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Title

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Permalink

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Journal

Journal of Wildlife Management, 80(4)

ISSN

0022-541X

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Publication Date

2016-05-01

DOI

10.1002/jwmg.1054

Peer reviewed

Habitat Selection by Juvenile Mojave Desert Tortoises

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ABSTRACT Growing pressure to develop public lands for renewable energy production places several protected species at increased risk of habitat loss. One example is the Mojave desert tortoise (*Gopherus agassizii*), a species often at the center of conflicts over public land development. For this species and others on public lands, a better understanding of their habitat needs can help minimize negative impacts and facilitate protection or restoration of habitat. We used radio-telemetry to track 46 neonate and juvenile tortoises in the Eastern Mojave Desert, California, USA, to quantify habitat at tortoise locations and paired random points to assess habitat selection. Tortoise locations near burrows were more likely to be under canopy cover and had greater coverage of perennial plants (especially creosote [*Larrea tridentata*]), more coverage by washes, a greater number of small-mammal burrows, and fewer white bursage (*Ambrosia dumosa*) than random points. Active tortoise locations away from burrows were closer to washes and perennial plants than were random points. Our results can help planners locate juvenile tortoises and avoid impacts to habitat critical for this life stage. Additionally, our results provide targets for habitat protection and restoration and suggest that diverse and abundant small-mammal populations and the availability of creosote bush are vital for juvenile desert tortoises in the Eastern Mojave Desert. © 2016 The Wildlife Society.

KEY WORDS California, development, *Gopherus agassizii*, habitat selection, Mojave Desert, renewable energy, restoration, solar energy.

Managing wildlife is often more about managing habitat than managing animals. Appropriate habitat management, however, requires knowing which habitat animals use to meet their needs. Studies that focus on third-order habitat selection (Johnson 1980)—habitat selection by animals within their home ranges—can reveal species' resource requirements; identify factors that affect its fitness, demography, and distribution; and thereby enable focused protection or restoration of habitat features (Manly et al. 2002). Such information is especially important for managing and recovering sensitive status species, defined as species protected by law or treated as being of conservation concern by management agencies; often, habitat needs of such species can affect regulatory decisions (Lovich and Ennen 2011).

The desert southwest of the United States lies at the center of many important regulatory decisions that affect wildlife habitat. This is influenced primarily by the strong and growing interest in developing public lands for renewable energy (Lovich and Ennen 2011) and by continued urban growth and occasional expansion of military training grounds (Darst et al. 2013). The conversion of native desert habitats for human land use affects many sensitive status species but also creates opportunities to make proposed development more sustainable. A better understanding of how habitat characteristics shape distributions of special status species can inform development planning to minimize impacts and help locate affected species (Stoms et al. 2013). In addition, understanding the habitat needs of species that are negatively affected by development provides actionable targets for habitat preservation or restoration as part of a larger portfolio of management or recovery options (Darst et al. 2013).

The Mojave desert tortoise (*Gopherus agassizii*, hereafter desert tortoise or tortoise) is an example of a protected species with sensitive status that frequently factors into policy

debates about public land development in the Southwest (Lovich and Ennen 2011). Development planning on public lands must consider impacts to the desert tortoise because of its status as threatened under the United States Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 2011). The desert tortoise was listed in 1990 as threatened in part because of population declines that ranged from 3% to 59% per year (USFWS 1994). Population densities have remained low, averaging 8.6 tortoises per km^2 from 2001 to 2007 (USFWS 2011), and recovery has remained elusive. Recovery is hampered in part by an incomplete understanding of its ecology. In particular, the ecology of juvenile North American tortoises is largely unknown (Morafka 1994, Smith et al. 2006). Field surveys generally fail to detect juveniles because of their small size and secretive behavior (Anderson et al. 2001, Freilich et al. 2005). As a result, most studies of North American tortoises have focused on adults. This knowledge gap represents a notable deficiency given the need for successful juvenile recruitment to promote recovery and persistence of wild desert tortoise populations (Reed et al. 2009). To address this gap, we conducted a study of the habitat selection of juvenile desert tortoises in the eastern Mojave Desert, California, USA. Because juvenile tortoises are encountered infrequently in the wild, we allowed female tortoises to nest in protected outdoor enclosures and then examined habitat selection of juveniles released in maternal habitats shortly after hatching (0–18 months). Our objective was to identify habitat characteristics preferred by juvenile tortoises to better guide habitat management for this declining species.

