Western Wildlife 12:6–14 • 2025
Submitted: 6 December 2024; Accepted: 19 March 2025.

HABITAT USE AND BURROW ARCHITECTURE OF THE ENDANGERED SAN BERNARDINO KANGAROO RAT (*DIPODOMYS MERRIAMI PARVUS*): IMPLICATIONS FOR CONSERVATION

DEBRA M. SHIER[1,2,4]***, PAIGE C. MILLER***[1]***, CHRISTIAN A. BRAUDRICK***[3]***, AND RACHEL Y. CHOCK***[1]

[1]*Recovery Ecology, San Diego Zoo Wildlife Alliance, 15600 San Pasqual Valley Road, Escondido, California 92027, USA.*
[2]*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 921 Charles E. Young Drive South, Los Angeles, California 90095, USA*
[3]*Stillwater Sciences, 2855 Telegraph Avenue, Berkeley, California 94705, USA*
[4]*Corresponding author, e-mail: dshier@dzwa.org*

Abstract.—**Suitable habitat is critical for the survival and reproductive success of subterranean mammals, with burrow sites playing a key role in shelter, predator evasion, food storage, and environmental regulation. For endangered San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*), burrow construction in suitable locations within alluvial fan sage scrub habitat of California is essential. Here we investigate the habitat use and burrow architecture of *D. m. parvus*, whose range has been dramatically reduced by habitat loss. We collected field data through burrow casting, structural analysis, and habitat surveys. Results indicate that burrows are typically located in open, sandy areas under sparse shrub cover, with entrances that minimize soil displacement and provide escape from predators. Root cohesion likely played a key role in soil stability, as most of the burrows were adjacent to vegetation, and only small amounts of silt were measured in the soil. Burrows varied in complexity, with shallower depths that may result from relatively recent site disturbance. Anecdotal observations of burrow sharing between females and independent offspring suggest natal philopatry. Conservation efforts should prioritize open, sandy habitats with low silt in river washes, minimizing surface impacts, and maintaining adequate buffers around burrow entrances. Our study provides the first detailed examination of *D. m. parvus* burrowing ecology, offering valuable guidance for habitat management and the preservation of suitable burrowing sites for this endangered species.**

Key Words.—burrow architecture; burrowing behavior; soil suitability; habitat suitability; natal philopatry.

INTRODUCTION

Availability of suitable habitat is a key determinant of survival and reproductive success for many animal species, shaping their ability to find shelter (Swan et al. 2009), evade predators (Lima and Dill 1990), and access food resources (Halliday and Blouin-Demers 2014). For subterranean mammals, appropriate burrowing habitat is especially critical, as burrows not only provide shelter during periods of rest, but they offer protection from predators (Lacey et al. 2000), serve as storage for food reserves (Randall 1993), are used to raise offspring (Hoogland 1995), aid in conserving body moisture, and regulate microclimate, enabling thermoregulation and survival in extreme environments (Reichman and Smith 1990; Riddell et al. 2021). As a result, understanding the habitat characteristics that an animal uses for burrowing is a key component of habitat suitability and critical for management of at-risk burrowing species.

The architecture of rodent burrows is influenced by various factors. Soil characteristics, for instance, significantly impact burrow dimensions among burrowing mammals. Hard soils, such as clay, are more energy-intensive to excavate (Reichman and Smith 1990; up to 9.5 times more than sandy loam soils; Lin et al. 2017) but tend to support more complex burrow systems (Laundre and Reynolds 1993). In contrast, sandy soils without cohesive silt and clay are prone to collapse, and thus require some type of bio-reinforcement such as root cohesion (Kinlaw 1999), biocementation (Akin et al. 2024; Tirkes et al. 2024), or compaction (Akin et al. 2024) to be suitable for burrowing. Soil moisture appears to play an important role in the depth of a burrow with deeper burrows found in soils with deeper soil moisture (Bienek and Grundmann 1971). The complexity of a burrow system is also thought to be related to its function: species that primarily use burrows for shelter and raising offspring tend to construct simpler burrows, while species that also store food often build more complex ones (Reichman and Smith 1990). Additionally, the age of a burrow may affect its architecture, as long-occupied burrows can become progressively longer and deeper over time (Fitch 1948; Smith and Gardner 1985).

Kangaroo rats (*Dipodomys* spp.) typically construct complex burrows (Vorhies and Taylor 1922; Culbertson 1946; Anderson and Allred 1964) with multiple entrances, creating a network of tunnels and chambers (Kenagy 1973; Reichman and Smith 1990; Randall 1993). Because kangaroo rats are scratch-diggers, using their claws to loosen the soil (Eisenberg 1963; Nikolai and Bramble 1983; Price 1993; Siciliano Martina et al. 2023), optimal burrow sites are typically located in sandy well-drained soils that are stable yet easy to excavate, allowing for long-term burrow maintenance (Kenagy 1973; Nikolai and Bramble 1983). Burrow placement can also depend on vegetation cover, which provides food resources, shading, and protection from predators (Kenagy 1973; Gerald Braden and Robert McKernan, unpub. report).

