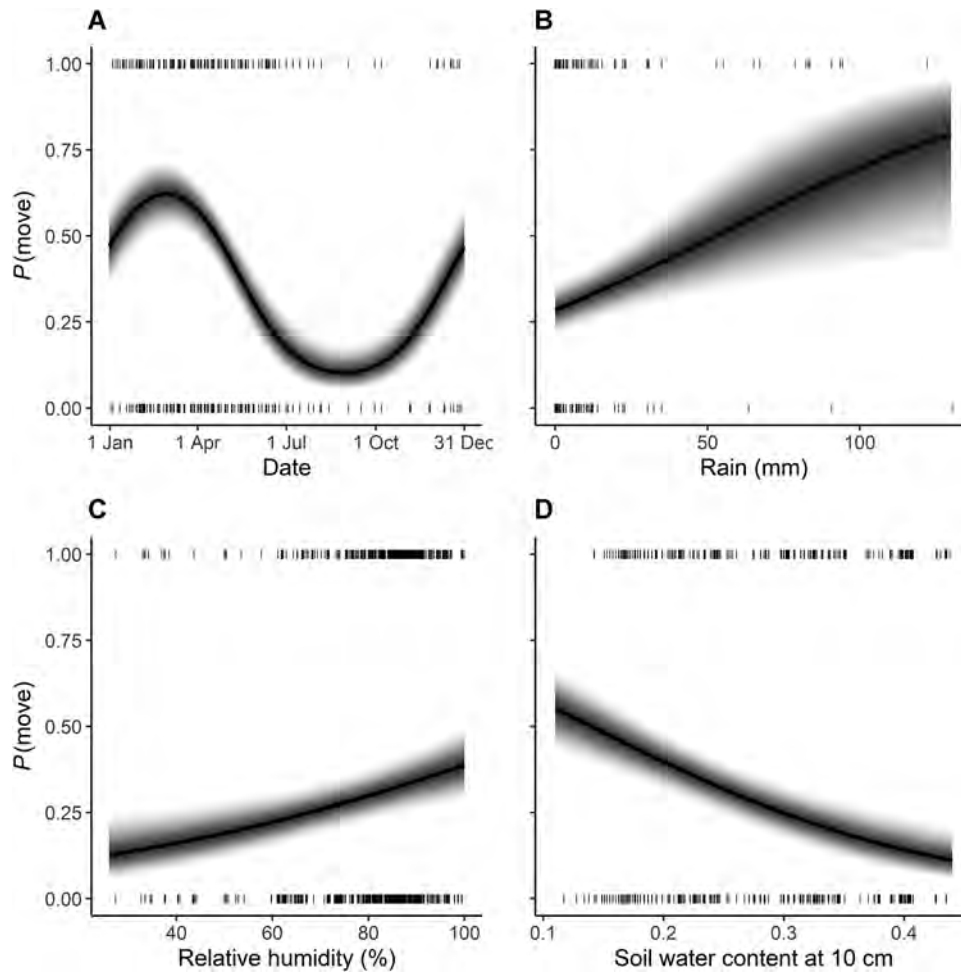


Figure 4. Probability western spadefoots moved between observations based on A) date, B) total rainfall, C) mean relative humidity, and D) mean soil water content at 10-cm depth in southern California, USA, 2018–2019. Black lines represent posterior medians and shading represents the posterior distribution in 2.5 percentile bands, with the outermost shading representing 95% credible intervals. Ticks represent observed values, with 0 = no movement between observations and 1 = movement between observations. Each plot holds the other variables at their mean values.

predictive distribution for the asymptotic distance from the breeding pool at Limestone Canyon (187 m) encompassed all observed spadefoot distances from the breeding pool at that site (max. = 145 m) but would have failed to encompass the maximum observed distances from the breeding pool for half (9 of 18) of the western spadefoots at Crystal Cove (Fig. 8). These differences emphasize the importance of site-specific information when making conservation decisions for amphibians (Fellers and Kleeman 2007, Searcy and Shaffer 2011, Searcy et al. 2013). Without further site-specific information, estimates of terrestrial habitat requirements for western spadefoots derived from Crystal Cove would provide a more conservative target for habitat conservation.