STUDY AREA

We conducted this study in the Eastern Mojave desert tortoise recovery unit in the northeastern portion of the Mojave National Preserve, San Bernardino County, California (UTM 11S 650787 E, 3913389 N). This area of the preserve is largely a flat valley bottom with little topography or human land use except for 2 paved roads and a dirt road. It lies in the Ivanpah Valley desert tortoise critical habitat unit (USFWS 2011). Elevation across the study site ranged from 800 m to 1,050 m and the habitat was dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) as is typical of many parts of the Mojave Desert (Pavlik 2008). The study site also included patches of big galleta (*Pleuraphis rigida*) and occasional Joshua tree (*Yucca brevefolia*), Mojave yucca (*Y. schidigera*), and littleleaf ratany (*Krameria erecta*) along with many other less abundant perennial plants in the community. The soil was largely a homogeneous mix of coarse-loamy torriothents and fine-loamy orthents with occasional mixed cobble (65–250-mm grain size) but very few boulders (>250 mm) and no exposed caliche layers. Temperatures range from typical overnight lows of 1°C in winter to daytime highs of 40°C in summer, with annual precipitation ranging from 8 cm to 18 cm, falling primarily in winter with as much as 34% of precipitation coming during summer monsoonal rains (Hereford et al. 2006). Vertebrate fauna include numerous rodents such as the desert woodrat (*Neotoma lepida*), round-tailed ground squirrel (*Xerospermophilus tereticaudus*), and Merriam's kangaroo rat (*Dipodomys merriami*), the latter 2 of which frequently dig burrows. Possible predators of juvenile desert tortoises at the study site include species such as American badger (*Taxidea taxus*), kit fox (*Vulpes macrotis*), coyote (*Canis latrans*), common raven (*Corvus corax*), and raptors such as shrikes (genus *Lanius*) and hawks (genus *Buteo*), among others.

METHODS

Beginning May 2011, we captured, marked, and radio-tagged adult female desert tortoises at the study site. We radio-tracked females ≥2 times/month during April–October each year when they were most active, and 1 time/month in November–March when their activity was reduced. In 2011–2013, we radiographed females (Diagnostic Imaging Systems, Poskam, Colorado, USA; 60 kvp, 0.8 mAS, 74 cm focal length) every 7–14 days from mid-April through early July when they were likely to produce their first clutch of eggs. When calcified eggs were visible on radiographs (Gibbons and Greene 1979), we placed females individually in outdoor predator-proof nesting pens at the Ivanpah Desert Tortoise Research Facility (IDTRF) 20 km northeast of the study area. We provided them with shelter from temperatures via hand-dug burrows and natural shrub cover inside the pens. We immediately returned females to their last burrow location after they laid eggs; females that did not lay eggs within 30 days were also released at their last burrow location. We allowed eggs to incubate in the ground where they were laid by females. Beginning August–September each year, approximately 80 days after nesting, we searched pens daily for emerging hatchlings. We removed hatchlings from nesting pens when we found them and immediately weighed (to nearest 0.1 g), measured (mid-line carapace length [MCL] to nearest 0.1 mm), and individually marked each one by notching the marginal scutes. We released juveniles at the field site where mothers were collected in fall 2012 (6 12-month-old juveniles, 12 newly hatched juveniles), spring 2013 (6 18-month-old juveniles, 12 6-month-old juveniles), and fall 2013 (10 newly hatched individuals; $n = 46$ released animals). We housed juveniles that we did not release immediately at the IDTRF in 10×10-m outdoor field enclosures that excluded predators and we minimized further contact by researchers before release. We staggered releases to keep data collection manageable and to allow continuous collection of habitat data despite attrition of study animals via mortality or less frequently, transmitter failure. We assumed that variation in the length of time juveniles were held captive prior to release (0–18 months) did not affect habitat selection, given that earlier work reported no evidence of homing in neonates released from a hatchery, in contrast to older juveniles held captive for 6–8 years (Hazard and Morafka 2002).

Immediately before release, we weighed and measured each juvenile tortoise. We attached a small very high frequency (VHF) transmitter (Holohil Systems Limited, type BD-2, 4-month battery life, 1.5 g, Carp, Ontario, Canada) to the fourth or fifth vertebral scute of each released animal using

