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A solitary Allen’s Big-eared Bat (*Idionycteris phyllotis*) roosting in a drill hole in the Sueños Mine 28 January 2021, Sierra County, New Mexico. (Photographed by Dillon S. Metcalfe).

2023 PEER REVIEWERS

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NOTES

WINTER OBSERVATIONS OF ALLEN'S BIG-EARED BAT (*IDIONYCTERIS PHYLLOTIS*) IN NEW MEXICO

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Abstract.—**Limited data are known about winter habits of Allen's Big-eared Bat (*Idionycteris phyllotis*) throughout the southwestern U.S. and northern and central Mexico. Herein, we report on several winter observations of the species in New Mexico. In central parts of the state, we observed a solitary individual in a drill hole of an abandoned mine during two consecutive winters, January 2020 and 2021, in the Caballo Mountains of Sierra County. In southwestern New Mexico, several museum specimens further demonstrate that abandoned mines are used as winter roosts, likely hibernacula, in the Burro Mountains and Little Bear Mountain of Grant County. These data on winter roosts as well as limited winter captures of volant individuals suggest that some Allen's Big-eared Bats might move to lower, more arid rocky habitats in New Mexico during cooler months. Winter observations, thus far in New Mexico, represent some of the lowest elevations for this species in the state. Observations from the Caballo Mountains also represent the easternmost records in New Mexico, and guano from species in another mine in the mountain range suggests the area possibly is used during warmer months of the year. Thus far, abandoned mines appear to be important winter roosts for this species. Additional studies on Allen's Big-eared Bat are warranted to better understand and protect this uncommon species in need of conservation.**

Key Words.—abandoned mines; bats; hibernacula; roost; Southwestern USA; winter ecology.

Allen's Big-eared Bat (*Idionycteris phyllotis*) occurs from the southwestern U.S. to central Mexico (Czaplewski 1983; O'Shea et al. 2018). In the U.S., Allen's Big-eared Bat is considered a sensitive species by all states in which the species occurs (O'Shea et al. 2018), and relatively little is known about many aspects of its biology (Adams 2003). This species resides in a variety of habitats from desert scrub to montane fir forests, although individuals primarily are captured in rocky forested montane areas during warmer months of the year (Findley et al. 1975; Czaplewski 1983; Hoffmeister 1986; O'Shea et al. 2018). Data on seasonal movements and winter hibernacula are limited or absent in many accounts for this species (Findley et al. 1975; Czaplewski 1983; Hoffmeister 1986; Adams 2003; O'Shea et al. 2018). Herein, we report on winter observations for Allen's Big-eared Bats from central and southwestern New Mexico.

We conducted surveys for bats in several mines in the Caballo Mountains, Sierra County, New Mexico, during the winters of 2019/2020 and 2020/2021 (Fig. 1). On 9 January 2020 and 28 January 2021, we surveyed for bats in the Sueños Mine (6.2 km N, 8.5 km E Caballo Post Office; 1,590 m elevation) on the eastern side of the Caballo Mountains. The Sueños Mine has two connected entrances (i.e., portals) with airflow between them. The main horizontal passageway (i.e., adit) was driven straight into an east-facing hillside for about 85 m. Along its length, four lateral short passageways (i.e., drifts; 1.5, 3, 4.5, and 7.6 m in length) were excavated at right angles, with only the longest drift having another right-angle bend within its 7.6 m total length. A vertical shaft connected the single adit to the surface 54.9 m from the adit portal. Rocks along the adit and short drifts had many domes, crevices, and cracks.

On 26 January 2021, we surveyed for bats in an unnamed abandoned mine located on the western side of the Caballo Mountains (8.1 km N, 6.7 km E Caballo Post Office; 1,421 m elevation; Fig. 1). This mine contained a single adit with a large underground room (i.e., stoping) that is open to the surface on the hillside above, creating an open 13.1 m trench about 9.1 m deep to the adit floor. The adit continued beyond the underground room for 12.2 m before the underground passageway bent at a right angle for another 8.5 m. For our research on winter observations, we also examined museum specimens and associated field notes, when available, in the natural history collections at Western New Mexico University (WNMU), Silver City. We also accessed museum databases via VertNet (VertNet.org) for additional specimens and data from late October through March throughout its entire distribution.

On 9 January 2020, we surveyed the first 30.5 m of the single horizontal adit of the Sueños Mine for bats and observed > 30 Townsend's Big-eared Bats (*Corynorhinus townsendii*) both in clusters and roosting solitarily, as well as a solitary Allen's Big-eared Bat (Fig. 2). In the first

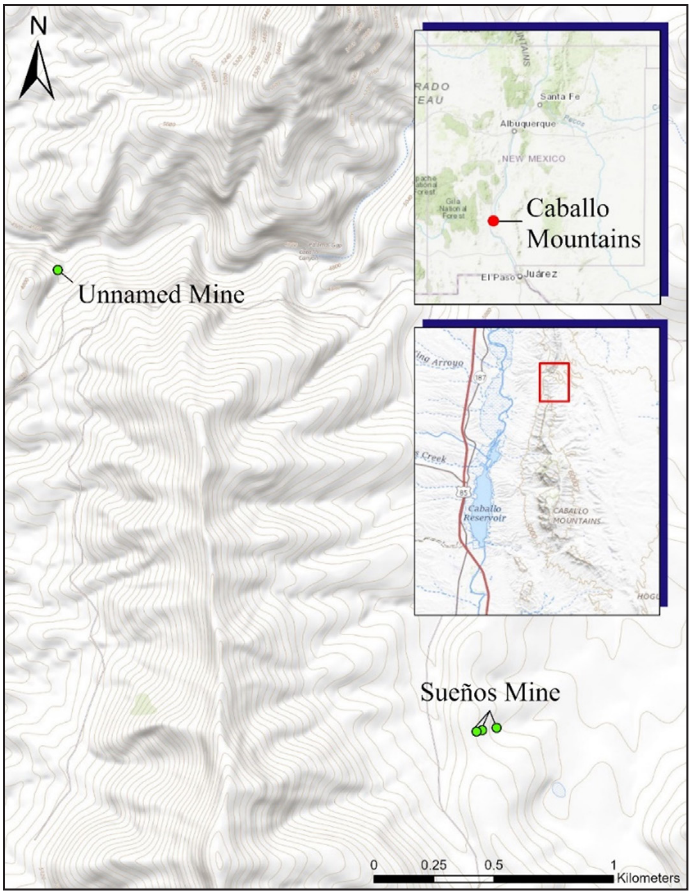

Figure 1. Topographic map showing the location of two mines in the north end of the Caballo Mountains, Sierra County, New Mexico, where observations of Allen's Big-eared Bats (*Idionycteris phyllotis*) were documented during winter surveys. Green dots represent openings of abandoned mines with observations of *I. phyllotis*, either live individuals or guano of this species.

short side drift about 9.1 m from the main entrance, an Allen's Big-eared Bat was situated in a drill hole roosting with its ventral side on the rocks about 1.4 m above the floor of the drift (Fig. 2). Climatic conditions generally were cool and humid at the site, as specific details on temperature and relative humidity were not recorded on this day of observation.

On 28 January 2021, we again surveyed the Sueños Mine for wildlife. We documented a solitary Allen's Big-eared Bat in the same side drift and same drill hole (Fig. 3). Other bats observed in the mine on this day included 41 Townsend's Big-eared Bats and two Pallid Bats (*Antrozous pallidus*). Townsend's Big-eared Bats roosted in clusters and solitarily from about 6.1 m to 30.5 m from the entrance along the single adit. Both Pallid Bats roosted deep in a ceiling crack about 39.6 m from the portal. We recorded temperatures throughout the mine from 5.0° C to 13.9° C, with the relative humidity at 28%. We documented airflow between the two portals on this date. The Sueños Mine of Sierra County represents the easternmost distributional record for Allen's Big-eared Bat in New Mexico and most arid location in the state (Findley et al. 1975; Keith Geluso, unpubl. report).

On 26 January 2021, we surveyed an unnamed mine on the western side of the Caballo Mountains. We observed one Townsend's Big-eared Bat and three Pallid Bats. A large pile of guano was located at the right-angle bend in the back of the adit as well as scattered guano throughout much of the mine, along with insect remnants. Through molecular sequence data of fecal pellets, analyses identified four species including Pallid Bats, Townsend's Big-eared Bats, Allen's Big-eared Bats, and either the Long-eared Myotis (*Myotis evotis*) or Fringed Myotis (*Myotis thysanodes*). These two Myotis species cannot be differentiated via molecular techniques at this time (Faith Walker, unpubl. report) but based on the habitat and distribution of these two species in New Mexico, the Fringed Myotis is the most likely species inhabiting the mine (Findley et al. 1975). We recorded temperatures throughout the mine from 5.6° C to 13.9° C, with the relative humidity at 41%. It is unclear when the guano from Allen's Big-eared Bat was deposited. Some individuals have been captured drinking during cooler months over water resources (Geluso 2007 and see below) suggesting bats might also feed during cooler months. In contrast, guano from Allen's Big-eared Bats might represent occupancy during warmer months in this low-elevation mountain range. Surveys in riparian habitats along the Rio Grande as well as surrounding arid foothills in Sierra County would be valuable to understand whether this species only occurs in the area during winter or also in summer.

Figure 2. A solitary Allen's Big-eared Bat (*Idionycteris phyllotis*) roosting in a drill hole in the Sueños Mine 9 January 2020, Sierra County, New Mexico. (Photographed by Jackson D. Bain).

Figure 3. A solitary Allen's Big-eared Bat (*Idionycteris phyllotis*) roosting in a drill hole in the Sueños Mine 28 January 2021, Sierra County, New Mexico. (Photographed by Dillon S. Metcalfe).

Via museum queries and searches, we discovered five other observations of Allen's Big-eared Bats collected from mines during colder months (late October to March). All specimens were from two localities in southwestern New Mexico. Four of the five specimens were from the Cora Miller Mine, Grant County, New Mexico (about 7 mi [11 km] south of Cliff; WNMU #2468, 2469, 2823, 2824). All four individuals were females, with collection dates of 31 October 1971 (WNMU#2468), 12 December 1970 (WNMU#2823 and 2824), and 17 December 1971 (WNMU#2469). Reported weights for two individuals were 13.5 and 14 g, whereas another individual was noted as being extremely fat. Another female (WNMU#3298) located in a drill hole 27 October 1974 in the Little Bear Mountain, 5 mi (8.1 km) northwest of Silver City was extremely fat with no embryos (Denise Friedrick, unpubl. report). To our knowledge, no other details are available for that specimen. Being at the upper limits of known weights for the species (Czaplewski 1983), these individuals had likely stored fat for prolonged hibernation, but more needs to be learned about the winter habits of this rare species. Although another specimen (WNMU#3941) was reported in museum databases as hibernating, original notes from Bruce J. Hayward on file at the museum at WNMU demonstrated that the individual was captured in a mist net 17 April 1982 (not 18 April) during a mammalogy field trip at a pond 0.4 km above the Gila River in Davis Canyon (about 7 mi [11 km] south of Cliff; Bruce Hayward, unpubl. report).

To date, all known winter observations of Allen's Big-eared Bats are female from both abandoned mines (observations discussed above) and captures over water sources from November to March: one female captured over stock tank 10 March 2005, Grant County, New Mexico, 1,542 m elevation (Geluso 2007) and one female captured over earthen pond 10 February 1996, Catron County, New Mexico, 1,761 m elevation (Museum of Southwestern Biology [MSB] #208513; William Gannon, unpubl. report). It is unclear whether males roost in different types of roosts or are not as active as some females during winter. In summer in northern Arizona, males and females roost in different habitats and types of roosts, with females selecting Ponderosa Pine (*Pinus ponderosa*) snags and males roosting in sandstone cliffs within Pinyon-juniper (*Pinus edulis-Juniperus* spp.) Woodlands (Solvesky and Chambers 2009). In Utah, however, females also roosted in cliffs (Siders and Jolley 2009).

During warmer months in New Mexico, most Allen's Big-eared Bats are known from Ponderosa Pine Forests and above, with some observations known from oak-piñon-juniper-pine transition and riparian cottonwood-sycamore forests (Jones 1965, 1966; Findley et al. 1975; Keith Geluso, unpubl. report). In the Gila National Forest of southwestern New Mexico, Bruce Hayward and Duston Hunt (unpubl. report) reported Allen's Big-eared Bats only from Ponderosa Pine Forests and Douglas Fir (*Pseudotsuga menziesii*) Forests at elevations ranging from 1,768 to 3,048 m, whereas there was no mention of the species in Pinyon-juniper Woodlands and Pine-oak Woodlands from elevations of 1,463 m to 2,469 m. In Arizona, several reports of Allen's Big-eared Bats exist from Mexican Pine-oak Woodlands with low lying areas consisting of riparian habitats (Commissaris 1961; Hoffmeister 1986); however, there is one observation of an individual captured 1.6 km away from woodland vegetation near Portal, Arizona, in mesquite (*Prosopis* sp.) and white-thorn acacia (*Acacia* sp.; Commissaris 1961) habitats. It was unknown whether the individual lived in this habitat or visited the water source to drink from nearby riparian areas (Commissaris 1961; Hoffmeister 1986).

These limited winter observations from New Mexico only were reported from pinyon-juniper oak habitats and desert scrublands (WNMU specimens; MSB #208513; Geluso 2007; this study). Elevations of winter observations were from 1,421 m in the unnamed mine in Sierra County (this study), 1,440 m in the Cora Miller Mine in Grant County (WNMU specimens), 1,541 m in the Big Burro Mountains in Grant County (Geluso 2007), 1,590 m in the Sueños Mine (this study), and 1,761 m in the Mogollon Mountains in Catron County (MSB #208513). The lowest reported captures during warmer months of the year were at the Glenwood Fish Hatchery, Catron County, in a riparian woodland surrounded by Pinyon-juniper Woodlands at 1,446 m (Jones 1961; Jones and Suttkus 1972; Keith Geluso, unpubl. report). The next lowest summer captures were at 1,960 m on the edge of the San Mateo Mountains (5.7 km east, by road, of Springtime Campground in Piñon/juniper and Oak Woodland, Keith Geluso, unpubl. report), with all other localities at higher elevations (Jones 1965, 1966; Findley et al. 1975; Bruce Hayward and Duston Hunt, unpubl. report; see Keith Geluso, unpubl. report). These data tend to suggest some individuals might move to lower, more arid habitats in winter, but more data are needed to understand the winter ecology of this species.

While we cannot confirm whether the same individual was observed in consecutive winters, observations of an Allen's Big-eared Bat in the same drill hole might suggest site fidelity. If accurate, site fidelity of winter roosts might be important for the species as other drill holes and cracks were common throughout the Sueños Mine. Specific environmental conditions potentially existed within and around the drill hole that enabled the individual to survive winter dormancy. O'Shea et al. (2018) commented on management practices and concerns regarding Allen's Big-eared Bats, but those authors only mention management practices regarding summer roosts in trees. We find that human access to abandoned mines in cooler months is another concern because, to date, all winter observations are from mines. Documentation of a few volant individuals during winter months suggests that automated acoustic recording devices might further assist in locating individuals, especially if individuals might move seasonally to lower elevations or into habitats/areas not suspected as normally inhabited by the species in New Mexico. Winter surveys for Allen's Big-eared Bat and studies following individuals to winter retreats throughout its distribution are warranted to better understand and protect this uncommon species in need of conservation.

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LITERATURE CITED

Adams, R.A. 2003. Bats of the Rocky Mountain West: Natural History, Ecology, and Conservation. University Press of Colorado, Boulder, Colorado.

Commissaris, L.R. 1961. The Mexican Big-eared Bat in Arizona. Journal of Mammalogy 42:61–65.

Czaplewski, N.J. 1983. *Idionycteris phyllotis*. Mammalian Species 208:1–4.

Findley, J.S., A.H. Harris, D.E. Wilson, and C. Jones. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, New Mexico.

Geluso, K. 2007. Winter activity of bats over water and along flyways in New Mexico. Southwestern Naturalist 52:482–489.

Hoffmeister, D.F. 1986. Mammals of Arizona. University of Arizona Press, Tucson, Arizona.

Jones, C.J. 1961. Additional records of bats in New Mexico. Journal of Mammalogy 42:538–539.

Jones, C. 1965. Ecological distribution and activity periods of bats of the Mogollon Mountains area of New Mexico and adjacent Arizona. Tulane Studies in Zoology 12:93–100.

Jones, C. 1966. Changes in populations of some western bats. American Midland Naturalist 76:522–528.

Jones, C., and R.D. Suttkus. 1972. Notes on netting bats for eleven years in western New Mexico. Southwestern Naturalist 16:261–266.

O'Shea, T.J., P.M. Cryan, and M.A. Bogan. 2018. United States bat species of concern: a synthesis. Proceedings of the California Academy of Sciences 65:1–279.

Siders, M.S., and W. Jolley. 2009. Roost sites of Allen's Lappet-browed Bats (*Idionycteris phyllotis*). Southwestern Naturalist 54:201–230.

Solvesky, B.G., and C.L. Chambers. 2009. Roosts of Allen's Lappet-browed Bat in northern Arizona. Journal of Wildlife Management 73:677–682.

Dillon Metcalfe, a Subterranean Specialist, joined Bat Conservation International part-time in June 2016 and became a full-time staff member in July 2019. Dillon works to identify and protect critical habitat for bats in the western U.S., specializing in rope access and safety. He has led subterranean habitat assessment and evaluation projects for the Bureau of Land Management, U.S. Forest Service, National Park Service, Department of Defense, and New Mexico Energy, Minerals, and Natural Resources Department. (Photographed by Janette Perez-Jimenez).

Jackson Bain, a Senior Subterranean Specialist, joined Bat Conservation International (BCI) part-time in October 2017 and became a full-time staff member in July 2019. His role on the Subterranean Team focuses on planning, implementing, and reporting on field projects in the western U.S. Prior to joining BCI, Jackson worked for a variety of governmental, academic, and private entities around the U.S., from the Bering Sea in Alaska to the southern international border, in a multitude of roles and on a diverse set of projects, pursuing a career in wildlife management. Jackson has worked with rattlesnakes, garter snakes, lizards, frogs, tortoises, leopard frogs, marine fisheries, crabs, corals, Mexican Spotted Owls (*Strix occidentalis lucida*), Northern Goshawks (*Accipiter gentilis*), Peregrine Falcons (*Falco peregrinus*), small mammals, and bats. (Photographed by Dillon Metcalfe)

Shawn Thomas, Subterranean Team Manager, joined Bat Conservation International (BCI) in July of 2014. He oversees the Subterranean Team by managing field projects and leading all aspects of program management, with the goal of protecting bat habitat in abandoned mines and cave. Prior to joining BCI, Shawn conducted cave management work for the National Park Service (NPS) in western U.S. cave parks, with most of his time at Carlsbad Caverns National Park (New Mexico) and Lava Beds National Monument (California). This work included cave mapping, biological surveys, photography, cave restoration, and development of NPS protocols for bat monitoring, with a focus on winter hibernacula surveys in western U.S. caves. Shawn has safely accessed thousands of natural caves and abandoned mines in pursuit of bat conservation. (Photographed by Abby Tobin).

Brett Andersen is the Wildlife Diversity Program Manager at the Nebraska Game and Parks Commission. He manages funding and the State Wildlife Action Plan aimed at conserving at-risk species. Prior to working for the state, Brett studied bat roosting behavior in Nebraska and New Mexico through the University of Nebraska at Kearney and investigated winter activity patterns of bats in the southeastern U.S. while at Texas Tech University, Lubbock. Additionally, he worked as an Environmental Consultant, conducting presence-absence surveys for threatened and endangered bat species throughout the eastern U.S. (Photographed by Ashby Simonton).

Keith Geluso is a Professor of Biology at the University of Nebraska at Kearney. He has spent decades studying bats and other vertebrates throughout the Great Plains and the Southwestern U.S. He is an avid supporter of publishing natural history data and focuses many of his projects with students on the distribution, seasonality, reproductive timing, and ecology of vertebrates. (Photographed by Mary Harner).

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NOTES

NORTHERNMOST RECORD OF THE LONG-NOSED BAT (*LEPTONYCTERIS* SP.) IN NEW MEXICO: CONSERVATION IMPLICATIONS

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Abstract.—**Three species of nectar feeding bats (Phyllostomidae: Glossophaginae) reach the northern edge of their geographic range in southwestern New Mexico. We report observations of bats drinking from a hummingbird feeder in Glenwood, Catron County, which is 46 km north of the next nearest record. We confirmed the bat as *Leptonycteris*, based on external morphology, and concluded that it likely represented the Lesser Long-nosed Bat (*L. yerbabuenae*), which was recently delisted from the Endangered Species Act. Our observations occurred from 29 September to 20 October 2022, which is consistent with the fall migratory period. This and other northern records from Grant County, New Mexico, corroborate a previously published species distribution model that predicted occurrence in this region during fall. Contrary to recent speculation that this species has expanded its range in New Mexico, we concluded that the occurrences of the species in Catron and Grant counties is not unexpected given that these locations occur within a large contiguous area of Madrean Woodland that contains *Agave* spp. (food resource) and the adjacent mountain ranges contain high densities of caves and mines (roost sites). Renewed mining activities in the region could pose a threat to these bats.**

Key Words.—distribution; *Leptonycteris yerbabuenae*; Lesser Long-nosed Bat; Madrean Encinal; Madrean Pinyon-juniper Woodland; Mogollon Mountains; range expansion

Three species of nectar-feeding bats, Mexican Long-tongued Bat (*Choeronycteris mexicana*), Mexican Long-nosed Bat (*Leptonycteris nivalis*), and Lesser Long-nosed Bat (*Leptonycteris yerbabuenae*; all Phyllostomidae: Glossophaginae), reach their northern distributional limits in southern Arizona and New Mexico (Hoffmeister 1986; Frey 2004; Burke et al. 2019). These bats roost colonially in caves and mines and are migratory in the northern portion of their range. In New Mexico, these bats occur in the southwestern portion of the state, but specifics about patterns of distribution, abundance, and habitat are poorly understood due to low densities, migratory behavior, and paucity of field survey work in most parts of this region. *Leptonycteris nivalis* is listed as Endangered by New Mexico and Endangered under the U.S. Endangered Species Act, whereas *L. yerbabuenae* is listed as Threatened by New Mexico and was recently removed from protections under the U.S. Endangered Species Act (New Mexico Department of Game and Fish [NMDGF]. 2022. Threatened and endangered species of New Mexico: 2022 biennial review. NMDGF. Available from https://www.wildlife.state.nm.us/download/conservation/threatened-endangered-species/biennial-reviews/2022-Biennial-Review.pdf [Accessed 15 November 2022]). Most specimen records of these three species of bats are from the years 1963–1966, with virtually no collections prior to 1958 and only sporadic collections in the years since (https://doi.org/10.15468/dl.zjgyc6). Over the past decade there has been renewed research focused on *Leptonycteris*. In part, this is due to completion of a 5-y review on the status of *L. yerbabuenae* in 2007 that recommended downlisting (New Mexico Department of Game and Fish. 2022. *op. cit.*). Further, the ubiquity of digital cameras and remote camera technology, public awareness that these bats can be attracted to hummingbird feeders, and citizen science programs aimed at documenting bats and other wildlife, has provided additional information about the occurrence and behavior of these species (Buecher and Sidner 2013; https://www.azcentral.com/story/news/local/arizona-science/2017/05/26/arizona-volunteers-help-rescue-lesser-long-nosed-bat/338194001/). Here we describe the northernmost record of one of these bats in New Mexico.

One of us (JL) first observed a bat drinking from a hummingbird feeder on 29 September 2022 at a residence in Glenwood, Catron County, New Mexico (elevation about 1,430 m). A video of the bat drinking at the feeder was taken 4 October 2022 and posted to YouTube (https://youtu.be/Ub9ZtAOD144). We identified the bat as *Leptonycteris* sp. on the basis of the shape of the rostrum and uropatagium (Fig. 1). Glenwood is a small town located at the junction of the San Francisco River and Whitewater Creek in the valley between the Brushy Mountains to the west and the Mogollon Mountains to the east. There is a high density of abandoned mines in the adjacent Mogollon Mountains, particularly the Mogollon mining district located about 12 km northeast of Glenwood (http://mindat.org). Within Glenwood, dominant vegetation consists of exotic trees and

Figure 1. Still photographs taken from a video showing a long-nosed bat (*Leptonycteris* sp.) feeding from a hummingbird feeder in Glenwood, Catron County, New Mexico, 5 October 2022. The reduced uropatagium and shape of the rostrum confirm it as *Leptonycteris* sp. versus Mexican Long-tongued Bat (*Choeroyncteris mexicana*).

cottonwoods (*Populus* sp.) in the riparian zones. The surrounding uplands are dominated by Madrean Encinal and Madrean Pinyon-Juniper (*Pinus* spp. - *Juniperus* spp.) Woodland, with smaller patches of Apacherian-Chihuahuan Semi-desert Grassland and Steppe and Mogollon Chaparral (NatureServe. 2004. Landcover descriptions for the southwest regional GAP analysis project. NatureServe. Available from https://slco.org/globalassets/1-site-files/watershed/watershed-library/landcoverswregionalgapanalproj2004.pdf [Accessed 16 November 2022]). The residence had abundant vegetation including morning glories (*Ipomoea* sp.), hollyhocks (*Alcea* sp.), native sunflowers (*Helianthus* sp.), and Millet (*Panicum miliaceum*) planted to attract birds. The residence maintained five hummingbird feeders that were deployed annually, generally from mid to late March to mid to late October depending on hummingbird activity. The feeders had their bee guard removed to facilitate use by hummingbirds. A remote baby monitoring video camera was aimed at one of the feeders under the eve of the house in an attempt to photograph hummingbirds and had been in place for about 3 y. After the first observation, a bat regularly visited the feeder each night, including during thunderstorms, generally arriving prior to 2230 and no later than 0400. The last observation of a bat at the feeder was 20 October 2022.

Leptonycteris nivalis has only been confirmed in New Mexico from the so-called bootheel in extreme southern Hidalgo County (Bogan et al. 2017). A bat identified as *L. nivalis* from the lower Gila River, Hidalgo County (Lewis 2001) was likely a misidentified *L. yerbabuenae* (Geluso and Geluso 2021). Ramsey and Whiteman (2011) reported capturing *L. yerbabuenae* in the Big Burro Mountains, Grant County. Other northern records of *L. yerbabuenae* in New Mexico are from near the base of the Mogollon Mountains in Grant County, including Silver City in 2021 (Laverty and Stoner 2022) and the valley of the Gila River in vicinity of Gila and Cliff in 2014, 2016, 2018, and 2019 (Jones et al. 2021; Geluso and Geluso 2021). In 2021 a *Leptonycteris* sp. was identified via acoustic recording from near Bear Creek, 7 km west of Gila, Grant County (Rachel Burke, pers. comm.). The nearest of these records to Glenwood was about 46 km south-southeast in the Gila-Cliff Valley. It seems likely that the bat observations in Glenwood were referable to *L. yerbabuenae* given their proximity to other verified records of the species in the same biogeographic region, although we cannot refute the possibility that it was a vagrant *L. nivalis*. All of the Gila-Cliff Valley and Silver City records were in September and October, which corresponds to the fall migration period, and were associated with hummingbird feeders. The dates of our observations are also consistent with the fall migratory period for *Leptonycteris* in New Mexico (Geluso and Geluso 2021).

Leptonycteris are closely associated with columnar cacti and paniculate *Agave* species, both following a corridor of blooming phenology of these species during migration and serving as the principal pollinator of them (Fleming et al. 1993; Burke et al. 2019). Although much of the literature on *Leptonycteris* centers on their specializations for feeding on the nectar and pollen of these plants, their diet may be more catholic outside of the maternal period during which they may require columnar cacti for pregnancy and lactation (Petit 1997; but see Laverty and Stoner 2022). For instance, emerging data indicate *L. yerbabuenae* regularly consume insects in New Mexico (Sellers 2018; Kathryn Stoner et al., unpubl. report), which has also been observed for *Leptonycteris* in other regions (Petit 1997), and *Leptonycteris* uses fleshy fruits from a diversity of cacti and diverse taxa of broadleaf plants (Petit 1997; Rojas-Martinez et al. 2012). Fruits may go unrecognized in their diet because the bats spit out the seeds at temporary feeding roosts (Godinez-Alvarez and Valiente-Banuet 2000; Rojas-Martinez et al. 2012). Thus, in the U.S., maternal colonies of *L. yerbabuenae* are limited to the Sonoran Desert in Arizona, which is the only region to contain columnar cacti. Following the maternal period, these bats may leave the maternal roosts to spread out more widely to use Chihuahuan Desert and Madrean ecological communities that harbor agaves (Buecher and Sidner 2013).

In New Mexico, *Leptonycteris* are thought to be associated with agaves and they may travel long distances (40 km) from day roosts to accesses foraging areas (Buecher and Sidner 2013; Bogan et al. 2017). Burke et al. (2019) found that while the overall distribution of *L. yerbabuenae* was primarily predicted by high richness of cacti, the fall distribution of *L. yerbabuenae* was predicted by diversity of food plants, especially agave. The distribution models predicted that *L. yerbabuenae* seasonally expands its distribution during fall and fall-to-winter migration well into the Mogollon Mountains in Catron and Grant counties, largely coincident with the distribution of agaves (Burke et al. 2019, 2021). Thus, the September and October records of *L. yerbabuenae* from Catron and Grant counties provide strong independent support for the species distribution models presented by Burke et al. (2019), which were based on independent data sources. Parry's Agave (*Agave parryi*) occurs at elevations up to about 2,400 m in the montane coniferous forest zone on the southern and southwestern aspects of the Mogollon Mountains, and northward in the San Francisco River drainage to the northern part of the Gila National Forest.

Given the recent population recovery of *L. yerbabuenae*, presence of abundant potential roost sites (mines and caves) and agave food resources in vicinity of Glenwood, and data suggesting that *L. yerbabuenae* may exhibit dietary plasticity, particularly within the nonmaternal periods, the fall occurrence of *L. yerbabuenae* in southern Catron County is not unexpected. Based on the available evidence, we disagree with the argument by Geluso and Geluso (2021) that records in northern Grant County, immediately south of Catron County, represent a recent range expansion. Geluso and Geluso (2021) appear to have based their conclusion of range expansion on the lack of prior records of *L. yerbabuenae* in the region. They cited Jones et al. (2014) as an example of a mammal that had altered migration pattern due to supplemental feeding, but that study did not demonstrate a range expansion, which is the establishment of new populations beyond the species historical range (Pacifici et al. 2020). Hummingbird feeders and gardens have been implicated in altering the winter distribution of Anna's Hummingbird (*Calypte anna*; Grieg et al. 2017). In the case of *Calypte anna*, the overarching pattern is one in which the birds remain on or near their summer range during winter (instead of migrating), thereby resulting in changed winter distribution. This is a fundamentally different process than supplemental food luring bats into a novel region that they did not previously occupy, as suggested by Geluso and Geluso (2021). Many other species that use anthropogenic foods have not substantially changed their geographic range. Buecher and Sidner (2021) found that *L. yerbabuenae* used hummingbird feeders in an urban area within a valley that contained few agaves or other traditionally recognized food resources, but this finding does not presuppose a shift in their geographic range. *L. yerbabuenae* shift core use areas within their expansive seasonal home ranges around day roosts to take advantage of temporarily and spatially variable food resources, returning to the same foraging areas nightly until the resource is depleted (Ober et al. 2018). This is consistent with our observations of nightly visitation over several weeks. Such foraging areas must be in proximity (within 40 km) of the day roost. Day roosts are relatively rare, used generationally, and roost site selection appears to be highly constrained given that population increases result in more bats per roost rather than the proliferation of new roosts (U.S.

Fish and Wildlife Service 2016). Further, roosts are often abandoned when disturbed, requiring up to two decades for *L. yerbabuenae* to recolonize abandoned roosts (U.S. Fish and Wildlife Service 2016). Thus, the determinant of geographic range in *L. yerbabuenae* is suitable roost site (coupled with availability of food resource). The association of *L. yerbabuenae* with hummingbird feeders in the autumn is likely a result of shifting core use areas around roosts as agave and other food resources dwindle. Because bird feeders are associated with humans, they make the presence of the bats easily detectable. Use of hummingbird feeders for food is a novel behavior, but it is unknown if the behavior is readily self-taught or socially transmitted via diffusion in a population (Duboscq et al. 2016). The manner and ease of bats learning to use feeders would dictate the speed and geographic distribution of the behavior making it an unreliable metric for ascertaining when a population started using a location.

Our record fills an important void in knowledge about the distribution of *Leptonycteris*. Most records of *L. yerbabuenae* in New Mexico are from areas dominated by the Madrean Lowland Evergreen Woodland (macrogroup ecosystem M010), which contains agaves (U.S. Geological Survey [USGS]. 2011. GAP/Landfire National Terrestrial Ecosystems 2011. USGS. Available from https://maps.usgs.gov/terrestrial-ecosystems-2011/ [Accessed 15 November 2022]). In southwestern New Mexico, this Madrean ecosystem occurs in the isolated mountain ranges of southern Hidalgo County and as a large continuous area around the southern periphery of the Mogollon Plateau, including the Burro Mountains. A northern peninsula of this ecosystem that includes Gila-Cliff and Glenwood extends northward along the San Francisco River to at least vicinity of Reserve, New Mexico (Catron County), and we anticipate that improved autumn sampling will reveal sporadic occurrence of *L. yerbabuenae* northward along the San Francisco River to the vicinity of Reserve. Similarly, we anticipate that future research may reveal sporadic autumn occurrence of *L. yerbabuenae* eastward to the Mimbres River and southern portion of the Black Range (Sierra and Luna counties).

Human disturbance of roosts is perhaps the greatest threat to populations of *Leptonycteris* and conservation efforts over the past several decades to close caves and abandoned mines to human entry has allowed some populations to recover (U.S. Fish and Wildlife Service 2018). One of the densest concentrations of abandoned mines in New Mexico is the Mogollon mining district (Ferguson 1927) located a short distance from Glenwood. Mining in this area largely ceased around 1950 (Eveleth 1978), which has allowed several decades of mine inactivity for bats to establish roosts. Because research typically focuses on places where a species is known to occur, and the occurrence of *Leptonycteris* in this region has not been previously recognized, no surveys have been conducted to determine presence of post-maternal roosts in the mining districts of the Mogollon Mountains region. Recent plans to develop silver mines in the Mogollon Mining District could pose a threat to any *Leptonycteris* roosts that may be present (https://nmpoliticalreport.com/2022/09/20/advocates-say-new-mining-claim-near-mogollon-threatens-ecosystem-and-sacred-sites/). Surveys are needed to ascertain the status of *Leptonycteris* in the Mogollon Mountains, and specifically in the Mogollon mining district.

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LITERATURE CITED

Bogan, M.A, P.M. Cryan, C.D. Weise, and E.W. Valdez. 2017. Landscape movements by two species of migratory nectar-feeding bats (*Leptonycteris*) in a northern area of seasonal sympatry. Western North American Naturalist 77:317–330.