The predictive distribution of distance from breeding pools can also be used to refine pool creation and restoration efforts to increase western spadefoot populations and re-establish a metapopulation dynamic within the reserve area (Smith and Green 2005, Baumberger et al. 2020). During the course of this telemetry study and Baumberger et al. (2019), no western spadefoots were observed moving between breeding pools or even moving far enough to reach another breeding pool. Notably, all western spadefoots, even

a male that had moved closer to a different breeding pool, moved back to the pool where originally captured in November and December 2019. This is not unexpected given that adult amphibians often breed in the same location year after year (Berven and Grudzien 1990, Hels 2002, Vasconcelos and Calhoun 2004). Adult use of the same breeding pools does not mean that pools are isolated, however, as juvenile dispersal might provide demographic and genetic connectivity among pools. The small size of juveniles has thus far precluded radio-telemetry studies of dispersal of this life stage. Nonetheless, based on observed movements in the reserves, building or restoring pools within 486 m of each other in Crystal Cove and within 187 m at Limestone Canyon could increase connectivity and promote metapopulation dynamics in the reserves.

In addition to spatial variation in distances from breeding pools, substantial temporal variation in the extent of terrestrial movements likely exists. For example, at Crystal Cove in 2012, the maximum observed distance from the breeding pool was 82 m (Baumberger et al. 2019), which was less than the observed maximum distance for 16 of 18 western spadefoots and <15% of the maximum value

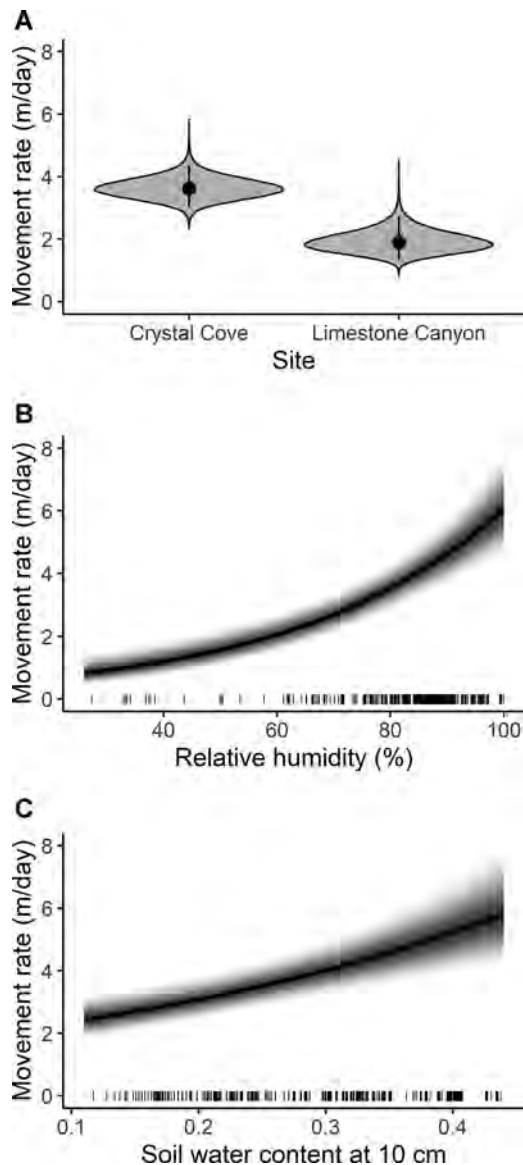


Figure 5. Movement rate of western spadefoots based on A) site, B) relative humidity, and C) soil water content at 10 cm below the surface in southern California, USA, 2018–2019. In A, shaded areas represent the posterior distribution, points represent posterior medians, and vertical lines represent 95% credible intervals. In frames B–C, the black lines represent posterior medians, and shading represents the posterior distribution in 2.5 percentile bands, with the outermost shading representing 95% credible intervals. Ticks along the x-axis represent observed values. Each plot holds the other variables at their mean values. Plots B and C represent movement rates at Crystal Cove State Park.