The San Bernardino Kangaroo Rat (*Dipodomys merriami parvus*) is listed as Endangered by both California state (https://wildlife.ca.gov/Data/CNDDB) and federal (U.S. Fish and Wildlife Service [USFWS] 1998) agencies. The species was historically found in Riversidean alluvial fan sage scrub in the floodplains and adjacent upland habitat at the base of the San Gabriel, San Bernardino, and San Jacinto mountain ranges in San Bernardino and Riverside counties (USFWS 2024). Primarily due to habitat loss associated with development, mining, and water management, it was estimated that the range of the species was reduced by 96% at the time of federal listing (USFWS 1998). Currently, it is patchily distributed with only three remaining populations, each having extremely small effective population sizes (Hendricks et al. 2020). Recovery of the species depends on conserving remaining high-quality habitat and improving the suitability of low to medium quality habitat (Chock et al. 2020; USFWS 2023). *Dipodomys merriami parvus* is solitary and primarily granivorous, and like other *D. merriami* spp. (Leaver and Daly 2001; Leaver 2004), they are thought to store seeds in pit caches rather than in larders within their burrow systems. Currently, we know almost nothing about shelter use, selection of habitat for burrows, or burrow architecture in the species.

Here we describe habitat characteristics of *D. m. parvus* burrowing locations and the architecture and use of their burrows. We quantified these observations as part of a mitigation project aimed at minimizing impacts on kangaroo rats during site remediation for heavy metal contamination (Deborah Wilson and David Allison, unpubl. report). Resident kangaroo rats were removed and relocated from a mitigation area before site remediation began. A better understanding of *D. m. parvus* burrowing ecology may help inform habitat restoration and management strategies for the long-term conservation of the species.

Methods

Study site.—We conducted burrow casting during spring 2022 on U.S. Bureau of Land Management lands in Highland, California, about 200 m north of the current path of Plunge Creek within the Santa Ana River wash (Latitude 34.104, Longitude -117.181, 393 m elevation). The site was historically part of the Santa Ana River and Plunge Creek alluvial fan complex and thus has sandy fluvial soils. From 1945 to mid-2009, the area was used as an open-air recreational shooting range. Buildings were removed from 2012–2013, leaving the alluvial fan sage scrub habitat 9–10 y to reestablish (Mikael Romich, pers. comm.) before the start of our study with early stage sage scrub, bare ground, and nonnative grass dominating. No other kangaroo rat species were documented on the site.

Burrow architecture.—We searched for kangaroo rats and documented burrow ownership throughout the footprint of the mitigation area (16.2 ha). To do this, we first live-trapped all kangaroo rats on the site using Sherman live-traps (7.62 × 7.62 × 30.48 cm; model XLKSD, H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) with modified shortened doors to avoid tail injury. We spaced traps 10 m apart in grids or long lines and we opened and baited traps before dusk with sterilized millet seed and checked traps at midnight and dawn, closing them during the dawn check. We weighed, determined the sex, inspected for reproductive condition, and marked all kangaroo rats with a Passive Integrated Transponder (PIT) tag (HPT8 8 mm FDX-B, Biomark, Inc., Boise, Idaho, USA), and then we released them at the point of capture. We documented the nearest open burrow entrances of the appropriate size (e.g., with an approximately 5.0–6.3 cm entrance; Kenagy 1973). Following trapping, we used night vision goggles and remote cameras set in front of potential *D. m. parvus* burrows to confirm ownership, as determined by observing kangaroo rats entering and exiting repeatedly during the night. Once burrow ownership was determined, we trapped the kangaroo rat and removed it from the area for relocation to a new site. Following removal, we verified that the burrow was unoccupied for 24 h via camera trap images before casting the burrow.

We created casts of all unoccupied kangaroo rat burrows in situ using plaster of Paris (Reynolds and Wakkinen 1987; Laundre 1989; Laundre and Reynolds 1993; Tschinkel 2010; Dentzien-Dias and Figueiredo 2015). We poured plaster into the burrow with a funnel and a hose until the chamber was full, as indicated by mushrooming of plaster at the burrow entrance. Once the plaster hardened, we took photos to document locations of the burrow entrances. We then excavated the cast by removing layers of soil from above the casts to maintain their morphology and determine their depth and direction. If an uncast tunnel or chamber was encountered, we paused excavation, filled the opening with plaster, and waited for it to harden before continuing. Occasionally, a tunnel remained unfilled with plaster due to its uphill trajectory. In such cases, we carefully shaved off soil layers to access the tunnel from above. If we were unable to access the tunnel from above, we used polyurethane expanding foam to fill the open tunnel. We began excavation of all casts at a burrow entrance and continued until the cast ended, met another cast, or opened to the surface. We captured only one lactating female and did not cast her burrow; instead, we carefully excavated her burrow by hand to remove her unweaned offspring, and then we took measurements of tunnels and chambers.

For each burrow system (n = 10), we used a measuring tape to document the greatest burrow depth (distance from the ground surface to the burrow floor), the greatest tunnel length (the greatest distance across a series of connected tunnels), the total length of the burrow system (including all tunnels), the total number of openings, and the dimensions (width and height) of each entrance. From photos and casts, we documented the orientation of burrow entrances assigned to eight compass directions: north, northeast, east, southeast, south, southwest, west, and northwest, and used the Rayleigh test for circular uniformity to determine whether orientation differed from a uniform (random) distribution (Torres et al. 2003). We measured the distance from each burrow entrance to the basal stem of the nearest shrub, the number of shrubs directly over the excavated burrow system, and the number of shrubs within 1 m of the excavated burrow.

Habitat surveys.—We conducted ocular habitat surveys (Cheryl Brehme et al., unpubl. report) at eight of the 10 burrows in a 10 × 10 m plot centered on each burrow entrance prior to casting. At each plot we visually assessed the percentage ground cover (< 10 cm) of the following variables: (1) bare ground; (2) bare sandy soil; (3) non-native grass; (4) forbs; (5) shrubs, woody debris/leaf litter; (6) cactus; (7) native bunchgrass; and (8) inhospitable cover (e.g., boulders, concrete, gravel or paved roads). Additionally, we measured shrub cover at the crown (e.g., > 10 cm) to better characterize the extent of shrub canopy.