Buecher, D.C., and R. Sidner. 2013. Long distance commutes by Lesser Long-nosed Bats (*Leptonycteris yerbabuenae*) to visit residential hummingbird feeders. Pp. 427–433 *in* Merging Science and Management in a Rapidly Changing World: Biodiversity and Management of the Madrean Archipelago III; 2012 May 1–5; Tucson, AZ. Proceedings. Gottfried, G.J., P.F. Ffolliott, B.S. Gebow, G. Lane, and L.C. Collins (Comps.). RMRS-P-67, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Burke, R., J.K. Frey, A.C. Ganguli, and K.E. Stoner. 2019. Species distribution modeling supports "nectar corridor" hypothesis for migratory nectarivorous bats and conservation of tropical dry forests. Diversity and Distributions 25:1399–1415.

Burke, R., J.K. Frey, and K.E. Stoner. 2021. Using species distribution modeling to delineate richness patterns of chiropterophyllic plants and allocate conservation efforts in Mexico and the southwestern United States. Natural Area Journal 41:85–92.

Duboscq, J., V. Romano, A. MacIntosh, and C. Sueur. 2016. Social information transmission in animals: lessons from studies of diffusion. Frontiers in Psychology 7:1147. http://dx.doi.org/10.3389/fpsyg.2016.01147.

Eveleth, R.W. 1978. New methods of working an old mine: case history of the Eberle Group, Mogollon, NM. New Mexico Geology 1:7–10.

Fleming, T.H., R.A. Nuñez, and L. da S. L. Sternberg. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia 94:72–75.

Frey, J.K. 2004. Taxonomy and distribution of the mammals of New Mexico: an annotated checklist. Occasional Papers, Museum of Texas Tech University 240:1–32.

Geluso, K., and K.N. Geluso. 2021. Lesser long-nosed bat (*Leptonycteris yerbabuenae*) range expansion into northern Grant County, New Mexico. Western North American Naturalist 81:273–279.

Godinez-Alvarez, H., and A. Valiente-Banuet. 2000. Fruit-feeding behavior of the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds. Biotropica 32:552–556.

Hoffmeister, D.F. 1986. Mammals of Arizona. University of Arizona Press, Tucson, Arizona.

Jones, A.K., S.W. Liphardt, J.L. Dunnum, T.W. Perry, J. Malaney, and J.A. Cook. 2021. An overview of the mammals of the Gila region, New Mexico. Therya 12:213–236.

Jones, J.D., M.J. Kauffman, K.L. Monteith, B.M. Scurlock, S.E. Albeke, and P.C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications 24:1769–1779.

Laverty, T.M., and K.E. Stoner. 2022. In search of bachelorettes: observations of male *Leptonycteris yerbabuenae* with dorsal patches across its range. Therya 13:163–170.

Lewis, L. 2001. Eighty mile range extension for *Leptonycteris nivalis*. Bat Research News 42:17.

Ober, H.K., R.J. Steidl, and V. M. Dalton. 2005. Resource and spatial use patterns of an endangered vertebrate pollinator, the lesser long-nosed bat. Journal of Wildlife Management 69:1615–1622.

Pacifici, M., C. Rondinini, J.R. Rhodes, A.A. Burbidge, A. Cristiano, J.E.M. Watson, J.C.Z. Woinarski, and M. Di Marco. 2020. Global correlates of range contracts and expansions in terrestrial mammals. Nature Communications 11:2840. https://doi.org/10.1038/s41467-020-16684-w

Petit, S. 1997. The diet and reproductive schedules of *Leptonycteris curasoae curasoae* and *Glossophaga longirostris elongata* (Chiroptera: Glossophaginae) on Curacao. Biotropica 29:214–223.

Ramsey, M., and K. Whiteman. 2011. Range extension for the Lesser Long-nosed Bat in New Mexico. Western Bat Working Group Newsletter 7:11.

Rojas-Martínez, A., H. Godinez-Alvarez, A. Valiente-Banuet, M. del Coro Arizmendi, and O. S. Acevedo. 2012. Frugivory diet of the Lesser Long-nosed Bat (*Leptonycteris yerbabuenae*), in the Tehuacán Valley of central Mexico. Therya 3:371–380.

Sellers, S. 2018. Metabarcoding indicates increased arthropod consumption at the northern range extent of long-nosed bats (*Leptonycteris* spp.). M.S. Thesis, New Mexico State University, Las Cruces, New Mexico. 83 p.

U.S. Fish and Wildlife Service. 2016. Species status assessment for the Lesser Long-nosed Bat. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, New Mexico. 96 p.

U.S. Fish and Wildlife Service. 2018. Removal of Lesser Long-nosed Bat from the federal list of endangered and threatened wildlife. Federal Register 83:17093–17110.

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Brood Parasitism and Communal Egg Dumping in the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*)

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***Abstract*.—Conspecific brood parasitism occurs in many species of birds, especially colonially breeding species with precocial offspring. During 2010–2019 we monitored nesting colonies of the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*Aechmophorus clarkii*) at Clear Lake, California. Maximum mean clutch size in three large colonies ranged from 2.29–3.12 eggs/nest (range, 1–14). Brood parasitism in 33 marked nests with 1–4 eggs occurred at a rate of 0.04–0.17 egg/nest/d and in 2.6–10.4% of nests/d. Nests with up to 10 eggs were usually incubated in well-maintained nests. We encountered 51 nests with unusually large clutches of 11–31 eggs, presumably laid by multiple females, representing 0.16% of all nests encountered. All were disintegrating nests unattended by grebes, except for one well-maintained nest with 18 eggs incubated by a mixed pair of grebes. Brood parasitism in three of these nests occurred at a rate of 0.0–4.0 eggs/nest/d. Such communal egg dumps occurred only in larger colonies with a minimum of 134 nests. The number of nests and number of communal egg dumps in a colony were positively correlated. Conspecific and interspecific brood parasitism by females of the two species is more extensive than previously realized and appears to be a common and potentially adaptive reproductive strategy.**

Key Words.—breeding; California; Clear Lake; clutch size; coloniality; nesting; Podicipedidae; reproduction.

Introduction

In birds, conspecific or intraspecific brood parasitism results from females laying eggs in the nests of conspecifics without subsequently incubating the eggs or caring for hatchlings (Yom-Tov 1980). It occurs across a wide taxonomic spectrum, including at least 256 species of 44 genera (Yom-Tov 2001; Yom-Tov and Geffen 2017), and is especially likely to occur among colonially breeding species with precocial offspring because they tend to lay larger clutches than species with altricial offspring, initiation of incubation is often delayed until most or all of the eggs are laid (which may leave the nest unguarded for several days), and the costs of raising parasitic offspring are lower than for species with altricial offspring that require more time to develop (Petrie and Møller 1991; Sorenson 1992; Johnsgard 1997; Yom-Tov 2001; Yom-Tov and Geffen 2017). Some species engage in an extreme form of conspecific brood parasitism, referred to as dump nesting (Mackie and Buechner 1963), pre-hatch brood amalgamation (Eadie et al. 1988), or egg dumping (Yom-Tov 1980), in which multiple females lay large numbers of eggs in a single unattended nest.

Many species of grebes (Podicipedidae) breed colonially and all have precocial offspring (Fjeldså 2004). Conspecific brood parasitism has been reported in at least six of the 23 species of grebes (Yom-Tov 2001): the Red-necked Grebe (*Podiceps grisegena*), Great Crested Grebe (*P. cristatus*), Eared Grebe (*P. nigricollis*), Silvery Grebe (*P. occipitalis*), Western Grebe (*Aechmophorus occidentalis*), and Clark's Grebe (*A. clarkii*). The Western Grebe and Clark's Grebe are large, morphologically similar, and occasionally hybridizing species of piscivorous birds that breed on floating nests in mixed-species colonies in lacustrine ecosystems in western North America (Storer and Nuechterlein 1992; http://birdsoftheworld.org/bow/species/wesgre; http://birdsoftheworld.org/bow/species/clagre). Up to six eggs are typically laid by a mated pair in a nest (Storer and Nuechterlein 1992; LaPorte et al. 2014, http://birdsoftheworld.org/bow/species/wesgre). Larger clutches and broods with mixed species may result from conspecific and interspecific brood parasitism (Storer and Nuechterlein 1992; LaPorte et al. 2014, http://birdsoftheworld.org/bow/species/wesgre). Nuechterlein (in Rohwer and Freeman 1989) reported brood parasitism in 1.8% of Western Grebe nests based on eggs added to incubated clutches. Finley (1907) was the first to report unusually large clutches of up to 16 eggs, that had never been incubated, in Oregon. Bent (1919) published a photograph of 11 eggs in a well-maintained nest in Saskatchewan and speculated that unusually large clutches were dumped indiscriminately by several birds, but never hatched. In this paper we provide new quantitative data on the occurrence of brood parasitism, including unusually large clutches of dumped eggs, and demonstrate that brood parasitism is much more extensive than previously realized in the Western Grebe and Clark's Grebe.

Methods

***Study area*.**—Clear Lake (39°01'N, 122°46'W) is a large and relatively shallow lake, comprising an area of 180 km^2 with 114 km of shoreline and a maximum depth of 18 m, in Lake County, northern California, USA (Horne and Goldman 1972). The Western Grebe and Clark's Grebe nest together in colonies of up to 4,721 nests at Clear Lake, with most nests (84.9%) attended by Western Grebes (Hayes et al. 2022). The natural history and anthropogenic impairments of the lake are summarized by Suchanek et al. (2003) and Richerson et al. (2008).

Sampling methods.**—**We conducted surveys of nesting grebes at Clear Lake and adjacent wetlands during 186 d of field work between 8 April and 3 October of 2010–2019, with an average of 18.6 surveys per year (standard deviation = 7.2; range, 7–29 due to variable funding). The surveys were usually conducted from a canoe but some were conducted from a motorboat or from land. During each survey we counted the number of nests and occasionally the number of eggs on nests within each colony. A colony was defined as one or more nests separated by a gap of at least 400 m or by a minimum swimming distance of 400 m around land or dense aquatic vegetation from the nearest nest of an adjacent colony, even if only one nest was present at the site.

To determine the typical clutch size, we counted the number of eggs in each nest in the two largest colonies: Rodman Slough South on 6 and 13 August 2010 and at Anderson Marsh Southeast on 6 and 15 August 2010. We chose the date with the largest clutch size at each colony and combined the data to represent the typical clutch size of *Aechmophorus* grebes. Although we often noted clutch size of nests during subsequent years, we did not repeat large-scale egg counts to avoid excessive disturbance of nesting grebes until we encountered an unusually large number of eggs in a colony at Indian Island on 30 July 2019. We identified the parent incubating eggs on some nests, but due to the difficulty of determining the species for both individuals of each pair attending each nest, we combined the data for all nests for analysis.

Brood parasitism can be difficult to detect. The interval between laying the first egg and the last egg ranges from 3–6 d (Storer and Nuechterlein 1992; http://birdsoftheworld.org/bow/species/wesgre). To determine whether new eggs were laid on nests more than 1 week after eggs were present, which is more suggestive of brood parasitism than a mated pairing adding new eggs, we marked nests at the Rodman Slough South colony with numbered flags on stakes and counted the number of eggs on each nest on 13 August 2010. We subsequently returned to count the eggs on each numbered nest on 20, 27, and 31 August 2010. We did not repeat this method to avoid excessive disturbance of nesting grebes. We identified the parent incubating eggs on some nests, but due to the difficulty of determining the species for both individuals of each pair attending each nest, we combined the data for all nests for analysis.

Although we did not make an effort to observe eggs in all nests during the study period, nests with unusually large numbers of eggs were more conspicuous than nests with typical clutches because the eggs were seldom covered by an incubating grebe. Because we often observed grebes incubating on nests with up to 10 eggs and rarely observed grebes incubating on nests with more than 10 eggs, we defined communal egg dumps as nests with > 10 eggs. On all such nests, we counted the number of eggs and identified any accompanying adults. We estimated distances (nearest 1 m) between closely spaced communal egg dumps visually if close or measured with a laser range finder.

During 2014–2017, we monitored selected nests with up to six motion-activated cameras (Trophy Cam Bone Collector RTAP Night Vision and Trophy Cam HD Aggressor No Glow; Bushnell Outdoor Products, Overland Park, Kansas, USA). Each camera was bolted to a U-channel post pushed into the substrate and aimed at one or more active nests with variable numbers of eggs. We subsequently examined photographs for evidence of brood parasitism.

Statistical analysis.**—**We combined data for all 10 y for analysis. We used Spearman Rank Correlation Coefficient ($\alpha = 0.05$; Zar 2010) to determine if the number of nests correlated to the number of egg dumps within colonies. All means are given ± 1 standard deviation.

Results

During 2010–2019, we counted 31,234 grebe nests in 150 colonies at 37 sites along the shores of Clear Lake. The maximum mean clutch size in the two largest colonies in 2010 occurred on 6 August, with 2.29 ± 0.94 eggs/nest (range, 1–5; n = 76 of 334 nests) at Rodman Slough South and 2.37 ± 1.09 eggs / nest (range, 1–7; n = 294 of 440 nests) at Anderson Marsh Southeast. The vast majority of nests (97%) in these colonies combined had 1–4 eggs, with only 3.0% of nests containing > four eggs (Fig. 1). The maximum mean clutch size in the largest colony in 2019 occurred on 30 July, with 3.12 ± 2.42 eggs / nest (range, 1–14; n =132 of 1,516 nests) at Indian Island. Although most nests had 1–4 eggs, 15.2% had > four eggs (Fig. 1).

Eggs laid by brood parasites after a clutch of eggs were laid by a host were often distinguishable from the eggs of a host by being distinctly paler in color because the pale blue color of freshly laid eggs was gradually stained brown by wet nest vegetation (Fig 2). Parasitic eggs laid before the final egg of a host was laid, however, should overlap in age with the eggs of a host and be similar in color. One or more distinctly paler eggs often occurred among darker eggs in clutches with as few as two eggs, but because of subtle variation in egg coloration across a continuum from pale blue to brown, it was often difficult to distinguish between host and parasitic eggs, so we did not attempt to quantify egg coloration.

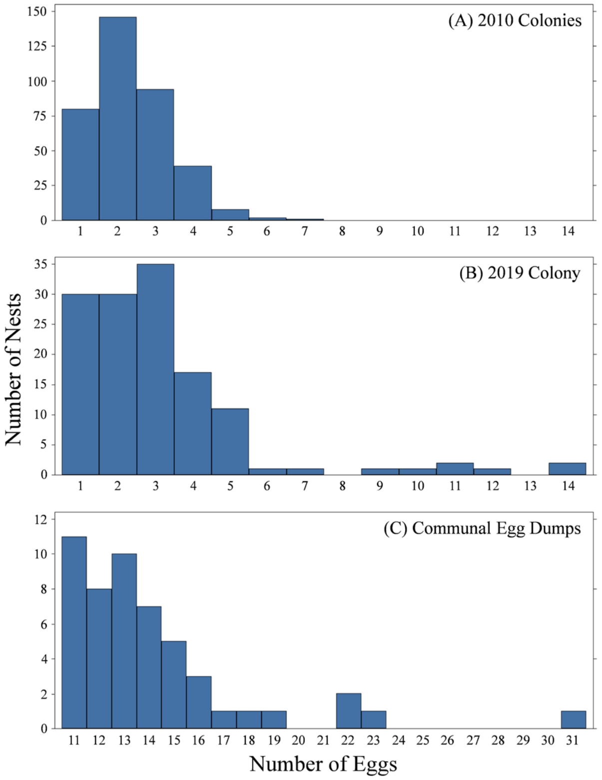

Figure 1. Examples of variation in clutch size (number of eggs in nest) of Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) nests at Clear Lake, California. (A) Rodman Slough South and Anderson Marsh Southeast colonies combined in 2010 (n = 370 nests). (B) Indian Island colony with six communal eggs dumps in 2019 (n = 132 nests). (C) Communal eggs dumps (> 10 eggs / nest) during 2010–2019 (n = 51 nests).

Of 102 marked nests with eggs (date of laying unknown) on 13 August 2010, 33 still had 1–4 eggs on both 20 and 27 August 2010. It was uncertain whether all of these eggs were being incubated. The number of eggs on 27 August (> 6 d after the first eggs were laid) decreased on 10 nests, remained the same on 16 nests, and increased by 1–3 eggs (mean = 1.7 new eggs/parasitized nest, n = 10 eggs) on six nests, including four nests with only one egg on 20 August. Thus, 10 eggs presumably laid by brood parasites were laid among 33 active nests during 7 d at a rate of 0.04 egg/nest/d, and 18.2% of nests were parasitized during 7 d at a rate of 2.6% of nests/d. Of 12 marked nests that still had eggs on both 27 and 31 August 2010, the number of eggs on 31 August decreased on four nests, remained the same on three nests, and increased by 1–2 eggs on five nests (mean = 1.7 new eggs/parasitized nest, n = 18 eggs), including two nests with only one egg on 27 August. Thus, eight eggs presumably laid by brood parasites were laid among 12 active nests during 4 d at a rate of 0.17 egg/nest/d, and 41.7% of nests were parasitized during 4 d at a rate of 10.4% of nests/d.

The grebes usually incubated and defended up to 10 eggs on well-maintained nests (Fig. 2); however, the grebes rarely incubated eggs on nests with > 10 eggs. During the study period we encountered 51 nests with 11–31 eggs in a nest (Figs. 1–2), representing at least 0.16% of all nests encountered. These communal egg dumps occurred in disintegrating nests unattended by grebes except for one well-maintained nest with 18 eggs (Fig. 2) incubated by a male Clark's Grebe and a female Western Grebe for at least 7 d (8–15 July 2016) in the Rodman Slough Northwest colony. Communal egg dumps occurred most frequently in large colonies (Table 1). The smallest colony with a communal egg dump had 134 nests. The colony with the most communal egg dumps (14) also had the most nests (4,721). The number of nests and the number of communal egg dumps in colonies were significantly positively correlated (r_s = 0.43, $P < 0.001$, n = 150). Some communal egg dumps were closely spaced. Three (with 13, 13, and 22 eggs) were within 12 m of each other and two of these (with 13 and 13 eggs) were 4 m apart in a colony of 844 nests. Another three (with 12, 13, and 14 eggs) were within 16 m of each other and two of these (with 13 and 14 eggs) were 4 m apart in a colony of 2,079 nests.

We documented the rate of increase or decrease in the number of eggs in several communal egg dumps. The number of eggs in a nest with 15 eggs increased to 19 by the following day at a rate of four eggs/d (the maximum rate recorded). The largest communal egg dump had 26 eggs on 15 July, 30 eggs (including fragments of one) on 19 July (Fig. 2), 31 eggs (including fragments of one) on 22 July, and 24 eggs on 29 July 2013. The number of eggs in this nest increased at a rate of 0.71 eggs/d and then decreased at a rate of 1.0 egg/d. In contrast, the communal egg dump with 18 eggs guarded by the Clark's Grebe had the same number of eggs when inspected 7 d later. The number of eggs in a nest with 11 eggs declined to four eggs 2 d later at a rate of 3.5 eggs/d, and all eggs disappeared 3 d later.

Our motion-activated cameras frequently documented frenzied copulation and occasional egg laying by grebes, during both day and night, on nests recently abandoned due to egg predation by mammals or transportation of nests to shallow water by wind-generated waves. In some cases, both species of grebes copulated and laid eggs on the same nest. Usually, the eggs on these nests

Table 1. Relationship between colony size and number of communal egg dumps (> 10 eggs in nest) for the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) at Clear Lake, California, during 2010–2019.

Number of nests in colony	Number of colonies	Number of egg dumps	Number of egg dumps per colony
1–99	109	0	0
100–199	9	2	0.22
200–299	5	1	0.20
300–499	11	3	0.27
500–999	8	11	1.38
1,000–4,721	8	34	4.25

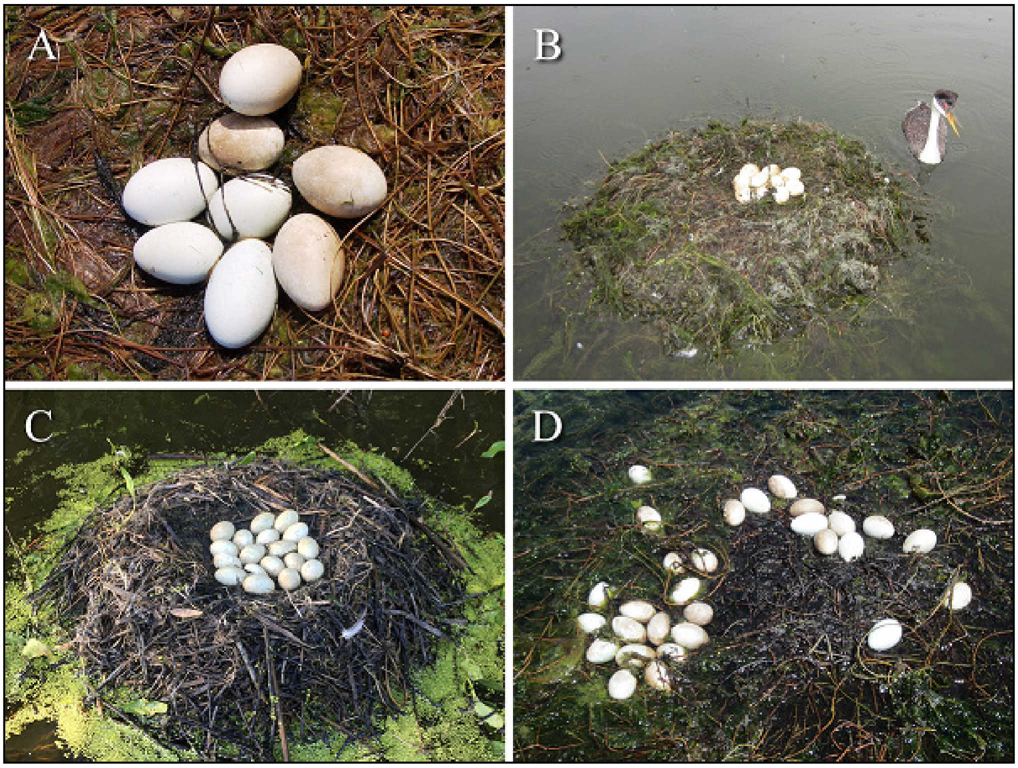

Figure 2. Examples of brood parasitism in Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) at Clear Lake, California. (A) A well-maintained nest with four pale eggs recently laid by a presumed brood parasite in a nest with four brown-stained eggs previously laid by a host. (B) A male Western Grebe vigorously defending 10 eggs in a well-maintained nest. (C) A well-maintained nest with 18 eggs incubated by a male Clark's Grebe and female Western Grebe. (D) An unmaintained nest with 30 eggs, including fragments of one egg (a 31st egg was present 2 d later). (Photographed by Floyd E. Hayes).

were not incubated but sometimes they were incubated intermittently. Two cameras documented an unusual instance of egg dumping after a windstorm on 18 July 2015, when numerous nests with at least 11 visible eggs were transported to shallow water. Although the grebes stopped incubating eggs in these nests, 25 copulations on at least five different nests were recorded during the next 7 h, two the following night, and four the following day. The grebes also dumped new eggs in the abandoned nests, with the number of visible eggs increasing from 11 to 13 during day 1, 17 eggs by day 4, and 20 eggs by day 5, with up to 11 eggs on a nest. None of the eggs were subsequently incubated and all gradually sank underwater as the nests disintegrated.

Discussion

Disturbance of nesting birds by researchers may negatively impact their breeding success (Fair et al. 2010). Our 2010 and 2019 surveys of clutch size in three large colonies and our repeated visits in 2010 to count eggs in marked nests at one colony did not result in colony abandonment, which often happens on Clear Lake for no apparent reason (Hayes et al. 2022). The number of days of our monitoring effort per breeding season varied by more than four-fold and was not significantly correlated with the number of nests, number of young, number of young per nest, or the productivity ratio of young to adults (Hayes et al. 2022). The number of young per nest, which we consider the best measurement of reproductive successive, was the second highest in 2010 and fourth highest in 2019 during our 10-y study (Hayes et al. 2022). These results indicate that our intrusions into colonies to count eggs in 2010 and 2019 did not significantly reduce breeding success.

The mean clutch size of typical grebe nests in the two 2010 colonies (2.29–2.37) is similar to previous reports from Clear Lake (2.10–2.40; Feerer and Garrett 1977) and Utah (2.6; Lindvall and Low 1982). The mean clutch size of the 2019 colony was much higher (3.12) but still lower than previous reports from British Columbia (up to 3.7; Forbes 1988), Colorado (up to 3.89; Davis 1961), and Manitoba (up to 4.2; LaPorte et al. 2014). Although only 3% of our nests contained > four eggs in the two 2010 colonies, up to 12.2% of nests contained > four eggs in Manitoba (http://birdsoftheworld.org/bow/species/wesgre), 13.7% in British Columbia (Forbes 1988), 15.2% in our 2019 colony, and 39.1% in Colorado (Davis 1961).

Our study provides new data on the maximum number of eggs incubated by the grebes. Lindvall and Low (1982) reported that clutches with > four eggs in Utah were not incubated. Forbes (1988) stated that all 19 clutches with > four eggs in British Columbia were incubated, but did not provide a maximum clutch size. LaPorte et al. (2014) reported that clutches with > six eggs in Manitoba were always cold and presumed abandoned. We occasionally observed grebes incubating clutches of up to 10 eggs, however, and in one case we observed a mixed pair of grebes incubating 18 eggs in a well-maintained nest (Fig. 2).

Our observations reveal that eggs frequently disappear and reappear on nests of all clutch sizes. New eggs appearing on nests well after the eggs of the initial host were laid provide evidence of brood parasitism. We provide the estimates of the daily rate of brood parasitism for these species, with a rate much higher (2.6–10.4% of nests/d) than the only previously published total rate of 1.8% of Western Grebe nests (Nuechterlein in Rohwer and Freeman 1989). Although our sample sizes are small, the daily rate of brood parasitism was lower for nests with 1–4 eggs than for nests with 15–31 eggs. Our methods did not exclude the possibility of parasitic eggs being laid prior to the last egg laid by the parents incubating the eggs. Brood parasites should have a stronger incentive to parasitize nests at an early period of the egg-laying cycle of a host, especially for species such as grebes with asynchronous egg laying and hatching because eggs laid earlier are more likely to hatch and less likely to be abandoned (Konter 2011).

The grebes appeared to be especially attracted to abandoned nests with failed clutches due to predation or windstorms. Because floating grebe nests are a valuable resource requiring considerable time and energy to construct and maintain daily to prevent disintegration in the water (Fjeldså 2004), the nests were frequently reused by the grebes for copulation, egg laying, and sometimes for incubation of laid eggs (Hayes and Turner 2017; Hayes et al. 2018a,b). Konter (2008) similarly reported an increase in egg parasitism on nests of the Great Crested Grebe after many eggs were destroyed by a storm. Brood parasites are presumably more successful in parasitizing abandoned nests than active nests because abandoned nests are not defended by a mated pair. The eggs laid in abandoned nests, however, are less likely to be incubated than those in active nests.

Communal egg dumping is probably initiated in abandoned nests with failed clutches, although the mixed pair incubating 18 eggs in a well-maintained nest may have been an exception. The large communal egg dumps of the Western Grebe and Clark's Grebe are unique among grebes (Fjeldså 2004). Our maximum count of 31 unincubated eggs in a nest nearly doubled the previously reported high of 16 eggs (Finley 1907). The maximum number of eggs reported in nests of other grebe species is 11 in the brood parasitic Great Crested Grebe (Moskal and Marszałek 1986) and non-brood parasitic Pied-billed Grebe (*Podilymbus podiceps*; Lee et al. 2008). Our data reveal that egg dumping is more likely to occur in larger colonies, where more nests with failed clutches are available. Hill et al. (1997) reported brood parasitism to be more common in a high-density colony than in a low-density colony of Eared Grebes. Konter (2008) reported that the largest clutches of the Great Crested Grebe, which presumably included parasitized eggs, occurred in areas of a colony with high nest density.

Grebes are indeterminate and prolific egg layers. The Horned Grebe (*Podiceps auritus*) can lay up to 50 eggs in a season (Fjeldså 2004), the Least Grebe (*Tachybaptus dominicus*) can lay up to 35 eggs during a breeding season (Gross 1949), and the Pied-billed Grebe can lay up to 13 eggs in 15 d (Fugle and Rothstein 1977). The Western Grebe and Clark's Grebe also appear to be prolific egg layers, frequently laying eggs in the nest of each other whether attended or unattended, and the Western Grebe has been reported parasitizing a nest of the Red-necked Grebe (*Podiceps grisegena*; Van Damme 2004, 2006). The rate of heterospecific brood parasitism remains unknown but could be documented by studying the DNA of eggs. It is unknown whether parasitic eggs are laid by unmated young females, mated females with active clutches, mated females with failed clutches, or a mixture of these groups. It is also unknown what proportion of females engage in brood parasitism. Given their ability to produce many eggs, it is possible that all females engage in brood parasitism.

Some species of birds react aggressively to conspecific brood parasites by removing parasitic eggs or hatchlings from their nests to reduce the costs of raising unrelated offspring. The best known example among grebes is the Eared Grebe, in which eggs are often destroyed, presumably by conspecifics (McAllister 1958), with a higher rate of egg loss and infanticide occurring in parasitized nests than in non-parasitized nests (Lyon and Everding 1996). In contrast, egg destruction is rare in the Western Grebe and Clark's Grebe (Hayes et al. 2018b) and infanticide has never been documented. These grebes respond more passively to brood parasites and tolerate the accumulation of more parasitic eggs in nests. Conspecific and interspecific brood parasitism by females of the two species is more extensive than previously realized and appears to be a common and adaptive reproductive strategy that potentially increases the probability of producing additional offspring without incurring the extra costs of parental care. Even though eggs dumped in failed nests are unlikely to be incubated, the incubation of 18 eggs by a mixed pair of grebes for at least 7 d indicates that there is always a chance, even if small, that dumped eggs will be incubated and the hatchlings raised by other grebes.

Acknowledgments.—We followed all applicable ethical guidelines for the use of birds in research (Fair et al. 2010). Funding was provided by Audubon California, the Luckenbach Trustee Council, the National Audubon Society, the National Fish and Wildlife Foundation, the National Oceanic and Atmospheric Administration, Pacific Union College, and the Redbud Audubon Society.

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Literature Cited

Bent, A.C. 1919. Life histories of North American diving birds, order Pygopodes. United States National Museum Bulletin 107:1–239.

Davis, D.G. 1961. Western Grebe colonies in northern Colorado. Condor 63:264–265.

Eadie, J. McA., F.P. Kehoe, and T.D. Nudds. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. Canadian Journal of Zoology 66:1709–1721.

Fair, J., E. Paul, and J. Jones (Eds.). 2010. Guidelines to the Use of Wild Birds in Research. 3rd Edition. Ornithological Council, Washington, D.C.

Feerer, J.L., and R.L. Garrett. 1977. Potential Western Grebe extinction on California lakes. California-Nevada Wildlife Transactions 13:80–89.

Finley, M.W. 1907. The grebes of southern Oregon. Condor 9:97–101.

Fjeldså, J. 2004. The Grebes. Oxford University Press, Oxford, UK.

Forbes, L.S. 1988. Western Grebe nesting in British Columbia. Murrelet 69:28–33.

Fugle, G.N., and S.I. Rothstein. 1977. Clutch size determination, egg size and eggshell thickness in the Pied-billed Grebe. Auk 94:371–373.

Gross, A.O. 1949. The Antillean Grebe at central Soledad, Cuba. Auk 66:42–52.

Hayes, F.E., B. McIntosh, D.G. Turner, and D.E. Weidemann. 2022. Historical and recent breeding of the Western Grebe and Clark's Grebe in a severely impaired ecosystem at Clear Lake, California. Monographs of the Western North American Naturalist 14:65–100.

Hayes, F.E., and D.G. Turner. 2017. Copulation behavior in the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*). Waterbirds 40:168–172.

Hayes, F.E., D.G. Turner, N.D. Zimmerly, and M.B. Peralta. 2018a. Nocturnal courtship, copulation, and egg laying in the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*Aechmophorus clarkii*). Journal of Ethology 36:65–75.

Hayes, F.E., D.G. Turner, N.D. Zimmerly, M.B. Peralta, B.J. McIntosh, and M.E. Hellie. 2018b. Egg destruction by males in the Western Grebe and Clark's Grebe. Western Birds 49:258–269.

Hill, W.L., K.J. Jones, C.L.L. Hardenbergh, and M. Browne. 1997. Nest distance mediates the costs of coloniality in Eared Grebes. Colonial Waterbirds 20:470–477.

Horne, A.J., and C.R. Goldman. 1972. Nitrogen fixation in Clear Lake, California. I. Seasonal variation and the role of heterocysts. Limnology and Oceanography 17:678–692.

Johnsgard, P.A. 1997. The Avian Brood Parasites: Deception at the Nests. Oxford University Press, New York, New York.

Konter, A. 2008. Colonial nesting in the Great Crested Grebe *Podiceps cristatus* (Linné 1758): research results from a colony on the Dutch IJsselmeer in comparison to other studies on colonial nesting in the species. Ferrantia 56:5–56.

Konter, A. 2011. Seasonal patterns of aggressiveness in colonial Great Crested Grebes *Podiceps cristatus*. Ardea 99:85–92.

Laporte, N., N. Koper, and L. Leston. 2014. Assessing the breeding success of the Western Grebe (*Aechmophorus occidentalis*) after 40 years of environmental changes at Delta Marsh, Manitoba. Waterbirds 37:30–42.

Lee, J.F., F.E. Durbian, R. Bell, and M. Voltz. 2008. Pied-billed Grebe nesting ecology on Squaw Creek National Wildlife Refuge, 1996–2007. Transactions of the Missouri Academy of Science 42:23–29.

Lindvall, M.L., and J.B. Low. 1982. Nesting ecology and production of Western Grebes at Bear River Migratory Bird Refuge, Utah. Condor 84:66–70.

Lyon, B.E., and S. Everding. 1996. High frequency of conspecific brood parasitism in a colonial waterbird, the Eared Grebe *Podiceps nigricollis*. Journal of Avian Biology 27:238–244.

Mackie, R. J., and H. K. Buechner. 1963. The reproductive cycle of the Chukar. Journal of Wildlife Management 27:246–260.

McAllister, N.M. 1958. Courtship, hostile behavior, nest-establishment and egg laying in the Eared Grebe (*Podiceps caspicus*). Auk 75:290–311.

Moskal, J., and J. Marszałek. 1986. Effect of habitat and nest distribution on the breeding success of the Great Crested Grebe *Podiceps cristatus* on Lake Żarnowieckie. Acta Ornithologica 22:147–158.

Petrie, M., and A.P. Møller. 1991. Laying eggs in others' nests: intraspecific brood parasitism in birds. Trends in Evolution and Ecology 6:315–320.

Richerson, P.J., T.H. Suchanek, R.A. Zierenberg, D.A. Olseger, A.C. Heyvaert, D.G. Slotton, C.A. Eagles-Smith, and C.E. Vaughn. 2008. Anthropogenic stressors and changes in the Clear Lake ecosystem as recorded in sediment cores. Ecological Applications 18 (Supplement):A257–A283.