observed at the same site in this study. The former study was in a much drier year than this study, which likely affected the activity patterns of western spadefoots and the distances western spadefoots were found from the breeding pool. It is likely that increased variability in precipitation in California (Swain et al. 2018) will also result in within-population variation in spatial ecology as we observed between wet and dry years at Crystal Cove. Therefore, as in other ephemeral pool-breeding grassland amphibians (Searcy et al. 2013) both spatial and temporal variation in western spadefoot spatial ecology are important to

characterize, and larger, more conservative conservation buffers such as those for Crystal Cove in this study are prudent when faced with the accompanying variation and uncertainty in western spadefoot behavior.

The maximum distance at which western spadefoots were located from their breeding pools was related to their home range areas. Western spadefoot home ranges were larger at Crystal Cove than at Limestone Canyon, but home range area of western spadefoots was generally small. Most spadefoots had home range areas in the low thousands of square meters, but 2 individuals, both at Crystal Cove, had home ranges $>10,000 \text{ m}^2$, with 1 individual having a home range area of $13,000 \text{ m}^2$ and the other having a home range area of $61,000 \text{ m}^2$. Home range area also varied temporally in addition to spatially. In 2012, maximum home range area for an individual western spadefoot at Crystal Cove was $2,300 \text{ m}^2$ (Baumberger et al. 2019). In 2019, 7 of 17 western spadefoots at Crystal Cove had larger home range areas than this 2012 maximum. Thus, as for other aspects of the spatial ecology of western spadefoots, spatiotemporal variation in home range area of western spadefoots is likely substantial. The sources of variation in home range area among individuals, sites, and years remains obscure, though movement data suggest that rainfall and humidity patterns play a role in frequency and rate of movement and, therefore, home range area.

Another potential source of variation in home range area is resource use and availability (Indermaur et al. 2009, Long and Prepas 2012). Although we did not assess prey availability, we examined habitat selection of western spadefoots. Western spadefoots did not appear strongly selective of habitat components, though selection varied between sites. Although no habitat components were selected disproportionately to their availability at Limestone Canyon, all evaluated vegetation types were avoided at Crystal Cove. It is unknown why vegetation might inhibit use by western spadefoots at the more coastal site, but some hypotheses include roots that inhibit digging or structural complexity that might negatively affect foraging success. Of course, other unevaluated habitat components might have influenced selection. We limited the analyses to fewer variables than those collected in the field to keep the number of observations per model parameter >10 ; evaluation of other variables might indicate unanticipated patterns in selection. For example, several western spadefoots appeared to select sites under trees or tall shrubs during aestivation. This pattern might have been obscured by using all locations to evaluate habitat selection of western spadefoots.

The lack of strong selection for most evaluated habitat components could have several sources. We used an individual random coefficient to allow for a different number of observations and variation in selection among individuals, and our focus on the population level could have obscured individual selection. Examination of individual medians and the standard deviation of the random coefficients indicates that this is unlikely the case. For most habitat components at most sites, individual odds of selection were similar to