We measured soil compaction at the same eight burrows using a penetrometer (Model #15585, Dickey-John Corporation, Auburn, Illinois, USA) with a 76.2 cm length probe and a 1.27 cm diameter tip. We recorded the depth at which the penetrometer read 2,068 kPa (300 psi), which is the pressure roots cannot penetrate (Aase et al. 2001), and may limit kangaroo rat burrowing. We measured compaction at 25 locations evenly spaced throughout each 10 × 10 m habitat survey plot centered on a burrow entrance. We also collected soil samples from each excavated burrow following burrow casting to determine the soil particle size. Each sample consisted of approximately 5.0–6.5 kg of soil. This material surrounded the burrow and is assumed to be representative of the material excavated by *D. m. parvus* to create the tunnel. Soil particle size analysis was conducted by the Eurofins Calscience laboratory (Tustin, California, USA) using laser light scattering. Their analysis categorized particles into seven grain size classes ranging from silt and clay (< 0.0625 mm) to gravel (> 2 mm). Although sparse cobbles (> 64 mm in diameter) were observed near some burrows, and in one case (burrow 10) the tunnel passed around cobbles, they were not part of the excavated material.

RESULTS

We found that all *D. m. parvus* burrows were excavated in alluvial fan sage scrub, with no burrows documented in areas dominated by nonnative grass (Fig. 1). The burrows can be highly complex (Fig. 2), with 1–4 entrances, multiple chambers, some which were terminal, blind laterals (tunnels that do not end in a chamber), T-junctions (one tunnel intersects another at a 90° angle) and bifurcations (tunnel splits at an acute angle; Fig. 2, Table 1). Five of the 10 burrow systems had tunnels that terminated just below the surface of the

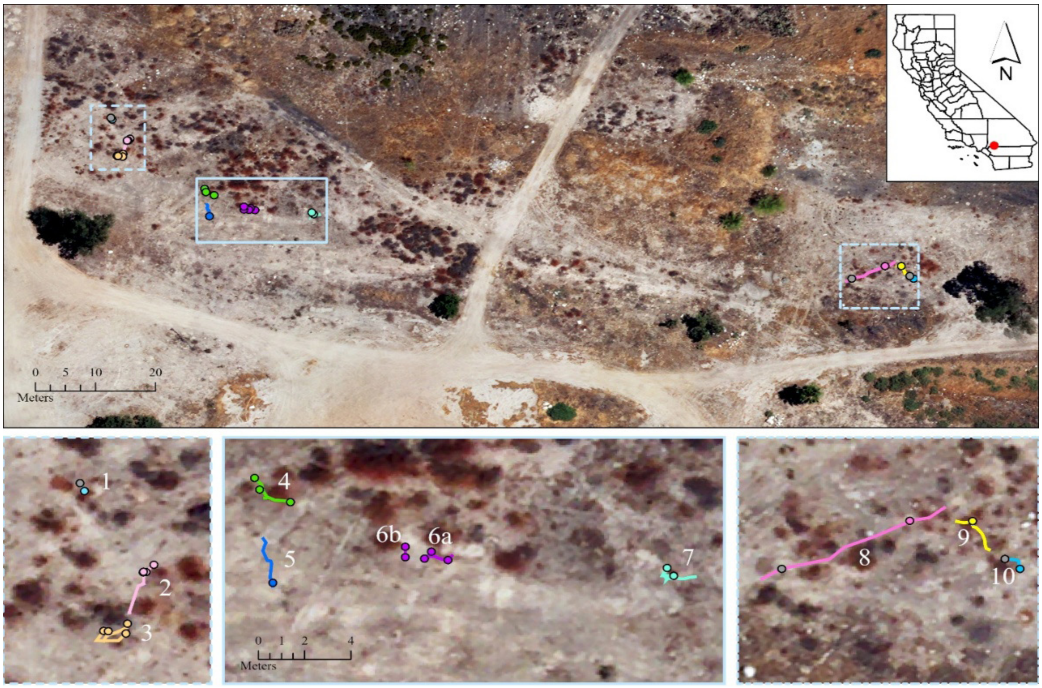

FIGURE 1. A map of the 10 burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) in Highland, California (red dot on map of California). The three inset panels are at the same scale as each other and show the burrows in greater detail. Lines represent tunnels and dots represent burrow entrances, with grey dots indicating plugged entrances.

Figure 2. Example photograph of burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) in Highland, California (left: Burrow 3; right: Burrow 2) showing plaster casts after burrow systems were excavated. Burrow entrances of each system are labeled 1–4. Inset photographs depict (a) chamber, (b) blind lateral, (c) T-junction, and (d) bifurcation. The shrubs over the burrows were trimmed during excavation; these and the surrounding shrubs are Deerweed (*Acmispon glaber*). The distance between the two burrow systems was 70 cm.

ground. Two burrow systems (1 and 6b) were relatively small and likely newly initiated or temporary refuges (i.e., subsidiary burrows, Tappe 1941) used for quick escape. Burrow entrances were roughly circular and often placed under or near shrubs with tunnels dug directly under shrubs (shrub canopy ranged from about 0.25 to 1.5 m in diameter; Table 1), and we found roots embedded in several of the plaster casts when exposed. Most burrows were oriented toward the north, but the distribution did not differ from a uniform distribution ($\bar{R} = 0.20$, $P = 0.359$; Fig. 3). Similar to other *D. merriami* spp., little to no soil was piled up in the vicinity of the entrance