Rohwer, F.C., and S. Freeman. 1989. The distribution of conspecific nest parasitism in birds. Canadian Journal of Zoology 67:239–253.

Sorenson, M.D. 1992. Comment: why is conspecific nest parasitism more frequent in waterfowl than in other birds? Canadian Journal of Zoology 70:1856–1858.

Storer, R.W., and G.L. Nuechterlein. 1992. Western Grebe (*Aechmophorus occidentalis*) / Clark's Grebe (*Aechmophorus clarkii*). Pp. 1–26 *in* The birds of North America, no. 26. Poole, A., P. Stettenheim, and F. Gill (Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Suchanek, T.H., P.J. Richerson, D.C. Nelson, C.A. Eagles-Smith, D.W. Anderson, J.J. Cech, Jr., R. Zierenberg, G. Schladow, J.F. Mount, S.C. McHatton, et al. 2003. Evaluating and managing a multiply-stressed ecosystem at Clear Lake, California: a holistic ecosystem approach. Pp. 1239–1271 *in* Managing for Healthy Ecosystems. Rapport, D.J., W.L. Lasley, D.E. Rolston, N.O. Nielsen, C.O. Qualset, and A.B. Damania (Eds.). Lewis Publishers, Boca Raton, Florida, USA.

Van Damme, L.M. 2004. Weather influences parenting behaviour among Red-necked Grebes and Western Grebes on Duck Lake, Creston Valley. Wildlife Afield 1:67–69.

Van Damme, L.M. 2006. Western Grebe parasitism of Red-necked Grebe nests on Duck Lake in the Creston Valley, British Columbia. Wildlife Afield 3:121–125.

Yom-Tov, Y. 1980. Intraspecific nest parasitism in birds. Biological Reviews 55:93–108.

Yom-Tov, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis 143:133–143.

Yom-Tov, Y., and E. Geffen. 2017. Conspecific brood parasitism among birds: the effects of phylogeny, mode of reproduction and geographic distribution. Pp. 95–103 *in* Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution. Soler, M. (Ed.). Springer, Cham, Switzerland.

Zar, J.H. 2010. Biostatistical Analysis. 5th Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Floyd Hayes is a Professor of Biology at Pacific Union College, Angwin, California. He previously worked for a year as a primary school teacher in Micronesia, 3 y as a U.S. Peace Corps Vertebrate Biologist at the National Museum of Natural History of Paraguay, 9 y as a Biology Professor at the University of the Southern Caribbean and University of the West Indies in Trinidad, and 1 y as a Wildlife Biologist at the Division of Fish and Wildlife in the U.S. Virgin Islands. Floyd has published research on a variety of invertebrates and vertebrates based on field work in 17 countries. (Photographed by Jessica Edens).

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Doug Weidemann is a Molecular Biology Research Technician for Virginia Tech, Blacksburg, Virginia. His work mainly focuses on understanding gene expression regulation, in particular RNA dynamics. Doug has also worked on a variety of ecology, wildlife biology, and evolutionary biology bird studies, including studying grebes at Clear Lake, California. (Photographed by Floyd Hayes).

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PEER-EDITED NOTES

NORTH AMERICAN DEERMOUSE (*PEROMYSCUS MANICULATUS*) PREDATION BY A STELLER'S JAY (*CYANOCITTA STELLERI*)

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Abstract.—**Predation events are uncommonly witnessed, but the increasing deployment of camera trap arrays has resulted in incidental capturing of predation events. Here we describe a Steller's Jay (*Cyanocitta stelleri*) preying upon a juvenile North American Deermouse (*Peromyscus maniculatus*) captured incidentally on a camera trap intended to record the movements of Mountain Lions (*Puma concolor*) in Sonoma County, California.**

Key Words.—arboreal; camera traps; diet; digital capture, foraging, Sonoma County.

Predation events are necessarily frequent because they are the occurrences by which predators achieve successful foraging, yet directly witnessing predation is uncommon (Major 1991; Van Vuren 2001). The increasing use of camera traps, however, along with their improving technologies (Smith et al. 2020), has facilitated the number of predation events witnessed, albeit remotely. In addition, because camera traps are triggered either by motion, or by thermal signals, they often capture unintended targets and thus reveal incident events. For example, Linnell and Lesmeister (2020) deployed a camera trap array on artificial nest platforms placed high in young coniferous forests to assess the predation and non-lethal avoidance behaviors of Red Tree Voles (*Arborimus longicaudus*) in response to two known predators. Incidentally, a camera trap captured a Steller's Jay (*Cyanocitta stelleri*) predating one of the tree voles in what may be the first report of Steller's Jays preying upon small mammals. Here, we report an incidental digital capture of a Steller's Jay predating a North American Deermouse (*Peromyscus maniculatus*).

Steller's Jays are generalist predators primarily inhabiting coniferous, mixed coniferous forests, and open woodlands from Alaska to Guatemala (Walker et al. 2020). Their diet consists of plant matter (nuts, berries, seeds, and mast) and insects (Bent 1946; Walker et al. 2020), but seasonal availability strongly influences their individual foraging habits (Vigallon and Marzloff 2005; Walker et al. 2020). Steller's Jays are known bird nest predators (Sieving and Willson 1999; Marzluff et al. 2000; Vigallon and Marzluff 2005; Linnell and Lesmeister 2020) but are also opportunistic predators of vertebrate prey (Carothers et al. 1972; Walker et al. 2020; Linnell and Lesmeister 2020).

An incidental digital capture event occurred on a camera within an existing trap array (Dellinger et al. 2020) designed to track the movements of Mountain Lions (*Puma concolor*) through the Mitsui Ranch on Sonoma Mountain; Sonoma County, 8 km east of Petaluma, California. The Mitsui Ranch is comprised of primarily of open Oak Savannah, where stands of California Bay-Laurel (*Umbellularia californica*) and Oregon White Oak (*Quercus garryana*) are confined to dense copse formations by the surrounding mosaic of Vertisol soils, which limit the growth of deep-rooted plants (Belsky 1990). The clustered trees create fragmented pockets of forest, creating the abundant edge habitat preferred by Steller's Jays (Walker et al. 2020).

Within the camera array, we mounted a High Knolls camera (Browning BTC-5HDPX; Browning Trail Cameras, Birmingham, Alabama, USA) to the bole of a small oak tree, approximately 60 cm from the ground, set to record 20 sec of digital video when triggered. We directed the camera toward a prominent game trail along a narrow ridge line under dense canopy, 10 m from the edge of the copse. The forest floor was characterized by a carpet of leaf litter, fallen branches, and large, moss-covered rocks forced from the substrate by the growing roots of the surrounding trees. At 1015 on 3 June 2021, the camera trap was actuated by a Steller's Jay landing on a rock in front of the camera. In its mouth was a live juvenile North American Deermouse (Fig. 1). We determined the age of the mouse by its uniform gray dorsal pelage, and small size (Ingles 1965). The jay, immediately after landing, beat the deer mouse on either side of the rock it stood upon, bending to rapidly slam the mouse, head exposed, on the flattish side of the rock. The jay then jumped down to a smaller rock (Fig. 1) and adjusted its hold on the mouse before disappearing by flying out of the camera view. The entire incident consumed only the first 5 sec of the 20-sec recording. Although we did not directly witness the Steller's Jay capture the mouse, the struggling mouse (legs flailing in the air) showed that this was a live capture and not scavenging by the jay. The subsequent repeated beating of the head of the mouse against the rock indicates the intent to subdue, therefore predate.

Figure 1. A trail camera photograph of a Steller's Jay (*Cyanocitta stelleri*) adjusting its hold on a Deer Mouse (*Peromyscus maniculatus*) before flying off with the mouse.

North American Deermice build nests of vegetative materials that may be located in trees, under rocks, or underground (Wolff and Durr 1986). Because the mouse was a juvenile, it may have only recently made a first venture from a nest site, and a lack of developed senses may have contributed to its vulnerability to predation. The increased deployment of camera traps may reveal that Steller's Jays are as adept at locating a concealed mouse nest as they are the arboreal nests of birds. This event occurred when Steller's Jays are likely to be raising young, and a high protein meal of that size would be an especially rewarding find for parents. Predation by Steller's Jays on rodents may occur more frequently than we realize and further targeted investigation is warranted.

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Literature Cited

Belsky, A.J. 1990. Tree/grass ratios in East African savannas: a comparison of existing models. Journal of Biogeography 17:483–489.

Bent, A.C. 1946. Life histories of North American jays, crows and titmice, Part I. United States National Museum Bulletin 191, Smithsonian Institution, Washington, D.C., USA.

Carothers, S.W., N.J. Sharber, and R.P. Balda. 1972. Steller's Jays prey on Gray-headed Juncos and a Pigmy Nuthatch during periods of heavy snow. Wilson Bulletin 84:204–205.

Dellinger, J.A., B. Cristescu, J. Ewanyk, D.J. Gammons, D. Garcelon, P. Johnston, Q. Martins Dellinger, C. Thompson, T.W. Vickers, et al. 2020. Using Mountain Lion habitat selection in management. Journal of Wildlife Management 84:359–371.

Ingles, L.G. 1965. Mammals of the Pacific States, California, Oregon, Washington. Stanford University Press, Stanford, California.

Linnell, M.A., and D.B. Lesmeister. 2020. Predator-prey interactions in the canopy. Ecology and Evolution 10:8610–8622.

Major, R.E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. Auk 108:190–195.

Marzluff, J.M., M.G. Raphael, and R. Sallabanks. 2000. Understanding the effects of forest management on avian species. Wildlife Society Bulletin 28:1132–1143.

Sieving, K.E., and M.F. Willson. 1999. A temporal shift in Steller's Jay predation on bird eggs. Canadian Journal of Zoology 77:1829–1834.

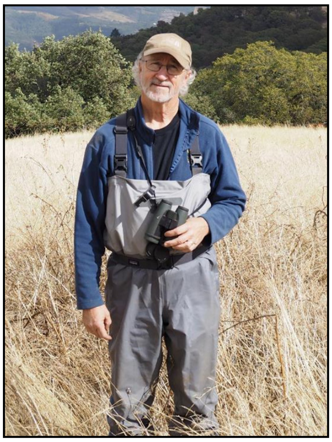
Smith, J.A., J.P. Suraci, J.S. Hunter, K.M. Gaynor, C.B. Keller, M.S. Palmer, J.L. Atkins, I. Castañeda, M.J. Cherry, P.M. Garvey, and S.E. Huebner. 2020. Zooming in on mechanistic predator-prey ecology: integrating camera traps with experimental methods to reveal the drivers of ecological interactions. Journal of Animal Ecology 89:1997–2012.

Van Vuren, D.H. 2001. Predation on Yellow-bellied Marmots (*Marmota flaviventris*). American Midland Naturalist 145:94–100.

Vigallon, S.M., and J.M. Marzluff. 2005. Is nest predation by Steller's Jays (*Cyanocitta stelleri*) incidental or the result of a specialized search strategy? Auk 122:36–49.

Walker, L.E., P. Pyle, M.A. Patten, E. Greene, W. Davison, and V.R. Muehter. 2020. Steller's Jay (*Cyanocitta stelleri*). Version 1.0. *In* Birds of the World. Rodewald, P.G. (Ed.). Cornell Lab of Ornithology, Ithaca, New York. https://doi.org/10.2173/bow.stejay.01.

Wolff, J.O., and D.S. Durr. 1986. Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 67:409–412.



Jeff Wilcox is the Managing Ecologist for the Mitsui Ranch Preserve near Petaluma County, California. He has worked with landscape-scale parcels to manage sites for endangered species, native grasses, and compatible uses such as organic cattle grazing, education, and research. Jeff has decades of experience working collaboratively on projects that include pond management and construction, native grasses restoration, and species-level projects with California Red-legged Frogs (*Rana draytonii*), Wild Pigs (*Sus scrofa*), American Bullfrogs (*Lithobates catesbeianus*), California Tiger Salamanders (*Ambystoma californiense*), and Foothill Yellow-legged Frogs (*Rana boylii*). (Photographed by Lou Silva).

Collen Sibanda spent his childhood in Bulawayo Province, Zimbabwe, where he learned cattle ranching and stockmanship from his grandfather, and where he provisioned wild game to the family kitchen. After graduating high school, he followed his dream of becoming a professional photographer, emigrating to Johannesburg, South Africa, to apprentice as a commercial photographer. There, he met and fell in love with an American traveler and soon after, came to the United States. After earning a college degree, he pursued a career in motion graphic design, but yearning for a better quality of life, he sought out ranching again. Collen joined the staff of the Mitsui Ranch Preserve in 2018. In addition to invasive weed management, welding and fabrication, woodworking, and stockmanship, Collen ran the camera trap program on the Mitsui Ranch Preserve. When not on the ranch, you will find Collen on the soccer pitch, guiding the youth of America to be better at this world game. (Photographed by Jeff Wilcox).

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NOTES

CATTLE WATER TROUGHS: DO THEY PROVIDE SUPPLEMENTAL WATER FOR WILDLIFE?

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***Abstract*.—Cattle water troughs are widely used on cattle ranches throughout the American west, including the U.S. Bureau of Land Management (BLM) cattle allotments. Many of these BLM water troughs were installed decades ago and have since become unusable; however, the spring box system that provides the water may remain functional. I assisted grazing lessees in replacing two water troughs on BLM allotments in 2020 and 2021. These galvanized steel water troughs were installed for cattle. I used this opportunity to assess whether these troughs provided supplemental water for wildlife. To investigate this question, I installed trail cameras to detect wildlife use at each water trough. Data were collected for approximately 18 mo and 22 bird and 11 mammal species were detected visiting the water troughs during that period. This study provides evidence that wildlife will readily use water troughs installed for cattle in the Sierra Nevada foothills.**

Key Words.—cattle; foothills; Sierra Nevada; spring box; thermoregulate; trail cameras; trough; wildlife.

Research has been conducted on wildlife use of water developments in Arizona and Southern California (Bleich et al. 1982; Broyles 1995; Rosenstock et al. 1999; Rich et al. 2019). These water resources were reported to show a benefit to wildlife species, but speculation remained that there may be negative impacts that are currently not studied or understood (Rosenstock et al. 1999). For instance, concentration of avian predators around water sources has been a concern in desert environments (Simpson et al. 2011). DeStafano et al. (2000) noted that a concern of water developments is the attraction of predators, which impact prey populations. In addition to a lack of systematic studies on the effects of these resources for wildlife, the few studies published are widely disparate in design, location, and detail reported. Of note, no published report, whether systematically evaluated or observational, is available for the Sierra Nevada foothills in California. This region supports a rich assemblage of wildlife species (Schoenherr 2007), and water resource availability has a high level of interannual variability. Following numerous anecdotal observations of various species of wildlife using cattle water troughs for drinking and other purposes, I elected to determine the extent of use at troughs by wildlife in my study area in the foothill region of central California.

I used two existing water troughs in Mariposa County, which are on U.S. Bureau of Land Management (BLM) land. This region experiences an average annual temperature range of 5°–20° C and an average annual rainfall of 93 cm, with a high level of year-to-year variation (Barreau et al. 2017). Both water troughs were in typical Chaparral habitat dominated by Toyon (*Heteromeles arbutifolia*), Buckbrush (*Ceanothus cuneatus*), Chamise (*Adenostoma fasciculatum*), White-leaf Manzanita (*Arctostaphylos viscida*), Poison Oak (*Toxicodendron diversilobum*), and Grey Pine (*Pinus sabiniana*). Additionally, Interior Live Oak (*Quercus wislizeni*) and Blue Oak (*Q. douglasii*) occurred in patches of habitat in the surrounding area. Understory vegetation included non-native annual grasses dominated by Medusahead (*Taeniatherum caput-medusae*). Lake McClure reservoir (28 km^2), a moderate-sized drinking water reservoir that provided year-round water, was approximately 1–1.5 km from both troughs. Two small stock ponds were also in the general vicinity; both of which were completely dry by late spring (May-June). Each trough was located adjacent to a small creek, which was the water source to each trough. These adjacent creeks provided year-round water, but access was limited due to dense vegetation growing over and around the water. Therefore, the only reliable water source for the immediate area was the water trough.

In the winter of 2020 and summer of 2021, I assisted two lessees in replacing one water trough within their respective BLM cattle allotment (Fig. 1). After new troughs were installed, I placed one Bushnell Trail Camera (Trophy Cam Model 119874 or Core DS Model 119977C; Bushnell, Overland Park, Kansas) at each trough to observe wildlife usage. Metal posts were installed at both ends of Trough 1 to protect the inflow/outflow plumbing. I placed the camera on one of these posts, which resulted in a clear view of the trough and any potential species that might visit. I placed the camera at Trough 1 at a height of approximately 1 m. At Trough 2, I mounted the camera to an adjacent tree (distance of approximately 3 m). To allow smaller species access to the water in the Trough 1, I attached a small section of wood to the side of the water trough to function as a small platform for access to the water by smaller species. In addition, I placed a wildlife escape ramp and large rocks (25–35 cm diameter) in a manner to facilitate access to and escape from the water.

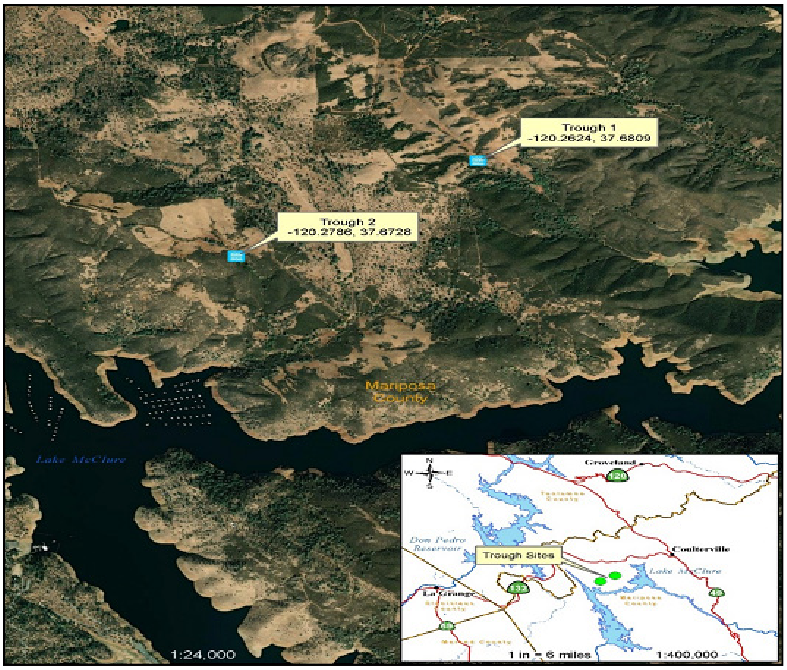

Figure 1. Vicinity and location of water troughs in Mariposa County, California.

I checked the trail cameras periodically (every 6–10 weeks), which may have led to a loss of detection of some species. For example, one trail camera was found, on more than one occasion, displaced by cattle and bear activity resulting in loss of potential species detections. The camera position had to be corrected periodically throughout the study. I collected trail camera data from July 2021 to January 2023. Direct photographic observations and presumed behavior of each species were the only data collected. I did not analyze species abundance for this pilot project; therefore, I did make statistical analyses.

The trail cameras documented 22 bird species at Troughs 1 and 2 (Table 1). Many species were documented drinking water from the trough, while others were observed either perched on the trough (e.g., Lawrence's Goldfinch, *Spinus lawrencei*), bathing in the water (e.g., American Black Bear, *Ursus americanus*), or foraging on insects drawn to the water (e.g., Black Phoebe, *Sayornis nigricans*). Although this data is not indicative of species abundance, these data suggest some species such as Mourning Doves (*Zenaida macroura*) attended the troughs in higher numbers than other species: I observed doves in groups of up to six individuals. Common Ravens (*Corvus corax*) were typically photographed in pairs, while nearly all other species were visiting troughs as individuals. I speculate that additional species visited the trough but

Figure 2. Trail camera photograph of an American Black Bear (*Urus americanus*) using a trough for bathing and presumably thermoregulating.

Table 1. Species of birds and mammals photographically recorded by trail cameras at water troughs in Mariposa County, California. I include their inferred behaviors, which included drinking (D), bathing (B), foraging (F), attempted but unable to drink (AD), and photographed at a trough but behavior was undetermined (U).

Species	Detected Use
Birds	
California Quail (*Callipepla california*)	U
Mourning Dove (*Zenaida macroura*)	D, B
Greater Roadrunner (*Geococcyx californianus*)	U
Turkey Vulture (*Cathartes aura*)	D
Cooper's Hawk (*Accipiter cooperii*)	U
Western Screech Owl (*Megascops kennicottii*)	F
Acorn Woodpecker (*Melanerpes formicivorus*)	D
Northern Flicker (*Colaptes auratus*)	D
American Kestrel (*Falco sparverius*)	B
Black Phoebe (*Savornis nigricans*)	D, F
California Scrub Jay (*Aphelocoma california*)	D
Common Raven (*Corvus corax*)	D
American Crow (*Corvus brachyrhynchos*)	D
Western Bluebird (*Sialia mexicana*)	AD
American Robin (*Turdus migratorius*)	U
House Finch (*Haemorhous mexicanus*)	AD
Lawrence's Goldfinch (*Spinus lawrencei*)	AD
California Towhee (*Melozone crissalis*)	D
Bullock's Oriole (*Icterus bullockii*)	D
Brown-headed Cowbird (*Molothrus ater*)	D
Mammals	
Unknown bat species (order: Chiroptera)	D
Virginia Opossum (*Didelphis virginiana*)	U
Coyote (*Canis latrans*)	D
Grey Fox (*Urocyon cinereoargenteus*)	D
American Black Bear (*Ursus americanus*)	D, B
Raccoon (*Procyon lotor*)	U
Bobcat (*Lynx rufus*)	D
Mountain Lion (*Puma concolor*)	U
Mule Deer (*Odocoileus hemionus*)	U
Western Gray Squirrel (*Sciurus griseus*)	U
Black-tailed Hare (*Lepus californicus*)	U

may have been out of the detection field of the camera. Notably, both House Finches (*Haemorhous mexicanus*) and Lawrence's Goldfinches visited the trough in small flocks but appeared to fail at reaching the water to drink. In addition to the species observed drinking, the cameras detected numerous observations of what I term bathing. For example, an American Kestrel (*Falco sparverius*) was detected bathing by using the escape ramp. Additionally, some species were photographed preying on insects that were present at the water.

I found 11 mammal species using the troughs, with five species photographed drinking water. In addition to using the trough as a water source, American Black Bears were frequently photographed entering the trough (Fig. 2), presumably to cool off during the heat of the day, which can exceed 38° C daily for several months in this region of California. Thermoregulatory behavior can help to mitigate heat stress and maintain homoeostasis for some mammalian species (Sawaya et al. 2017). Research conducted by Sawaya et al. (2017) suggested that natural and artificial water sources play an important role in allowing black bears to thermoregulate and counteract the negative physiological effects of heat stress. It is important to note that the trail camera data was collected during the drought of 2020–2022, and photos of bears bathing were frequently collected during summer and early fall.

During my study, I observed various mammalian predator species but no signs of a predator-prey interaction (e.g., feathers, blood, hair). In one photograph, an owl appeared to capture an unknown prey on the water surface. Use of cattle water troughs has allowed, at the least, some species to expand into areas that, without a water source, was not previously preferred habitat. For example, Black Phoebes are seldom found far from water (Wolf 1991), yet an adult Black Phoebe established a territory at one of the troughs and, therefore, likely expanded the species local range away from Lake McClure. Everlyn et al. (2004) found that the Yuma Myotis (*Myotis yumanensis*) selected roost sites within 132.6 ± 167.5 (standard deviation) m of a water source. In another study, Fringed Myotis (*Myotis thysanodes*) choose roost sites within 117.4 ± 27.3 m of a water source (Weller et al. 2001). Cameras detected bats using the troughs for dinking, and possibly for foraging, but I could not determine the particular species.

My study demonstrates that water troughs installed for cattle will be used by a suite of wildlife species. Although no attempt was made to determine invertebrate use, I speculate that the supplemental water attracted species use to both troughs. A more systematic study of the use of supplemental water sources or the use of livestock water troughs should be considered. Studies should include modifications to water troughs that would facilitate access for smaller seed-eating bird species. Additionally, future studies should include a strict schedule for data collection to limit potential data loss. Artificial water sources, such as water troughs, will likely continue to be used by wildlife in this region of California. This is particularly true during the frequent drought conditions that California is now experiencing, and when other natural water sources are scarce.

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LITERATURE CITED

Barreau, T., D. Conway, K. Haught, R. Jackson, R. Kreutzer, A. Lockman, and S. Minnink. 2017.

Physical, mental, and financial impacts from drought in two California Counties. American Journal of Public Health 5:783–790.

Bleich, V.C., L.J. Coombes, and J.H. Davis. 1982. Horizontal wells as a wildlife habitat improvement technique. Wildlife Society Bulletin 10:324–328.

Broyles, B. 1995. Desert wildlife water developments: questioning use in the Southwest. Wildlife Society Bulletin 23:663–675.

DeStefano, S., S. Schmidt, and J.C. deVos, Jr. 2000. Observations of predator activity at wildlife water developments in southern Arizona. Journal Rangeland Management 53:255–258.

Evelyn, M., D. Stiles, and R. Young. 2004. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. Biological Conservation 115:463–473.

Rich, L.N., S.R. Beissinger, J.S. BrasHares, and B.J. Furnas. 2019. Artificial water catchments influence wildlife distribution in the Mojave Desert. Journal of Wildlife Management 83:855–865.

Rosenstock, S.S., W.B. Ballard, J.C. deVos, Jr. 1999. Viewpoints: benefits and impacts of wildlife water developments. Journal of Rangeland Management 52:302–311.

Sawaya, M.A., J.B. Ramsey, and P. Ramsey. 2017. American Black Bear thermoregulation at natural and artificial water sources. Ursus 27:19–135.

Schoenherr, A. 2007. A Natural History of California, 2nd Edition. University of California Press, Berkeley, California, USA.

Simpson, N.O., K. Stewart, and V. Bleich. 2011. What have we learned about water developments for wildlife? Not enough! California Fish and Game 97:190–209.

Wolf, B.O. 1991. The reproductive biology and natural history of the Black Phoebe (*Sayornis nigricans Swainson*) in central California. M.S. Thesis, San Jose State University, San Jose, California. 99 p.

Weller, T., and C. Zabel. 2001. Characteristics of Fringed Myotis day roosts in Northern California. Journal of Wildlife Management 65:489–497.

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THE EFFECTIVENESS OF AN UNMANNED AERIAL VEHICLE IN CONTROLLED FECAL PELLET SURVEYS

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Abstract.—**The declining costs and increasing capabilities of unmanned aerial vehicles (UAVs) have led to their expanded use in natural resources research and management. Generally, UAV-based data collection involves larger (i.e., more visible) components (e.g., large mammals, blocks of forest) that are more easily observed by UAV cameras. Little research has focused on UAV effectiveness in researching and monitoring relatively small and less visible objects. Fecal surveys are broadly applied methods for determining wildlife occupancy, population abundance and trends, and land use. Potentially, UAVs could improve, or augment, fecal surveys by reducing time and effort expenditures, expense, and impacts on focal species behavior. Yet, their effectiveness and ability to produce accurate and precise estimates have not yet been evaluated. We compared UAV surveys at multiple observation altitudes to traditional in-person on-the-ground surveys to test relative UAV effectiveness. We created artificial survey plots with a randomly assigned number of cereal pellets that mimicked the morphology of rabbit pellets. UAVs provided similar data to in-person counts for presence-absence inference. Additionally, raw counts were similar in pattern to in-person observations for pellets across a range of cover classes but were biased low in most circumstances. Heavy cover negatively affected both methods but resulted in higher undercounting with the UAV. The density of vegetation cover impacts pellet detection for both in-person and UAV-based surveys. Our research demonstrates that UAV-based fecal surveys are viable strategies. Further research in different conditions and fecal shapes is required for full implementation.**

Key Words.—drone; fecal surveys; *Sylvilagus palustris hefneri*; unmanned aerial vehicle.

INTRODUCTION

Unmanned aerial vehicles (UAVs) are an emerging technology improving data collection capabilities, data accuracy, research efficiency, cost, and human and wildlife safety in natural resources fields (Linchant et al. 2015; Nowak et al. 2019). The technology includes high-definition camera options, technological integration (e.g., Global Positioning Systems), improving battery life and battery replacement options, modularity and customization, software interface and command capability, commercial availability, and maturing legislation for UAV operation (Christie et al. 2016; Rosario et al. 2020). The increasing capability and diminishing cost of UAVs has spurred their use in natural resources research and management. Over time UAV applications have expanded to include a variety of subfields including wildlife biology (Lopez and Mulero-Pázmány 2019; Scarpa and Piña 2019). Much of the documented use of UAVs in natural resources fields has focused on large-scale subject matter such as analyzing landscape-level vegetation parameters, conducting large-bodied animal counts, and general wildlife population analyses (e.g., Witczuk et al. 2018; Castellanos-Galindo et al. 2019; Scarpa and Piña 2019). We found a variety of research focused on use of UAVs for surveying small or cryptic objects (e.g., Martin et al. 2012; Weissensteiner et al. 2015; Landeo-Yauri et al. 2022). Of note, Martin et al. (2012) tested the ability of UAVs to detect smaller or hidden test objects (tennis balls) in an approximation of wildlife surveys. In some instances, researchers have found UVA-derived estimates of medium sized animals (e.g., sea birds) to be more accurate compared to traditional enumeration methods (Hodgson et al. 2016, 2018). We did not, however, find literature evaluating the use of UAVs to identify or estimate the numbers of very small objects such as rabbit fecal pellets or in pellet-related wildlife surveys.

The attractiveness of UAVs partially stems from research efficiency and safety. They are often able to access areas faster and more safely than walking, driving, boating, or flying and can have a lower level of auditory and visual intrusion than conventional vehicles (e.g., cars, helicopters; Lisein et al. 2013; Linchant et al. 2014). For instance, Castellanos-Galindo et al. (2019) used UAVs to access remote coastal areas including mangroves and rocky coasts during tropical habitat mapping surveys. Natural resources workers face a variety of job-related dangers (Sasse 2003; Watts et al. 2010). Aerial-wildlife surveys in traditional aircraft is a leading cause of death for biologists (Sasse 2003). UAVs are increasingly capable of replacing humans in dangerous situations (e.g., using UAVs instead of humans in helicopters for surveys). As such, UAVs are a relatively low-cost option to increase human and wildlife safety.

UAV capabilities are a continued subject of exploration despite their demonstrated benefits in a variety of natural resources fields. For example, the ability of UAVs to effectively observe small or obscured objects such as fecal pellets is relatively unknown. Fecal pellet surveys are broadly applied in wildlife conservation and management and often require significant amounts of fieldwork. This is generally expensive, time-consuming, physically difficult, and potentially dangerous due to environmental hazards. Ideally, we would reduce fecal pellet fieldwork without reducing data quantity and quality. The pertinent question is whether UAVs produce similar estimates of pellet presence or abundance to provide useful inferences for management and research. If we find UAVs yield biased or inaccurate estimates, can we predict or identify causes for those errors?

We used Lower Keys Marsh Rabbits (LKMR; *Sylvilagus palustris hefneri*) as a model for testing UAV capabilities of seeing cryptic or small animal sign. Fecal-pellet surveys are an important LKMR data collection strategy (Faulhaber 2003; Schmidt et al. 2010; Dedrickson 2011). LKMR habitat primarily consists of areas with low to heavy herbaceous cover including native salt grasses and forbs with little or no forest canopy. We survey hundreds of pre-selected survey plots throughout the LKMR range as part of ongoing population monitoring efforts. Although UAVs preclude some methods related to in-person surveys (e.g., pellet removal for certain density estimation techniques), LKMR surveys are an excellent candidate for UAV-based surveys if researchers can sufficiently detect fecal pellets in UAV-captured photos. Additionally, UAV-based fecal surveys may have broad application. Fecal surveys are a common survey method for a variety of taxa such as lagomorphs (e.g., Hodges and Mills 2008; Murtze et al. 2014), cervids (e.g., DeCalesta 2013), and mustelids (e.g., Birks et al. 2005). Our primary goal was to evaluate the effectiveness of a UAV in detecting objects similar in size and distribution to LKMR pellets. Our objective was to compare accuracy of on-the-ground surveys with UAV-based aerial surveys in multiple cover types.

Methods

Study site.—We conducted our experiment in College Station, Texas, USA, 15 February 2019. College Station is in southeastern Texas in the Post Oak (*Quercus stellata*) Savannah ecoregion (https://enrta.tamu.edu/restoration/). Much of the rural acreage is a mix of upland and bottomland grasslands, with scattered Post Oak Woodlands located both in the upland and bottomland zones. We did not conduct this experiment in the Lower Florida Keys, Florida (location of LKMR), for several reasons. LKMR habitat co-occurs with significant human presence or in areas with restricted access and airspace. Local authorities are reluctant to approve use of UAVs without evidence that supports research effectiveness. College Station was selected due to proximity to research staff, availability of remote testing sites, and presence of vegetation structure similar to LKMR habitat.

Distribution of responsibility.—We carefully separated study setup and data collection responsibilities among the three primary researchers. Separate individuals performed each task of: (1) plot setup and UAV operation; (2) surveyor 1 / ground surveys; and (3) surveyor 2 / image analyses to avoid any observer contamination across surveys. Both surveyors were highly experienced with fecal pellet surveys in general and LKMR surveys in particular.

UAV and operation specifications.—We used a Phantom 4 UAV (Da-Jiang Innovations [DJI], Shenzhen, China) to conduct plot surveys. Our UAV was equipped with a 12.4-megapixel camera (field of view was 94°, 1/2.3” Complementary Metal Oxide Semiconductor [CMOS] sensor) and was capable of a hover-accuracy range (vertical) of ± 0.1–0.5 m depending on positioning method (dji.com/mobile/phantom-4). We kept camera settings at factory defaults: aperture = auto, white balance = auto, style = standard. We flew the UAV using the DJI Go 4 application in P-mode in free flight altitude hold (UAV will hold position). We conducted all flights in Class G airspace (usually classified as uncontrolled airspace 0–1,200 m above ground level). We cleaned the camera lens between each flight as low altitude flying can mobilize dust that coats the equipment. We flew the UAV when wind speed was < 5 kph to improve stability and reduce battery drain. The UAV operator held a U.S. Federal Aviation Administration (FAA) 107 Remote Pilot Certificate at the time of the study. Additionally, the UAV was registered with the FAA as required under U.S. law with all study flights following FAA and Texas A&M University (TAMU) rules and safety guidelines. We submitted a flight plan, which was approved by the TAMU UAV committee prior to our study.