liquid 5-minute 2-part epoxy. The combined weight of transmitter and epoxy was <10% of tortoise body mass (Beaupre et al. 2004). Prior to release, we checked each tortoise to ensure it could right itself with the attached transmitter. We released animals under cover at sites in the area where females were collected during weeks where daytime temperatures did not exceed 32°C or fall below 10°C. We subsequently radio-tracked released juveniles twice each week when they were active, typically March–May each spring and late July–November each fall. We tracked animals weekly or bi-weekly during other times of the year when they were less active. When an animal was located, we recorded its location with a handheld global positioning system (GPS; ±3 m accuracy). We collected habitat data for each animal on each occasion the animal had moved ≥10 m from its previous location. We collected habitat data beginning shortly after the initial release of animals in October 2012 through October 2014. We collected data March–May and late July–November, when ephemeral annual and perennial forbs and grasses were flowering and available as a forage resource for desert tortoises. We conducted all animal handling in full accordance with approved Institutional Animal Care and Use Committee protocols (no. 15997 to the University of California, Davis; no. A2010-04-059-Y3-A0 to the University of Georgia) and all relevant permits (USFWS no. TE-17838A; California Fish and Wildlife no. SC-0011221; National Park Service Mojave National Preserve no. MOJA-2011-SCI-0023).

We collected habitat data in a case-control fashion. We considered an animal's observed location as the case and a random point as a temporally and spatially paired control. Each paired random control point was located 200 m, a distance at which juveniles in the study region were capable of moving within 1 day, from the animal's location at a random azimuth. We collected habitat data at both locations using the same protocol on the same day as described below.

We recorded whether each animal was at a burrow or away from a burrow for each tracking event, being careful to identify each inhabited burrow (hereafter used burrow point) or to detect the animal visually when it was active away from a burrow (hereafter used surface point). At each used or random point, we recorded whether the animal or the center of the random point was under a cover object (typically a perennial or large annual plant). For each point, we measured the distance to the nearest wash or rivulet and the distance to the center of the nearest 3 perennial plants (≥10 cm height). Washes were areas incised into the desert floor that supported water flow during heavy rains. Rivulets were smaller drainages that supported some water flow during rains but which were not deeply incised. We also counted the number of small-mammal burrows, typically those of rodents or rarely kit foxes or American badgers, within a 1-m^2 plot centered at the tortoise or random point location.

At each plot, we established 6 transects that extended from the plot center at 60° azimuths, with the first transect having an azimuth in the direction the observed tortoise was facing or the direction of the burrow entrance in which a tortoise was found. Along each 5-m transect at 1-m intervals (0 m recorded only on first transect; total 31 points), we recorded surface composition, including ground cover, substrate type, and presence of a dry wash or rivulet following the methods of Grandmaison et al. (2010). We categorized ground cover in a hierarchical manner: live perennials and live and dead annual vegetation, followed by litter or duff, and finally bare soil or rock if no vegetation was present at the point. Where vegetation was present, we recorded the type of live annual vegetation (grass or forb) and its height (cm). Substrate types included fine soil (particle size <0.05 mm), sand (0.05–2 mm), gravel (3–64 mm), cobble (65–250 mm), boulder (>250 mm), and mixed substrate. We recorded the perennials that intersected each transect line and their distances to center. At 5 1 × 1-m quadrats placed randomly along the 6 transects with 1 located at the center of the plot, we recorded percent perennial and annual vegetation cover, annual species richness, and substrate type. Finally, we recorded the species of the first 3 perennial plants closest to the tortoise or random point.

Statistical Analysis

We used a Bayesian analysis of hierarchical case-control logistic regression models, which treated used points as the cases and the paired random points as controls. The model was hierarchical in that it included an individual-level random effect for model coefficients (the paired case-control model does not contain an intercept). The inclusion of these random effects properly places the individual as the sample unit, from which observations are considered sub-samples (Gillies et al. 2006). Treating the individual as a random effect also weights individuals by the number of locations, resulting in individuals that contribute fewer data being pulled toward the population mean (i.e., shrinkage; Gelman and Hill 2006). The output of this model is a resource selection function, which is the relative probability that a resource unit will be used, given its covariate profile (Keating and Cherry 2004).

We fit 2 separate logistic regression models to the data to 1) estimate the selection of habitat components from animals at (or in) burrows, and 2) estimate the selection of habitat components from animals away from burrows. We modeled used burrow points and used surface points separately because habitat use in these instances may reflect different selection processes by the animals. Animals likely select burrows because of characteristics that identify them as a valuable refuge, whereas animals away from burrows may be selecting foraging areas, areas that present the lowest cost to movement, or areas that enhance crypsis. We excluded variables with a Pearson correlation coefficient ≥ |0.60| with another variable in the model to reduce collinearity among habitat variables. On such occasions, we retained in models the variable hypothesized to have the largest direct effect on habitat selection and excluded the other correlated variable. We also excluded any habitat characteristics for which >50% of the used and random observations were 0. This resulted in the exclusion of the identity of perennial species from logistic regression models, necessitating the use of a separate analysis

described below to evaluate which perennial plants contributed to patterns of habitat selection. The final model sets included 18 habitat characteristics in the logistic regression models (Table 1).