Table 1. Characteristics of 10 burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) on Bureau of Land Management property in Highland, California, excavated during spring 2022. All measurements are in centimeters. An asterisk (*) indicates that the system had a plugged burrow entrance not included here or a tunnel that ended <10 cm below the surface. A plus sign (+) indicates the orientation for one burrow entrance was not documented. Abbreviations are GD = greatest depth, LLT = length of longest tunnel, TSL = total system length, NE = number of entrances, OBE = orientation of burrow entrances, MWE = mean width of entrances, MHE = mean height of entrances, MDEBS = mean distance of entrances to base of nearest shrub, NST = number of shrubs over tunnels, NSMD = number of shrubs < 1 m to burrow system, and SD = standard deviation.

Burrow ID	GD	LLT	TSL	NE	OBE	MWE	MHE	MDEBS	NST	NSMD
1*	10.2	128.3	156.2	2	E,W	8.1	8.4	55.3	1	3
2*	35.6	327.7	396.2	4	N,N,W,SW	6.4	5.9	15.2	2	8
3	35.5	254.0	458.5	4	SE, SW,N,N	6.1	6.8	27.8	4	5
4	35.5	231.1	271.2	3	NW, SE, SW	8.7	9.3	31.3	2	3
5	17.7	306.1	306.1	1	N	4.3	4.2	320.0	0	1
6a	16.5	201.9	226.1	3	E,N,E	8.3	7.6	16.9	3	5
6b	10.2	58.4	58.4	2	N,S	6.0	6.8	83.3	0	2
7*	31.8	222.9	329.6	2	E,N	6.9	6.4	41.5	1	2
8*	27.3	894.7	1078.2	2	NE, N	8.9	10.2	33.0	0	6
9	21.6	252.1	268.0	1	N	6.7	6.0	30.5	1	6
10*	19.7	109.2	138.4	2	S	7.0	6.4	31.8	1	6
Mean	23.8	271.5	335.2	2.6		7.0	7.0	46.8	1.5	4.5
SD	9.8	222.4	271.9	1.4		1.4	1.7	61.3	1.3	2.2

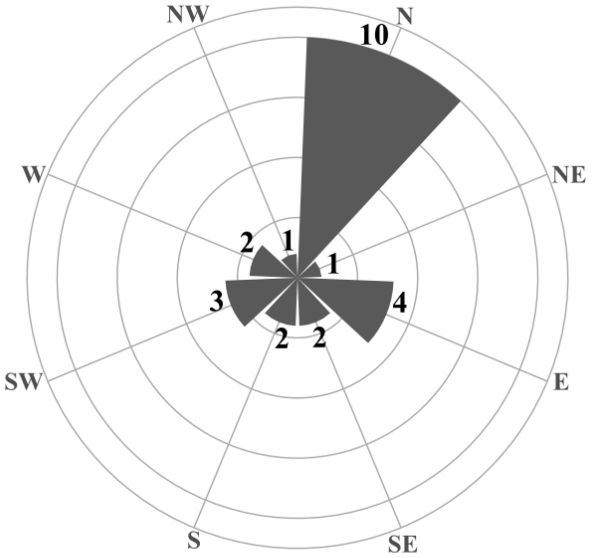

Figure 3. Orientation of 25 burrow entrances across 10 burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) in Highland, California. The number on each bar denotes the number of entrances in each direction. Although there were more entrances oriented towards the north, this was not a significant deviation from a random distribution.

(Monson and Kessler 1940). During observations we saw *D. m. parvus* scatter hoarding, and we found no seed caches or nesting material in the excavated burrow systems.

We documented three adult females sharing burrow systems with offspring. One was a natal burrow with unweaned pups (Burrow 5). We trapped the other two adult females in the same trap locations as recently weaned independent offspring. We designated these offspring as young-of-the-year based on weight and pelage color, and we determined them to be independent based on the reproductive condition of the suspected mother (i.e., nipples had returned to normal following lactation). Based on trapping results, camera trap videos, and focal observations of burrow use, these two females each appeared to share multiple burrow systems with their weaned offspring: one female used Burrows 4 and 6a/b with a single female offspring, and one female used burrows 8, 9 and 10 with one male and one female offspring). There was a mean distance of 6.32 m between any two shared burrow systems.

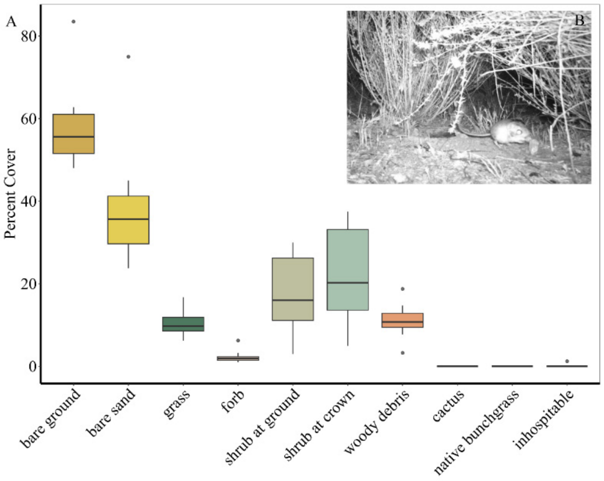

Figure 4. (A) Vegetation ground cover (< 10 cm) at eight burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) in Highland, California, measured on 10 × 10 m plots centered on the observed burrow entrance prior to excavation. The box plots depict medians (horizontal lines) and interquartile ranges, (IQR; boxes). Whiskers extend to the extreme values of the data or 1.5 × IQR from the center, whichever is less. Dots represent outlier values that fall outside of the whiskers. (B) Camera trap image of a *D. m. parvus* to the right of a burrow entrance on bare ground under shrub cover.