Experimental design: setup.—We surveyed in areas of mixed herbaceous cover with no woody vegetation. We designated four broad herbaceous vegetation cover classes based on conditions we experienced working in LKMR habitat: (1) absent cover (0% herbaceous cover [bare ground]); (2) low cover (< 20% herbaceous cover); (3) moderate cover (20–50% herbaceous cover); and (4) high cover (> 50% herbaceous cover). We assigned 12 circular 1 m^2 plots per cover class (48 plots total; Fig. 1). The field researcher assigned a plot to its respective cover class. We determined the locations for plots in the field (in Texas) based on previous experience with similar cover classes in LKMR research (in Florida). We fully outlined plots using biodegradable marking chalk and we placed survey flags in the center of plots.

We used Kix cereal pieces (General Mills, Minneapolis, Minnesota, USA) as a substitute for rabbit fecal pellets due to their similar size, shape, weight, and coloration (adult pellets ≥ 6.7 mm; Forys 1995; Fig. 2). We based cereal dispersal amount on individual

Figure 1. Unmanned aerial vehicle photograph taken at 3 m altitude of 1 m^2 plots with pseudo rabbit pellets in low vegetation cover, College Station, Texas, USA, in 2020. (Photographed by Ian Gates).

plots on four categories: (1) Absent (0 pellets); (2) low (1–15 pellets); (3) moderate (16–100 pellets); and (4) high (101–300 pellets). These categories were derived from the distributions of counts from current LMKR data collection efforts (Roel Lopez et al., unpubl. reports) and provide useful population monitoring information such as rough occupancy, population trends, and overall range. Each cover class had all four pellet distributions (four plots per cover class). We determined the exact number of pellets placed into each non-zero plot by random number generation within the limits of the category (e.g., moderate = random number within 16–100 pellets). Pellets were placed in plots by the UAV operator who did not reveal these numbers to the other researchers until all data collection was complete.

Experimental design: UAV operation.—After cereal was placed on plots**,** we first surveyed with the UAV and then conducted on-the-ground data collection. We chose this order of survey to minimize the impact of vegetation or pellet disturbance from on-the ground surveys. UAV flights began in the morning and continued through the afternoon to ensure direct overhead sunlight to minimize shadows. We flew the UAV above the plots at multiple altitudes (3 m, 4 m, 5 m) and took one photograph at each altitude or three photographs total at each plot. These altitudes corresponded to ground sampling distances of 0.13 cm/pixel (3 m), 0.17 cm/pixel (4 m), and 0.21 cm/pixel (5 m). The UAV remained stationary directly above each plot and took a picture at each assigned altitude.

Experimental design: data collection.—One experienced surveyor counted pellets at all ground plots and another counted pellets in UAV images displayed on a 27” 4K monitor. Counts of pellets using the UAV photographs were done sequentially from the highest altitude to the lowest. Consequently, the final count was not independent of the other counts. We took this approach because we assumed that surveys on actual locations would most likely take numerous photographs or videos once over a plot. Throughout the manuscript, references to what we call altitude should be considered a combined effect from altitude and increased vigilance within the surveys. We do make specific comparisons to only the highest altitude to reduce inference based on multiple observations at different altitudes.

Experimental design: data analysis.—We expected that UAVs could be useful tools for monitoring LKMR at various levels of investigation or need. If they could be used accurately to document presence and absence of pellets, then they could be used within an occupancy approach whereas if they effectively reflected patterns of pellet density they may serve as a correlate to existing population estimates (e.g., Schmidt et al. 2010). Ideally,

Figure 2. Comparison of the appearance of (A) pellets of Lower Keys Marsh Rabbits (*Sylvilagus palustris hefneri*) and (B) pseudo pellets. (Photographed by Andrea Montalvo).

estimates derived from UAVs would recapitulate the true numbers of pellets within plots, but if they produced consistently biased estimates, quantifying those biases could be important. We evaluated the ability of UAV-based estimates to provide similar estimates to in-person surveys for presence-absence data, their relative patterns of abundance, and their precision relative to the true number of pellets on a plot. For each level of analyses, we compared the highest altitude of the drone (5 m) to in-person estimates first and as our primary comparison because these estimates were independent. Nevertheless, we also evaluated the lowest altitude to see how increased evaluation across multiple photos and altitude changed patterns and biases in estimates relative to human efforts.

For each plot we quantified the true absence or presence of any pellets to counts made using UAV and in-person surveys. If there was disagreement between the respective methods and the true presence on plot, we coded it as a 0 where we coded the records as a 1 if the method agreed with the true presence on a plot. We used PROC Logistic (SAS; Cary, North Carolina) to quantify the rates, and odds, that a method was correct. For the in-person data set, we used the cover class as a discrete variable and then modeled this as the explanatory variable to the true presence. We modeled the cover as a discrete variable to evaluate differences among the cover classes. For comparison to the in-person data, we used only the information collected at 5 m altitude and evaluated the 95% Confidence Interval (CI) for differences among cover groups. We also modeled information at 3 m altitude to see if it differed from either the 5 m or in-person methods. We report the odds-ratios values for these comparisons with 95% CIs.

We conducted initial plots of the raw count data using both methods, and all altitudes for UAV data, against the true numbers of pellets deployed. These initial plots indicated a potential non-linear response between count methods as the total number of pellets increased. Therefore, to assess the relationship of counts to the true number for similarity in their general pattern, we used General Linear Models with 2nd and 3rd degree polynomial terms as well as single order term where the true numbers of pellets deployed was used as the explanatory variable. We compared the 2nd and 3rd order models to the single order model using Akaike Information Criteria corrected for small sample size (AICc; Burnham and Anderson 2004) to identify which model best described the data. For comparison between the two methods, we examined the 95% CIs around their respective beta estimates for overlap.

We evaluated the precision of counts by calculating a relative deviance of the observed counts versus the true numbers deployed. Because some plots had no pellets deployed, we calculated deviance as:

$$\text{Relative deviance} = \frac{(\text{observed - true})}{(1 + \text{true})}$$

where the observed were the numbers of pellets counted on an individual plot, and at specific altitudes for the UAV, and the true number was the numbers of pellets actually deployed on a plot. For the purposes of statistical analyses, we took the absolute value of this relative deviance value but included the sign and magnitude of this value when we report mean values. The sign of the value was important to consider as it reflected under-detection (negative values) or over-detection (positive values).

We conducted two analyses using these data. In the first analyses, we directly compared the relative deviance of estimates directly between the two methods. Here we made all comparisons between in-person counts and UAV-based counts at 5 m altitude. We evaluated six distinct models in these analyses with explanatory variables considered as follows: (1) A single term model using the method (UAV vs in-person); (2) A single term model with cover class; (3) A single term model with the numbers of pellets deployed on a plot. We considered pellet count as an explanatory variable based on our earlier analyses which indicated changes in estimates based on the numbers of pellets; (4) An additive model with both cover and methods included as discrete variables; (5) An interactive model with terms for method, cover class, and an interaction between method and cover class; and (6) An interactive model with terms for method and the true numbers of pellets deployed on a plot.

We constructed all models in PROC GENMOD using a Poisson distribution with a log link and type III sums of squares. We evaluated other distributions, but the Poisson fit our data best based on our evaluation of histograms and residual plots. We compared these models using AICc and used parameter estimates from the top model. We report all estimates from these models with 95% CIs. We also examined *P*-values from respective effects to make a secondary evaluation of the effects relative to their descriptive ability on deviation in our counts. We used an alpha of 0.05 for rejecting a null hypothesis of no effect. If we found significant differences from specific main effects, we used Nelson-Hsu comparisons to identify groups that were different from one another.

In a secondary analysis of relative deviation, we examined only the UAV data. Our primary goal was to examine the effects of altitude on percentage deviation. Because we felt cover class could potentially exert additive or interactive effects across levels of altitude, we also tested several models including those terms. We tested four models with the UAV data as such: (1) A single effect model with altitudinal effect across 3 m, 4 m, and 5 m altitudes; (2) A single effect cover class model; (3) An additive model with terms from both altitude and cover class; and (4) An interactive model with terms from altitude, cover class, and interactions between cover class and altitude. We tested these four models as we did with our analyses of methods as described above.

RESULTS

For in-person surveys, across all cover types, 47 of 48 (97%) were categorized properly based presence-absence. Only the highest cover class had one of 12 plots that were mis-categorized for presence-absence. At this single plot, we detected no pellets when five were on the plot. For the UAV method, across all altitudes and cover types, 126 of 144 (88%) were correctly categorized for having pellets present or absent. Of the 18 (across all altitudes) that were improperly classified, two (11%) detected pellets when no pellets were present and (88.9%) failed to detect when they were present (Table 1). For in-person surveys, we detected no differences among cover class ($\chi^2 = 0.015$, df = 3, $P = 0.997$). For UAV data, we could not reject the null hypothesis of no effect based on cover classes at either the 5 m ($\chi^2 = 0.208$, df = 3, $P = 0.976$) or 3 m level ($\chi^2 = 0.010$, df = 3, $P = 0.997$).

Regression analyses on the raw count data indicated modest but significant differences between the in-person vs UAV count relative to their true numbers of pellets on the plot. Both methods showed significant positive relationships to the true number of pellets on plots (Fig. 3). In-person counts were best described with a second-order polynomial regression (AICc = 428.38, χ^2= 46.80, df = 1, $P < 0.001$, $\beta = 0.927$ [0.722–1.12], $\beta^2 = -0.0012$ [-0.002, - 0.0004]) formulation as AICc values for this model were > 4 different from the single-order model (AICc = 433.85, χ^2 = 93.86, df = 1, $P < 0.001$, $\beta = 0.638$ [0.0.564–0.710],). A 3rd order model was not well supported by the data (AICc = 338.7). In contrast, UAV-based counts (5 m altitude only) were best described with a 1st order model (AICc = 474.01, χ^2= 44.33, df = 1, $P < 0.001$, $\beta = 0.484$ [0.373–0.595]) model compared to the 2nd (AICc = 476.08, χ^2= 10.24, df = 1, $P = 0.001$, $\beta = 0.578$ [0.0.242–0.913]) and 3rd (AICc = 479.23) order models. This beta-estimate for the 1st order model was significantly lower than the comparable parameter for the in-person counts indicating an on-average negative bias for the UAV-counts relative to in-person methods. A regression using UAV-counts at the 3 m altitude was similar to the one we conducted at 5 m ($\beta = 0.55$ [0.34–0.65]). Both in-person and UAV surveys methods under-detected pellets on plots on average. In-person surveys had a mean deviance of -0.18 ± 0.231 (standard deviation) whereas UAV surveys had a mean of -0.24 ± 0.852. Commensurate with these means, in-person surveys were negatively biased on 28 of 48 (58%) of plots whereas UAVs were negatively biased on 30 of 48 (62%). In contrast, both methods reported two plots with higher numbers of pellets than were actually on plots. When we examined only the 3 m altitude for UAVs the mean values were -0.31 ± 0.321 but the same proportion were negatively biased.

TABLE 1. The total number plots (n) and the number and percentage identified correctly for presence-absence status for in-person surveys and Unmanned Aerial Vehicles (UAV) surveys by altitude (meters) at a study site at College Station, Texas.

Type	Cover	n	Correct	Percentage
In-person	Absent	12	12	100%
	Low	12	12	100%
	Medium	12	12	100%
	High	12	11	92%
UAV				
3 m	Absent	12	12	100%
	Low	12	12	100%
	Medium	12	10	83%
	High	12	10	83%
4 m	Absent	12	12	100%
	Low	12	12	100%
	Medium	12	8	66%
	High	12	9	75%
5 m	Absent	12	12	100%
	Low	12	12	100%
	Medium	12	8	66%
	High	12	9	75%

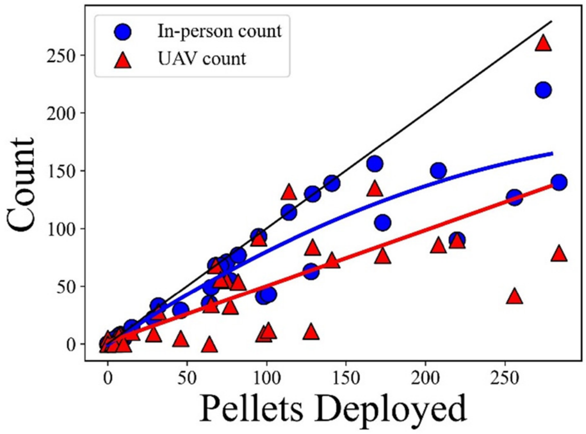

FIGURE 3. Linear Regression of the counts versus pellets during Unmanned Aerial Vehicles (UAV) test, College Station, Texas, in 2020. The black diagonal line represents the hypothetical ideal relationship between the number of actual pellets and the number of pellets counts. The blue line represents a 2nd order polynomial regression line for in-person counts and the red line a 1st order regression line fit for UAV-based counts.

Our examination of factors that best explained relative deviation revealed that both the method and cover class were important (Table 2). The best model included an effect from both method and cover class with a ΔAICc value of 3.64 compared to the next best model, which included only a cover term. From this top model the effects from both method ($\chi^2 = 5.87$, df = 1, $P = 0.015$) and cover class ($\chi^2 = 18.05$, df = 1, $P < 0.001$) were significant when we considered their P-values. All other models we tested included significant effects from both method and

Table 2. Comparison of five competing models hypothesized to explain the percentage deviance of count versus true data for pseudo-pellet surveys conducted using in-person and Unmanned Aerial Vehicles (UAV) methods. Metrics used to compare models follow the form of Burnham and Anderson (2002) where the number of estimable parameters (k), number of observation (n = 96 for all) are used to construct Akaike's Information Criterion corrected for sample size (AICc), the difference between top model and other models (ΔAICc), the model likelihood, and model weight (*w*).

Model	AICc	ΔAIC	k	likelihood	weight
Method + Cover	119.01	0.00	6	1.00	0.83
Cover	122.65	3.64	5	0.16	0.13
Method × Cover	125.13	6.12	16	0.05	0.04
Method × Pellets Deployed	133.15	14.14	6	0.00	0.00
PelletsDeployed	135.51	16.50	2	0.00	0.00
Method	216.69	97.68	3	0.00	0.00

cover class. Across all methods the summed weights indicated cover class to be most influential (cumulative weight = 1.0) where all models with method included as an explanatory variable equaled 0.83. Largely, the results of our analyses indicated that differences in method and cover class were additive rather than interactive (Fig. 4). Mean values of deviance were lowest on average for in-person estimates compared to UAV estimates similarly across all cover classes. Deviations were lowest for both methods when cover was absent (mean = 0.036 ± 0.061), and highest in the moderate (mean = 0.58 ± 0.981) and high cover classes (mean = 0.50 ± 0.357). This pattern is consistent within individual methods although for UAV estimates, the moderate cover class had the highest deviation (mean = 0.92 ± 1.31, z-value = 2.84, $P < 0.010$; Fig. 4). This value was inflated by a single plot where five pellets were counted when none were truly present and yielding a value of five. Had we eliminated this one plot, then the deviation for UAVs in the moderate cover class (mean = 0.54 ± 0.295) would have been lower but similar to mean deviations in the high cover class.

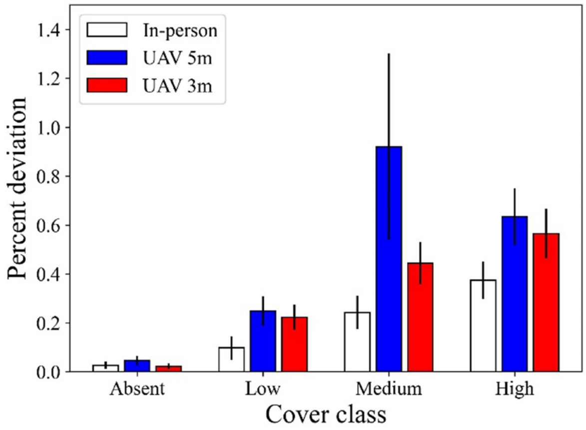

Figure 4. The average percentage deviation ± standard deviation from the true pellet count for in-person surveys and unmanned aerial vehicle surveys conducted at 5 m and 3 m above the observation plot within four vegetation cover class categories (absent = 0% herbaceous cover, low = < 20% herbaceous cover, medium = 20–50% herbaceous cover, and high = > 50% herbaceous cover) for 48 plots surveyed in College Station, Texas, in 2020.

Our analyses of the UAV data indicated no strong effects on deviations from the true value based on altitude but did retain a signal from cover class. Among the models we tested, altitude was not well supported (ΔAICc = 28.6 from top model). Accordingly, no significant effect was detected for altitude in any model we tested ($\chi^2 = 1.41$, df = 2, $P < 0.491$). Although we did not formally examine the data from the 3 m altitude, the patterns of mean values were similar in pattern to our formal analyses across cover class (Fig. 4). The average deviation at the 3 m altitude was lower (mean = 0.33 ± 0.350) than those at the 4 m (mean = 0.39 ± 0.372) or 5 m (mean = 0.40 ± 0.394) altitudes. Cover class was far more powerful in describing deviation in our UAV data (e.g., Fig. 4). Models that included cover and altitude either additively (ΔAICc = 2.9 from top model) or interactively (ΔAICc = 15.8 from top model) seemed not as important as cover class by itself.

DISCUSSION

The use of UAVs in natural resources research and management is widespread and well-documented. This has overwhelmingly tended towards more easily observable phenomena such as basking or foraging animals, vegetation communities, and fire effects (e.g., Biserkov and Lukanov 2017; Witczuk et al. 2018; Castellanos-Galindo et al. 2019; Nowak et al. 2019; Scarpa and Piña 2019). Much of the relevant natural resources work, however, requires observation of small items like fecal pellets.

Our analyses indicate that UAVs and in-person counts of fecal pellets are largely correlated with one another, and to the true numbers of pellets on plots. Both UAVs and in-person surveyors are, on average, biased low in their assessments of the true numbers of pellets on plots. UAVs appear to have a high degree of negative bias and produce more variability in estimates. Both in-person and UAV counts perform well when vegetation cover is absent or low but are less reliable when there is moderate or high vegetation cover. The altitude of the drone heights we used (3–5 m above the ground) were largely uninformative or increased the precisions of counts. We acknowledge that our counts below 5 m were ultimately not independent of one another, but this provides compelling evidence that modest differences in altitude or photographic examination effort did little to improve the precision of the counts. Conceivably had we flown the UAV to a lower altitude (1 m), taken more photographs, or spent more time examining any one of the photographs, our precision would have improved. Nonetheless, our results highlight that even in-person counts are biased low in thick cover. Therefore, we recommend estimating or adjusting the effort for searching when either UAVs or on-the-ground surveyors examine locations with high ground cover. Alternatively, researchers could include an adjustment of pellet counts based on the known biases associated with cover or surveyor skill. For example, our data suggests a modest adjustment of 4% detection rate when vegetation is absent but as much as 63% in vegetation > 75%. We recognize, however, that our results are unlikely to be consistent in all scenarios but in most field settings human-based and drone-based surveys are infrequently going be completely independent. UAVs could work with surveyors on an initial visit to empirically estimate the detection probably on specific plots or in cover classes that are then used on subsequent surveys by the UAV alone.

We found that in-person surveyors were more accurate in their assessments compared to UAVs. Yet, our analyses suggested that when there are large numbers of pellets (> 100), in-person counts became more negatively biased. Human estimates were nearly identical to the true numbers until roughly 100 pellets but appeared to reach an asymptote thereafter. We hypothesize that this resulted from our surveyor not being able to precisely keep track of pellets when they became more numerous. Moreover, the researcher could not revisit counts after having left the plot. Here, drones could ultimately offer an improvement because the photographs are stored for future review by multiple observers or by the potential of using image processing algorithms or even Deep Learning to improve upon counts.

In general, UAVs seem adequate to identify presence and absence of pellets on plots irrespective of cover. Our results did not indicate a significant decline in the ability of UAVs to adequately categorize a plot for presence or absence. Our results highlight the potential limitations of UAVs, but also provide potential approaches for overcoming specific biases. For example, taking photographs (or video) from multiple angles or heights could help improve detection and counts and could conceivably be used within occupancy analytical frameworks to explicitly estimate the probability of detections. In future studies of this nature, we recommend mixing roles so that each researcher is not solely responsible for a single data collection effort (i.e., in-person versus photographs). This would help separate surveyor effects from test effects; however, we note that such observer differences are likely common in most research.

Our research demonstrated several important points. UAVs provided similar, low-biased, numbers to in-person observations for pellets across a range of cover types. Similarly, Goebel et al. (2015) found no significant difference between UAV-based chick counts and ground counts when conducting penguin surveys (Gentoo Penguin, *Pygoscelis papua* and Chinstrap Penguin, *P. antarctica*). Cover type appears to have some capacity to bias UAV results modestly but once the differences in method were accounted for, cover type did not seem to impose an interactive effect where UAVs had additional biases with higher or lower cover. Other studies have found stronger correlations between vegetation cover and detection such as Barr et al. (2018) who found lower colonial waterbird detection by a UAV when vegetation canopy cover was present. More interestingly, there was no important difference in the deviation from the observed to the true numbers based on the survey method. Cover density is likely to reduce the precision and accuracy of pellet counts for both in-person and UAV based surveys, but it is unlikely to alter the relative assessment of the number of pellets among surveyed plots. Both UAV-based surveys and on-the-ground surveys accurately detected categorical pellet abundances (low, moderate, high). For most surveys, UAVs appear to provide sufficient information to determine if pellets are present and their relative abundance. Additionally, altitudes of 3–5 m in height had only modest effects on the raw numbers of pellets detected even though the relative deviance was unaffected. Although focusing on much larger objects, Hodgson et al. (2013) found that UAV altitude did not impact Dugong (*Dugong dugon*) sighting rates or identification capability.

UAVs did relatively well in detecting fecal pellets in a variety of real-world scenarios. As experienced rabbit biologists, we would feel comfortable using UAVs to conduct fecal pellet surveys in absent and low vegetation cover. The ability of UAVs to traverse rough habitat could provide an extensive reduction in field-time and associated survey costs. As such, the relative efficacy of UAV-based pellet surveys must be calibrated for each project with detection rates and reliability evaluated prior to data collection. Researchers must understand the local impact of vegetation cover density on pellet detection.

Our primary UAV-related concern was that propeller wash (air pushed from the rotors) would move pellets or vegetation thus impacting detection. This concern proved unwarranted as we detected no impacts. Our pseudo pellets were often evenly spread throughout plots without being blown to the edges or next to obstacles such as vegetation. This was true even for bare-ground plots with minimal rolling resistance. For studies where this is a concern, researchers should conduct pre-study data collection to determine propeller wash impact.

We believe that UAVs can provide data on small phenomena such as fecal pellet surveys. These can provide flexibility for natural resources agencies conducting critical work with decreasing budgets. The relatively low cost and availability of UAVs and associated components make the adoption of UAV technology a low-risk endeavor for agencies seeking higher returns on investments. We strongly recommend additional evaluation of UAV accuracy in various cover types and scenarios. Additionally, we recommend that UAV operators understand the local, state, and federal laws prior to use of any UAVs. Ultimately, UAVs are like any other research and conservation tool. They will provide quality data if the project design is robust and the limitations of the equipment are understood.

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LITERATURE CITED

Barr, J.R., M.C. Green, S.J. DeMaso, and T.B. Hardy. 2018. Detectability and visibility biases associated with using consumer-grade unmanned aircraft to survey nesting colonial birds. Journal of Field Ornithology 89:242–257.

Birks, J., J. Messenger, T. Braithwaite, A. Davison, R. Brookes, and C. Strachan. 2005. Are scat surveys a reliable method for assessing distribution and population status of Pine Martens? Pp. 235–252 *in* Martens and Fishers (*Martes*) in Human-Altered Environments. Harrison, D.J., A.K. Fuller, and G. Proulx (Eds.). Springer, Boston, Massachusetts.

Biserkov, V.Y., and S.P. Lukanov. 2017. Unmanned aerial vehicles (UAVs) for surveying freshwater turtle populations: methodology adjustment. Acta Zoologica Bulgarica 10:161–163.

Burnham, K.P., and D.R. Anderson. 2004. Multimodal inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Castellanos-Galindo, G.A., E. Casella, J.C. Mejía-Rentería, and A. Rovere. 2019. Habitat mapping of remote coasts: evaluating the usefulness of lightweight unmanned aerial vehicles for conservation and monitoring. Biological Conservation 239:108282. https://www.sciencedirect.com/science/article/abs/pii/S0006320719308092.

Christie, K.S., S.L. Gilbert, C.L. Brown, M. Hatfield, and L. Hanson. 2016. Unmanned aircraft systems in wildlife research: current and future applications of a transformative technology. Frontiers in Ecology and Environment 14:241–251.

DeCalesta, D.S. 2013. Reliability and precision of pellet-group counts for estimating landscape-level deer density. Human-Wildlife Interactions 7:60–68.

Dedrickson, A.J. 2011. Effects of vegetation structure and elevation on Lower Keys Marsh Rabbit density. M.S. Thesis, Texas A&M University, College Station, Texas. 33 p.

Faulhaber C.A. 2003. Updated distribution and reintroduction of the Lower Keys Marsh Rabbit. M.S. Thesis, Texas A&M University, College Station, Texas. 223 p.

Forys, E.A. 1995. Metapopulations of Marsh Rabbits: a Population Viability Analysis of the Lower Keys Marsh Rabbit (*Sylvilagus palustris hefneri*). Ph.D. Dissertation, University of Florida, Gainesville, Florida. 257 p.

Goebel, M.E., W.L. Perryman, J.T. Hinke, D.J. Krause, N.A. Hann, S. Gardner, and D.J. LeRoi. 2015. A small unmanned aerial system for estimating abundance and size of Antarctic predators. Polar Biology 38:619–630.

Hodges, K.E., and L.S. Mills. 2008. Designing fecal pellet surveys for Snowshoe Hares. Forest Ecology and Management 256:1918–1926.

Hodgson, A., N. Kelly, and D. Peel. 2013. Unmanned aerial vehicles (UAVs) for surveying marine fauna: a Dugong case study. PLoS ONE 8:e79556. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0079556.

Hodgson, J.C., S.M. Baylis, R. Mott, A. Herrod, and R.H. Clarke. 2016. Precision wildlife monitoring using unmanned aerial vehicles. Scientific Reports 6:22574. https://pubmed.ncbi.nlm.nih.gov/26986721/.

Hodgson, J.C., R. Mott, S.M. Baylis, T.T. Pham, S. Wotherspoon, A.D. Kilpatrick, R.R. Segaran, I.Reid, A. Terauds, L.P. Koh. 2018. Drones count wildlife more accurately and precisely than humans. Methods in Ecology and Evolution 9:1160–1167.

Landeo-Yauri, S.S., D.N. Castelblanco-Martínez, Y. Hénault, M.R. Arreola, and E.A. Ramos. 2022. Behavioural and physiological responses of captive Antillean Manatees to small aerial drones. Wildlife Research 49:24–33.

Linchant J., J. Lisein, J. Semeki, P. Lejeune, and C. Vermeulen. 2015. Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. Mammal Review 45:239–252.

Lisein, J., J. Linchant, P. Lejeune, P. Bouché, and C. Vermeulen. 2013. Aerial surveys using an unmanned aerial system (UAS): comparison of different methods for estimating the surface area of sampling strips. Tropical Conservation Science 6:506–520.

Lopez, J.J., and M. Mulero-Pázmány. 2019. Drones for conservation in protected areas: present and future. Drones 3:10.3390/drones3010010. https://www.mdpi.com/2504-446X/3/1/10.

Martin, J., H.H. Edwards, M.A. Burgess, H.F. Percival, D.E. Fagan, B.E. Gardner, J.G. Ortega-Ortiz, P.G. Ifju, B.S. Evers, and T.J. Rambo. 2012. Estimating distribution of hidden objects with drones: from tennis balls to manatees. PLoS ONE 7:1–8. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0038882.

Murtze, G., B. Cooke, M. Lethbridge, and S. Jennings. 2014. A rapid survey method for estimating population density of European rabbits living in native vegetation. Rangeland Journal 36:239–247.

Nowak, M.M., P. Bogawski, and K. Dzióbm. 2019. Unmanned aerial vehicles (UAVs) in environmental biology: a review. European Journal of Ecology 4:56–74.

Rosario, R.G., M.K. Clayton, and I.T. Gates. 2020. Use of unmanned aerial vehicles in wildlife ecology. Pp. 387–394 *in* The Wildlife Techniques Manual. 8th Edition. Silvy, N.J. (Ed.). Johns Hopkins University Press, Baltimore, Maryland.

Sasse, D.B. 2003. Job-related mortality of wildlife workers in the United States, 1937–2000. Wildlife Society Bulletin 31:1015–1020.

Scarpa, L.J., and C.I. Piña. 2019. The use of drones for conservation: a methodological tool to survey caimans nests density. Biological Conservation 238:108235. https://www.sciencedirect.com/science/article/abs/pii/S0006320719312017.

Schmidt, P.M., R.A. McCleery, R.R. Lopez, N.J. Silvy, and J.A. Schmidt. 2010. Habitat succession, hardwood encroachment and raccoons as limiting factors for Lower Keys Marsh Rabbits. Biological Conservation 143:2703–2710.

Watts, A.C., J.H. Perry, S.E. Smith, M.A. Burgess, B.E. Wilkinson, Z. Szantoi, P.G. Ifju, and H.F. Percival. 2010. Small unmanned aircraft systems for low-altitude aerial surveys. Journal of Wildlife Management 74:1614–1619.

Weissensteiner, M.H., J.W. Poelstra, and J.B.W. Wolf. 2015. Low-budget ready-to-fly unmanned aerial vehicles: an effective tool for evaluating the nesting status of canopy-breeding bird species. Journal of Avian Biology 46:425–430.

Witczuk J., S. Pagacz, A. Zmarz, and M. Cypel. 2018. Exploring the feasibility of unmanned aerial vehicles and thermal imaging for ungulate surveys in forests - preliminary results. International Journal of Remote Sensing 39:5504–5521.

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Roel Lopez provides leadership in the field of wildlife ecology and natural resource management. Roel works with internal and external stakeholders in developing institute priorities for research and extension programs and leads interdisciplinary teams to address these natural resource challenges. His research focuses on endangered and fragmented wildlife populations, sustainability of military lands, and rural land trends and demographics. (Photographed courtesy of Texas A&M Natural Resources Institute staff).

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RODENT COMMUNITIES IN CISMONTANE CALIFORNIA: COMPOSITION, DIVERSITY, AND SPECIFIC STUDY LOCATIONS FOR FUTURE REFERENCE

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Abstract.—**We investigated composition and species diversity of rodent communities in six vegetation types on the cismontane slope of the San Jacinto Mountains, Riverside County, California. The Deer Mouse (*Peromyscus maniculatus*) occurred in all vegetation types, and we captured the Western Harvest Mouse (*Reithrodontomys megalotis*) in five and the Agile Kangaroo Rat (*Dipodomys agilis*) in four of the six vegetation types. The California Vole (*Microtus californicus*), California Mouse (*Peromyscus californicus*), Brush Mouse (*P. boylii*), Pinyon Mouse (*P. truei*), Desert Woodrat (*Neotoma lepida*), Dusky-footed Woodrat (*N. fuscipes*), and California Pocket Mouse (*Perognathus californicus*) were less abundant and far more restricted in occurrence. We captured all 10 species in the Interior Live Oak vegetation type, but only the Deer Mouse, Western Harvest Mouse, and Agile Kangaroo Rat were captured in the Graminoid vegetation type. Species diversity of rodents was greatest in the Black Oak and Interior Live Oak vegetation types; slightly lower, but similar to each other, in the Chamise-Manzanita, Graminoid, and Riparian vegetation types; and least in the Coast Live Oak vegetation type. We provide precise locations for each of the study plots to ensure the sites can be relocated by future investigators interested in the long-term effects of a warming climate or anthropogenic manipulation of those vegetation types.**

Key Words.—baseline data; climate; habitat; history; San Jacinto Mountains; succession.

INTRODUCTION

Data collected nearly half-a-century earlier seldom appear in a contemporary journal but as prophesized by Bob Dylan (Gray 2006), "The times, they are a-changin'." Indeed, the planet has been experiencing a warming trend and, despite the skepticism of some (Smith and Leiserowitz 2012), there is increasing interest in the ways that ecosystems will be altered and how the biota will adapt or evolve in response (Millien et al. 2006; Hoffman and Sgro 2011; and many others). Additionally, there is a pressing need to minimize impacts of habitat loss or resource exploitation (Caro et al. 2021) and, if biodiversity existing today is to be conserved, it is essential that contemporary threats to habitat be a primary concern so that issues remain to be addressed in the future (Caro et al. 2022). In addition, all of this has been compounded by a substantial decline in the recognition of natural history as a respected discipline in wildlife education, wildlife science, and conservation (Noss 1996; Kessler and Booth 1998; Bleich and Oehler 2000; Bury 2006). As a result, acquisition of information that may serve as baseline data against which to assess future changes, whether climate-related or otherwise the result of anthropogenic meddling, has received little attention in the recent past. Much of the data upon which future ecological comparisons may be based was obtained during basic natural history investigations or observations, but few site-specific locations for such investigations appear in the literature.

Southern California is characterized by exceptional levels of biodiversity (Chen et al. 2005; Mooney and Zavaleta 2016) and cismontane southern California is rapidly being developed (Erickson and Patten 1999). Anticipated ecosystem-level changes will include distributional shifts in plants and animals, species extirpations, range expansions, altered life-history strategies, and behavioral adaptations, among others (Ostberg et al. 2013; and references therein). Additionally, anthropogenic activities will continue to transform habitats in profound ways, including increased frequency of fires that will continue to convert native shrublands to nonnative grasslands (Keeley 2001; Klinger et al. 2006; Keeley et al. 2011; Keeley and Safford 2016). Moreover, long-term shifts in management prescriptions will continue to affect community structure within and among habitat types (Bowyer and Bleich 1980, 1984; Bleich 2021).

Nearly 50 y have passed since a devastating wildfire (the Soboba Burn) occurred on the western slope of the San Jacinto Mountains, Riverside Co., California (Moore et al. 1979). That conflagration burned nearly 7,300 ha in 1974, of which almost 4,700 ha were within the San Bernardino National Forest (SBNF). Following that event, personnel representing the SBNF and the California Department of Fish and Game (CDFG; now California Department of Fish and Wildlife) cooperated on the development of a vegetation management plan for what was known as the Soboba Management Area (SMA). Although our investigation occurred after 4 y of post-fire vegetation succession, a variety of anthropogenic manipulations (Bleich and Holl 1982) were planned to improve wildlife habitat and simultaneously to reduce, or otherwise manage, fuels across the variety of low-elevation habitat types within the SMA (Berg 1978; Blong et al. 1978; Roberts 1980, 1981; Quinn 1983). A similar project, the Laguna-Morena Demonstration Area (LMDA) in San Diego County, also was initiated following a series of disastrous wildfires of the early 1970s, but with an emphasis on fuel reduction on chaparral-dominated ranges and secondarily on habitat enhancement for large mammals inhabiting that vegetation type (Bowyer 1981; White et al. 1982). Thus, the SMA differed from the LMDA in that there was an emphasis on: (1) the management of multiple types of vegetation; (2) the creation and improvement of wildlife habitat as a primary goal; and (3) habitat management for both game and nongame species (Quinn 1983).