We analyzed models using standard Markov chain Monte Carlo (MCMC) methods (Gelman et al. 2004). The predictor variables in each model were a vector of differences between the used and random pairs for each variable at each location. We selected vague priors, with N (0, 3.16; $\bar{x}$, SD) priors on model coefficients and a uniform density U (0, 10) priors on standard deviations, both on the logit scale. Posterior inference was based upon 5 chains of 100,000 iterations each, after a burn-in period of 100,000 iterations. We thinned each chain by a factor of 50, keeping 10,000 iterations to describe the posterior distribution of each parameter. We analyzed each model with JAGS 3.4.0 (Plummer 2013) called from R 3.1.0 (R Core Team 2014) using the package rjags (Plummer 2014). We diagnosed convergence by visual examination of history plots and using the Gelman-Rubin statistic (Gelman and Rubin 1992); we observed no evidence for lack of convergence ($\hat{R} < 1.02$ for all monitored parameters).

We also used canonical analysis of principal coordinates (CAP) to further examine differences in habitat between used points and paired random points (Anderson and Willis 2003). This analysis first uses a principal coordinate analysis (PCO) to reduce multiple habitat characteristics into composite variables that best correlate with the presence or absence of an animal at a given point, and that capture the most variance in the data. This is followed by a canonical discriminant analysis. The canonical discriminant analysis determines whether the primary PCO axis can be used to differentiate between used points and paired random points. The CAP method uses a leave-one-out approach to determine the misclassification error of all points in the

model as a measure of the goodness of fit of the model. Finally, a permutation test is used to determine whether there is a significant difference in multivariate space between used points and paired random points along the primary canonical axis. Anderson and Willis (2003) provide complete details about CAP.

Because ordination methods cannot account for repeated measures made on individuals, we used the mean habitat characteristics of used points for each tortoise and of its paired random points in CAP. We transformed all data to $\ln(x + 1)$ with no standardization and the analysis was based on Bray–Curtis distance for calculating dissimilarities. We performed 2 CAP analyses: one for used burrow points (data for 45 tortoises) and a separate one for used surface points (data for 35 tortoises). Habitat characteristics used in CAP analyses included the same variables as used in the logistic regression case-control analysis described above (Table 1). Additionally, we included mean counts for each of the following perennial plant species identified among the 3 nearest a point (observed or random point): white bursage, burrobrush (*Ambrosia salsola*), silver cholla (*Cylindropuntia echinocarpa*), diamond cholla (*C. ramosissima*), sacred thorn-apple (*Datura wrightii*), cottontop barrel cactus (*Echinocactus polycephalus*), Nevada Mormon tea (*Ephedra nevadensis*), littleleaf ratany, creosote bush, Anderson's desert thorn (*Lycium andersonii*), hoary aster (*Machaeranthera canescens*), bush muhly (*Muhlenbergia porteri*), beavertail cactus (*Opuntia basilaris*), big galleta, bladder sage (*Salazaria mexicana*), and Mojave yucca.

RESULTS

We collected 356 observations from 46 radio-tracked juveniles from 22 October 2012 to 16 October 2014. Of these, 201 observations were made on 45 animals that were found at burrows when they were radio-tracked. In contrast,

Table 1. Mean odds of use by juvenile Mojave desert tortoises in the eastern Mojave Desert, California, USA from October 2012 to October 2014 based on habitat characteristics at used burrow points compared to paired random points. Values in parentheses after each habitat characteristic indicate the scale of measurement followed by the scale at which we calculated odds of use, with 10% indicating a 10% increase in coverage. An asterisk (*) next to the median odds of use denotes credible intervals that do not overlap 1.