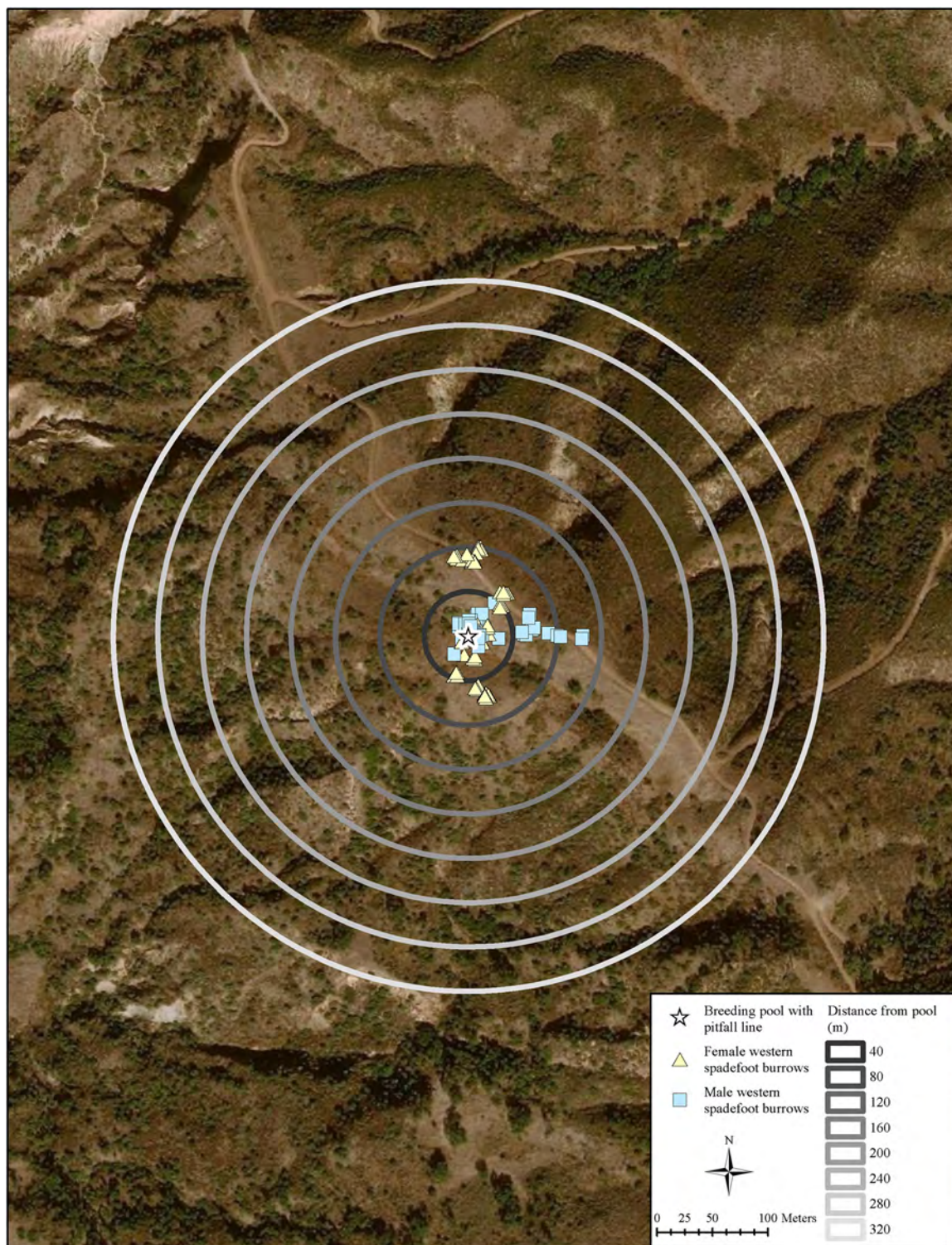


Figure 6. Overview of western spadefoot burrow points at Limestone Canyon in southern California, USA, 2018–2019. Circles represent distance from breeding pool.

and clustered around the population mean for odds of selection. The exception was for the effect of the number of burrows on selection of locations by western spadefoots at Crystal Cove, for which individual variation in selection was more evident, but credible intervals for odds of selection for number of burrows by individual spadefoots all overlapped one. The sample size for estimating selection at both sites

also was lower than one might expect because we added an additional level representing western spadefoot location to the hierarchical model to avoid treating selection of a single location by a western spadefoot as multiple independent observations. By adding location to the hierarchy of selection, we avoided artificially increasing the precision of our results but reduced our statistical power to detect selection.