The multiple vegetation types in the SMA promulgated several intensive resource inventories (Blong et al. 1978). During May 1978, we investigated the distribution and relative abundance of small mammals occurring among a diversity of vegetation types in the SMA. Published reports detailing the mammalian fauna of the San Jacinto Mountains were few and remain so; to add to the sparse information in that area, we report the results of our 1978 survey and the locations at which the investigations were conducted. Such information is especially relevant given current concerns about continued habitat loss, resource exploitation, and a warming climate, and their respective effects on the biodiversity of small mammals and the paucity of specific study locations in the published literature.

Methods

The Soboba Management Area (approximate centroid 36.87°N, 116.87°W) was located on the San Jacinto Ranger District of the San Bernardino National Forest, Riverside Co., California, proximate to the San Gorgonio Pass (36.92°N, 116.76°W; Fig. 1), an area of long-standing biogeographic interest (Grinnell 1908; Grinnell and Swarth 1913). We selected and defined a single study plot in six distinct vegetation types (Table 1) representative of those within the SMA (Berg 1978; Paysen et al. 1980). We placed an emphasis on the vegetation types most apt to be subjected to manipulation pending implementation of the management plan for the SMA (Berg 1978). Thus, we established trapping plots in those vegetation types deemed most suitable for habitat modification by methods involving: (1) direct rehabilitation of ranges whose capability had declined because of natural processes or past management strategies; (2) direct enhancement of existing habitat; or (3) modification of other resource management practices (Scotter 1980) using manual, mechanical, chemical, or pyrotechnic methods, or by manipulation with livestock (Green 1977a,b; Bleich and Holl 1982; Bleich et al. 2020).

Figure 1. The Soboba Management Area (SMA) encompassed 4,735 ha and was located on the San Jacinto Ranger District of the San Bernardino National Forest, Riverside County, California (Berg 1978). Shown in red is the approximate boundary of the SMA and its juxtaposition to the city of Banning and to San Gorgonio Pass, which separates the San Bernardino Mountains from the San Jacinto Mountains and is a topographic feature long of interest to mammalogists and biogeographers (Grinnell 1908; Grinnell and Swarth 1913).

Table 1. Species of rodents and the vegetation type in which each was captured to establish baseline data on the composition of small mammal communities in the Soboba Management Area, San Bernardino National Forest, Riverside County, California, May 1978. Total numbers of each species (n) captured in six vegetation types are presented, followed parenthetically by the relative abundance (captures/100 trap-nights) in each type of vegetation. As ordered in the table, species captured were the Deer Mouse (*Peromyscus maniculatus*), California Mouse (*P. californicus*), Pinyon Mouse (*P. truei*), Brush Mouse (*P. boylii*), Desert Woodrat (*Neotoma lepida*), Dusky-footed Woodrat (*N. fuscipes*), California Vole (*Microtus californicus*), Western Harvest Mouse (*Reithrodontomys megalotis*), Agile Kangaroo Rat (*Dipodomys agilis*), and California Pocket Mouse (*Perognathus californicus*). The Chamise-Manzanita Association refers to the Chamise or Manzanita Vegetation Series of Paysen et al. (1980) and the Chamise-Manzanita Association of Berg (1978); Interior Live Oak, Graminoid, Riparian, Black Oak, and Coast Live Oak vegetation types are those described by Paysen et al. (1980).

	Vegetation Type							
Species	Chamise-Manzanita Association	Interior Live Oak Series	Graminoid Subformation	Riparian	Black Oak Series	Coast Live Oak Series	Total (n)	Total (%)
P. maniculatus	11 (2.04)	41 (6.51)	8 (1.27)	1 (0.32)	2 (1.75)	1 (0.16)	64	25.8
P. californicus	10 (1.85)	22 (3.49)	0	0	1 (0.88)	1 (0.16)	34	13.7
P. truei	3 (0.55)	3 (0.48)	0	0	0	0	6	2.4
P. boylii	4 (0.74)	2 (0.32)	0	13 (4.13)	3 (2.63)	16 (2.54)	38	15.3
Peromyscus sp.	1 (0.18)	1 (0.16)	0	0	0	0	2	0.8
N. lepida	1 (0.18)	4 (0.63)	0	2 (0.63)	0	0	7	2.8
N. fuscipes	0	1 (0.16)	0	0	0	0	1	0.4
M. californicus	0	2 (0.32)	0	0	0	0	2	0.8
R. megalotis	0	3 (0.48)	2 (0.32)	1 (0.32)	1 (0.88)	1 (0.16)	8	3.2
D. agilis	32 (5.92)	29 (4.60)	6 (0.95)	0	0	2 (0.32)	69	27.8
P. californicus	1 (0.18)	16 (2.54)	0	0	0	0	17	6.9
Captures (n)	63	124	16	17	7	21	248	
Captures (%)	25.4	50.0	6.5	6.8	2.8	8.5		100.0
Trap Nights	540	630	630	315	114	630		
Relative Abundance	11.7	19.7	2.5	5.4	6.1	3.3		

At each sampling location we established two parallel trap-lines separated from each other by 15 m, and placed trap-stations at 15-m intervals along each trap-line. We placed two Museum Special traps (Woodstream Corporation, Lititz, Pennsylvania) and a Victor rat trap (Woodstream Corporation) at each station, and the total number of stations per vegetation type ranged from 19 to 70. We baited each trap with moistened rolled oats each evening, and traps were active for three consecutive nights on each study plot 10–19 May 1978. We visited every study plot early each morning, collected specimens and placed them in plastic bags on ice, and rebaited or re-set each trap as necessary. We relied on our extensive familiarity with the taxa encountered (Bleich 1973, 1977) and identified all but 13 individual specimens to species; these were submitted to the Bird and Mammal Museum, California State University Long Beach (unpubl. report, 27 August 1978), where experts used morphological and cranial attributes to identify those individuals (David G. Huckaby, unpubl. report, 11 September 1978; David R. Bontrager, unpubl. report, 24 August 1979). Several taxonomic or nomenclatural changes have occurred since the field work was completed (Bradley et al. 2014; Blood 2021), but we have retained the common and scientific names in use during our research and shortly thereafter (Jones et al. 1973, 1975, 1979) because much of the literature cited herein relied on the earlier nomenclature. We have summarized systematic or nomenclatural revisions that have occurred since 1978 (Appendix).

We expressed relative abundance of the various species as captures/100 trap-nights. We calculated Simpson's (1949) Diversity Index (D) as a measure of rodent species diversity for each habitat type, where D ranges from 0 to 1, but increases as species diversity declines (Simpson 1949) and, as a result, is counter intuitive. Thus, we present the Gini-Simpson Index of Diversity (1-D), which also ranges from 0 to 1 but has a positive relationship with species diversity (Guiasu and Guiasu 2010). We also used that metric to index rodent species diversity among the six vegetation types. Calculation of the Simpson Index (and the Gini-Simpson Index) is not dependent solely on the number of species detected but, instead, is an overall index to species diversity and incorporates both the number of species present and the relative abundance of each (Simpson 1949).

Results

We captured 248 specimens representing 10 species in 2,859 trap-nights for an overall capture rate of 8.67

animals/100 trap-nights, including two mice (*Peromyscus* sp.) that could not be identified because they had been partially consumed (Table 1). We captured Deer Mice (*Peromyscus maniculatus*) in all six vegetation types, and Western Harvest Mice (*Reithrodontomys megalotis*) and Agile Kangaroo Rats (*Dipodomys agilis*) in five and four of the habitats, respectively. The California Vole (*Microtus californicus*), California Mouse (*P. californicus*), Brush Mouse (*P. boylii*), Pinyon Mouse (*P. truei*), Desert Woodrat (*Neotoma lepida*), Dusky-footed Woodrat (*N. fuscipes*) and California Pocket Mouse (*Perognathus californicus*) were less abundant and far more restricted in distribution (Table 1). We captured all 10 species of rodents in the Interior Live Oak vegetation type, but we only caught Deer Mice, Western Harvest Mice, and Agile Kangaroo Rats in the Graminoid vegetation type. The Gini-Simpson Index of Diversity was greatest for rodents in the Black Oak and Interior Live Oak vegetation types; slightly lower but similar to each other in the Chamise-Manzanita, Graminoid, and Riparian vegetation types; and lowest in the Coast Live Oak vegetation type (Table 2).

Discussion

Our purpose here was to memorialize descriptions of the rodent communities following a severe conflagration and is based on an intensive trapping effort at a specific place and time following that event; in addition, we ensure the locations of those efforts are available to future investigators. Although there has been some historical interest in the composition of rodent communities in cismontane Southern California, much of the early work centered on biotic surveys of specific mountain ranges (Grinnell 1908; Grinnell and Swarth 1913; Pequegnat 1951; Vaughan 1954; Kolb and White 1974) or nearby geographic areas (Bleich 1973; Bontrager 1973; Quinn 1979, 1983; Wirtz 1982). More recent efforts have, however, concentrated on changes in rodent communities shortly after fires in vegetation types subject to periodic conflagrations, and particularly in chaparral (Quinn 1979; Wirtz 1982; Price and Wasser 1984; Schwilk and Keeley 1998; Borchert et al. 2014).

It has become clear that the effects of fire on small mammals vary spatially, temporally, with habitat type, and by species (Brehme et al. 2011; Bond 2015), but those effects generally are of short duration. Moreover, few study plots have been described adequately to ensure they can be located by future investigators (Pequegnat 1951; Bleich 1973; Kolb and White 1974; Quinn 1979, 1983), but references to permanent grids occasionally appear in the literature (Price and Wasser 1984). Information presented herein adds to this list of true permanent study sites, which will become of increasing interest in view of upward-trending ambient temperatures and their anticipated long-term effects in Southern California (Dong et al. 2019).

Table 2. Location (quarter section, section, township, and range, San Bernardino Base and Meridian) and elevation (Elev.) of study plots; trapping effort (total number of trap nights); number of rodent species (n) caught per vegetation type; and rodent species diversity (SpD; expressed as the Gini-Simpson Index of Diversity [1-D] and also known as Simpson›s Index of Diversity or the Dominance Index) for six vegetation types in the Soboba Management Area, San Bernardino National Forest, San Jacinto Mountains, Riverside County, California. The Chamise-Manzanita Vegetation Type includes the Chamise or Manzanita Series of Paysen et al. (1980) and the Chamise-Manzanita Association of Berg (1980). The Graminoid Vegetation Type was dominated by a variety of annual grass species, but a specific series was not identified by Paysen et al. (1980). The Riparian, Black Oak, Interior Live Oak, and Coast Live Oak vegetation types were defined by Paysen et al. (1980).

Vegetation Type	Location of Study Plot	Elev. (m)	Trap-Nights	n	SpD
Chamise-Manzanita	SE¼, 13, 4S, 1E	1,095	540	7	0.68
Interior Live Oak	NW¼, 7, 4S, 2E	1,527	630	10	0.79
Graminoid	NW¼, 12, 4S, 1E	1,290	630	3	0.63
Riparian	SE¼ 24, 4S, 1E	932	315	5	0.63
Black Oak	SW¼, 6, 4S, 2E	1,510	114	4	0.81
Coast Live Oak	SW¼, 13, 4S, 1E	1,097	630	5	0.47

The trending shift away from natural history as an academic discipline, increasing fascination with, and reliance on, technology (Bleich 2018), and the tendency of what is considered old data to be of little interest to contemporary investigators all contribute toward the ubiquity of what has been described as generational amnesia (Robert Fisher. 2021. The Memory Loss that Harms the Planet. British Broadcasting Corporation, London, UK. Available from https://www.bbc.com/future/columns/wise-words [Accessed 31 December 2021]). As a result, well-documented historical data are becoming increasingly meaningful and more important to future investigators (Bleich et al., in press). Fortunately, there is renewed enthusiasm for the important role that natural history has played, currently plays, and will play in the future in terms of its relevance to ecological science (Tewksbury et al. 2014; Barrows et al. 2016; Callaghan et al. 2017; McKeon et al. 2020).

The portending increase in global temperature and its effect on ecosystem structure or function further enhances the value of the information presented here. Thus, the relative abundance and species diversity of these small mammals, at a specific time and at permanent locations memorialized in the formal literature, have the potential to serve as baselines regarding alteration of habitat, whether the result of a warming climate or of anthropogenic manipulation (Hope et al. 2017; Caro et al. 2021). Given these changing times, interest in those data and location information will increase, because it complements other, albeit less-detailed, data from a region of Southern California that long has been at the forefront of interest in mammalian biogeography (Grinnell and Swarth 1913). Indeed, our study area was proximate to the San Gorgonio Pass of Riverside County, an area that has been of substantial interest to recent investigators (Best et al. 1986; Sullivan and Best 1997; Erickson and Patten 1999; Patton et al. 2014). Had a greater number of earlier investigators provided information of the type included here many additional specific locations at which to assess changes rodent community composition would be available in the literature.

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Literature Cited

Barrows, C.W., M.L. Murphy-Mariscal, and R.R. Hernandez. 2016. At the crossroads: the nature of natural history in the twenty-first century. BioScience 66:592–599.

Berg, K. 1978. Soboba Vegetation Mapping: a resource inventory in conjunction with the Soboba Vegetation Management Plan. San Bernardino National Forest, San Jacinto Ranger District, Idyllwild, California. 27 p.

Best, T.L., R.M. Sullivan, J.A. Cook, and T.L. Yates. 1986. Chromosomal, genic, and morphologic variation in the Agile Kangaroo Rat, *Dipodomys agilis* (Rodentia: Heteromyidae). Systematic Zoology 35:311–324.

Bleich, V.C. 1973. Ecology of rodents at the United States Naval Weapons Station Seal Beach, Fallbrook Annex, San Diego County, California. M.A. Thesis, California State University, Long Beach, California. 102 p.

Bleich, V.C. 1977. *Dipodomys stephensi*. Mammalian Species 73:1–3.

Bleich, V.C. 2018. Maintaining momentum for conservation: bighorn sheep as an example. Wildlife Society Bulletin 42:540–546.

Bleich, V.C. 2021. Fire on the mountain - run boys, run! California Fish and Wildlife 107:33–43.

Bleich, V.C., and S.A. Holl. 1982. Management of Chaparral habitat for Mule Deer and Mountain Sheep in Southern California. Pp. 247–254 *in* Proceedings of the Symposium on the Dynamics and Management of Mediterranean-type Ecosystems. Conrad, C.E., and W.C. Oechel (Tech. Coord.). General Technical Report PSW-58, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Bleich, V.C., and M.W. Oehler. 2000. Wildlife education in the United States: thoughts from agency biologists. Wildlife Society Bulletin 28:542–545.

Bleich, V.C., M.W. Oehler, and J.G. Kie. 2020. Managing rangelands for wildlife. Pp. 126–148 *in* The Wildlife Management Techniques Manual. Volume 2: Management. 8th Edition. Silvy, N.J. (Ed.). Johns Hopkins University Press, Baltimore, Maryland.

Bleich, V.C., G.W. Sudmeier, M.W. Wolter, and R.A. Weaver. In press. The first translocation of bighorn sheep in California: a critical review of the activities of William Franklin Frakes. Human-Wildlife Interactions.

Blong, B., V.C. Bleich, F.L. Botti, and R.R. Celentano. 1978. Wildlife investigations of the Soboba Burn, San Bernardino National Forest. California Department of Fish and Game, Long Beach, California. 27 p.

Blood, B.R. 2021. An annotated checklist of the terrestrial mammals of Los Angeles County, part I: Didelphimorphia, Lagomorpha, and Rodentia. Bulletin of the Southern California Academy of Sciences 120:99–127.

Bond, M.L. 2015. Mammals and mixed- and high-severity fire. Pp. 89–117 *in* The Ecological Importance of Mixed-Severity Fires. DellaSala, D.A., and C.T. Hanson (Ed.). Elsevier Scientific Publishers B.V., Amsterdam, The Netherlands.

Bontrager, D.R. 1973. Rodent ecology of the Santa Rosa Plateau, Riverside County, California. M.A. Thesis, California State University, Long Beach, California. 115 p.

Borchert, M.I., D.P. Farr, M.A. Rimbenieks-Negrete, and M.N. Pawlowski. 2014. Responses of small mammals to wildfire in a mixed conifer forest in the San Bernardino Mountains, California. Bulletin of the Southern California Academy of Sciences 113:81–95.

Bowyer, R.T. 1981. Management guidelines for improving Southern Mule Deer habitat on the Laguna-Morena Demonstration Area. Final Report, Contract 40-9AD6-9-622, U.S. Forest Service, Cleveland National Forest, San Diego, California. 80 p.

Bowyer, R.T., and V.C. Bleich. 1980. Ecological relationships between Southern Mule Deer and California Black Oak. Pages 292–296 *in* Proceedings of the Symposium on the Ecology, Management, and Utilization of California Oaks. Plumb, T.R. (Tech. Coord.). General Technical Report PSW-44, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Bowyer, R.T., and Bleich, V.C. 1984. Effects of cattle grazing on selected habitats of Southern Mule Deer. California Fish and Game 70:240–247.

Bradley, R.D., L.K. Loren, R.J. Baker, L.C. Bradley, J.A. Cook, R.C. Dowler, C. Jones, D.J. Schmidly, F.B. Stangl, Jr., R.A. Van Den Bussche, and

B. Wursig. 2014. Revised checklist of North American mammals north of Mexico, 2014. Occasional Papers of the Museum of Texas Tech University 327:1–27.

Brehme, C.S., D.R. Clark, C.J. Rochester, and R.N. Fisher. 2011. Wildfires alter rodent community structure across four vegetation types in southern California, USA. Fire Ecology 7:81–96.

Bury, R.B. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. Herpetological Conservation Biology 1:56–61.

Callaghan, C.T., J.M. Martin, R.T. Kingsford, and D.M. Brooks. 2018. Unnatural history: is a paradigm shift of natural history in 21st century ornithology needed? Ibis 160:475–480.

Caro, T., Z. Rowe, J. Berger, and A. Dobson. 2022. Now is not tomorrow. Conservation Letters 15:e12922. https://doi.org/10.1111/conl.12922.

Caro, T., Z. Rowe, J. Berger, P. Wholey, and A. Dobson. 2021. An inconvenient misconception: climate change is not the principal driver of biodiversity loss. Conservation Letters 15:e12868. https://doi.org/10.1111/conl.12868.

Chen, X., B.-L. Li, T.A. Scott, T. Tennant, J.T. Rotenberry, and M.F. Allen. 2005. Spatial structure of multispecies distributions in Southern California, USA. Biological Conservation 124:169–175.

Dong, C., G. MacDonald, G.S. Okin, and T.W. Gillespie. 2019. Quantifying drought sensitivity of Mediterranean climate vegetation to recent warming: a case study in Southern California. Remote Sensing 11(24), 2902. https://doi.org/10.3390/rs11242902.

Erickson, R.A., and M.A. Patten. 1999. Identification and distribution of spiny pocket mice (*Chaetodipus*) in cismontane Southern California. Bulletin of the Southern California Academy of Sciences 98:57–65.

Gray, M. 2006. The Bob Dylan Encyclopedia. Continuum International Publishing Group, New York, New York.

Green, L.R. 1977a. Fuel reduction without fire - current technology and ecosystem impact. Pp. 163–171 *in* Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. Mooney, H.A., and C. E. Conrad (Tech. Coord.). General Technical Report WO-3, U.S. Forest Service, Washington, D.C.

Green, L.R. 1977b. Fuelbreaks and Other Fuel Modifications for Wildland Fire Control. Agriculture Handbook 499. U.S. Department of Agriculture, Washington, D.C.

Grinnell, J. 1908. The biota of the San Bernardino Mountains. University of California Publications in Zoology 5:1–170.

Grinnell, J., and H.S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of Southern California. University of California Publications in Zoology 10:197–406.

Guiasu, R.C., and S. Guiasu. 2010. The Rich-Gini-Simpson quadratic index of biodiversity. Natural Science 2:1130–1137.

Hafner, J.C., and M.S. Hafner. 1983. Evolutionary relationships of heteromyid rodents. Great Basin Naturalist Memoirs 7:3–29.

Hoffman, A.A., and C.M. Sgro. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Hope, A.G., E. Waltari, N.R. Morse, J.A. Cook, M.J. Flamme, and S.L. Talbot. 2017. Small mammals as indicators of climate, biodiversity, and ecosystem change. Alaska Park Science 16:71–76.

Jones, J.K., Jr., D.C. Carter, and H.H. Genoways. 1973. Checklist of North American mammals north of Mexico. Occasional Papers of the Museum of Texas Tech University 12:1–14.

Jones, J.K., Jr., D.C. Carter, and H.H. Genoways. 1975. Revised checklist of North American mammals north of Mexico. Occasional Papers of the Museum of Texas Tech University 28:1–14.

Jones, J.K., Jr., D.C. Carter, and H.H. Genoways. 1979. Revised checklist of North American mammals north of Mexico, 1979. Occasional Papers of the Museum of Texas Tech University 62:1–17.

Keeley, J.E. 2001. Fire and invasive species in Mediterranean-climate ecosystems of California. Pp. 81–94 *in* The Role of Fire in the Control and Spread of Invasive Species. Galley, E.E.M., and T.P. Wilson (Ed.). Tall Timbers Research Station, Tallahassee, Florida.

Keeley, J.E., J. Franklin, and C. D'Antonio. 2011. Fire and invasive plants on California landscapes. Pp. 193–221 *in* The Landscape Ecology of Fire. McKenzie, D., C. Miller, and D.A. Falk (Ed.). Springer Science+Business Media B.V., New York, New York.

Keeley, J.E., and H.D. Safford. 2016. Fire as an ecosystem process. Pp. 2–3 *in* Ecosystems of California: Threats and Responses - Supplement for Decision-making. Mooney, H.A., and E. Zavaleta (Ed.). University of California Press, Berkeley, California.

Kessler, W.B., and A.L. Booth. 1998. Professor Leopold, what is education for? Wildlife Society Bulletin 26:707–712.

Klinger, R.C., M.L. Brooks, and J.M. Randall. 2006. Fire and invasive plant species. Pp. 499–515 *in* Fire in California's Ecosystems. Sugihara, N.G., J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thoede (Ed.). University of California Press, Berkeley, California.

Kolb, J.A., and M. White. 1974. Small mammals of the San Bernardino Mountains. Southwestern Naturalist 19:112–114.

Matocq, M. 2002. Morphological and molecular analyses of a contact zone in the *Neotoma fuscipes* species complex. Journal of Mammalogy 83:866–883.

McKeon, S., L. Weber, A.J. Adams, and T.L. Fleischner. 2020. Natural history as the innate foundation of ecology. Bulletin of the Ecological Society of America 101(1):e01656. https://doi.org/10.1002/bes2.1656.

Millien, K., S.K. Lyons, L. Olson, F.A. Smith, A.B. Wilson, and Y. Yom-Tov. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. Ecology Letters 9:853–869.

Mooney, H.A., and E. Zavaleta (Ed.). 2016. Ecosystems of California: Threats and Responses - Supplement for Decision-making. University of California Press, Berkeley, California.

Moore, J.C., C.E. Taylor, and B.C. Moore. 1979. The *Drosophila* of Southern California. I. Colonization after a fire. Evolution 33:156–171.

Noss, R.F. 1996. The naturalists are dying off. Conservation Biology 10:1–3.

Ostberg, S., W. Lucht, S. Schaphoff, and D. Gerten. 2013. Critical impacts of global warming on land ecosystems. Earth System Dynamics 4:347–357.

Patton, J.L., D.G. Huckaby, and S.T. Alvarez-Castañeda. 2007. The evolutionary history and a systematic revision of woodrats of the *Neotoma lepida* group. University of California Publications in Zoology 135:1–411.

Paysen, T.E., J.A. Derby, H. Black, Jr., V.C. Bleich, and J.W. Mincks. 1980. A Vegetation Classification System Applied to Southern California. General Technical Report PSW-45, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Albany, California.

Pequegnat, W.E. 1951. The biota of the Santa Ana Mountains. Journal of Entomology and Zoology 42:1–84.

Price, M.V., and N.M. Waser. 1984. On the relative abundance of species: postfire changes in a Coastal Sage Scrub rodent community. Ecology 65:1161–1169.

Quinn, R.D. 1979. Effects of fire on small mammals in the Chaparral. Transactions of the Western Section of The Wildlife Society 15:125–133.

Quinn, R.D. 1983. Short-term effects of habitat management on small vertebrates in Chaparral. Transactions of the Western Section of The Wildlife Society 19:55–66.

Roberts, T.A. 1980. Approaches to Chaparral management for wildlife. Transactions of the Western Section of The Wildlife Society 16:112–119.

Roberts, T.A. 1981. The Soboba Project: preliminary evaluation of habitat improvement techniques. Transactions of the Western Section of The Wildlife Society 17:100–105.

Schwilk, D.W., and J.E. Keeley. 1998. Rodent populations after a large wildfire in California Chaparral and Coastal Sage Scrub. Southwestern Naturalist 43:480–483.

Scotter, G.W. 1980. Management of wild ungulate habitat in the western United States and Canada: a review. Journal of Range Management 33:16–27.

Simpson, E.H. 1949. Measurement of diversity. Nature 163:688.

Smith, N., and A. Leiserowitz. 2012. The rise of global warming skepticism: exploring affective image associations in the United States over time. Risk Analysis 32:1021–1032.

Sullivan, R.M., and T.L. Best. 1997. Systematics and morphologic variation in two chromosomal forms of the Agile Kangaroo Rat (*Dipodomys agilis*). Journal of Mammalogy 78:775–797.

Tewksbury, J.J., J.G.T. Anderson, J.D. Bakker, T.J. Billo, P.W. Dunwiddie, M.J. Groom, S.E. Hampton, S.G. Herman, D.J. Levey, N.J. Machnicki, et al. 2014. Natural history's place in science and society. BioScience 64:300–310.

Vaughan, T.A. 1954. Mammals of the San Gabriel Mountains of California. University of Kansas Publications of the Museum of Natural History 7:513–582.

White, T.C., G.L. Larsen, and K.K. Bergstrom. 1982. Laguna-Morena Demonstration Area: a multiagency Chaparral management project. Pp. 575–580 *in* Proceedings of the Symposium on the Dynamics and Management of Mediterranean-type Ecosystems. Conrad, C.E., and W.C. Oechel (Tech. Coord.). General Technical Report PSW-58, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Wirtz, W.O. 1982. Postfire community structure of birds and rodents in Southern California Chaparral. Pp. 241–246 *in* Proceedings of the Symposium on the Dynamics and Management of Mediterranean-type Ecosystems. Conrad, C.E., and W. C. Oechel (Tech. Coord.). General Technical Report PSW-58, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

APPENDIX

Several systematic or taxonomic revisions have occurred since completion of the survey of small mammals occupying the Soboba Management Area, Riverside County, California, in 1978. These changes are noted here to ensure readers are aware that specimens collected during our research have been subjected to systematic or taxonomic review, and that identifications of specimens obtained during our research should be reviewed and confirmed. Common and scientific names of these species that were in use during our research precede each discussion.

Desert Woodrat (*Neotoma lepida*). The *Neotoma lepida* group of woodrats was revised by Patton et al. (2007). We have retained the nomenclature existing at the time of our survey, but specimens obtained during our investigation may represent either, or both, of the two species, *N. lepida*, and Bryant's Woodrat, *N. bryanti*, as currently recognized and occur in the vicinity of San Gorgonio Pass (Patton et al. 2007).

Dusky-footed Woodrat (*Neotoma fuscipes*). The *Neotoma fuscipes* species complex was revised by Matocq (2002). In this paper, we retained the nomenclature existing at the time of our survey, but what we refer to in the text as *N. fuscipes* now is recognized as *Neotoma macrotis*, the Big-eared Woodrat. The Dusky-footed Woodrat, *N. fuscipes*, occurs north of the range of *N. macrotis* as currently understood.

Agile Kangaroo Rat (*Dipodomys agilis*). In this paper, we have retained the nomenclature existing at the time of our survey, but the species *Dipodomys agilis* has been revised and split into two separate species, *D. agilis* and *D. simulans* (Sullivan and Best 1997), the latter being referred to as the Dulzura Kangaroo Rat (Bradley et al. 2014). Similar to specimens that we identified as *Neotoma lepida*, specimens of kangaroo rats collected during our investigation and identified at the time as *D. agilis* may represent *D. agilis*, *D. simulans*, or both species.

California Pocket Mouse (*Perognathus californicus*). In this paper, we have retained the nomenclature existing at the time of our survey. Since then, the subgenus *Chaetodipus* has been elevated to full generic status, and this species now is recognized as *Chaetodipus californicus* (Hafner and Hafner 1983; Bradley et al. 2014).

VERNON C. BLEICH was employed by the California Department of Fish and Game (CDFG) for 34 y, during which time he worked extensively with large mammals occupying the Great Basin, Mojave, and Sonoran deserts of California. He received B.S. and M.A. degrees from California State University Long Beach, and a Ph.D. from the University of Alaska Fairbanks. He currently is Research Professor at the University of Nevada Reno, and remains actively involved in conservation and research activities. He currently serves on the Advisory Board of the Texas Bighorn Society and is the Science Advisor for the Society for the Conservation of Bighorn Sheep, is a member of the Professional Resource Advisory Board of the Wild Sheep Foundation, and recently completed a 3-y appointment to the Wild Horse and Burro Advisory Board of the Bureau of Land Management, on which he represented wildlife conservation issues. In 2023, Vern received the Aldo Leopold Award from the American Society of Mammalogists in recognition of his lasting contributions to the conservation of mammals and their habitats. (Photographed by 'Stasia Mitzel).

BONNAR BLONG was employed by the California Department of Fish and Game (CDFG) for 34 y, during which he became well known as an advocate for conservation, particularly with respect to Mule Deer (*Odocoileus hemionus*) occupying the chaparral-dominated mountains of southern California and the Desert Bighorn Sheep (*Ovis canadensis nelsoni*) inhabiting the Santa Rosa Mountains and other Sonoran Desert areas. Bonnar was a veteran of World War II, during which time he served in the U.S. Marine Corps. Following an honorable discharge from military service, he completed his education at Washington State University, Pullman, before joining CDFG. Among his earliest assignments was an investigation of food habits of Mule Deer in Santa Barbara County, California, following which he became the Biologist for the San Jacinto Wildlife Management Unit of CDFG, and rose to the rank of Field Supervisor prior to retirement. (Photograph courtesy of The Riverside Press-Enterprise).

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NOTES

NORTHWESTERN POND TURTLES (*ACTINEMYS MARMORATA*) UNDER ICE

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Abstract.—**Freshwater turtles on the North American continent have adapted to endure seasonal cold weather across a range of climatic conditions. The Northwestern Pond Turtle may move around within its chosen overwintering habitat, whether it be terrestrial or aquatic. Here we report observations of overwintering turtles active under a frozen pond surface. Remote sensors recorded the edaphic conditions under which our observations were made. Conditions under the ice were less severe than those in the adjacent terrestrial habitat. For turtles, the reduced risk of predation, and protection from extreme temperatures, make overwintering in lentic habitat a better fitness choice than overwintering on land.**

Key Words.—basking; brumation; cloacal breathing; hibernation; Northwestern Pond Turtle; overwintering; remote sensor.

In the Northern Hemisphere, freshwater turtles have adapted to cope with the seasonal cold temperatures of winter (Ultsch 2006; Bury and Germano 2008; Rödder et al. 2013). During winter months, most turtles enter a prolonged period of inactivity referred to as hibernation, or brumation, but turtles may become intermittently active when winter temperatures warm periodically (Holland 1994; Bury et al. 2012). Herein we refer to this prolonged inactive period as overwintering. In overwintering, turtles have adapted to lower their metabolic rate to a low constant that minimizes energy consumption (Ultsch 2006). During this metabolic depression, turtles choose a location that provides a suitable environment; one in which they are least likely to succumb to freezing temperatures, prolonged anoxia, or predation (Ultsch 2006; Bury and Germano 2008). Freshwater turtles may overwinter on land, or in lakes and ponds, but overwintering mortalities are generally lower in aquatic overwintering sites (Ultsch 2006).

Northwestern Pond Turtles (*Actinemys marmorata*) inhabit a range that extends from the San Francisco Bay in the south, northward to the Puget Sound area of Washington (Bury and Germano 2008; Spinks et al. 2016; Todd et al. 2022), and along the Pacific Coast west of the Sierra Nevada and Cascade Range peaks, with few isolated populations east of the Sierra Nevada (Storer 1930; Seeliger 1945; Thomson et al. 2016; Bury 2017). *Actinemys marmorata* generally overwinters aquatically if living in lakes and ponds, and on land when it occurs in riverine habitats (Ultsch 2006; Bury et al. 2012). Often, *A. marmorata* from lentic systems overwinter under water, while those in lotic systems overwinter on land to escape seasonal scouring flows (Reese and Welsh 1997; Ultsch 2006; Bury and Germano 2008; Bury et al. 2012). There appears to be plasticity in overwintering behavior; however, as individual turtles may alternate between overwintering aquatically and terrestrially from year to year (Dan Holland, unpub. report), perhaps due to extremes in the Mediterranean climate that predominates throughout much of their distribution (Ultsch 2006; Bury et al. 2012).

During the depressed metabolic state of overwintering, *A. marmorata* may move around in their overwintering sites, whether terrestrial or aquatic, including occasional basking (Reese and Welsh 1997). *Actinemys marmorata* have been found basking in temperatures as low as 6º C in a lake in Oregon, and a radio-telemetry study suggested that *A. marmorata* may actively move under the frozen surface of a mountain lake in central Oregon (Dan Holland, unpubl. report). Here, we offer evidence of *A. marmorata* moving under an ice-covered pond in northern California. We also provide clarity on the thermal conditions of the pond environment immediately surrounding these active turtles, and discuss the possible benefits for *A. marmorata* to overwintering aquatically under the threat of such extreme environmental conditions.

We found *A. marmorata* moving under the ice at Bonnie's Pond, which is located on the Mitsui Ranch Preserve, 8 km east of Petaluma in Sonoma County, California. The pond is a small (0.18 ha surface area), relatively deep (3.5 m) stock pond constructed in the 1980s, at an elevation of 682 m, for the purpose of watering livestock (M. E. Mitsui, pers comm). Bonnie's Pond hosts a breeding population of California Red-legged Frogs (*Rana draytonii*; Wilcox et al. 2017).

As part of a research project to determine conditions of oviposition by *R. draytonii*, various environmental sensors were previously installed in and around the pond (unpubl. data). A Hobo UA-001-64 temperature logger (Onset Corp., Bourne, Massachusetts, USA) was mounted on a 1 m-tall post approximately 1 m from the pond shore to record temperatures every half hour. A Hobo MX-2202 temperature/light data logger mounted approximately 5 cm under and parallel to the water surface on a PVC pipe, collected data on light falling on the pond surface (in lumens), in addition to water temperature, every 30 min. Finally, from a raft in the pond center, a Hobo U26-001 dissolved oxygen logger was suspended at a depth of 1 m in the water column (unpubl. data). This unit also recorded water temperature and dissolved oxygen every 15 min.