Habitat surveys indicated that *D. m. parvus* burrows were located in habitat with open bare ground or open sand with shrub canopy and little grass, woody debris, or forb cover (Fig. 4). The dominant shrub present at the site was Deerweed (*Acmispon glaber*), which is a fast growing early successional species that grows in well-drained soils (https://research.fs.usda.gov/treesearch/57245). Soil at the site was relatively compacted. Although the soil compaction measurements had a wide range (Fig. 4), the median depth to 300 psi was only 5.3 cm. In addition, 96% of the soil compaction measurements were < 24 cm, the average maximum depth of the tunnels. These results suggest that the 300 psi threshold used for root growth is not a threshold for *D. m. parvus* burrowing. The median grain size for soil samples was 0.5 mm, just at the cusp between medium and coarse sand (Fig. 5). Five of the burrows (1, 2, 3, 4, and 7) were dominantly

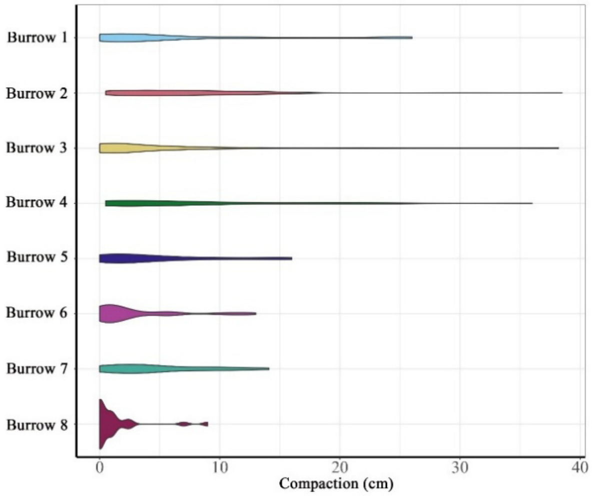

Figure 5. Soil compaction measurements in pounds per square inch (psi) across a 10 ×10 m square centered on the observed entrance prior to excavation at eight burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) in Highland, California. Depth to 300 psi was measured in centimeters; smaller compaction values are the most compact, and larger values are less compact (greater depth to 300 psi).

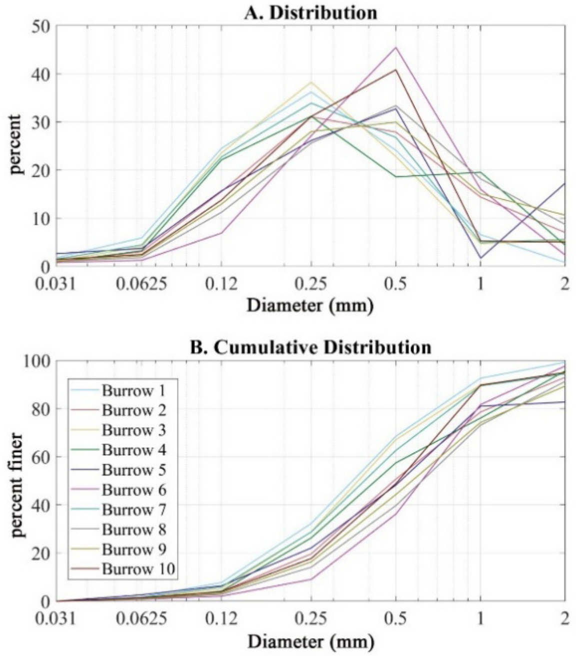

Figure 6. Grain size distribution of material removed during burrow excavation of burrow systems of San Bernardino Kangaroo Rats (*Dipodomys merriami parvus*) in Highland, California. Excavated sediment included silt and clay (< 0.0625 mm), very fine sand (0.0625–0.125 mm), fine sand (0.125–0.25 mm), medium sand (0.25–0.5 mm), coarse sand (0.5–1.0 mm), and very coarse sand (1.0–2.0 mm).

medium sand, four burrows were dominantly coarse sand (6, 8, 9, 10), and one burrow (9) had similar coarse and medium sand percentages. Silt was rare in the burrow samples, comprising an average of 1.4% of the samples. Silt made up < 2.7% of the material in all the sediment samples, suggesting that silt is not present in sufficient amounts to increase the soil strength. In addition, a cryptogamic soil crust, which is observed elsewhere in the alluvial fan, was not present (Burk et al. 2007; Brian Root, unpubl. report).

Discussion

Understanding the habitat requirements of endangered species is critical for recovery, but with low numbers remaining in the wild, opportunities for filling information gaps are often rare. Our study adds to the growing body of knowledge on the habitat use of the endangered *D. m. parvus*. We found that burrow systems were located in areas with bare ground or open sand, with entrances often situated adjacent to or beneath shrub canopy. This suggests that while the soil surface remains largely unvegetated, burrow entrances may be positioned in locations where overstory vegetation provides cover. There was no significant pattern to burrow entrance orientation, which in other species have been found to be associated with wind and sun direction (Torres et al. 2003). Given the small sample size in our study, however, it remains possible that burrow orientation to the north may play a role in thermal regulation or reduced flooding as the current path of the Plunge Creek is to the south. Burrow entrances were often under shrub canopy cover, which may help mitigate these environmental factors.