Habitat characteristic	Used burrow points		Random points		$\bar{x}$ odds of use		
	$\bar{x}$	Range	$\bar{x}$	Range	Median	0.025 quantile	0.975 quantile
Presence of cover	0.83	0–1	0.12	0–1	3,806.07*	24.11	>10,000
No. small-mammal burrows per m^2	2.22	0–9	0.04	0–10	7,356.24*	205.02	>10,000
Distance to wash (cm; 1 m)	372.54	0–6,500	433.40	0–4,700	0.59	0.20	1.13
Perennial species richness	3.29	1–9	3.06	1–7	1.72	0.05	63.97
$\bar{x}$ distance to closest 3 perennials (cm; 10 cm)	77.86	8–270	95.38	7–390	0.92	0.80	1.03
$\bar{x}$ percent cover perennials in quadrats (1%; 10%)	23.60	<1–65	16.15	<1–53	95.10*	3.06	4,255.73
% cover dead annuals (1%; 10%)	15.58	0–77	15.15	0–61	0.14	0.00	12.50
% cover live annuals (1%; 10%)	7.33	0–71	6.00	0–52	32.75	0.24	4,311.09
% cover litter and debris (1%; 10%)	5.04	0–32	4.82	0–26	2.04	0.01	363.39
% cover live perennials (1%; 10%)	1.87	0–29	1.27	0–16	0.10	0.03	3,416.11
% cover rock (1%; 10%)	11.50	0–48	10.87	0–48	10.82	0.12	1,000.22
% cover bare soil (1%; 10%)	36.29	3–81	43.10	3–84	0.05	0.00	1.89
% substrate fine soil (1%; 10%)	28.40	0–100	33.97	0–100	0.76	0.02	17.52
% substrate gravel (1%; 10%)	13.22	0–74	13.99	0–77	0.52	0.01	28.18
% substrate sand (1%; 10%)	24.11	0–100	23.77	0–100	0.44	0.01	17.25
% no. wash or rivulet (1%; 10%)	86.31	13–100	89.18	10–100	0.10	0.00	4.27
% rivulet (1%; 10%)	7.87	0–42	8.17	0–55	0.74	0.01	50.79
$\bar{x}$ % cover annuals in quadrats (1%; 10%)	5.34	0–72	5.37	0–73	0.64	0.00	100.57

155 observations were made on 35 animals that were found away from burrows when they were radio-tracked. We found that juvenile desert tortoises showed strong evidence of selection for and against several habitat characteristics in the eastern Mojave Desert; patterns were relatively consistent despite using 2 different methods to analyze the data. Habitat selection, however, differed depending on whether animals were at or away from burrows when they were located during radio-tracking.

The analysis of used burrow points using logistic regression identified evidence for selection of 3 habitat characteristics: the presence of cover, small-mammal burrow density, and perennial plant cover (Table 1). The presence of cover increased the odds of selection by juvenile tortoises in burrows by 3,806 times. For every additional small-mammal burrow/1 m^2, the odds of selection by juvenile tortoises in burrows increased by 7,356 times. For every 10% increase in mean percent cover of perennials, the odds of selection by juvenile tortoises in burrows increased by 95 times. No other habitat characteristics were identified in this model as being significantly associated with used burrow points.

The CAP analysis of mean habitat characteristics at used burrow points and paired random points identified 6 PCO axes that achieved the maximum proportion of correct allocations (85.6%). These 6 PCO axes explained 83.2% of the variability in the original dissimilarity matrix. The CAP yielded 1 canonical axis with a squared correlation of $\partial^2 = 0.58$. The canonical test revealed a significant difference in the multivariate space between used burrow points and paired random points along the primary canonical axis ($P \leq 0.001$ using 9,999 permutations). The correlations of the original habitat characteristics with canonical axis 1 showed that used burrow points were associated with a greater number of small-mammal burrows within 1 m^2, had a greater average percent coverage of perennial plants along transects, a greater number of creosote bush among the 3 closest perennials, and a greater average proportion of washes, rivulets, and mixed fine soil and gravel along the transects than did paired random points (Table 2). In contrast, random points had fewer areas with washes along transects and had more white bursage among the closest 3 perennials than did used burrow points (Table 2).

The analysis of used surface points using logistic regression identified evidence for selection of 2 habitat characteristics, which differed from those identified in the analysis of used burrow points: distance to wash and mean distance to the 3 nearest perennial plants (Table 3). Juvenile tortoises on the surface were 2.9 times more likely to select a location for every 1 m that it was closer to a wash, and 1.2 times more likely to select a location for every 10 cm that it was closer to the 3 nearest perennial plants (Table 3). No other habitat characteristics were identified in this model as being significantly associated with used surface points.

The CAP analysis of mean habitat characteristics at used surface points and paired random points identified 8 PCO axes that achieved the maximum proportion of correct allocations (52.9%). These 8 PCO axes explained 93.2% of the variability in the original dissimilarity matrix. The CAP yielded 1 canonical axis with a squared correlation of $\partial^2 = 0.12$. The canonical test found no significant difference in the multivariate space between used surface points and paired random points along the primary canonical axis ($P = 0.39$ using 9,999 permutations). Because there was no difference between used surface points and paired random points, correlations of individual habitat characteristics with canonical axis 1 are not described.