Between 1 and 2 January 2019, the minimum overnight temperature (Mitsui Ranch weather station; about 300 m southeast of Bonnie's Pond) was -5.35º C (RX-3000, Onset, Corp.), and by 0840 had increased to -3.89° C, resulting in an approximately 1 cm-thick layer of ice over the entire surface of Bonnie's Pond (Fig. 1). Given the rarity of temperatures this low, we visited the pond to photographically record the freezing event. Standing on the earthen berm of the pond, we noticed movement approximately 2 m away along the shoreline. Closer inspection revealed two adult *A*. *marmorata* under the ice, one larger pond turtle slowly moving near the frozen edge in shallow water, and the other smaller pond turtle less active, nestled in a vegetated substrate (Fig. 2). Our initial observations occurred over 10 min, with the larger turtle slowly exploring the pockets and depressions where the ice met the shoreline. The turtles moved slowly and our presence did not seem to elicit any kind of flight response.

We investigated the remainder of the shoreline, and discovered four additional turtles a few meters from the first two. One of the four was exploring the shoreline in the same manner as the first turtle (Fig. 3), with two others exploring the substrate in the shallows of the pond. We observed another turtle swimming at an upward angle from deep within the pond but the turtle turned immediately and swam at a faster speed back in the direction from which it had come. Our last observation involved a turtle that had been at rest near the shore and swam away at our approach, but not before we captured a digital image showing it had a large leech attached to the posterior end of its carapace (Fig. 3). We recorded the air temperature at the Mitsui Ranch weather station on the day of our observations, but the remainder of the temperatures were downloaded from sensors retrieved later in the spring. Remote sensor readings at or around 0830 on 2 January 2019 contrasted with sensor readings from mid-afternoon (1530) on the same day (Table 1), illustrating the large temperature fluctuation on that winter day.

Figure 1. A layer of ice covers the surface of Bonnie's Pond on the Mitsui Ranch Preserve in Sonoma County, California. We detected six Northwestern Pond Turtles (*Actinemys marmorata*) near the shoreline in the lower right corner of the photo, under the ice. (Photographed by Jeffery T. Wilcox).

We observed six *A*. *marmorata* of various sizes active under ice on the morning of 2 January 2019. Previous researchers inferred turtles were moving under the ice of a frozen lake in Oregon while tracking movements with radio transmitters (Dan Holland, unpubl. report). Conditions at the surface of Bonnie's Pond on the morning of 2 January seemed extreme to us, but just under the ice, conditions were more tolerable for turtles. Air temperatures at 0830 were well below freezing, but just under the ice surface, 4 m from shore, the MX-2202 remote sensor recorded water temperature of 1.12º C, and the U26-001 sensor recorded a temperature of 6.24º

Figure 2. (Left) Two Northwestern Pond Turtles (*Actinemys marmorata*) under ice in Bonnie's Pond on a January morning in 2019 at the Mitsui Ranch Preserve near Petaluma, California. The turtle farthest right was slowly exploring the pond substrate at the ice edge, while the smaller turtle, at bottom center, moved very little during our observation. (Right) A single adult Northwestern Pond Turtle (*Actinemys marmorata*) shown leaving the shallow edge of an ice-covered pond making its way to deeper water. (Photographed by Jeffery T. Wilcox).

Figure 3. An adult Northwestern Pond Turtle (*Actinemys marmorata*) under ice in Bonnie's Pond, Sonoma County, California. Note the large leech attached to the rear marginal scute of the carapace. (Photographed by Jeffery T. Wilcox).

Table 1. Remote sensor readings from two times of the day during 2 January 2019 on the Mitsui Ranch Preserve, Sonoma County, California. The sensors UA-001-64, MX-2202, and U26-001 were located at or in Bonnie's Pond, and the RX-3000 weather station was located approximately 400 m east of the pond. The abbreviation Temp. = temperature.

Sensor	Time	Temp. (ºC)	Light intensity (lumens/m^2)	Dissolved Oxygen (mg/L)
RX-3000	0830	-3.89	—	—
	1530	9.24	—	—
UA-001-64	0830	-3.28	—	—
	1530	11.2	—	—
MX-2202	0830	1.12	16	—
	1530	5.10	1,033	—
U26-001	0830	6.24	—	5.06
	1530	6.83	—	5.69

C at a depth of 1 m in the pond center (Table 1). By mid-afternoon on that same day, the surface temperature had increased by 5º C and ice had largely melted from the surface.

Most turtles in the Emydidae family (including *Actinemys*) are capable of cloacal breathing, where oxygen is exchanged with water absorbed across areas of dense capillaries in the cloacal walls (Carr 1995; Ultsch 2006). Turtles also have a very low metabolic rate in cold water, which lowers their oxygen demand, and also have relatively high tolerance to lactic acid build-up in the tissues, which allows them to use anaerobic respiration in low-oxygen conditions (Carr 1995; Ultsch 2006). Cold water has a higher capacity for holding dissolved oxygen, and the dissolved oxygen levels on that January morning were within the normal range of many other California water bodies sampled during warmer months (Silbernagel et al. 2013; see Table 1). Additionally, enough light was penetrating the water surface for algae in the water column to respire, likely contributing to oxygen production in the water column beneath the ice (Yang et al. 2017).

The Mediterranean climate of coastal northern California is not generally characterized by cold weather extremes, but periods of prolonged drought alternating with those of high rainfall are not uncommon (Schoenherr 1992). Prior to European settlement, *A. marmorata* primarily occupied stream habitat because ponded water was not a common feature in historically unglaciated areas of California (Trenham et al. 2001; Wilcox 2015; McMurry 2020). Thus, periodic high flows may have necessitated *A. marmorata* leaving lotic waters and overwintering on land to escape winter flooding (Reese 1996; Reese and Welch 1997; Ultsch 2006). The construction of stock ponds and reservoirs over the past century in California, however, has provided *A. marmorata* safer alternative water bodies in which to overwinter (Bury et al. 2012; Tu and Trulio 2022).

Water, in general, is thought to be a more favorable environment for overwintering turtles because the risk of predation is reduced (Ultsch 2006). Furthermore, water temperatures are less susceptible to the dramatic fluctuations that are physiologically stressful to ectotherms; and turtles are not forced to expose themselves to predation and desiccation as they search for suitable terrestrial overwintering sites (Ultsch 2006). Therefore, the temporary disadvantage of sequestration under a frozen surface may outweigh the risk of terrestrial overwintering for *A. marmorata*.

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LITERATURE CITED

Bury, R.B., and D.J. Germano. 2008. *Actinemys marmorata* (Baird and Girard 1852) - Western Pond Turtle, Pacific Pond Turtle. Conservation Biology of Fresh Water Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Rhodin, A.G.J., P.C.H. Pritchard, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, J.B. Iverson, and R.A. Mittermeier (Eds.). Chelonian Research Monographs No. 5, doi:10.3854/crm.5.090.affinis.v1.2015.

Bury, R.B., D.T. Ashton, H.H. Welsh, Jr., D.A. Reese, and D.J. Germano. 2012. Synopsis of biology. Pp. 9–19 in Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation, and Management. Bury, R.B., H.H. Welsh, Jr., D.J. Germano, and D.T. Ashton (Eds.). Northwest Fauna 7.

Bury, R.B. 2017. Biogeography of Western Pond Turtles in the western Great Basin: dispersal across a northwest passage? Western Wildlife 4:72–80.

Carr, A. 2018. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, New York.

McMurry, S. 2020. The American farm pond. Buildings and landscapes: Journal of the Vernacular Architectural Forum 27:39–58.

Reese, D.A. 1996. Comparative demography and habitat use of Western Pond Turtles in northern California: the effects of damming and related alterations. Ph.D. Dissertation, University of California, Berkeley, California. 253 p.

Reese, D.A., and H.H. Welsh, Jr. 1997. Use of terrestrial habitat by Western Pond Turtles, *Clemmys marmorata*: implications for management. Pp. 352–357 *In* Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference. J. Van Abbema (Ed.). New York Turtle and Tortoise Society, New York, New York.

Rödder, D., A.M. Lawing, M. Flecks, F. Ahmadzadeh, J. Dambach, J.O. Engler, J.C. Habel, T. Hartmann, D. Hörnes, F. Ihlow, et al. 2013. Evaluating the significance of paleophylogeographic species distribution models in reconstructing Quaternary range-shifts of Nearctic chelonians. PLoS ONE 8(10): e72855. https://doi.org/10.1371/journal.pone.0072855

Schoenherr, A.A. 1992. A Natural History of California, University of California Press, Berkeley, California.. 773 p.

Seeliger, L.M. 1945. Variation in the Pacific Mud Turtle. Copeia 1945:150–159.

Silbernagel, C., D.L. Clifford, J. Bettaso, S. Worth, and J. Foley. 2013. Prevalence of selected pathogens in Western Pond Turtles and sympatric introduced Red-eared Sliders in California, USA. Diseases of aquatic organisms 107:37–47.

Spinks, P.Q., R.C. Thomson, E. McCartney-Melstad, and H.B. Shaffer. 2016. Phylogeny and temporal diversification of the New World pond turtles (Emydidae). Molecular Phylogenetics and Evolution 103:85–97.

Storer, T.I. 1930. Notes on the range and life-history of the Pacific Fresh-water Turtle (*Clemmys marmorata*). University of California Publications in Zoology 32:449–441.

Thomson R.C., A.N. Wright, and H.B. Shaffer. 2016. California Amphibian and Reptile Species of Special Concern. California Department of Fish and Wildlife and University of California Press, Oakland, California.

Todd, B.D., T S. Jenkinson, M. Escalona, E. Beraut, O. Nguyen, R. Sahasrabudhe, P.A. Scott, E. Toffelmier, I.J. Wang, and H.B. Shaffer. 2022. Reference genome of the Northwestern Pond Turtle, *Actinemys marmorata*. Journal of Heredity 113:624–631.

Trenham, P.C., W.D. Koenig, and H.B. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82:3519–3530.

Tu B., and L. Trulio. 2022. Livestock ponds as long-term habitat for Southwestern Pond Turtles (*Actinemys pallida*) in rangeland landscapes. Chelonian Conservation and Biology 21:277–282.

Ultsch, G.R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biological Review 64:435–516.

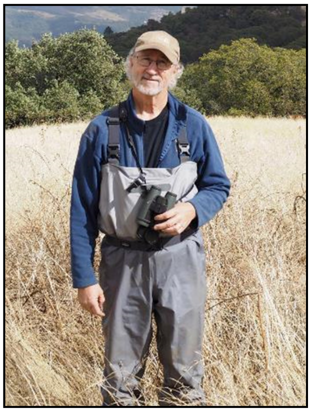
Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Review 81:339–367.

Wilcox, J.T., M.L. Davies, K.D. Wellstone, and M.F. Keller. 2017. Traditional surveys may underestimate *Rana draytonii* egg masses in perennial stock ponds. California Fish and Game 103:66–71.

Wilcox, J.T., G.E. Padgett-Flohr, J.A. Alvarez, and J.T. Johnson. 2015. Possible phenoytypic influence of superinvasive alleles on larval California Tiger Salamanders (*Ambystoma californiense*). American Midland Naturalist 173:168–175.

Yang, B., J. Young, L. Brown, and M. Wells. 2017. High-frequency observations of temperature and dissolved oxygen reveal under-ice convection in a large lake. Geophysical Research Letters 44:12218–12226.

Zaragoza, G., J.P. Rose, K. Purcell, and B.D. Todd. 2015. Terrestrial habitat use by Western Pond Turtles (*Actinemys marmorata*) in the Sierra foothills. Journal of Herpetology 49:437–441.



Jeff Wilcox is the Managing Ecologist for the Mitsui Ranch Preserve near Petaluma in Sonoma County, California. He has worked with landscape-scale parcels to manage sites for endangered species, native grasses, and compatible uses such as organic cattle grazing, education, and research. Jeff has decades of experience working collaboratively on projects that include pond management and construction, native grasses restoration, and species-level projects with California Red-legged Frogs (*Rana draytonii*), Wild Pigs (*Sus scrofa*), American Bullfrogs (*Lithobates catesbieanus*), California Tiger Salamanders (*Ambystoma californiense*), and Foothill Yellow-legged Frogs (*Rana boylii*). (Photographed by Lou Silva).

Jeff Alvarez is a Herpetologist who has specialized in California reptiles and amphibians for 37 y. He has worked with California Red-legged Frogs (*Rana draytonii*), California Tiger Salamanders (*Ambystoma californiense*), western pond turtles (*Actinemys* spp.), and Alameda Whipsnakes (*Masticophis euryxanthus*) for much of his career. His focus is on the conservation and natural history of herpetofauna, survey techniques development, and conducting peer-level special-status species workshops. (Photographed by Jorge Valdez-Villavicencio).

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NOTES

ROLE OF BURROW SYSTEMS OF CALIFORNIA GROUND SQUIRRELS (*OTOSPERMOPHILUS BEECHEYI*) IN SUSTAINING NATIVE WILDLIFE

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***Abstract*.—California Ground Squirrels (*Otospermophilus beecheyi*) are known to create and modify habitat and microhabitat that is routinely colonized or used by other common and special-status species. It follows that ground squirrel control, whether as a result of pest control or by displacement or ground disturbance in the course of resource management activities, may have unforeseen consequences on native wildlife. I identified 74 obligate species (24.3% of which are special-status) and 76 facultative species (13.1% special-status) specifically associated with *O. beecheyi* burrow systems. No previously published accounts indicate the scope of the use of these systems by native wildlife that I have found. The number of burrow-associated species suggests that the *O. beecheyi* is a keystone species and that wildlife managers should consider the effects of squirrel control on ancillary wildlife, in particular, special-status species.**

Key Words.—burrow; habitat; keystone species; management implications; microhabitat; special-status species.

Although all species play a role in the ecological processes with which they are associated, some species play a particularly profound role as habitat modifier, prey base, dispersal agent, and/or other ecological contributor. Species that support this complexity of roles are often referred to as keystone species, a concept first suggested by Pain (1969). His definition was complex but narrow, concentrating on the role of a predator within an ecological community. He suggested that, inasmuch as the activities of certain native species naturally modify the local ecosystem, population attrition by predation likely alters the physical appearance and composition of the habitat (Pain 1969; Zhao-hua et al. 2001). In the mid-1990s, the concept of keystone species gradually broadened to include the parallel or conceptually similar role of ecosystem engineer (Mills et al. 1993; Lawton 1995). Broadening the definition helped to incorporate species whose critical contributions to local ecology and concomitant species would otherwise have been more obscure. This augmented definition was critical to understanding the ecological role that species play outside of the predator-prey relationship, in particular, on relationships between a species and its environment.

Keystone species, and more specifically ecosystem engineers, come in the form of a range of taxa, but are often represented by a variety of rodents. The North American Beaver (*Castor canadensis*) is an excellent example of a species that fits the subcategory of ecosystem engineer. The beaver creates and modifies habitat for its own needs, but in so doing, creates and supports habitats and microhabitats that meet the needs of numerous other species (Rutherford 1955; Hanson and Campbell 1963; Jones et al. 1994; Karraker and Gibbs 2009), fulfilling the role of a keystone species (Naiman et al. 1986). Another well-known ecosystem engineer is the prairie dog (*Cynomys* spp.; Kotliar et al. 1999). Previous authors have reported that prairie dog towns modify habitat and provide microhabitat for numerous species that might otherwise not occur there (Koford 1958; Sharps and Uresk 1990; Kotliar et al.1999). A reported 146 vertebrate species, both obligate and facultative, have been associated with prairie dog burrow systems, such as the Texas Toad (*Anaxyrus speciosus*), and special-status species including the Black-footed Ferret (*Mustela nigripes*; Koford 1958; Clark et al. 1982; Loredo-Prendeville et al. 1994; Sharps and Uresk 1990; Kotliar et al. 1999). This large range of syntopic (ecologically associated) species notwithstanding, prairie dogs are considered an agricultural pest in many areas, and as such, are subjected to lethal control efforts and burrow-system destruction or disruption (Clark 1989).

In California, the closest prairie dog surrogate is the California Ground Squirrel (*Otospermophilus beecheyi*), which also constructs and depends on extensive underground burrow systems (Grinnell and Dixon 1918). Early researchers working with *O. beecheyi* noted at least 25 syntopic species within its burrow complexes (Grinnell and Storer 1924; Linsdale 1946; Fitch 1948). The burrow systems of this species have been described by Grinnell and Dixon (1918) and Fitch (1948) as ranging from relatively simple (i.e., one roughly straight tunnel with two entrances) to very complex (i.e., numerous tunnels, refuse sumps, nest chambers, and exits). Each burrow system can be up to 8.5 m deep and 226 m (total) in length (Linsdale 1946). Van Vuren and Ordeñana (2012) and Van Vuren et al. (2014) summarized the mean depth and length as 0.6–0.75 m and 7.5–8.2 m, respectively. *Otospermophilus beecheyi* can alter and create habitat and microhabitat as they move large amounts of soil and maintain burrow systems in the course of creating secure refuge, birthing areas, and rearing

Figure 1. Two Species of Special Concern in California using California Ground Squirrel (*Otospermophilus beecheyi*) burrows. (Left) Burrowing Owls (*Athene cunicularia*) using a burrows for a nest site and for refuge, Stanislaus County, California. (Right) American Badger (*Taxadea taxus*) foraging and seeking refuge in a burrow, Contra Costa County, California. (Photographed by Jeff A. Alvarez).

microhabitat for the entire ground squirrel colony (Grinnell and Dixon 1918; Linsdale 1946). These activities mound and ventilate the soil; amend it with vegetation, feces, and urine; and create underground refugia (Grinnell and Dixon 1918; Grinnell and Storer 1924; Linsdale 1946). Ground squirrel complexes are reported (Lenihan 2007) to provide habitat and microhabitat for numerous other species in the form of underground refugia (e.g., favorable for California Tiger Salamander, *Ambystoma californiense*), thermal stability (Baudinette 1972), bare mounds for basking (i.e., conducive to reptiles, etc.), access to waste materials for decomposers (Hawkins 1996), and nesting sites for Burrowing Owls (*Athene cunicularia*; Fig. 1)

Direct observations of numerous species across a wide range of taxa associated with *O. beecheyi* suggested that their burrow systems may be an important microhabitat for many species. Here I report data on native California species that occupy or use the burrow systems of *O. beecheyi* and identify deleterious implications for these syntopic species from activities driven by resource management, and in particular, the National Environmental Policy Act (NEPA) and California Environmental Quality Act (CEQA), conservation measures that require ground squirrel burrow system eradication. These measures are required by the California Department of Fish and Wildlife and the U.S. Fish and Wildlife Service, as part of Biological Opinions and Incidental Take Permits (and other permits) when ground disturbing projects are initiated. Typically, this would include the hand excavation of every burrow in the project area (area of disturbance) and a buffer (sometimes up to 65 m) to its terminal end to move listed species outside the area that will be impacted by a project.

I conducted a formal literature review including materials from agricultural divisions of colleges and universities, integrated observations from my own studies, and I extended a request to other professional biologists engaged in *O. beecheyi* burrow excavation to report what native species they found associated with squirrel burrows. Personal communications were compiled and added to the literature review. Additionally, I added direct observations that were used to compile a list of species found during routine burrow excavation following NEPA and CEQA driven conservation measures. These data came from observations during the excavation of approximately 8,000–9,000 ground squirrel burrows from 1996 through 2022. From the list of compiled data, species were categorized as either common (i.e., not believed to be in decline throughout their range) or as special-status (i.e., California Species of Concern, and federally or CESA-listed species, or candidates for that category). The role or use of ground squirrel habitat and microhabitat by other species was subjectively categorized as being for refuge, nesting, denning, foraging, and/or reproduction/egg-laying. Also, burrows of the closely related, range-overlapping Douglas Squirrel (*O. douglasii*), which was only recently separated as a species from *O. beecheyi*, likely provide similar habitat and microhabitat for sympatric species within its range in northern California, but I did not include information for this species here.

The aggregate literature, personal observations, and input from peers revealed 76 mostly terrestrial, obligate species reported to consistently use *O. beecheyi* burrows for some portion of their natural history (Appendix Table 1). Of these 74 species, 24.3% were categorized as special status. Although work by Lenihan (2007) suggested that numerous avian species were also supported by or use habitat manipulated or occupied by *O. beecheyi* (e.g., Horned Larks, *Eremophila alpestris*, which favors barren surface patches created by the ground squirrels), those data were not systematically analyzed here. With the exception of *Athene cunicularia*, which depend on *O. beecheyi* burrows for nesting, those avian associations appear to be primarily facultative. I also list species associated with *O. beecheyi* burrow systems (use the excavation piles, barren areas, groomed vegetation, etc.; Appendix Table 2). This list includes 76 species that feed on vegetation groomed

Figure 2. Adult male California Tiger Salamander (*Ambystoma californiense*), listed as Threatened under the California Endangered Species Act, emerging from a California Ground Squirrel (*Otospermophilus beecheyi*) burrow, Merced County, California. (Photographed by Jeff A. Alvarez).

Figure 3. Adult Botta's Pocket Gopher (*Thomomys bottae*) after emerging from an excavated California Ground Squirrel (*Otospermophilus beecheyi*) burrow system, San Joaquin County, California. (Photographed by Jeff A. Alvarez).

by *O. beecheyi* activity (e.g., Tule Elk, *Cervus canadensis nannodes*) or consistently avail themselves of the aboveground microhabitat created by the ground squirrels (e.g., Western Meadowlark, *Sturnella neglecta*). It is clear that far more species are associated with ground squirrel burrows systems than are reported here, particularly invertebrates, of which only 30 have been identified.

Despite supporting numerous common and special-status species, *O. beecheyi*, like prairie dogs, are often perceived as an agricultural pest, feeding on fruits and grains, and disrupting planting areas (Storer 1958; Marsh 1998; Van Vuren et al. 2014). Their ground-displacing activity can also compromise levee safety (Grinnell and Dixon 1918; Ordeñana et al. 2012; Van Vuren and Ordeñana 2012; Van Vuren et al. 2014), threaten other infrastructure (Longhurst 1957), and create physical hazards to livestock (Marsh 1998). Land managers have historically responded to the pernicious effects of *O. beecheyi* by gassing, baiting, trapping, shooting, poisoning, burrow collapsing (i.e., entombment of live squirrels), burrow-system excavating, and other measures (Storer 1938, 1958; pers obs.). These systematic efforts to reduce, eliminate, or displace *O. beecheyi*, even within known special-status species habitat, have been done for more than 100 y (Storer 1958, Salmon and Lickliter 1984; Loredo-Prendeville et al. 1994; Berentsen and Salmon 2001).

Such extirpative practices continue even decades following institution of the California Endangered Species Act (1970), CEQA (1970), the federal Endangered Species Act (1973), NEPA (1969), and other regulatory frameworks designed to protect special-status species. Even as resource managers struggle to maintain declining populations of at-risk species in California (Shuford and Gardali 2008; Thomson et al. 2016), local municipalities, state and federal agencies, industrial and small-scale farmers and ranchers, and the public at large are permitted to broadly control *O. beecheyi* with relatively little assessment of the impacts of those activities on special-status species, common concomitants, or the local ecology.

Ironically, biologists themselves may be contributing to this process because regulatory compliance frequently requires that they preemptively evacuate an area of potential special-status species to avert lethal encounters during planned development or resource-management activities. For example, burrow systems may be excavated to reduce habitat suitability for protected species such as San Joaquin Kit Fox (*Vulpes macrotis mutica*), *Ambystoma californiense* (Fig. 2), and the San Francisco Garter Snake (*Thamnophis sirtalis tetrataenia*), for what is termed proactive protection against upcoming ground-disturbance projects. Ground squirrel burrow systems and the burrows of other fossorial (burrowing) mammals (kangaroo rats (*Dipodomys* spp.), pocket gophers (*Thomomys* spp.; Fig. 3), etc., are routinely excavated based on such reasoning. The regulatory mandate does not, however, systematically consider the greater, fundamental ecological value of the ground squirrel colonies to sympatric or syntopic species. Direct experience suggests that burrow excavation may indeed save a few endangered individuals but likely at the cost of numerous other species and their habitat. Killing individual ground squirrels may have little impact on a resident or migratory population of closely associated wildlife species, but removing entire colonies or their habitat can and likely does sever ecological connectivity, break genetic flow, and facilitate or compound declines locally (pers. obs.). Removal of *O. beecheyi* colonies may actually eradicate slow-moving syntopic species (e.g., *A. californiense*) that have a limited ability to escape habitat destruction during manual excavation activity.

Not all the species (common or special status) that I have listed in the appendix tables depend on *O. beecheyi* burrow systems, only that long-term, unforeseen impacts of eliminating habitat and microhabitat on species that make use of these systems are rarely monitored or quantified. These findings portend that if ground squirrel control activities and removal of *O. beecheyi* burrows are not assessed in the present, we risk the decline of special-status species, such as *A. californiense* and *Athene cunicularia*, that depend on this habitat and microhabitat as refuge, hibernacula, foraging sites, and/or for other critical needs. Continued, wholesale destruction of these burrow systems may likely lead to declines in these species, as well as numerous syntopic rodents (i.e., *Dipodomys* spp.), dependent predators (i.e., *V. m. mutica* and American Badger, *Taxadea taxus*), and understudied invertebrates that are, or may soon be, legally protected. Although *O. beecheyi* may be a scourge to farmers, ranchers, and water authorities, it is a keystone species to some species where it occurs.

This work relied heavily on direct observations of individual or small numbers of detected species that were identified and recorded, but not monitored closely. This data should be used with some level of caution in that it was focused on preconstruction surveys and habitat management that was associated with ground disturbing activities related to various infrastructure developments (i.e., solar panel installation, road construction, reservoir inundation, etc.). Future work on these ecological associations must include long-term assessment of the persistence and extent of use of burrow systems by syntopic species. Until these studies are conducted, *O. beecheyi* (and other rodent species) burrow destruction should be conducted only in areas where ground disturbing activity is a certainty but should avoid adjacent (buffer) areas.

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LITERATURE CITED

Baudinette, R.V. 1972. The physiological ecology of a burrowing rodent, *Spermophilus beecheyi*. Ph.D. Dissertation, University of California, Irvine, California. 99 p.

Berentsen, A.R., and T.P. Salmon. 2001. The structure of California Ground Squirrel burrows: control implications. Transactions of the Western Section of the Wildlife Society 37:66–70.

Clark, T.W. 1989. Conservation biology of the Black-footed Ferret. Special Scientific Report No. 3, Wildlife Preservation Trust, Philadelphia, Pennsylvania, USA. 175 p.

Clark, T.W., T.M. Campbell, III, D.G. Socha, and D.E. Casey. 1982. Prairie dog colony attributes and associated vertebrate species. Great Basin Naturalist 42:572–582.

Fitch, H.S. 1948. Ecology of the California Ground Squirrel on grazing lands. American Midland Naturalist 39:513–596.

Grinnell, J., and J. Dixon. 1918. Natural history of the ground squirrels of California. Monthly Bulletin of the State Commission of Horticulture 7:597–708.

Grinnell, J., and T.I. Storer. 1924. Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. University of California Press, Berkeley, California, USA.

Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. University of California Publications in Zoology 25:1–594.

Hanson, W.D., and R.S. Campbell. 1963. The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a North Missouri stream. American Midland Naturalist 69:136–149.

Hawkins, L.K. 1996. Burrows of kangaroo rats are hotspots for desert soil fungi. Journal of Arid Environments 32:239–249.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Karraker, N.E., and J.P. Gibbs. 2009. Amphibian production in forested landscapes in relation to wetland hydroperiod: a case study of vernal pools and beaver ponds. Biological Conservation 142:2293–2302.

Koford, C.B. 1958. Prairie dogs, Whitefaces, and Blue Grama. Wildlife Monographs 3:3–78.

Kotliar N.B., B.W. Baker, A.D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177–192.

Lawton, J.H, and C.G. Jones. 1995. Linking species & ecosystems: organisms as ecosystem engineers. Pp. 373–386 *in* Linking Species & Ecosystems. Jones, C.G., and J.H. Lawton (Eds.). Chapman and Hall, New York, New York, USA.

Lenihan C.M. 2007. The ecological role of the California Ground Squirrel (*Spermophilus beecheyi*). Ph.D. Dissertation, University of California, Davis, California, USA. 109 p.

Linsdale, J.M. 1946. The *O. beecheyi*. University of California Press, Berkeley, California, USA.

Longanecker, D.S., and A.L. Burroughs. 1952. Sylvatic plague studies, IX. Studies of the microclimate of the California Ground Squirrel burrow and its relation to seasonal changes in the flea population. Ecology 33:488–499.

Longhurst, W.M. 1957. A history of squirrel burrow gully formation in relation to grazing. Journal of Range Management 10:182–183.

Loredo-Prendeville, I., D. Van Vuren, A.J. Kuenzi, and M.L. Morrison. 1994. California Ground Squirrels at Concord Naval Weapons Station: alternatives for control and the ecological consequences. Pp. 72–77 *in* Proceedings of the 26th Vertebrate Pest Conference. Timm, R.M., and J.M. O'Brian (Eds.). Davis, California.

Marsh, R.E. 1998. Historical review of ground squirrel crop damage in California. International Biodeterioration & Biodegradation 42:93–99.

Mills, L.S., M.E. Soulé, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. BioScience 43:219–224.

Montanucci, R.R. 1965. Observations on the San Joaquin Leopard Lizard, *Crotaphytus wislizenii silus* Stejneger. Herpetologica 21:270–283.

Morrell, S.H. 1972. Life history of the San Joaquin Kit Fox. California Fish and Game Journal 58:162–174.

Naiman, R.J., J.M. Melillo, and J.E. Hobbie. 1986. Ecosystem alteration of Boreal Forest streams by Beaver (*Castor canadensis*). Ecology 67:1254–1269.

Ordeñana, M.A., D.H. Van Vuren, and J.P. Draper. 2012. Habitat associations of California Ground Squirrel and Botta's Pocket Gophers on levees in California. Journal of Wildlife Management 76:1712–1717.

Paine R.T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91–93.

Rutherford, W.H. 1955. Wildlife and environmental relationships of Beavers in Colorado forests. Journal of Forestry 53:803–806.

Salmon, T.P., and R.E. Lickliter. 1984. Wildlife Pest control around gardens and homes. Division of Agriculture and Natural Resources, Oakland, California, USA. 90 p.

Sharps, J.C., and D.W. Uresk. 1990. Ecological review of Black-tailed Prairie Dogs and associated species in western South Dakota. Great Basin Naturalist 50:339–345.

Shuford, W.D., and T. Gardali (Eds.). 2008. California bird species of special concern: a ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. Studies of Western Birds No. 1, Western Field Ornithologists, Camarillo, California, and California Department of Fish and Wildlife, Sacramento, California, USA.

Storer, T.I. 1938. Control of injurious rodents in California. Circular 79, California Agricultural Extension Service, Berkeley, California. 62 p.

Storer, T.I. 1958. Controlling field rodents in California. Division of Agriculture Sciences, University of California, Davis, California. 50 p.

Thomson, R.C., A.N. Wright, and H.B. Shaffer. 2016. California amphibian and reptile species of special concern. University of California Press, Berkeley, California, USA. 390 p.

van Hattem, M.G. 2004. Underground ecology and natural history of the California Tiger Salamander. M.S. Thesis, San Jose State University, Santa Clara, California, USA. 65 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.

Van Vuren, D.H., M.A. Ordeñana, and M.C. McGrann. 2014. Managing California Ground Squirrels on levees using habitat modification. Pp. 180–183 *in* Proceedings of the 26th Vertebrate Pest Conference. Timm, R.M., and J.M. O'Brian (Eds.). Davis, California.

VerCauteren, K., M.J. Pipas, and J. Bourassa. 2002. A camera and hook system for viewing and retrieving rodent carcasses from burrows. Wildlife Society Bulletin 30:1057–1061.

U.S. Fish and Wildlife Service (USFWS). 1998. Recovery plan for upland species of the San Joaquin Valley. USFWS, Portland, Oregon, USA. 319 p.

Zhao-hua, L., M. Ling, and G. Qing-xi. 2001. Concepts of keystone species and species importance in ecology. Journal of Forestry Research 12:250–252.

Jeff A. Alvarez is a Herpetologist who has specialized in California reptiles and amphibians for more than 30 y. He has worked with California Red-legged Frogs (*Rana draytonii*), California Tiger Salamanders (*Ambystoma californiense*), Northwestern Pond Turtles (*Actinemys marmorata*), Southwestern Pond Turtles (*A. pallida*), and Alameda Whipsnakes (*Masticophis lateralis euryxanthus*) for much of his career. His focus is on the conservation and natural history of herpetofauna, survey techniques development, and conducting peer-level special-status species workshops. (Photographed by Kelly Davidson).

APPENDICES

APPENDIX TABLE 1. Species and subspecies reported or observed to use the internal (i.e., below ground level) structure of *O. beecheyi* burrow systems for some part of their natural history. Letters are D = denning; EL = egg laying; F = foraging; N = nesting; R = refugia; and U = Unknown use. Original source reflects first published or reported occurrences. Species in **boldface** are special status.

Species	Presumed Use	Original Source
INVERTEBRATES		
Earthworm (Order: Megadrilacea)	F, R	Jeffery Wilcox, pers comm.
Isopoda (Order: Isopoda)	F, R	pers. obs.
Centipede (Order: Scolopendromorpha)	F, R	Sarah Foster, pers. comm.
Louse (*Neohaematopinus laeviusculs*)	F	Linsdale 1946
Louse (*Enderleinellus suturalis*)	F	Linsdale 1946
Rodent Flea (*Holopsyllus anomalus*)	F, R	Longanecker and Burroughs 1952
Rock Squirrel Flea (*Diamanus montanus*)	F, R	Longanecker and Burroughs 1952
Pacific Coast Tick (*Dermacentor occidentalis*)	F	Linsdale 1946
Deer Tick *(Ixodes* sp.)	F	Linsdale 1946
Pseudoscorpion (*Hesperochernes* sp.)	R	Linsdale 1946
Field Cricket (subfamily: Gyllinae)	F, R	pers. obs.
Jerusalem Cricket *(Stenopelmatus* sp.)	F, R	pers. obs.
Camel Cricket *(Ceuthophilus* sp.)	F, R	Jeffery Wilcox, pers comm.
Snake Millipede (*Paeromopus angusticeps*)	F, R	van Hattem 2004
Staphylinid Beetles (*Quedius explanatus*)	U	Linsdale 1946
California Broad-necked Darkling Beetle (*Coelocnemis californica*)	F, R	pers. obs.
Ground Beetles (Family: Carabidea)	F, R	pers. obs.
Tick Wasp [*Ixodiphagus hookeri* (= *Hunterellus hookeri*)]	F	Linsdale 1946
Moth (Order: Lepidoptera)	U	van Hattem 2004
Tarantula *(Aphonopelma* sp.)	F, R	Fitch 1948
Western Black Widow (*Latrodectus hesperus)*	F, R	pers. obs.
Spiders (Order: Araneae)	F, R	pers. obs.
AMPHIBIANS		
California Tiger Salamander (*Ambystoma californiense*)	R	Storer 1925, Fitch 1948
California Slender Salamander (*Batrachoseps attenuatus*)	R	Sarah Foster, pers. comm.
Arboreal Salamander (*Aneides lugubris*)	R	Sarah Foster, pers. comm.
California Red-legged Frog (*Rana draytonii*)	R	pers. obs.
Western Toad (*Anaxyrus boreas*)	R	Grinnell & Dixon 1918, Grinnell & Storer 1924
American Bullfrog (*Lithobates catesbieanus*)	R	pers. obs.
Pacific Chorus Frog (*Pseudacris regilla*)	R	pers. obs.
Western Spadefoot (*Spea hammondii*)	R	Fitch 1948
REPTILES		
Cope's Leopard Lizard (*Gambelia copeii*)	R	pers. obs.
Blunt-nosed Leopard lizard (*G. sila*)	R	Montanucci 1965
Western Side-blotched Lizard (*Uta stansburiana*)	R	Fitch 1948
Western Fence Lizard (*Sceloporus occidentalis*)	R	pers. obs.
Sagebrush Lizard (*S. graciosus*)	R	pers. obs.
Western Whiptail (*Aspidocelus tigris*)	R	Linsdale 1946, Fitch 1948
Western Skink (*Plestiodon skiltonianus*)	R	pers. obs.
Gilbert's Skink (*P. gilberti*)	EL	Brian Mori, pers. comm.
Alligator Lizard (*Elgaria* sp.)	R	Brian Mori, pers. comm.