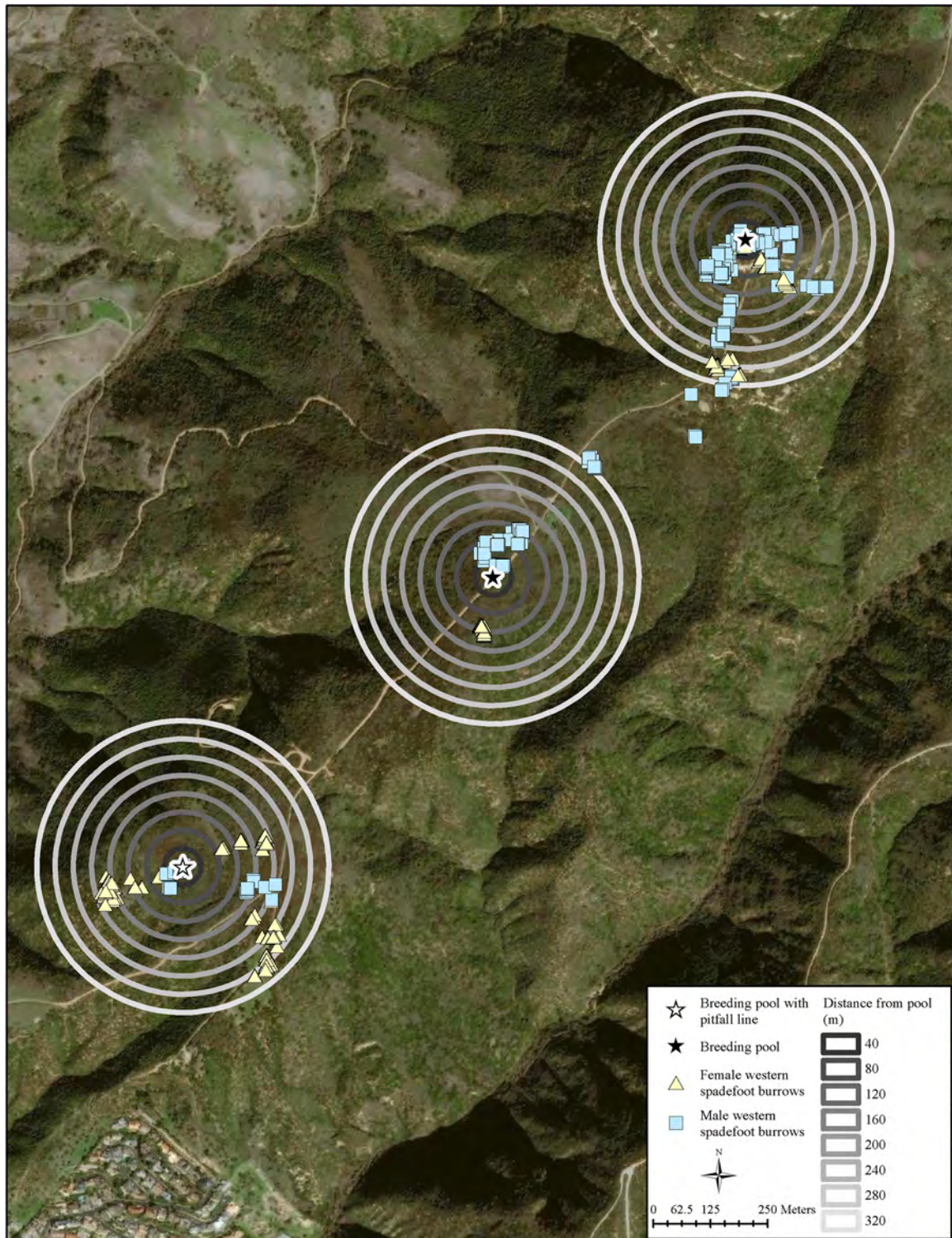


Figure 7. Overview of western spadefoot burrow points at Crystal Cove State Park in southern California, USA, 2018–2019. Circles represent distance from breeding pools.