DISCUSSION

Understanding how desert tortoises select habitat is important when making decisions about land use that affects the species or the habitat on which it relies. To date, studies of habitat selection in Mojave desert tortoises have focused on second- or first-order habitat selection (Johnson 1980) at large spatial scales to identify factors associated with tortoise occupancy across hundreds of hectares or to predict range-wide habitat suitability (Andersen et al. 2000, Nussear et al. 2009). These types of studies can be useful for avoiding impacts to the species, provided that decision-makers heed such information and guide development toward lower quality areas. Unfortunately, the majority of siting decisions still place utility-scale solar energy infrastructure in areas deemed incompatible (Hernandez et al. 2015), a term describing areas that present development challenges owing to environmental conflicts or resource constraints. A plurality of these sites lie on undeveloped public lands with intact natural ecosystems, often within 5–7 km of protected areas (Hernandez et al. 2015). They often include areas of high predicted habitat suitability for desert tortoises (Nussear et al. 2009), or other areas with high conservation value (Cameron et al. 2012). It may, however, be possible to adjust

Table 2. Habitat characteristics associated with juvenile Mojave desert tortoises in burrows with correlations of $|r| \geq 0.20$ with canonical axis 1 from a canonical analysis of principal coordinates, along with their mean values at used burrow points and paired random points from a study in the eastern Mojave Desert, California, USA, October 2012–October 2014.

Habitat characteristic	Correlation with canonical axis 1	$\bar{x}$ at used burrow points	$\bar{x}$ at random points
No. small-mammal burrows per m^2	0.86	2.58	0.55
$\bar{x}$ % coverage of perennials	0.54	23.36	16.53
No. creosote bush in 3 closest perennials	0.47	0.81	0.61
$\bar{x}$ proportion of washes	0.29	0.07	0.03
$\bar{x}$ proportion of washes and rivulets combined	0.25	0.15	0.11
$\bar{x}$ proportion of mixed fine soil and gravel	0.22	0.33	0.29
$\bar{x}$ proportion of area without washes	−0.23	0.85	0.89
No. white bursage in 3 closest perennials	−0.42	1.33	1.70

Table 3. Mean odds of use by juvenile Mojave desert tortoises in the eastern Mojave Desert, California, USA from October 2012 to October 2014 based on habitat characteristics at used surface points compared to paired random points. Values in parentheses after each habitat characteristic indicate the scale of measurement followed by the scale at which we calculated odds of use, with 10% indicating a 10% increase in coverage. An asterisk (*) next to the median odds of use denotes credible intervals that do not overlap 1.

Habitat characteristic	Used surface points		Random points		$\bar{x}$ odds of use		
	$\bar{x}$	Range	$\bar{x}$	Range	Median	0.025 quantile	0.975 quantile
Presence of cover	0.53	0–1	0.19	0–1	144.66	0.79	26,626
No. small-mammal burrows per m²	0.09	0–10	0.04	0–7	12.11	0.20	883.80
Distance to wash (cm; 1 m)	333.90	0–5,500	333.50[a]	0–7,500	0.39*	0.08	0.86
Perennial species richness	3.35	1–9	3.24	1–8	1.94	0.04	111.47
$\bar{x}$ distance to closest 3 perennials (cm; 10 cm)	84.59	13–267	94.85	7–350	0.90*	0.78	1.00
$\bar{x}$ % cover perennials in quadrats (1%; 10%)	19.32	0–65	16.30	0–55	4.19	0.08	255.15
% cover dead annuals (1%; 10%)	11.70	0–68	12.67	0–74	0.76	0.01	59.80
% cover live annuals (1%; 10%)	8.32	0–74	8.05	0–65	4.45	0.04	437.17
% cover litter and debris (1%; 10%)	4.94	0–32	5.16	0–29	0.17	<0.01	39.77
% cover live perennials (1%; 10%)	1.99	0–39	2.07	0–55	1.24	<0.01	337.48
% cover rock (10%)	14.22	0–71	11.57	0–87	15.13	0.20	1,025.48
% cover bare soil (1%; 10%)	40.25	0–90	43.22	0–87	0.59	0.01	28.12
% substrate fine soil (1%; 10%)	27.00	0–100	29.57	0–100	0.07	<0.01	4.62
% substrate gravel (1%; 10%)	18.81	0–90	18.06	0–90	0.68	0.01	72.41
% substrate mixed gravel and fine soil (1%; 10%)	22.57	0–87	20.95	0–87	3.29	0.05	263.73
% substrate sand (1%; 10%)	28.20	0–97	28.41	0–100	0.21	<0.01	13.19
% rivulet (1%; 10%)	9.49	0–68	8.57	0–52	1.71	0.04	87.85
$\bar{x}$ % cover annuals in quadrats (1%; 10%)	6.42	0–82	5.38	0–61	20.49	0.10	3,517.23