Appendix Table 1 (continued). Species and subspecies reported or observed to use the internal (i.e., below ground level) structure of *O. beecheyi* burrow systems for some part of their natural history. Letters are D = denning; EL = egg laying; F = foraging; N = nesting; R = refugia; and U = Unknown use. Original source reflects first published or reported occurrences. Species in **boldface** are special status.

Species	Presumed Use	Original Source
Lizard eggs (Suborder: Sauria)	EL	Sarah Foster, pers. comm.
Common Sharp-tailed Snake (*Contia tenius*)	R	pers. obs.
Gopher Snake (*Pituophis catenifer*)	R	Grinnell & Dixon 1918, Grinnell & Storer 1924
Alameda Whipsnake (*Masticophis lateralis euryxanthus*)	R	pers. obs.
Chaparral Whipsnake (*M. lateralis lateralis*)	R	Fitch 1948
California Kingsnake (*Lampropeltus getulus*)	R	pers. obs.
Red-sided Garter Snake (*Thamnophis sirtalis infernalis*)	R	Brian Mori, pers. comm.
Giant Garter Snake (*T. giga*)	R	Eric Hansen, pers comm.
Western Rattlesnake (*Crotalus oreganus*)	R	Grinnell and Storer 1924, Linsdale 1946,
Western Diamond-backed Rattlesnake (*C. atrox*)	R	VerCauteren et al. 2002
Snake eggs (Suborder: Serpentes)	EL	Sarah Foster, pers. comm.
BIRDS		
Burrowing Owl (*Athene cunicularia*)	N, R	Grinnell & Dixon 1918, Grinnell & Storer 1924
MAMMALS		
California Ground Squirrel (*Otospermophilus beecheyi*)	N, R	putative
San Joaquin Antelope Squirrel (*Ammospermophilus nelsoni*)	R	USFWS 1998
San Joaquin Pocket Mouse (*Perognathus inornatus*)	R	Fitch 1948
California Pocket Mouse (*Chaetodipus californicus*)	R	Fitch 1948
California Kangaroo Rat (*Dipodomys californicus*)	R	Grinnell et al. 1930
Heerman's Kangaroo Rat (*D. heermani*)	R	Fitch 1948
Short-nosed Kangaroo Rat (*D. nitratoides brevinasus*)	R	pers. obs.
Tipton Kangaroo Rat (*D. nitratoides mitatoides*)	R	USFWS 1998
Giant Kangaroo Rat (*D. ingens*)	R	Oliver Miano, pers comm.
Deer Mouse (*Peromyscus maniculatus*)	R	Fitch 1948
Pinyon Mouse (*P. truei*)	R	Fitch 1948
Brush Mouse (*P. boylii)*	R	Fitch 1948
Dusky-footed Woodrat (*Neotoma fuscipes*)	R	Fitch 1948
Tulare Grasshopper Mouse (*Onychomys torridus tularensis*)	R	USFWS 1998
Western Harvest Mouse (*Reithrodontomys megalotis*)	R	VerCauteren et al. 2002
California Meadow Mouse (*Microtus californicus*)	R	Fitch 1948
House Mouse (*Mus musculus*)	R	Lenihan 2007
Botta's Pocket Gopher (*Thomomys bottae*)	F	Fitch 1948
Desert Cottontail (*Sylvilagus audubonii*)	R	Linsdale 1946
Black-tailed Hare (*Lepus californicus*)	R	pers. obs.
San Joaquin Kit Fox (*Vulpes macrotis mutica*)	F, R	Morrell 1972
Red Fox (*V. vulpes*)	D, F	pers. obs.
Coyote (*Canis latrans*)	D, F	pers. obs.
American Badger (*Taxadea taxus*)	D, F	Linsdale 1946, Fitch 1948
Striped Skunk (*Mephitis mephitis*)	D, F	Linsdale 1946, Fitch 1948
Long-tailed Weasel (*Mustela frenata*)	F	pers. obs.

Appendix Table 2. Species and subspecies directly observed to use the external (i.e., above ground level) structure of *O. beecheyi* burrow systems (i.e., soil deposition pile or surrounding groomed vegetation, or associated with scat, remains, etc.) for some part of their natural history. Usage includes foraging on, calling from, or taking refuge within soil deposition piles. Species in **boldface** are special status. Source is direct observation or visual confirmation by the author, unless otherwise noted. Letters B = basking; C = calling of vocalizing; D = denning; F = foraging; N = nesting; and R = refugia. Superscript 1 is a species also reported by Lenihan (2007), and superscript 2 indicates special-status species.

Species	Presumed or Observed Use
INVERTEBRATES	
Silverfish (Family: Lepismatidae)	F, R
Isopoda (Order: Isopoda)	F, R
Centipede (Order: Scolopendromorpha)	F, R
Snake Millipede (*Paeromopus angusticeps*)	F, R
Short-horned Grasshoppers (Family: Acrididae)	R
Camel Crickets (Family: Gryllacrididae)	R
Field crickets (Family: Gryllidae)	F, R
Cockroaches (Family: Blattidae)	F, R
Earwigs (Family: Forficulidae)	R
Stinkbugs (Family: Pentatomidae)	F, R
Tiger Beetles (Family: Cicindelidae)	F
Carrion Beetles (Family: Silphidae)	F, R
Rove Beetles (Family: Staphylinidae)	F, R
Dermestid Beetles (Family: Dermestidae)	F, R
Ladybird Beetles (Family Coccinellidae)	R, F
Blister Beetles (Family Meloidae)	F, R
Darkling Beetles (Tenebrionidae)	F, R
Scarab Beetles (Scarabaeidae)	F, R
Ground Beetles (Family: Carabidea)	F, R
Hover Flies (Family: Syrphidae)	B, F, R
Horse Flies (Family: Tabanidae)	B, F, R
Soldier Flies (Family: Stratiomyidae)	F, R
Spider Wasps (Family: Pompilidea)	F, R
Velvet Ants (Family: Mutillidae)	F, R
Ants (Family: Formicidae)	F, R
Bees (Family: Apoidae)	F, R
Moths (Order: Lepidoptera)	F, R
Tarantula *(Aphonopelma* sp.)	F, R
Wolf spiders (Family: Lycosidae)	F, R
Spiders (Order: Araneae)	F, R
AMPHIBIANS	
Western Toad (*Anaxyrus boreas*)	F, R
Western Spadefoot (*Spea hammondii*)	F, R
REPTILES	
Coast Horned Lizard (*Phrynosoma blainvillii*)	B, F, R
Cope's Leopard Lizard (*Gambelia copeii*)	B, F, R
Blunt-nosed Leopard Lizard (*G. sila*)	B, F, R
Western Side-blotched Lizard (*Uta stansburiana*)	B, F, R
Western Fence Lizard (*Sceloporus occidentalis*)	B, F, R
Sagebrush Lizard (*S. graciosus*)	B, F, R
Western Whiptail (*Cnemidophorus tigris*)	B, F, R

Appendix Table 2 (continued). Species and subspecies directly observed to use the external (i.e., above ground level) structure of *O. beecheyi* burrow systems (i.e., soil deposition pile or surrounding groomed vegetation, or associated with scat, remains, etc.) for some part of their natural history. Usage includes foraging on, calling from, or taking refuge within soil deposition piles. Species in **boldface** are special status. Source is direct observation or visual confirmation by the author, unless otherwise noted. Letters B = basking; C = calling of vocalizing; D = denning; F = foraging; N = nesting; and R = refugia. Superscript 1 is a species also reported by Lenihan (2007), and superscript 2 indicates special-status species.

Species	Presumed or Observed Use
Western Skink (*Plestiodon skiltonianus*)	B, F, R
Alligator Lizard (*Elgaria* sp.)	B, F, R
Gopher Snake (*Pituophis catenifer*)	B, F, R
California Kingsnake (*Lampropeltus getulus*)	B, F, R
Western Rattlesnake (*Crotalus oreganus*)	B, F, R
Western Diamond-back Rattlesnake (*C. atrox*)	B, F, R
Speckled Rattlesnake (*C. mitchellii*)	B, F, R
Red Diamond Rattlesnake (*C. ruber*)	**B, F, R**
BIRDS	
Killdeer (*Charadrius vociferus*)	C, F
Great Blue Heron (*Ardea herodias*)	F
[1]**Burrowing Owl (*Athene cunicularia*)**	F, B
[1]American Kestrel (*Falco sparverius*)	F
Mourning Dove (*Zenaida macroura*)	F
Loggerhead Shrike (*Lanius ludovicianus*)	F
Rock Wren (*Salpinctes obsoletus*)	C, F
Say's Phoebe (*Sayornis saya*)	C, F
[1]Western Kingbird (*Tyrannus verticalis*)	C, F
[1]Horned Lark (*Eremophila alpestris*)	C, F
[1]American Pipet (*Anthus rubescens*)	C, F
[1]Savannah Sparrow (*Passerculus sandwichensis*)	C, F
[1]**Grasshopper Sparrow (*Ammodramus savannarum*)**	C, F
Lark Sparrow (*Chondestes grammacus*)	C, F
Western Meadowlark (*Sturnella neglecta*)	C, F
[1]Brewer's Blackbird (*Euphagus cyanocephalus*)	C, F
MAMMALS	
California Ground Squirrel (*Otospermophilus beecheyi*)	B, C, D, F, N, R
[2]**Heerman's Kangaroo Rat (*Dipodomys heermani*)**	D, F, N, R
Deer Mouse (*Peromyscus maniculatus*)	D, F, N, R
Black-tailed Hare (*Lepus californicus*)	F, R
San Joaquin Kit Fox (*Vulpes macrotis mutica*)	F
Red Fox (*Vulpes vulpes*)	F
Gray Fox (*Urocyon cinereoargenteus*)	F
Coyote (*Canis latrans*)	F
Pallid Bat (*Antrozous pallidus*)	F
Cattle (*Bos taurus*)	F
Black-tailed Deer (*Odocoileus hemionus*)	F
Tule Elk (*Cervus canadensis nannodes*)	F
Wild Pig (*Sus scrofa*)	F

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MANAGEMENT CONSIDERATIONS RELATED TO THE OVIPOSITING PHENOLOGY OF THE CALIFORNIA RED-LEGGED FROGS (*RANA DRAYTONII*) IN THE SIERRA NEVADA OF CALIFORNIA

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***Abstract*.—Timing of ovipositing is typically a function of environmental conditions for amphibians. The timing of this natural history function is often predictable, particularly for bi-phasic species that occur in temperate environments. For declining species, aspects of the reproductive natural history are used to facilitate detection of occupied habitats. Using regular winter and spring breeding egg mass counts, we found that the California Red-legged Frog (*Rana draytonii*) breeding season is consistent between two disparate populations: coastal sites and sites in the Sierra Nevada. In the Sierra Nevada, frogs breed through the winter and early spring months with an average peak in the number of egg mass observations occurring in mid-March, which is approximately one month prior to the onset of egg mass surveys recommended by regulatory agency survey guidelines. We recommend conducting egg mass surveys in the Sierra Nevada from mid-February to mid-April to accurately detect breeding for this species.**

Key Words.—coastal; egg mass surveys; inter-annual variability; phenology; populations; opportunistic; ovipositing

Amphibian reproductive events are typically timed with climatic conditions associated with the habitats in which they are live (Duellman and Trueb1994; Stebbins and Cohen 1995; Saenz et al. 2006). Many species are capable of breeding over long periods, while others breed only during seasonal rain events (Bragg 1965; Rastogi 1980; Jørgensen 1988; Stebbins and Cohen 1995; Stebbins and McGinnis 2012). Breeding timing is associated with optimal environmental conditions that can support successful reproduction (Duellman and Trueb1994; Stebbins and Cohen 1995). The environmental conditions that amphibians experience may change throughout the range of a species, within different habitat types, or due to anthropogenic activities, particularly for those wide-ranging species that may occur in various types of habitats (Schoenherr 2007; Wheeler et al. 2015, 2018).

In California, many anuran species have a very wide geographical range, can use a wide range of habitats, and may occur over a varied elevational gradient (e.g., Western Toad, *Anaxyrus boreas*, American Bullfrog, *Lithobates catesbaeinus*, and California Red-legged Frog, *Rana draytonii*). In northern and southern California, bi-phasic amphibians (having both an aquatic larval and a terrestrial adult life stage) occur within a wide variety of habitats, including grasslands, woodlands, and riparian and chaparral habitats; and can range from sea level to > 2,000 m elevation (Stebbins and McGinnis 2012; Flaxington 2021). The resulting variation in environmental conditions may alter various aspects of the breeding phenology of a species within their ranges.

The California Red-legged Frog, which occurs from Mendocino County south to the Santo Domingo watershed in Baja California, Mexico (Shaffer et al. 2004; Peralta-Garcia 2016), experiences significant variation in the available conditions under which it may occur (Schoenherr 2007). This species breeds in the winter and spring throughout its range (Storer 1925; Stebbins 1951; Alvarez et al. 2013; Wilcox et al. 2017; North et al. 2022). Additionally, there appears to be a high level of interannual variability in the period when egg masses are observed, with coastal populations appearing to breed earlier in the year (December/January) than inland populations (February/March; Alvarez et al. 2013). Moreover, the latest calendar date when an egg mass was observed was at an inland population (eastern Contra Costa County, California) on 17 April 2012 (Alvarez et al. 2013). To date, oviposition phenology has not been considered for populations in the Sierra Nevada. Herein we examine the time period when California Red-legged Frog egg masses have been observed among surveyed populations in the Sierra Nevada and consider the management implications associated with species surveys and detecting reproduction.

MATERIALS AND METHODS

We examined data from three sites in two counties (Placer and El Dorado) in the central Sierra Nevada of California. The sites are California Red-legged Frog localities with historical records (Barry and Fellers 2013) that are monitored regularly (4–12 times annually). We sought but were not able to examine data for an extant population of California Red-legged Frogs translocated to Yosemite National Park, Mariposa County; therefore, that population was not included in our analysis. We used multi-observer data from annual surveys at three sites. Surveys were not systematic or consistent across sites or years and are therefore the data are characterized as opportunistic observations. Because these egg mass surveys were documented for disparate reasons and without coordination among the authors, these observations consisted of egg mass observation date, with little to no attempt to determine the date at which the egg mass was laid, or the developmental stage of the egg mass.

The Placer County site (Big Gun Mitigation) is owned and operated by Westervelt Ecological Services and was managed as California Red-legged Frog habitat. The site is in the town of Michigan Bluff, California, at 930 m elevation. Most of the site was covered by a mixed density Ponderosa Pine (*Pinus ponderosa*) forest, with patches of manzanita (*Manzanita* spp.) with rural residential development nearby. Six ponds on the site ranged from 1–2 m deep, three of which have had annually reproducing populations of California Red-legged Frog. One El Dorado County site (Spivey Pond) was an Area of Critical Environmental Concern site designated and managed by the U.S. Bureau of Land Management specifically as, but not exclusively, California Red-legged Frog habitat. The site was located south of the town of Sly Park, at an elevation of 980 m. The majority of the site was mixed coniferous forest and White Alder (*Alnus rhombifolia*), with rural residential development in the vicinity. Two ponds occurred on this site and range from 2–3 m deep, with one pond consistently supporting California Red-legged Frog reproduction. The third site, in El Dorado County (Bear Creek drainage), was owned and managed by the U.S. Forest Service. The site is located near the Lake of the Cross (Georgetown, California) at 710 m elevation. Most of the site was covered by a mixed density Ponderosa Pine Forest, with rural residential development in the vicinity. Four ponds occurred on the site that range from 0.3–1 m deep, one of which had a reproducing population of California Red-legged Frog on a consistent basis. Snow fell on all three sites each year, but typically occurred fewer than 5 d/y.

We collected a variety of physical data from each site, which included one or more of the following: (1) presence of California Red-legged Frogs; (2) surface water temperature adjacent to each the egg mass; (3) air temperature; (4) snow presence; (5) substrate attachment; and (6) presence of potential predators. We did not consistently collect physical data, however, across sites or visits, and we only collected surface water temperature and presence of snow regularly. Data used for our analysis were opportunistic and not always precise (Table 1). Therefore, we assigned a calendar week to the egg mass observation date to represent the

Table 1. Date of observations of egg masses of California Red-legged Frog (*Rana draytonii*) in the central Sierra Nevada of California.

Location name	Date Observed	Numerical Week	Source
Spivey	29 April 1998	17	Kathleen Freel (Berry and Fellers 2013)
Spivey	29 April 1998	17	Kathleen Freel (Berry and Fellers 2013)
Spivey	29 April 1998	17	Kathleen Freel (Berry and Fellers 2013)
Bear Creek	24 February 2016	8	Maura Santora
Bear Creek	24 February 2016	8	Maura Santora
Bear Creek	10 March 2016	10	Maura Santora
Spivey	late-April	17	Peggy Cranston - U.S. Bureau of Land Management
Spivey	late-April	17	Peggy Cranston - U.S. Bureau of Land Management
Bear Creek	24 February 2017	8	Maura Santora
Bear Creek	15 February 2018	7	Maura Santora
Bear Creek	03 March 2019	10	Maura Santora
Big Gun	22 March 2019	12	Matt Coyle
Bear Creek	18 April 2019	15	Maura Santora
Bear Creek	18 April 2019	15	Maura Santora
Spivey	30 March 2020	13	Jeff Alvarez
Big Gun	22 March 2020	11	Matt Coyle
Bear Creek	20 February 2020	7	Maura Santora
Bear Creek	27 February 2020	8	Maura Santora
Bear Creek	27 February 2020	8	Maura Santora
Spivey	03 April 2021	13	Jeffrey Jones
Spivey	03 April 2021	13	Jeffrey Jones
Spivey	08 April 2021	14	Jeffrey Jones
Spivey	08 April 2021	14	Jeffrey Jones
Bear Creek	21 February 2021	8	Maura Santora
Bear Creek	21 February 2021	8	Maura Santora
Bear Creek	29 March 2021	13	Maura Santora

period of egg mass presence (hereafter: observed week). For example, we assigned egg masses reported as the third week of March or 17 March to the same time period (i.e., calendar week 11).

RESULTS

We examined 26 reported observations of egg masses from three counties in the central Sierra Nevada over a 25-y period. Twenty-four observations included specific egg mass observation dates, whereas two were reported as a portion of a month (i.e., mid-April; Table 1). We found that California Red-legged Frog egg masses were observed in the central Sierra from 15 February (7th calendar week) to 29 April (17th calendar week), an ovipositing season occurring over approximately 11 weeks. The average egg mass observation time across all sites was calendar week 11 (approximately 15 March). The observation mode was the 8th calendar week (21 February).

Lower elevations appeared to have an earlier average observed week for egg masses. For Bear Creek, the lowest elevation site, the average week egg masses were observed was week 9 (approximately the first week of March); Big Gun had an average observed week of 11 (approximately mid-March); and the highest elevation site, Spivey Pond, had the latest average observed week (approximately week 15; early April). Surface water temperatures collected from 21 egg masses at the time of first observation ranged from 3.9°–21.0° C (mean = 10.5° C). Air temperatures were not reported for most observations, and snow was reported on the ground at only two egg masses during their initial observation in March 2021. Although snow falls on each of the sites and remains on the ground for a short period (1 to 5 d), snow was reported on the ground at the time of egg mass presence only at the lowest elevation site; Big Creek drainage in El Dorado County.

DISCUSSION

Though the observations used in this study were the opportunistic, the data used to support our conclusion that California Red-legged Frog ovipositing season in the Sierra Nevada is similar to, but slightly later than, that found along the coast and inner coast ranges of California. Over 12 years, Alvarez et al. (2013) found egg masses at eight sites located throughout most of the California Red-legged Frog coastal range from 11 December through 17 April, an ovipositing season of 18 weeks. The average range among the eight sites, however, was 25 January through 12 March (a 6.5-week ovipositing season).

The approximate average time for all egg masses reported by Alvarez et al. (2013) was the first week of March. This is similar to but only a week earlier than found in this study for the Sierra Nevada (mid-March). Both studies show extensive inter-annual variability and inter-site variability. This is likely due to local climatic conditions, including water levels in the aquatic breeding habitat. Because sites in this study were in adjacent counties, we did not expect to see any difference in timing of egg mass deposition.

Elevation may have an effect on ovipositing timing in the Sierra Nevada; however, we did not examine this statistically due to a small sample size. We note that higher elevations had slightly later average observed dates for ovipositing, but our data are only indicating that egg masses were observed on a certain date, not the actual oviposition date. Further examination of the effects of elevation or other site-level variables on oviposition phenology would require more precise data at these and additional sites in the Sierra Nevada. We speculate that the effect of elevation is more closely related to microclimate conditions than to elevation itself.

The U.S. Fish and Wildlife Service (USFWS) provides California Red-legged Frog survey guidelines for the breeding and non-breeding period (https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=83914&inline. [Accessed 20 July 2023]). In the section identified as Survey Periods, section IV.B., the guidelines suggest that egg mass surveys be conducted under the best survey period, which, for the California Red-legged Frog Sierra Nevada population, should not begin before April 15. If this starting time were adhered to, only 25% of the observed egg masses in our study would have been identified, and no egg masses would have been identified at the Big Gun site. With 75% of the egg masses observed between mid-February and mid-April in the Sierra Nevada, it appears that the survey guidelines should be shifted to include a broader time frame that would include the months of February, March, and April.

For comparison, over a 3-y period, egg masses oviposited at El Potrero, Santo Domingo Watershed, Baja California, Mexico, at a similar elevation (900 m) to the sites we examined, were oviposited from early March to mid-April. This suggests that despite, the location of the El Potrero site at the southernmost extent of the range of California Red-legged Frogs, the timing of ovipositing appears similar to that for the Sierra Nevada populations. It also suggests an absence of a latitudinal effect of ovipositing because the Baja population is approximately 1,000 km south of the Sierra Nevada populations, yet the approximate timing of reproduction is nearly the same.

There appears to be significant inter-annual variability in the phenology of ovipositing in the California Red-legged Frog (Alvarez et al. 2013; this study). Others studying the closely related Foothill Yellow-legged Frog (*R. boylii*) found a similar pattern that included inter-annual variability and an extended breeding season, which varied based on location, water temperature, flows, and other factors (Storer 1925, Wheeler et al. 2003, 2015, 2018, Rose et al. 2023). In the context of an extended breeding season, we observed only minor ovispositing timing differences between the populations of California Red-legged Frogs that occur on the coast and those that occurred in the Sierra Nevada. Further, although there appears to be a minor elevational effect, it is likely that local conditions related to temperature preferences may be affecting timing of ovipositing, which appears similar to Foothill Yellow-legged Frogs (Catenazzi and Kupferberg 2013; Wheeler et al. 2015, 2018; Rose et al. 2023). The California Red-legged Frog appears to remain a winter and spring breeder, with an oviposition phenology that typically ranges from mid-December (extreme coastal populations) to late-April (inland populations), irrespective of latitude.

Although an egg mass was observed at Point Reyes National Seashore in the first week of November (Patrick Kleeman, pers comm.), November breeding is likely uncommon to rare for California Red-legged Frogs. A larger, range-wide assessment, which includes earlier (November and December), and later (April and May) surveys is needed to better understand understudied and or underreported populations (i.e., Butte County, Baja California, and central coast populations) and potential extremes in oviposition timing for this species. For example, California Red-legged Frogs at La Grulla Meadow, Baja California, Mexico (1,850 m elevation), may oviposit later in the year due to persistent snow and cold weather, potentially limiting activity of frogs perhaps into late April or May. Populations in the northernmost extent of the range (i.e., Butte County) are understudied, and no reports exist for the timing of ovipositing or the presence of egg masses.

Surveys for California Red-legged Frogs, including USFWS-approved surveys, should consider the best available information about the breeding phenology of the species to detect egg masses in aquatic breeding habitat. This should include updating current survey guidelines for the species. Egg masses may not be easy to detect in some habitat types (Wilcox et al. 2017) but may also be missed if the timing of those surveys begins at the later stages of breeding activity, which the current (i.e., 2005) USFWS survey guidelines suggest. We recommend USFWS survey guidelines be updated to reflect the current understanding of the species reproductive natural history.

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LITERATURE CITED

Alvarez, J.A., D.G. Cook, J.L. Yee, M.G. Hattem, D.R. Fong, and R.N. Fisher. 2013. Comparative microhabitat characteristics at oviposition sites of the California Red-legged Frog (*Rana draytonii*). Herpetological Conservation and Biology 8:539−551.

Barry, S.J., and G.M. Fellers. 2013. History and status of the California Red-legged Frog (*Rana draytonii*) in the Sierra Nevada, California, USA. Herpetological Conservation and Biology 8:456–502.

Bragg, A.N. 1965. Gnomes of the Night: The Spadefoot Toads. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.

Catenazzi, A. and S.J. Kupferberg. 2013. The importance of thermal conditions to recruitment success in stream-breeding frog populations distributed across a productivity gradient. Biological Conservation 168:40–48.

Duellman, W.E., and L. Trueb. 1994. Biology of Amphibians. Johns Hopkins University Press, Baltimore, Maryland, USA.

Flaxington, W.C. 2021. Amphibians and Reptiles of California: Field Observations, Distribution, and Natural History. Fieldnotes Press, Anaheim, California, USA.

Jørgensen, C.B. 1988. The role of endogenous factors in seasonal maturation in temperate zone female toads, *Bufo bufo*. Journal of Herpetology 22:295–300.

North S., J.Q. Richmond, F.E. Santana, A. Peralta-García, E.A. Gallegos, A.R. Backlin, C.J. Hitchcock, B.D. Hollingsworth, J.H. Valdez-Villavicencio, Z. Principe, et al. 2022. Taking the leap: a binational translocation effort to close the 420-km gap in the Baja California lineage of the California Red-legged Frog (*Rana draytonii*). Frontiers in Conservation Science 3:908929. https://doi.org/10.3389/fcosc.2022.908929.

Rastogi, R.K. 1980. Seasonal cycle in anuran (Amphibia) testis: the endocrine and environmental controls. Bollettio di Zoologia 43:151–172.

Rose, J.P., S.J. Kupferberg, R.A. Peek, D. Ashton, J.B. Bettaso, S. Bobzien, R.M. Bourque, K.G.H. Breedveld, A. Catenazzi, J.E. Drennan, et al. 2023. Identifying drivers of population dynamics for a stream breeding amphibian using time series of egg mass counts. Ecosphere 14:e4645. https://doi.org/10.1002/ecs2.4645.

Peralta-Garcia, A., B.D. Hollingsworth, J.Q. Richmond, J.H. Valdez-Villavicencio, G. Ruiz-Campos, R.N. Fisher, P. Cruz-Hernandez, and P. Galina-Tessaro. 2016. Status of the California Red-legged Frog (*Rana draytonii*) in the state of Baja California, México. Herpetological Conservation and Biology 11:168–180.

Saenz, D., L.A. Fitzgerald, K.S. Baum, and R.N. Conner. 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. Herpetological Monographs 20:64–82.

Schoenherr, A.A. 2007. A Natural History of California. 2nd edition. University of California Press, Berkeley, California, USA.

Shaffer, H.B., G.M. Fellers, S.R. Voss, J.C. Oliver, and G.B. Pauly. 2004. Species boundaries, phylogeography and conservation genetics of the Red-legged Frog (*Rana aurora draytonii*) complex. Molecular Ecology 13:2667–2677.

Stebbins, R.C. 1951. Amphibians of Western North America. University of California Press, Berkeley, California, USA.

Stebbins, R.C., and N.W. Cohen. 1995. A Natural History of Amphibians. Princeton University Press, Princeton New Jersey, USA.

Stebbins, R.C., and S.M. McGinnis. 2012. Field Guide to Amphibians and Reptiles of California. University of California Press, Berkeley, California, USA.

Storer, T.I. 1925. A synopsis of the amphibia of California. University of California Publications in Zoology 27:1–342.

Wheeler, C.A., H.H. Welsh, Jr., and L.L. Heise. 2003. *Rana boylii* (Foothill Yellow-legged Frog). Oviposition behavior. Herpetological Review 34:234.

Wheeler, C.A., J.B. Bettaso, D.T. Ashton, and H.H. Welsh, Jr. 2015. Effects of water temperature on breeding phenology, growth, and metamorphosis of Foothill Yellow-legged Frogs (*Rana boylii*): a case study of the regulated mainstem and unregulated tributaries of California's Trinity River. River Research and Applications 31:1276–1286.

Wheeler, C.A., A.J. Lind, H.H. Welsh, Jr, and A.K. Cummings. 2018. Factors that influence the timing of calling and oviposition of a lotic frog in northwestern California. Journal of Herpetology 52:289–298.

Wilcox, J.T., M.L. Davies, K.D. Wellstone, and M.F. Keller. 2017. Traditional surveys may underestimate *Rana draytonii* egg-mass counts in perennial stock ponds. California Fish and Game 103:66–71.

Jeff A. Alvarez is a Herpetologist who has specialized in California reptiles and amphibians for more than 35 y. He has worked with California Red-legged Frogs, California Tiger Salamanders (*Ambystoma californiense*), Northwestern and Southwestern Pond Turtles (*Actinemys marmorata* and *A. pallida*), and Alameda Whipsnakes (*Masticophis lateralis euryxanthus*) for much of his career. His focus is on the conservation and natural history of herpetofauna, survey techniques development, and conducting peer-level special-status species workshops. (Photographer unknown).

Jeff Jones is a Wildlife Biologist working for the Motherlode office of the U.S. Bureau of Land Management (BLM) in El Dorado Hills, California. He chiefly works with Spotted Owls (*Strix occidentalis*), Great Gray Owls (*S. nebulosa*), California Red-legged Frogs, Foothill Yellow-legged Frogs (*R. boylii*), and Northwestern Pond Turtles (*Actinemys marmorata*), along with numerous cattle ranchers that lease BLM lands. (Photographed by Sophia Weinmann).

Maura Santora is an Aquatic Biologist with the Eldorado National Forest, Placerville, California, USA. She has a B.S. in Aquatic Biology from the University of California, Santa Barbara, California, and a M.S. in Fisheries Resources from the University of Idaho, Moscow, Idaho, USA. She has been investigating the movements of California Red-legged Frogs in the Georgetown Ranger District of the Eldorado National Forest in the Sierra Nevada, as it can inform forest management. (Photographed by Jessie Bushell).

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Matt Coyle is a Restoration Ecologist who has specialized in habitat restoration and endangered species conservation efforts for over 25 y. He has restored wetland habitats, conducted species monitoring and detection, and led land managed activities supporting listed large branchiopods, California Tiger Salamander (*Ambystoma californiense*), Giant Garter Snake (*Thamnophis gigas*), and Northwestern Pond Turtle (*Actinemys marmorata*) throughout California. (Photograph by Tara Collins).

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ACTIVITY PATTERNS OF THE ENDANGERED AMARGOSA VOLE (*MICROTUS CALIFORNICUS SCRIPENSIS*)

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***Abstract*.—Examining the activity patterns of wildlife is an important aspect of understanding the ecology of a species and may be especially important for species of conservation concern. We used remotely triggered cameras to describe the daily and seasonal activity patterns and examine ecological factors that influence the activity of the Amargosa Vole (*Microtus californicus scirpensis*), a California endemic listed federally and by the state as Endangered, and is a marsh habitat-specialist in the Mojave Desert. We found that vole activity was greatest during crepuscular periods, followed by nocturnal and diurnal periods. We saw strong seasonal effects, with the highest activity occurring in spring (March-May). Daily activity patterns varied at different times of the year, with lower activity during periods of seasonal temperature extremes. Daily high temperatures, however, were only weakly related to activity, and precipitation was not associated with changes in activity patterns. Of the factors we examined, marsh area was the most important factor in predicting vole activity, with larger marshes having higher vole activity than smaller marshes. Predation seemed to be strong driver of vole activity, with higher activity during periods of lower potential predation risk (crepuscular and new-moon periods), suggesting that voles may decrease their activity to avoid predators during periods when predators may more easily detect them (e.g., full moon). By highlighting factors that influence vole activity, we show the importance of understanding activity patterns relative to the ecology and conservation of this species.**

Key Words.—Camera trap; ecological interactions; Mojave Desert; seasonal

INTRODUCTION

The daily and seasonal activity patterns of a wildlife species reveal critical information about their ecology and behavior, with implications for their population dynamics (Sutherland and Singleton 2003), evolution (Kronfeld-Schor and Dayan 2008; Gerkema et al. 2013), energetics (Kenagy 1973; Tachinardi et al. 2017), and habitat use (Kenagy 1973; Brown et al. 1994). Activity patterns may also affect how a particular species interacts with other species, such as through competition and predation (O'Farrell 1974; Arias-Del Razo et al. 2011; Harrison 2019). Knowledge of activity patterns is particularly important to inform conservation actions for species at risk of decline or extinction without management intervention.

The Amargosa Vole (*Microtus californicus scirpensis*) is a federally and California state-listed Endangered rodent that is found within a small range of extremely isolated spring-fed marshes in the Mojave Desert (U.S. Fish and Wildlife Service [USFWS] 1997). The species is threatened by anthropogentic and climate change induced loss and degradation of habitat, alterations in hydrology, and the impacts from non-native species (USFWS 1997; Haswell et al. 2022). Studies on the ecology of the vole, including its distribution (Janet Foley et al., unpubl. report), demography and habitat use (Klinger et al. 2013; Klinger et al. 2015; Janet Foley et al., unpubl. report), predators (Roy et al. 2019), survival (Klinger et al. 2013), and general biology and behavior (Allan et al. 2018; Pesapane et al. 2018) have proven useful in understanding and managing this species. Understanding how activity of these voles varies seasonally and is affected by various factors will be important to their conservation. Moreover, previous studies of Amargosa Voles have relied upon live-trapping data (Klinger et al. 2013), which provides a snapshot of activity around set time intervals (e.g., day-time trapping vs night-time trapping), but is limited by both the timing of trap checks (every 6–8 h) and the need to avoid trapping during extreme temperature and weather events.