Nonetheless, we think this was the appropriate manner in which to treat selection by animals that choose a retreat site and remain there for an extended period of time (Halstead et al. 2016).

Another mechanism by which selection could go undetected is a restricted range of values of habitat components at a site, or more specifically, at random locations

within 25 m of a spadefoot. For example, if western spadefoots could easily burrow at all values of proportion clay or soil compaction at the sites, then these habitat components would not be selected at these sites. This does not mean that these variables are not important elsewhere, but rather that they did not reach values that would affect western spadefoot selection of locations at Limestone Canyon or Crystal

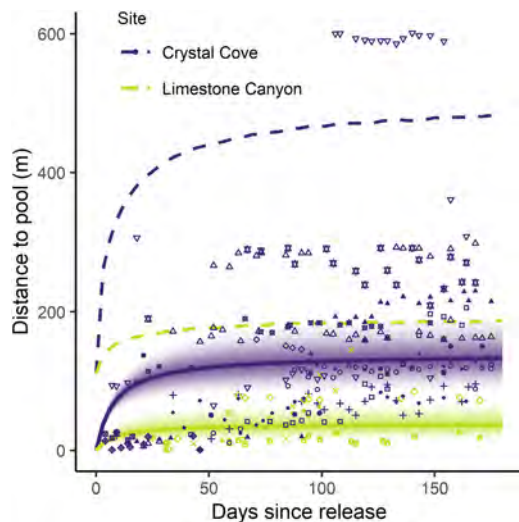


Figure 8. Distance from pool of western spadefoots in southern California, USA, 2018–2019, as a function of days since release at Crystal Cove State Park (indigo) and Limestone Canyon (chartreuse). Bold solid lines represent posterior medians; shading represents posterior distributions in 2.5 percentile bands, with the outermost shading representing 95% credible intervals; dashed lines represents the 95th percentile of the posterior predictive distribution. Points represent observed values, with different symbols representing individual western spadefoots; note that some symbols are used for more than one individual.

Cove. This is a limitation of all observational field studies of habitat selection, and not a unique limitation of this study. Without evidence for strong selection of habitat components by western spadefoots at our study sites, it is unlikely that measured habitat conditions affected western spadefoot spatial ecology at these sites. Further exploration of western spadefoot selection at larger spatial scales using geographic information system data, however, could reveal important patterns in habitat selection between the microhabitat components evaluated herein and larger scale distributional patterns (Rose et al. 2020).

Demographic information is an essential component of effective conservation of wildlife. Our estimate of annual survival indicates that about half of adult spadefoots breeding in 1 year would be expected to survive until the next breeding season, at least under similar conditions to those at our study sites in a relatively wet year. The relative importance of adult survival to western spadefoot population growth could be further elucidated using population models as done for many other amphibians (Caswell 2001, Trenham and Shaffer 2005, Canessa et al. 2014, Earl 2019, Rose et al. 2021).

In contrast to most aspects of the terrestrial ecology of spadefoots, adult survival did not vary between our study sites, though this lack of a difference could be caused by a small sample of observed deaths ($n=10$, excluding 1 spadefoot that died in a pitfall trap) and by the sometimes extreme interval censoring (i.e., the difference between the last observation where the spadefoot was observed alive and the first observation where the spadefoot was observed dead sometimes spanned months), which increases uncertainty in time-to-event models. Nonetheless, our piecewise constant hazard model indicated

that, as expected, survival was lower in the winter and spring active season than during summer and fall aestivation.