[a] The distribution of distance to wash was highly skewed, and a normal distribution was a poor fit to the data. The mean of log-transformed distance to wash for surface random points was 131.2 cm.

siting of planned development at a finer scale by altering footprints of proposed designs. For example, the footprint of the Ivanpah Solar Electric Generating System was reduced to some extent in areas deemed highly suitable for desert tortoises (U.S. Bureau of Land Management 2010). For these reasons, fine-scale studies of third-order habitat selection, as represented by the present study, are useful for minimizing impacts when designing and locating sites and may also guide restoration when reviewing mitigation options.

To examine fine-scale habitat selection in desert tortoises, we used 2 analytical approaches whose results were generally complementary. Conditional logistic regression models accounted for repeated observations on individuals with random effects but could not include plant species identities in the model structure. Canonical analysis of principal coordinates could not account for repeated measures or random effects but could accommodate plant species identities. Slight variation in the results of the 2 analyses was expected, given that a CAP analysis partitions variation in the data to accentuate habitat differences between groups. For example, because creosote and white bursage were included and were significant in the CAP analysis and explained much of the variation in the data between the used burrow points and paired random points, some other habitat factors were not identified as significant in the CAP analysis, whereas they were significant in the logistic regression models. Results from the 2 methods analyzing used burrow points were otherwise qualitatively similar, providing added support for the overall findings. The lack of significant results from the CAP analysis using data from used surface points may stem from low power (35 paired points in the CAP versus 155 in the logistic regression model). Reduction in the number of data points by using individual means in CAP was necessitated by the inability of this analysis to handle repeated measures.

The habitat characteristics selected by juvenile tortoises can provide insight into environmental factors important for their survival. Perennial plants were selected by tortoises when they were at burrows. Among these, creosote in particular was most often associated with tortoise habitat use. Creosote bush likely provides at least a few key resources to juvenile tortoises. First, they tend to be among the largest perennial plants by volume in the creosote-white bursage communities that dominate much of the Mojave Desert (Lathrop and Rowlands 1983, Barbour et al. 2007). Thus, they provide the greatest canopy to buffer animals from heat and excessive water loss during warmer parts of the day and year. Shade plants are important determinants of movement and activity of tortoise species in arid environments (Moulherat et al. 2014). In fact, environmental exposure may be a strong source of mortality in desert tortoises (Lovich et al. 2014), and this risk is likely higher for juveniles because they appear to be at greater risk of water loss than adults (Wilson et al. 2001). Creosote bush may also limit predation by concealing tortoises, making them harder to find by visual predators such as raptors and ravens. Our findings agree with a study on adult Sonoran desert tortoises (*G. morafkai*) that reported that availability of cover plants was the single most important factor explaining habitat selection in the Sonoran Desert (Grandmaison et al. 2010). Other larger scale habitat selection studies have similarly reported that characteristics associated with shelter sites are important for Mojave desert tortoises, such as loamy soils for burrows (Andersen et al. 2000), and are important for Sonoran desert tortoises, such as deeply incised washes that

provide exposed concrete-like caliche caves for refuge (Averill-Murray and Averill-Murray 2005, Riedle et al. 2008). The present study site lacks the exposed caliche layers typical of Sonoran Desert habitats.

Creosote bush is likely also critical to juvenile desert tortoises indirectly because it supports small mammals that benefit juvenile tortoises. Many desert-dwelling small mammals rely on creosote bushes for food and shelter, including the desert woodrat (Karasov 1989), round-tailed ground squirrels (Walsberg 2000), and the especially abundant Merriam's kangaroo rat (Nagy and Gruchacz 1994). Juvenile tortoises in turn appear to rely on diverse and abundant small-mammal communities that excavate extensive burrow complexes near the base of creosote bushes. In the present study, the vast majority of radio-tracked juvenile tortoises made extensive use of small-mammal burrows and often repurposed them for their own use; very few of the burrows that juvenile tortoises used appeared to have been dug exclusively by the tortoise. Hazard and Morafka (2002, 2004) reported that neonate and juvenile desert tortoises in the central Mojave Desert almost exclusively used existing rodent burrows for shelter. Similarly, Riedle et al. (2008) reported that adult Sonoran desert tortoises used white-throated woodrat (*Neotoma albigula*) middens in the absence of caliche caves. Both our logistic regression analysis and CAP analysis indicated that juvenile tortoises selected burrow locations with greater densities of small-mammal burrows than found at random points, suggesting that small-mammal communities and the burrows they create are important for persistence of juvenile tortoises, and thus recruitment into adult populations.