There was a great deal of variation in burrow lengths, depths and complexity within the 10 burrows cast. Burrow length and depth are typically correlated with body size in rodents (Van Vuren and Ordeñana 2012). When comparing these metrics across kangaroo rat species for which burrow characteristics have been documented, no clear pattern emerged. *Dipodomys merriami parvus* appears to have longer main tunnels (mean main burrow length = 311 cm) than both Tipton's Kangaroo Rat (*D. n. nitratoides*), which has approximately the same body size, and Heermann's Kangaroo Rat (*D. heermanni*), which is substantially larger (*nitratoides*: mean burrow length = 182 cm; *heermanni*: mean burrow length = 161 cm), although some burrows of *D. n. nitratoides* reached 350 cm in length (Germano and Rhodehamel 1995).

The burrows of *D. m. parvus* at this disturbed site were fairly shallow (greatest depth = 10.2–35.6 cm, mean = 23.8 cm) compared to burrows of other *D. merriami* spp. (greatest depth 175 cm; Bienek and Grundmann 1971; Kenagy 1973). Given the high energetic cost of excavating soil (Reichman and Smith 1990), it would be advantageous for kangaroo rats to construct burrow systems that are only as long and deep as necessary to meet basic needs. Soil serves as an effective insulator, with temperatures below depths of 30–40 cm remaining largely unaffected by daily fluctuations in aboveground temperatures (Chappell and Bartholomew 1981). As a result, rodents that burrow deeper than approximately 40 cm are unlikely to experience additional thermal benefits.

Significant ground disturbance from building removal in 2012–2013 suggests that these burrows were < 10 y old. Rodent burrow depth has been shown to be correlated with burrow age (Reichman and Smith 1990). In kangaroo rats, burrow excavation may take years (Tappe 1941) with burrow systems often used by multiple generations (Best 1972). Our results provide evidence of solitary occupancy of burrow systems by *D. m. parvus* except when females are raising offspring. We documented two females sharing burrows with their presumed independent offspring after weaning. These results are consistent with natal philopatry, or the retention of offspring in natal home ranges past the age of independence from parents (Armitage 1981; Jones 1984), as documented in other kangaroo rat species (Jones 1984, 1993; Shier and Swaisgood 2012). It is possible that *D. m. parvus* burrows in areas undisturbed for longer periods may be deeper than those documented here.

Soil cohesion from biologic crust and finer soils (e.g., fine/medium sand and silt/clay) did not play a large role in stabilizing the soils at our study site. The shrub roots observed in the burrow casts at this site are a possible source of additional soil strength (Kinlaw 1999). Tirkes et al. (2024) used a soil stability model to demonstrate that kangaroo rat burrows in the Sonoran Desert are likely unstable without additional strength from cohesion provided by biologic crusts. Their study observed relatively larger burrow diameters (12 cm compared to 7 cm in this study) and finer soils (median grain size, d50 = 0.16 mm versus 0.5 mm in this study). These factors likely result in less stable soils at their Sonoran Desert site in the absence of cohesion. Further investigation throughout the remaining range of *D.m. parvus*, particularly at upland sites that likely differ in soil composition, is needed to understand the burrow architecture and soil strength and cohesive properties of soils that support *D.m. parvus* burrows. Such studies would provide insights into the conditions that promote their stability and inform conservation and restoration practices.

We provide the first information on the subterranean habitat use of the endangered *Dipodomys merriami parvus*. For a species with habitat that is heavily impacted by human activities, research from even a single site can provide important information for minimizing impacts on below-ground habitat. Burrows were longer (up to about 900 cm for a single main tunnel; > 1,000 cm total system length) and shallower (as shallow as 10.2 cm at greatest depth) than expected compared to similarly sized species of kangaroo rat. If project fencing is needed to reduce impacts to the species, we recommend that fencing is constructed a minimum of 10 m from identified burrow entrances to ensure all entrances remain on the same side of the fence. The shallow burrow depths also suggest surficial impacts of off-road vehicles could collapse burrow systems in sandy wash habitat. Burrows were in habitat comprised primarily of open bare ground, though shrub canopy may be important for buffering entrances from sun and wind or providing shelter from predators. Additionally, the relationship between roots, soil strength and cohesion, and burrow architecture needs to be investigated across multiple sites with varying vegetation and soil characteristics. Our research emphasizes the need to preserve open, sandy areas that include shrub cover to support burrowing in this species, and additional studies are needed to identify critical burrowing habitat across the remaining range of *D.m. parvus*.

Acknowledgments.—This research followed guidelines by the American Society of Mammalogists (Sikes et al. 2016). It was approved under the Institutional Animal Care and Use Committee protocol (21-005), federal 10A1A permit ESPER0002526 and a Memorandum of Understanding from the state of California. Our study was conducted with permission from the U.S. Bureau of Land Management (BLM). We thank Mikael Romich, Stewart White (BLM), Amanda Swaller, William Sherwin and Karin Cleary Rose (U.S. Fish and Wildlife Service) and Kim Freeburn (California Department of Fish and Wildlife) for project coordination. We thank Hannah Bartholomaus and Talisin Hammond for assisting with field work. This work was funded by the San Diego Zoo Wildlife Alliance, the BLM, and the San Bernardino Valley Municipal Water District. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the views of our funders.