The greater risk of mortality of western spadefoots in the active season is likely related to their behavior. Western spadefoots are more likely to be visible on the surface and to move during the winter and spring, and this surface activity likely results in greater risk of predation for adult spadefoots. Indeed, of the 10 spadefoots that died of seemingly natural causes, 6 were definitely or likely eaten by predators. We did not know the exact time of death for spadefoots, but identified predators (a rattlesnake and birds of prey) are unlikely to have unearthed burrowed spadefoots, further suggesting a positive link between surface activity and mortality.

Spadefoot surface activity and movement patterns were positively related to conditions that reduced the risk of desiccation. Surface activity of western spadefoots was most likely when air temperatures were cool, at night, and during the winter and spring. These patterns are consistent with other studies of western spadefoots (Richmond et al. 2016, Baumberger et al. 2019). The higher mean probability of surface activity at Limestone Canyon than at Crystal Cove was likely because we tracked most western spadefoots at Limestone Canyon for a shorter time period during and immediately after the breeding season, when western spadefoots are more likely to be active. In contrast, tracking for many individuals at Crystal Cove continued into the summer and even autumn, when surface activity was less likely. Because we were unable to assess surface activity without physically locating western spadefoots, it is likely that they were surface active on many occasions that we did not detect them. Although we are unable to assess surface activity between observations if western spadefoots returned to the same burrow, those that moved to different burrows provided additional information about the conditions related to surface activity.

Western spadefoots moved relatively frequently during the late winter and early spring, with movement very likely during intervals with 50 mm or more of rain. The positive effect of relative humidity and negative effect of soil water content at 10 cm were of much smaller magnitude than the effects of date and amount of rain. Nonetheless, these contrasting effects of relative humidity and soil water content on the probability of movement suggest that western spadefoots are especially likely to move on wet nights following dry periods. These conditions might trigger emergence and movement to breeding pools by a large proportion of the population. Other explanations include moisture after dry periods eliciting foraging behavior or selection of a new burrow. These potential explanations are not mutually exclusive, and the cause of movement might vary depending on time of year, amount of precipitation, duration of aestivation, or nutritional status of the western spadefoot.

Although amount of rain was the strongest predictor of whether a spadefoot would move, wetness, as measured by relative humidity and soil water content, was a stronger predictor of how far western spadefoots moved. The positive relationship between wet conditions and movement rates was likely because more moisture reduces the risk of desiccation