Although desert tortoises do not typically forage on creosote bush or its seeds (Jennings and Berry 2015), creosote bush still indirectly provides added foraging opportunities for desert tortoises. Biomass of annual plants and smaller perennial plants is often greater in the canopy zone beneath creosote bush than outside the dripline (Muller 1953, Rowlands 1986); intershrub spaces also appear to have low biomass of annuals (Reichman 1984, Rowlands 1986, Jennings and Berry 2015). Although we recorded several measures of annual plant abundance (i.e., proportion of ground covered by annual plants, no. transects intersecting annual plants), there was no direct support for selection of these elements by juvenile tortoises in any of our models. Annual plant germination and biomass, however, can be highly variable among seasons and years (Beatley 1974, Andersen et al. 2000); it may be easier or more reliable for juvenile desert tortoises to select areas with creosote bush and higher perennial plant density that correlates with foraging resources rather than trying to track annual plants themselves.

Despite white bursage being a co-dominant perennial plant alongside creosote bush, the habitat selection models showed that used burrow points were more likely to be found in areas with fewer white bursage plants than at paired random points. White bursage and creosote bush often compete for resources and can displace one another (Fonteyn and Mahall 1978); these 2 plants are often evenly spaced as a result

(Wallace et al. 2000). Thus, selection by juvenile desert tortoises against white bursage probably reflects the animals' greater affinities for the larger and less numerous creosote bush for the aforementioned reasons rather than any specific avoidance of smaller white bursage plants per se.

Washes were an additional habitat characteristic for which there was evidence of tortoise selection. Habitat in areas of used burrow points tended to have more washes or rivulets than that found at paired random points based on the CAP analysis. Also, at used surface points, tortoises were closer to washes or rivulets than were paired random points. Although Grandmaison et al. (2010) reported a similar pattern of selection for washes by adult Sonoran desert tortoises, their result likely reflected a different selection process than that taking place among the juvenile desert tortoises in the present study. Grandmaison et al. (2010) suggested that washes were important to Sonoran desert tortoises because they were deeply incised and offered ample shelter sites in the form of caliche burrows. The habitat where we tracked juvenile desert tortoises in the present study does not have any caliche burrows; even incised washes here were typically in highly friable, loose sandy soils. Instead, washes are likely important to juvenile desert tortoises in the Mojave Desert because they offer foraging opportunities and because they facilitate movement (Barrett 1990, Jennings 1997, Riedle et al. 2008). Jennings and Berry (2015), for example, reported that Mojave desert tortoises preferentially feed on rare plants such as the desert perennial widow's milkvetch (*Astragalus layneae*), which is found more frequently along washes than elsewhere. Reichman (1984) reported that within actual washes, seedbanks and desert plants are less common; washes thus may pose fewer obstacles to small desert tortoises as they move across the landscape. In fact, washes were a habitat characteristic associated with used surface points in the present study. Juvenile tortoises away from burrows were likely seeking corridors that facilitate movement or foraging. Because both washes and perennial plants were also correlated with used burrow points, it is probable that studies that focus only on desert tortoise burrow locations are succeeding in identifying important habitat characteristics. However, a higher frequency of spatial data collection, as offered by GPS loggers, for example, may provide additional insights into habitat characteristics associated with tortoise movements away from burrows.

MANAGEMENT IMPLICATIONS

As public policies continue to support and promote investment in utility-scale solar energy infrastructure, it will be important to provide information about species distributions and habitat selection that can inform decisions about land use. Findings from our fine-scale research on desert tortoise habitat use can help reduce infrastructure footprints, discover animals requiring relocation, and shape mitigation strategies. We have shown that avoiding development of specific areas with high perennial plant abundances, creosote bush, and more washes and rivulets can help conserve high-quality juvenile tortoise habitat and promote recovery of this protected species. When aiming to

manage or restore habitat for desert tortoises, ensuring recovery of small-mammal communities is likely to be critical for success. Additionally, enhancing cover by creosote bush via planting or fencing during restoration and mitigation efforts would likely benefit juvenile desert tortoises.

ACKNOWLEDGMENTS

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Associate Editor: Cynthia Paszkowski.