LITERATURE CITED

Aase, J.K., D.L. Bjorneberg, and R.E. Sojka. 2001. Zone-subsoiling relationships to bulk density and cone index on a furrow-irrigated soil. Transactions of the American Society of Agricultural Engineers 44:577–583.

Akin, I.D., S. Tirkes, and C.E. Collins. 2024. Geotechnical insights of mammal burrows in loose desert sand. Acta Geotechnica 19:1449–1459.

Anderson, D.R., and D.M. Allred. 1964. Kangaroo rat burrows at the Nevada test site. Great Basin Naturalist 24:93–101.

Armitage, K.B. 1981. Sociality as a life-history tactic of ground squirrels. Oecologia 48:36–49.

Best, T.L. 1972. Mound development by a pioneer population of the Banner-tailed Kangaroo Rat, *Dipodomys spectabilis baileyi* Goldman, in eastern New Mexico. American Midland Naturalist 87:201–206.

Bienek, G.K., and A.W. Grundmann. 1971. Burrowing habits of two subspecies of *Dipodomys merriami* in California and Utah. Great Basin Naturalist 31:190–192.

Burk, J., C. Jones, W. Ryan, and J. Wheeler. 2007. Floodplain vegetation and soils along the upper Santa Ana River, San Bernardino County, California. Madroño 54:126–137.

Chappell, M.A., and G.A. Bartholomew. 1981. Standard operative temperatures and thermal energetics of the antelope ground squirrel *Ammospermophilus leucurus*. Physiological Zoology 54:81–93.

Chock, R.Y., S.M. Hennessy, T.B. Wang, E. Gray, and D.M. Shier. 2020. A multi-model approach to guide habitat conservation and restoration for the endangered San Bernardino Kangaroo Rat. Global Ecology and Conservation 21:e00881. https://doi.org/10.1016/j.gecco.2019.e00881.

Culbertson, A.E. 1946. Observations on the natural history of the Fresno Kangaroo Rat. Journal of Mammalogy 27:189–203.

Dentzien-Dias, P.C., and A.E.Q. Figueiredo. 2015. Burrow architecture and burrowing dynamics of Ctenomys in foredunes and paleoenvironmental implications. Palaeogeography, Palaeoclimatology, Palaeoecology 439:166–175.

Eisenberg, J.F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology 69:1–100.

Fitch, H.S. 1948. Habits and economic relationships of the Tulare Kangaroo Rat. Journal of Mammalogy 29:5–35.

Germano, D.J., and W.M. Rhodehamel 1995. Characteristics of kangaroo rat burrows in fallow fields of the southern San Joaquin Valley. Transactions of the Western Section of the Wildlife Society 31:40–44.

Halliday, W.D., and G. Blouin-Demers. 2014. Red Flour Beetles balance thermoregulation and food acquisition via density-dependent habitat selection. Journal of Zoology 294:198–205.

Hendricks, S., A.Y. Navarro, T. Wang, A. Wilder, O.A. Ryder, and D.M. Shier. 2020. Patterns of genetic partitioning and gene flow in the endangered San Bernardino Kangaroo Rat (*Dipodomys merriami parvus*) and implications for conservation management. Conservation Genetics 21:819–833.

Hoogland, J.L. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal. University of Chicago Press, Chicago, Illinois.

Jones, W.T. 1984. Natal philopatry in Bannertailed Kangaroo Rats. Behavioral Ecology and Sociobiology 15:151–155.

Jones, W.T. 1993. Social systems of heteromyid rodents. Pages 575–595 *in* Biology of the Heteromyidae. Genoways, H.H., and J.H. Brown (Eds.). American Society of Mammalogists, Shippensburg, Pennsylvania.

Kenagy, G.J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201–1219.

Kinlaw, A. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. Journal of Arid Environments 41:127–145.

Lacey, E., J.L. Patton, and G. Cameron. 2000. Life Underground: The Biology of Subterranean Rodents. University of Chicago Press, Chicago, Illnois.

Laundre, J.W. 1989. Horizontal and vertical diameter of burrows of five small mammal species in southeastern Idaho. Great Basin Naturalist 49:646–649.

Laundre, J.W., and T.D. Reynolds. 1993. Effects of soil structure on burrow characteristics of five small mammal species. Great Basin Naturalist 53:358–366.

Leaver, L.A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology 15:729–734.

Leaver, L.A., and M. Daly. 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. Oecologia (Berlin) 128:577–584.

Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Candian Journal of Zoology 68:619–640.

Lin, Y.-F., A. Chappuis, S. Rice, and E.R. Dumont. 2017. The effects of soil compactness on the burrowing performance of sympatric eastern and Hairy-tailed Moles. Journal of Zoology 301:310–319.

Monson, G., and W. Kessler. 1940. Life history notes on the Banner-tailed Kangaroo Rat, Merriam's Kangaroo Rat, and the White-throated Wood Rat in Arizona and New Mexico. Journal of Wildlife Management 4:37–43.

Nikolai, J.C., and D.M. Bramble. 1983. Morphological structure and function in desert heteromyid rodents. Great Basin Naturalist Memoirs 7:44–64.

Price, M.V. 1993. A functional-morphometric analysis of forelimbs in bipedal and quadrupedal heteromyid rodents. Biological Journal of the Linnean Society 50:339–360.

Randall, J.A. 1993. Behavioural adaptations of desert rodents (Heteromyidae). Animal Behaviour 45:263–287.