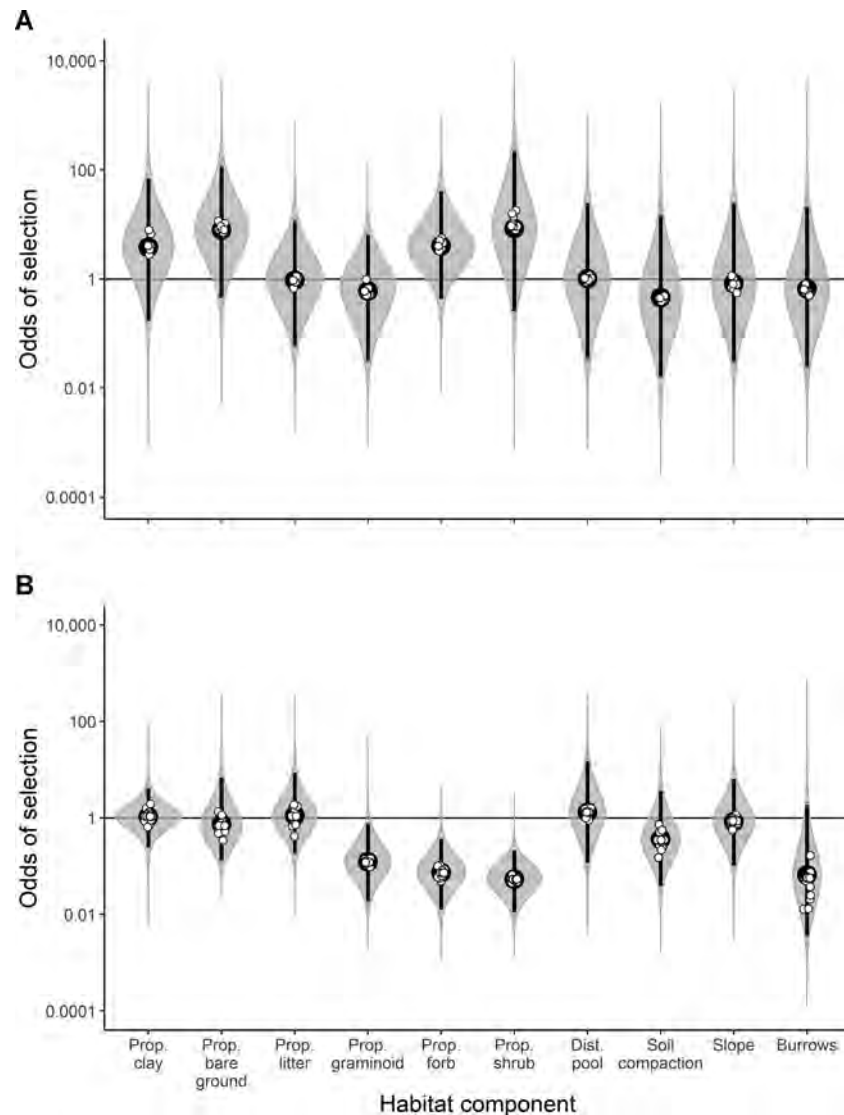


Figure 9. Western spadefoot odds of selection based on selected habitat components at A) Limestone Canyon and B) Crystal Cove State Park, California, USA, 2018–2019. Shaded areas represent posterior distributions, black dots represent posterior medians, and vertical bars represent 95% credible intervals. White points indicate estimated median odds of selection for individual spadefoots. The horizontal line at 1 represents no selection for or against the habitat component. Prop. = proportion; Dist. = distance. The effect size for proportions was scaled to a unit representing a change of 0.1; other variables were standardized to mean = 0, standard deviation = 1.

while western spadefoots are active on the surface. Perhaps because of the generally moister conditions near the coast, mean movement rates at Crystal Cove were higher than those at Limestone Canyon. Nonetheless, movement rates averaged <10 m/day across sites and environmental conditions. Two individuals, however, exhibited single large movements of >100 m/day, with a maximum movement rate of 154 m/day.

The ecology of western spadefoots is in many ways similar to that of other arid-region amphibians dependent on ephemeral resources. The low movement rate of western spadefoots in our study was similar to that of arroyo toads (*Anaxyrus californicus*) in coastal southern California (Mitrovich et al. 2011). In our relatively wet study year, western spadefoots moved farther from breeding sites than arroyo toads did in 2004, although western spadefoots at Crystal Cove in a dry year (Baumberger et al. 2019)

remained nearly as close to breeding sites as arroyo toads (Mitrovich et al. 2011). Neither species appears to disperse readily as adults; even in a wet year, adult arroyo toads did not disperse away from the stream channel and terrace habitats (Griffin and Case 2001). The dependence of adults on reliable seasonal water availability likely increases the susceptibility of desert amphibians to extirpation caused by increasingly stochastic precipitation in California, including more severe flood and drought cycles (Swain et al. 2018).

MANAGEMENT IMPLICATIONS

The spatial separation between breeding pools and adult terrestrial home ranges of western spadefoots suggests that fragmentation between these 2 essential habitat components can be detrimental to their populations. Furthermore, the extensive variation in activity periods

and movements between sites and years suggests that a one-size-fits-all approach to western spadefoot conservation is likely insufficient. Perhaps most important, differences between this study and others suggest that even within the same sites, western spadefoot behavior varies drastically between years. Thus, a study conducted in one or a few years will likely fail to capture the temporal variation in western spadefoot ecology. Conserving species with complex life histories, particularly those whose life stages need different habitats, requires understanding the requirements of each life stage and how those requirements vary in space and time.

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