Reichman, O.J., and S.C. Smith. 1990. Burrows and burrowing behavior by mammals. Pp. 197–244 *in* Current Mammalogy. Genoways, H.H. (Ed.). Plenum Press, New York, New York.

Reynolds, T.D., and W.L. Wakkinen. 1987. Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho. American Midland Naturalist 118:245–250.

Riddell, E., K. Iknayan, L. Hargrove, S. Tremor, J. Patton, R. Ramirez, B. Wolf, and S. Beissinger. 2021. Exposure to climate change drives stability or collapse of desert mammal and bird communities. Science 371:633–636.

Shier, D.M., and R.R. Swaisgood. 2012. Fitness costs of neighborhood disruption in translocations of a solitary mammal. Conservation Biology 26:116–123.

Siciliano Martina, L., D. Guerra, and J. Veech. 2023. Forelimb morphology as an adaptation for burrowing in kangaroo rat species (genus Dipodomys) that inhabit different soil substrates. Journal of Mammalogy 104:1377–1389.

Sikes, R.S., t.A. Care, and U.C.o.t.A.S.o. Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Smith, D.J., and J.S. Gardner. 1985. Geomorphic effects of ground squirrels in the Mount Rae area, Canadian Rocky Mountains. Arctic and Alpine Research 17:205–210.

Swan, M., J. Di Stefano, A. Greenfield, and G. Coulson. 2009. Fine-scale habitat selection by adult female Swamp Wallabies (*Wallabia bicolor*). Australian Journal of Zoology 56:305–309.

Tappe, D.T. 1941. Natural history of the Tulare Kangaroo Rat. Journal of Mammalogy 22:117–148.

Tirkes, S., D. Aydin, M. Thompson, C. Collins, H. Beyenal, and I. Akin. 2024. Stability of kangaroo rat burrows in the Sonoran Desert: evidence of biocementation. Canadian Geotechnical Journal https://doi.org/10.1139/cgj-2024-0225.

Torres, M.R., C.E. Borghi, S.M. Giannoni, and A. Pattini. 2003. Portal orientation and architecture of burrows in *Tympanoctomys barrerae* (Rodentia, Octoodontidae). Journal of Mammalogy 84:541–546.

Tschinkel, W.R. 2010. Methods for casting subterranean ant nests. Journal of Insect Science 2010:10:88. https://doi.org/10.1673/031.010.8801.

U.S. Fish and Wildlife Service (USFWS). 1998. Endangered and threatened wildlife and plants: Final rule to list the San Bernardino Kangaroo Rat as endangered. Federal Register 63:51005–51017.

U.S. Fish and Wildlife Service (USFWS). 2024. Recovery plan for the San Bernardino Kangaroo Rat (*Dipodomys merriami parvus*). U.S. Fish and Wildlife Service, Portland, Oregon. 11 p.

Van Vuren, D.H., and M.A. Ordeñana. 2012. Factors influencing burrow length and depth of ground-dwelling squirrels. Journal of Mammalogy 93:1240–1246.

Vorhies, C.T., and P. Taylor. 1922. Life history of the kangaroo rat *Dipodomys spectabilis spectabilis* Merriam. Bulletin No. 1091, U.S. Department of Agriculture, Washington, D.C.

Debra M. Shier is the Brown endowed Associate Director of Recovery Ecology at the San Diego Zoo Wildlife Alliance, Escondido, California, and an Adjunct Assistant Professor in Ecology and Evolutionary Biology at the University of California, Los Angeles. She earned her Bachelor's degree in Biopsychology from the University of California, Santa Barbara, her Master's in Biology with an emphasis in Ecology and Systematics from San Francisco State University, California, and a Master's and Ph.D. in Animal Behavior with an emphasis in Wildlife Conservation from the University of California, Davis. Debra runs several programs focused on threatened and endangered mammals and frogs in Southwestern U.S. She studies the ways in which an understanding of animal behavior, ecology, and genetics can be applied to conservation strategies such as reintroductions and translocations and has been researching the San Bernardino Kangaroo Rat since 2012. (Photographed by Samantha Fox).

Paige C. Miller is an early career professional and a Research Associate II at the San Diego Zoo Wildlife Alliance, Escondido, California. She earned her Bachelor's and Master's degrees in Biology at Idaho State University, Pocatello, where she studied the nesting ecology of Trumpeter Swans (*Cygnus buccinator*). Her research interests are in animal behavior and ecology, and their applications in conservation. Since 2022, Paige has broadened her experience to include mammals, working primarily with rodents including the San Bernardino Kangaroo Rat. (Photographed by Betsy Wagner).

Christian A. Braudrick is a Geomorphologist at Stillwater Sciences in Berkeley, California. He earned a Ph.D. in Earth and Planetary Science from the University of California, Berkeley. His work focuses on the interaction between fluvial and ecological processes to restore habitat for aquatic and riparian species. Christian has been working on habitat conditions for San Bernardino Kangaroo Rats since 2019. (Photographed by Maya Hayden).

Rachel Y. Chock is a Researcher II at the San Diego Zoo Wildlife Alliance, Escondido, California. She earned her Bachelor's and Master's degrees in Biology at Clark University, Worcester, Massachusetts, and her Ph.D. in Biology from the University of California, Los Angeles. As a behavioral ecologist, her research involves combining the fields of animal behavior, ecology, and applied conservation. Rachel is particularly interested in the recovery of local endangered species and has been working with San Bernardino Kangaroo Rats since 2018. (Photographed by Aliya McCarthy).