A better understanding of vole activity and behavior can aid in species management by targeting times of day or year to conduct surveys or limit disruptive human-use or the impacts of conservation activites on the species. Here we describe the activity patterns of Amargosa Voles using camera traps, which allow for continuous monitoring of animal activity. Our specific goals were to define the daily and seasonal activity patterns across the geographic range of the Amargosa Vole and to explore how ecological factors (time of day, temperature, precipitation, marsh location and size, and potential intra- and interspecific interactions) influence these patterns.

METHODS

***Study site*.**—We studied voles in marshes in the Mojave Desert near Tecopa, California (35.8481° -116.2267°; Fig. 1). The climate is characterized by wide daily and annual fluctuations in temperature, from a mean winter

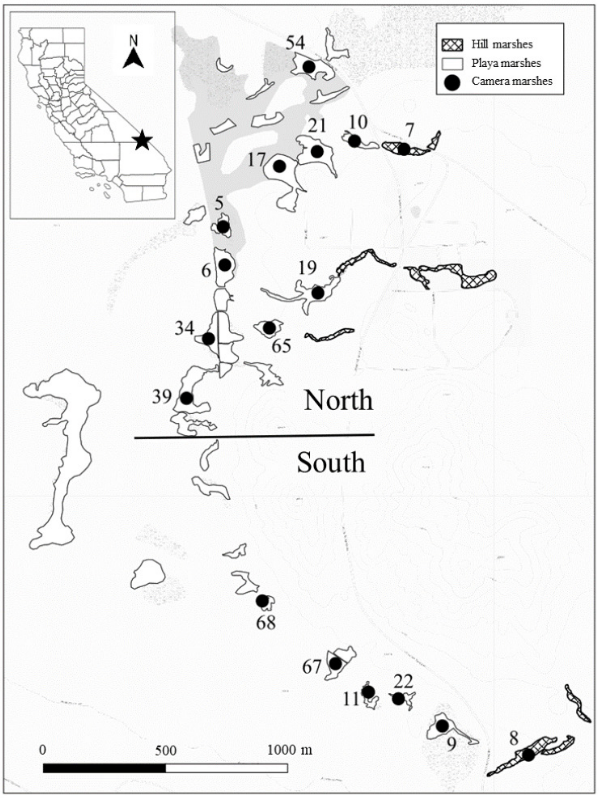

Figure 1. Locations of marshes near Tecopa, Inyo County, California (35.871°, -116.233°), where monthly camera trapping surveys of Amargosa Vole (*Microtus californicus scirpensis*) activity were conducted during 2015–2016. The black star represents the approximate location of the study area within California. Shaded areas in the base map represent ephemeral wetland habitats. Additional marshes are included in the map; however, only numbered marshes were included in this study.

Table 1. Sample marsh characteristics and total number of independent activity events of Amargosa Voles (*Microtus californicus scirpensis*) recorded by remote cameras in 17 marshes in Tecopa, Inyo County, California. Activity data were collected over approximately bi-monthly, five-day periods during 2015–2016. All marshes were located in Playa habitat except for marshes 7 and 8, which were located in Hill habitat (see Fig. 1).

Marsh ID #	Marsh size	Habitat	Marsh area (ha)	Activity events
North				
6	Large	Playa	1.20	17
17		Playa	2.21	161
19		Playa	1.44	163
21		Playa	1.61	181
39		Playa	1.75	132
54		Playa	1.28	145
5	Small	Playa	0.52	91
10		Playa	0.47	61
34		Playa	0.87	82
65		Playa	0.64	46
7		Hill	0.64	114
South				
9	Large	Playa	1.00	92
8		Hill	1.10	83
11	Small	Playa	0.32	5
22		Playa	0.25	22
67		Playa	0.66	98
68		Playa	0.24	1

low of 3.2° C to a mean summer high of 41.0° C, with a mean annual rainfall of 12.3 cm (www.ncdc.noaa.gov). Elevation of the marshes range from 290–420 m (Roy et al. 2019). Vole habitat is dominated by Olney's Bulrush (*Schoenoplectus americanus*), with additional common species including rushes (*Juncus* spp.), Common Reed (*Phragmites australis*), Southern Cattail (*Typha dominguensis*), Salt Grass (*Distichlis spicata*), Yerba Mansa (*Anemopsis californica*), Boraxweed (*Nitrophila occidentalis*), Slender Arrowgrass (*Triglochin concinna*), Alkali Sacaton (*Sporobolus airodes*), mesquite (*Prosopis* spp.), and other wetland and desert plants (Rado and Rowlands 1984).

Activity methods.—From December 2015 through November 2016, we placed cameras in 17 marshes (Fig. 1, Table 1) as part of Amargosa Vole range-wide surveys (Janet Foley et al., unpubl. report). Because the presence of voles is highly associated with Olney's Bulrush (Klinger et al. 2013), all marshes used in this study contained bulrush, except for Marsh 68, which was dominated by rushes. Eleven of the marshes studied were in the northern part of the range of the vole, which is considered to have more stable subpopulations (Castle et al. 2020a), and six marshes were in the southern portion of the range (Fig. 1, Table 1). Fifteen of the marshes were located along the Amargosa River floodplain (playa), and two were located above the floodplain (hills; Fig. 1, Table 1). We calculated the area of each marsh using Google Earth (earth.google.com/web), and we categorized marshes into large (≥ 1 ha) and small (< 1 ha) sizes (Table 1).

We deployed three NatureView CAMHD (Bushnell Overland Park, Kansas) or Reconyx PC900 (Holmen, Wisconsin) cameras at each marsh. We attached each camera using wire to a metal U-post (approximately 0.5 m above the ground surface), which we angled downward at approximately 45°. To minimize overexposure, we modified Bushnell cameras by placing black duct tape over half of the LED lights, and we attached a 600 mm lens for close-range photographs. We baited areas in front of cameras by distributing approximately 200 g of oats, peanut butter, alfalfa, and 4-way horse feed (oats, corn, barley, molasses) in a pile on the day we deployed each camera. To minimize false triggers, we trimmed vegetation within the field of view of each camera as needed. Vegetation trimming was minimal and only occurred in a small area (< 400 cm^2) to avoid substantially altering vole habitat use. We programmed cameras to take five photographs when triggered, with no delay between images. The cameras remained active for approximately six weeks, although at some sites, memory cards were filled with digital images sooner than six weeks. Due to limited numbers of cameras, we rotated cameras between half of the marshes every six weeks so that activity was recorded in marshes at least once per season (seasons defined below).

Experineced biologists reviewed images to identify small mammals to species. When voles were observed on an image, the date, time, and the number of voles in the image were recorded. We used Sanderson's AllPictures Method (Sanderson and Harris 2013) to calculate the number of activity events per hour. We considered images taken 15 min or more apart independent activity events (Rendall et al. 2014). At a few cameras, all bait was consumed within 5 d. Therefore, we analyzed only the first 5 d of camera images from each sampling period for all cameras.

We collected data on ecological variables such as time of sunrise and sunset, mean daily temperature, total precipitation, and moon phase (new moon and full moon) for the 5 d of data per sample period from National Oceanic and Atmospheric Administration (www.ncdc.noaa.gov) and Weather Underground (www.weatherunderground.com/history). For moon phase analysis, we only used nocturnal vole activity events that occurred during nocturnal periods within 3 d of the full moon or new moon periods. We assigned independent activity events to time of day categories based on sunrise and sunset times: crepuscular (one hour before and after both sunrise and sunset), diurnal (one hour after sunrise to one hour before sunset), and nocturnal (one hour after sunset to one hour before sunrise). We also assigned data to seasonal categories following Roy et al. (2019): (1) winter (December-February); (2) spring (March-May); (3) summer (June-August); and (4) fall (September-November). We also compiled vole demographic data from a range-wide study that occurred concurrently with this study (Janet Foley et al., unpubl. report), including monthly range-wide vole abundance. We assumed that vole population cycles were synchronous among marshes.

Statistical analyses.—We performed analyses with R (R v4.1.2, www.r-project.org) using an alpha of 0.05 for inferring statistical significance. We report all metrics as mean (± standard error). We used non-parametric tests whenever data could not be normalized using data transformations (e.g., log transformations for right-skewed data). We evaluated differences in the number of independent vole events among nightly and seasonal categories using a Two-way Analysis of Variance (ANOVA) followed by Tukey's Post-hoc Multiple Comparisons tests. We used Pearson's Product Moment Correlations to examine relationships between the number of monthly independent vole events and mean daily high and between daily low temperatures and mean precipitation during the first 5 d of each camera trapping period. Using a Wilcoxon Rank-sum Test, we compared the number of nocturnal independent vole events between full- and new-moon periods. Using a Pearson's Product Moment Correlation, we examined the correlation between vole activity (mean monthly independent activity events across all marshes) and monthly range-wide abundance estimates for the species. Finally, we compared the number of activity events between large and small marshes, between marsh regions (northern and southern), and between marsh locations (Playa and Hill) using Student's *t*-tests or Wilcoxon Rank-sum Tests. We then constructed Random Forest (RF) Models (Prasad et al. 2006) to determine which factors influenced the number of monthly independent vole events. Only predictor variables deemed significant in earlier tests were used in the model. We built RF models using bootstrapped subsamples of the original data and aggregated the results (Segal and Xiao 2011). The RF models were constructed in R using the randomForest package (Liaw and Wiener 2022), and variable importance was then estimated and plotted using the varImpPlot function.

RESULTS

Cameras were active for 815 camera days across all 17 marshes, resulting in 1,494 independent vole events (Table 1). Voles were detected in every month sampled (December 2015-November 2016) in 13 marshes (Marshes 5, 6, 7, 9, 10, 17, 19, 21, 22, 34, 39, 54, 67), but were only detected during spring and summer (i.e., not in fall or winter) in Marshes 8 and 11, and only during summer in Marshes 65 and 68. Mean hourly activity (number of of independent events/h) was highest in the spring (2.17 ± 0.34 independent events/h, n = 835), followed by summer (1.02 ± 0.17 independent events/h, n = 416), winter (0.90 ± 0.33 independent events/h, n = 194), and fall (0.68 ± 0.66 independent events/h, n = 49; Fig. 2). Furthermore, mean hourly activity was highest during crepuscular hours (1.95 ± 0.25 independent events/h, n = 343), followed by nocturnal hours (1.44 ± 0.24 independent events/h, n = 610) and diurnal hours (1.14 ± 0.18 independent events/h, n = 541; Fig. 2). Daily patterns of activity varied throughout the year with a significant Season and Time of Day interaction ($F_{6,1068}$ = 10.23, $P < 0.001$). Diurnal activity in summer was 4.5 times lower than both summer crepuscular and summer nocturnal activity (Tukey's HSD, $P < 0.001$), and in winter, crepuscular activity was 2.9 times higher than winter nocturnal activity (Tukey's HSD, $P = 0.011$;

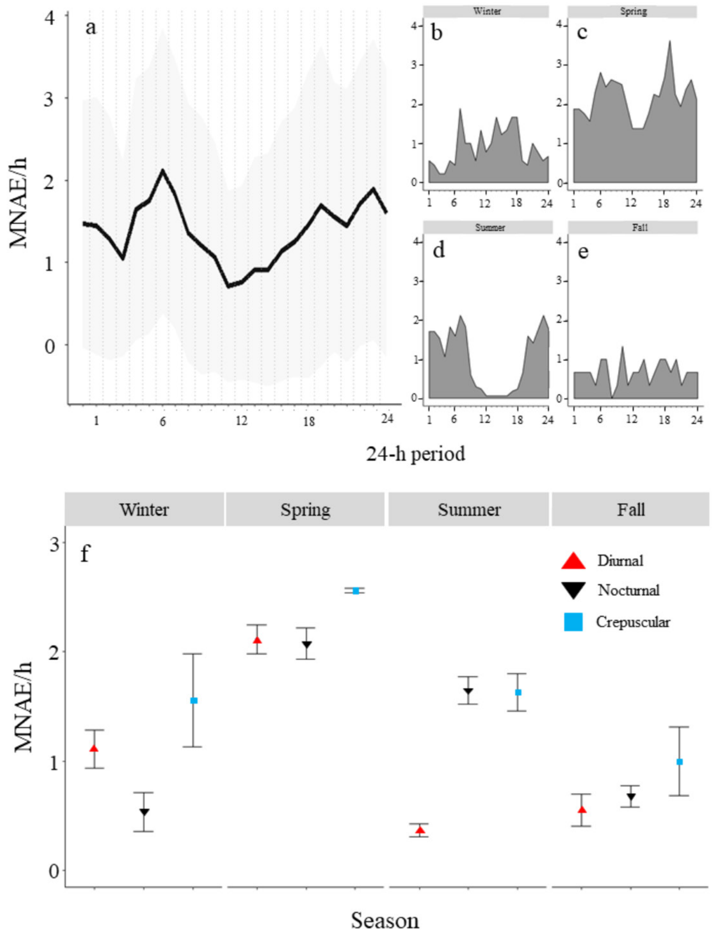

Figure 2. Daily activity patterns (mean number of activity events [MNAE]/h) of Amargosa Voles (*Microtus californicus scirpensis*) across the entire study period (a) and separately by season, during winter (b), spring (c), summer (d), fall (e), and (f) MNAE/h (± standard deviation) of Amargosa Voles during diurnal, nocturnal, and crepuscular periods for each season: winter (n = 194), spring (n = 835), summer (n = 416), and fall (n = 49). The shaded area of subgraph a represents the standard deviation around the mean. Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California, using remote camera traps.

Fig. 2). There was no significant difference in activity between winter diurnal periods and other winter periods (Tukey's HSD, $P > 0.050$) nor in daily activity patterns in the spring or fall seasons (Tukey's HSD, $P > 0.050$; Fig. 2).

Six marshes (21, 19, 17, 54, 39, 7) had high total activity over the course of the study (> 100 events per marsh; Fig. 1, Table 1). Activity was very low (< 50 independent events per marsh) at five marshes (68, 11, 6, 22, 65; Fig. 1, Table 1). On average, large marshes (> 1 ha) had 1.6 times more activity events than smaller marshes ($t = 6.989$, df = 1075.6, $P < 0.001$), and we observed a positive correlation between marsh area and the number of activity events within a marsh ($r = 0.33$, $t = 11.43$, df = 1,078, $P < 0.001$, Fig. 3). Northern marshes had significantly more vole activity (2.2 times) than southern marshes ($t = 10.06$, df = 919.6, $P < 0.001$; Fig. 3). There was no significant difference in mean vole activity between marshes in Playa habitat and marshes in Hill habitat ($W = 51674$, $P = 0.052$), but only two marshes were in Hill habitat and statistical power was low.

Lunar phase influenced vole activity, with 2.3 times more mean hourly events occurring during the new moon than the full moon ($W = 11425$, $P < 0.001$). We found a weak negative correlation between mean daily high temperatures and the number of activity events ($r = -0.09$, $t = -2.83$, df = 1,078, $P = 0.005$) but no significant correlation between vole activity and mean daily low temperature ($t = -0.13$, df = 1,078, $P = 0.898$) or mean precipitation ($t = -0.18$, df = 1,078, $P = 0.858$). Monthly vole activity was negatively correlated with range-wide vole abundance, but this relatioship was also weak ($r = -0.09$, $t = -2.89$, df = 1,078, $P = 0.004$; Fig. 4).

Due to statistically insignificant effects, we did not retain mean daily low temperature, mean precipitation, and habitat type in the RF model. The RF model ultimately included marsh area, marsh region (North, South), Season, Time of Day, Moon Phase, mean daily high temperature, and range-wide vole abundance. The RF model with these factors accounted for 60.7% of the variance in the number of monthly vole activity events, with marsh area being the most important predictor of vole activity (Fig. 5).

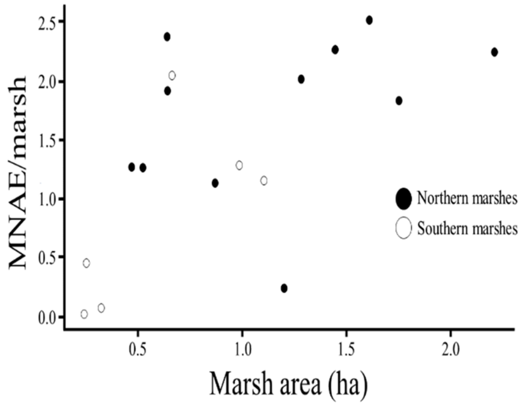

Figure 3. Correlation between the mean number of activity events (MNAE)/marsh of Amargosa Voles (*Microtus californicus scirpensis*) within each sampled marsh to the sample marsh area (ha) within northern marshes (closed circles) and southern marshes (open circles). Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California using remote camera traps.

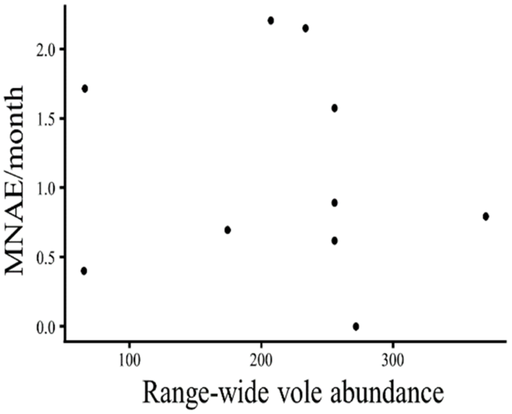

Figure 4. Correlation between the mean number of activity events (MNAE)/month of Amarogsa Voles (*Microtus californicus scirpensis*) to the range-wide abundance of voles during sampling periods. Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California, using remote camera traps.

Discussion

Our remote camera research fills previous data gaps and reveals new insights in the behavior and ecology of the Amargosa Vole by providing fine temporal-scale data that could not be inferred using other methods. We revealed differences in both daily and seasonal activity patterns of voles. Activity was highest during crepuscular periods and in the spring. We also found that activity changed seasonally, with higher diurnal vole activity than nocturnal activity in winter, and a reversed pattern in summer. Finally, we identified multiple factors that have important influences on Amargosa Vole activity.

Marsh area was identified as the most important factor in predicting vole activity. It is intuitive that in this system where larger marshes generally have higher abundances and densities of voles (Janet Foley et al., unpubl. report), there was also more vole activity. As such, the increased activity we observed in these marshes can likely be attributed to both higher vole numbers and more interactions between individual voles. These larger marshes generally have higher Olney's Bulrush cover and lower plant diversity compared to smaller marshes (Janet Foley et al., unpubl. report), and these differences in resources can also account for difference in activity (Abrams 1991; Fortier and Tamarin 1998; Blake and Loiselle 2018). The northern marshes are also mainly comprised of larger marshes, and any regional effects we observed are likely correlated with marsh area effects. That there was higher vole activity in the more demographically stable portion of the range of the vole highlights the importance of larger marshes in the biology of the species, metapopulation dynamics, and conservation (Foley and Foley 2016; Castle et al. 2020a). By conserving and managing for larger marshes, species managers can both maintain population dynamics and promote increased vole activity, which may provide beneficial intraspecific interactions (e.g., mating) and aid in recovering the species.

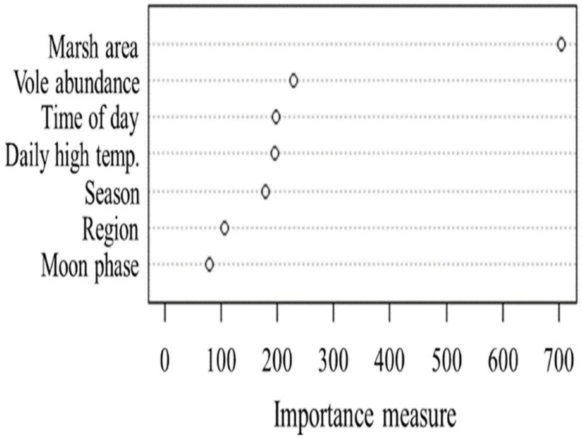

Figure 5. Variable importance plot depicting the importance measure (mean decrease in node impurity) of factors used in the Random Forest Model in predicting Amargosa Vole (*Microtus californicus scirpensis*) activity. Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California, using remote camera traps.

Several other factors also had important effects on vole activity and inform the biology of the species. Temperature factors have a strong role in shaping vole activity patterns as voles seem to avoid hot diurnal hours during the summer and cold nocturnal hours in winter, allowing them to optimize temperature and energy balance (Vieira et al. 2010; Tachinardi et al. 2017). This helps to explain how a wetland-dependent species can survive in extreme Mojave Desert envirornmental conditions (Körtner and Geiser. 2009). Predation risk also seems to have a strong influence on vole activity, with Amarogsa Voles being more active during periods of potentially lower predation risk (e.g., crepuscular periods, new moon nights; Daly et al. 1992). As the vole population is very small, fewer than 500 individuals on average (Janet Foley et al., unpubl. report), and predators have been identified as a key regulator of population abundance (Klinger et al. 2013), these predator avoidance strategies (Halle and Lehmann 1987; Halle 2000; Hoffmann et al. 2018; Monterroso et al. 2013) help to understand how the species can maintain viable population levels. Furthermore, in a system where marsh patches are relatively disconnected (Castle et al. 2020a), periods of heightened vole activity when predator pressure is low may allow for voles to safely disperse between marsh patches (Jacob and Brown 2000) and allow for the species to maintain metapopulation dynamics. Finally, our data suggest that vole activity seems to be influenced by population abundance. Although the inverse relationship between range-wide vole abundance and activity was weak, it may suggest that voles decrease their activity during periods of high density to avoid negative intraspecific interactions, such as aggression events between Amarogsa Voles during periods of high density (Pesapane et al. 2018). Intraspecific interactions may also explain some of the seasonal trends we observed, such as the the increase in activity in the spring potentially being related to mating or competition for resources. Increases in intraspecific interactions in summer may also explain why we observed voles in all marshes during periods of peak activity (summer) and not during periods of low activity (winter, fall). This suggests that animals are dispersing between habitat patches due to intraspecific competition in the larger marshes. The activity data collected here can aid to inform multiple aspects of vole biology and ecology.

For cryptic and rare species such as Amargosa Voles, remote camera studies such as ours complement traditional methods of studying occupancy, abundance, activity, and interactions between individuals but provide unique information that could not be collected otherwise. The vole activity data we have provided can be used to inform Amargosa Vole research and conservation. The data we provide can be used to make vole surveys more efficient by targeting research events to when voles are most active and therefore detectable, both seasonally and daily. Also, managers may use identified active periods to inform timing of management actions to maximize success (e.g., translocations) or reduce impacts to voles (e.g, habitat restoration activities). While predator management is not feasible in this system, by understanding that predator pressure impacts vole activity and potentially vole dispersal, managers can conduct conservation activities to limit predation pressure on the species (e.g., construct dispersal corridors between marshes, promote greater cover of Bulrush litter in marshes). Our survey occurred in bulrush-dominated habitats, but the data we provide can also be used to detect and monitor vole populations in other habitat types that may be used for foraging and dispersal (López-Pérez et al. 2019; Castle et al. 2020b). Finally, our results provide baseline ecological data for assessing the ecological interactions of Amargosa Voles, in support of the conservation needs of this species (USFWS 1997).

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LITERATURE CITED

Abrams, P.A. 1991. Life history and the relationship between food availability and foraging effort. Ecology 72:1242–1252.

Allan, N., R. Pesapane, J. Foley, and D. Clifford. 2018. Successful care and propagation of the endangered Amargosa Vole (*Microtus californicus scirpensis*) in captivity. Zoo Biology 37:59–63.

Arias-Del Razo, I., L. Hernández, J.W. Laundré, and O. Myers. 2011. Do predator and prey foraging activity patterns match? A study of coyotes (*Canis latrans*), and lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*). Journal of Arid Environments 75:112–118.

Blake, J.G., and B.A. Loiselle. 2018. Annual and spatial variation in composition and activity of terrestrial mammals on two replicate plots in lowland forest of eastern Ecuador. PeerJ 6:e4241. https://doi.org/10.7717/peerj.4241.

Brown, J.S., B.P. Kotler, and T.J. Valone. 1994. Foraging under predation - a comparison of energetic and predation costs in rodent communities of the Negev and Sonoran deserts. Austalian Journal of Zoology 42:435–448.

Castle, S.T., P. Foley, D.L. Clifford, and J. Foley. 2020a. A stochastic structured metapopulation model to assess recovery scenarios of patchily distributed endangered species: case study for a Mojave Desert rodent. PLoS ONE 14:e0237516. https://doi.org/10.1371/journal.pone.0237516.

Castle, S.T., N. Allan, D. Clifford, C.M. Aylward, J. Ramsey, A.J. Fascetti, R. Pesapane, A. Roy, M. Statham, B. Sacks, and J. Foley. 2020b. Diet composition analysis provides new management insights for a highly specialized endangered small mammal. PLoS ONE 15:e0240136. https://doi.org/10.1371/journal.pone.0240136.

Daly, M., P.R. Behrends, M.I. Wilson, and L.F. Jacobs. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. Animal Behaviour 44:1–9.

Foley, J., and P. Foley. 2016. Rapid assessment and stochastic modeling to avert extinction in the endangered Amargosa Vole. Wildlife Biology in Practice 12:369. https://doi.org/10.2461/wbp.2016.12.1.

Fortier, G.M., and R.H. Tamarin. 1998. Movement of meadow voles in response to food and density manipulations: A test of the Food-Defense and Pup-Defense hypotheses. Journal of Mammalogy 79:337–345.

Gerkema, M.P., W.I.L. Davies, R.G. Foster, M. Menaker, and R.A. Hut. 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. Proceedings of the Royal Society B: Biological Sciences 280:20130508. https://doi.org/10.1098/rspb.2013.0508.

Halle, S. 2000. Ecological relevance of daily activity patterns. Pp. 67–90 in Activity Patterns in Small Mammals: An Ecological Approach. Halle, S., nd N.C. Stenseth (Ed.). Springer, Heidelberg, Germany.

Halle, S., and U. Lehmann. 1987. Circadian activity patterns, photoperiodic responses and population cycles in voles. Oecologia 71:568–572.

Harrison, R.L. 2019. Temporal niche separation of Desert Cottontails (*Sylvilagus audobonii*) and Black-tailed Jackrabbits (*Lepus californicus*) in the Chihuahuan Desert. Southwestern Naturalist 63:153–160.

Haswell, P.M., A.M. López-Pérez, D.L. Clifford, and J.E. Foley. 2022. Recovering an endangered vole and its habitat may help control invasive house mice. Food Webs 34:e00267. https://doi.org/10.1016/j.fooweb.2022.e00267.

Hoffmann, J., R. Palme, and J.A. Eccard. 2018. Long-term dim light during nighttime changes activity patterns and space use in experimental small mammal populations. Environmental Pollution 238:844–851.

Jacob, J., and J.S. Brown. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in Common Voles. Oikos 91:131–138.

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

Klinger, R., M. Cleaver, S. Anderson, P. Maier, and J. Clark. 2015. Implications of scale-independent habitat specialization on persistence of a rare small mammal. Global Ecology and Conservation 3:100–114.

Klinger, R.C., M. Cleaver, S. Anderson, P. Maier, and J. Clark. 2013. Short-term population dynamics, demography, and habitat selection by the Amargosa Vole: USGS Final Report to the Bureau of Land Management. U.S. Geological Survey, Oakhurst, California. 72 p.

Körtner, G., and F. Geiser. 2009. The key to winter survival: daily torpor in a small arid-zone marsupial. Naturwissenschaften 96:525–530.

Kronfeld-Schor, N., and T. Dayan. 2008. Activity patterns of rodents: the physiological ecology of biological rhythms. Biological Rhythm Research 39:193–211.

Liaw, A., and M. Wiener. 2022. Package ‘randomForest’: Breiman and Cutler’s Random Forests for classification and regression. R news 2:18–22.

López-Pérez, A.M., J. Foley, A. Roy, R. Pesapane, S. Castle, A. Poulsen, and D.L. Clifford. 2019. Subpopulation augmentation among habitat patches as a tool to manage an endangered Mojave Desert wetlands-dependent rodent during anthropogenic restricted water climate regimes. PLoS ONE 14:e0224246. https://doi.org/10.1371/journal.pone.0224246.

Monterroso, P., P.C. Alves, and P. Ferreras. 2013. Catch me if you can: diel activity patterns of mammalian prey and predators. Ethology 119:1044–1056.

O’Farrell, M.J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809–823.

Pesapane, R., D.L. Clifford, J.C. Lam, N. Allan, A. Roy, N. Bellini, O. Rivett, and J. Foley. 2018. The biology and ecology of the Amargosa Vole (*Microtus californicus scirpensis*). Western Wildlife 5:43–52.

Prasad, A.M., L.R. Iverson, and A. Liaw. 2006. Newer classification and regression tree techniques: bagging and random forests for ecological prediction. Ecosystems 9:181–199.

Rado, T., and P. Rowlands. 1984. A small mammal survey and plant inventory of wetland habitats in Amargosa Canyon and Grimshaw Lake Areas of Critical Environmental Concern. U.S. Bureau of Land Management, Barstow Resource Area Office, Barstow, California. 27 p.

Rendall, A.R., D.R. Sutherland, R. Cooke, and J. White. 2014. Camera trapping: a contemporary approach to monitoring invasive rodents in high conservation priority ecosystems. PLoS ONE 9:e86592. https://doi.org/10.1371/journal.pone.0086592.

Roy, A.N., D.L. Clifford, A.D. Rivera Roy, R.C. Klinger, G.M. Wengert, A.M. Poulsen, and J. Foley. 2019. Survey of potential predators of the endangered Amargosa Vole (*Microtus californicus scirpensis*). Western Wildlife 6:5–13.

Sanderson, J., and G. Harris. 2013. Automatic data organization, storage, and analysis of camera trap pictures. Journal of Indonesian Natural History 1:11–19.

Segal, M., and Y. Xiao. 2011. Multivariate random forests. Wiley Interdisciplinary Reviews: Data Mining and Knowledge Discovery 1:80–87.

Sutherland, D.R., and G.R. Singleton. 2003. Monitoring activity patterns and social interactions of small mammals with automated event recording system: wild House Mice (*Mus domesticus*) as a case study. Pp. 159–164 *In* Rats, Mice, and People: Rodent Biology and Management. Singleton, G.R., L.A. Hinds, C.J. Krebs, and D.M. Sprat (Ed.). Australian Centre for International Agricultural Research, Canberra, Australia.

Tachinardi, P., V.S. Valentinuzzi, G.A. Oda, and C.L. Buck. 2017. The interplay of energy balance and daily timing of activity in a subterranean rodent: a laboratory and field approach. Physiolgical and Biochemical Zooloy 90:546–552.

U.S. Fish and Wildlife Service (USFWS). 1997. Recovery plan for the Amargosa Vole (*Microtus californicus scirpensis*). USFWS, Portland, Oregan. 43 p.

Vieira, E.M., L.C. Baumgarten, G. Paise, and R.G. Becker. 2010. Seasonal patterns and influence of temperature on the daily activity of the diurnal neotropical rodent *Necromys lasiurus*. Canadian Journal of Zoology 88:259–265.

Austin Roy is a small mammal ecologist interested in understanding how the different roles of wildlife affect how they influence their habitats and ecosystem function. He has been working with the Amargosa Vole since 2013. He received his B.S. in Wildlife from Humboldt State University, Arcata, California, and Ph.D. in Ecology and Evolutionary Biology from the University of Texas at El Paso. Austin seeks to use his knowledge and skillset to better conserve wildlife and other natural resources for the public at large. (Photographed by Anna Rivera Roy).

Anna Rivera Roy is a Wildlife Biologist with the U.S. Forest Service. She received her B.S. in Wildlife Conservation Biology and Applied Vertebrate Ecology from Humboldt State University, Arcata, California, and her M.S. in Earth, Environmental, and Marine Sciences from the University of Texas, Rio Grande Valley, Brownsville. Anna is experienced in endangered and sensitive species management on public lands and using camera traps to study wildlife ecology. (Photographed by Austin Roy).

Deana Clifford received her B.S. in Wildlife Conservation Biology, Doctor of Veterinary Medicine, and Master's and Ph.D. in Epidemiology from the University of California (U.C.), Davis. She is currently the Veterinarian for Nongame, Threatened and Endangered Species at the California Department of Fish and Wildlife and an Assistant Clinical Professor at U.C. Davis. (Photograph courtesy of the California Department of Fish and Wildlife).

Janet Foley is a Professor and Researcher for the Department of Veterinary Medicine and Epidemiology in the School of Veterinary Medicine at the University of California, Davis. She studies the ecology and epidemiology of infectious diseases in complex communities. Research in her lab aims to understand how community complexity contributes to disease persistence and emergence, and how driving factors are affected by anthropogenic change. (Unknown photographer).

2023 Annual Meeting Review

70th Annual Meeting, Hybrid

Program Chair: **Randi McCormick, McCormick Biological**

Attendance: 588 participants including 105 students and 54 Early Career Professionals.

Plenary Theme: Challenge Accepted! Confront Obstacles, Create Opportunities

Plenary Speakers:

- **Dr. Lisa Shipley**, Washington State University – Saving a tiny rabbit in the declining sagebrush sea: conservation of endangered Columbia Basin pygmy rabbit
- **Dr. Cali Crampton**, Kauai Forest Bird Recovery Project – Challenge Accepted: Ensuring the Survival of Kaua'i's Native Forest Birds
- **Dr. Deana Clifford**, CA Dept of Fish and Wildlife and UC Davis – Revolutionizing the Mojave – Amargosa Vole Recovery

Keynote Address:
- **Celeste Carlisle**, Return to Freedom Wild Horse Conservation
- **Dr. Nicki Frey**, Associate Extension Professor at Utah State University
- **Dr. Jim Sedinger**, Emeritus Faculty – University of Nevada, Reno

Capstone Presentation: **Joel Sartore,** National Geographic, Photo Ark

2023 Pre-Conference Workshops:
- Symposium: Burrowing Owl
- Wildlife Biologist Construction Awareness Training (WildCAT)

Awards Bestowed:
- The Raymond F. Dasmann Award for the Professional of the Year went to **Kathryn Purcell**
- The Conservationist of the Year Award went to **Beth Pratt**
- The Chapter of the Year Award went to the **California Southern California and the Sacramento-Shasta Chapters**
- The James D. Yoakum for Outstanding Service and Commitment to The Western Section of The Wildlife Society went to **Janine Payne**
- The Barrett A. Garrison Mentor of the Year Award went to **Melissa Price**
- The TWS Fellows Award went to **John McNerney**

Student Presentation Awards:

ORAL PRESENTATION:

- **1st: Jaran Hopkins—**Detecting and Monitoring Rodents Using Camera Traps and Machine Learning Versus Live Trapping for Occupancy Modeling
- **2nd: Keyanna Pinto—**Effect of Radio-Transmitter Collar Color on Predation Probability in Endangered Blunt-Nosed Leopard Lizards (*Gambelia sila*) in the Panoche Plateau
- **2nd: Marissa Rykowski—**Changing Sex Ratios Due to Global Warming for the Northwest Atlantic Loggerhead Sea Turtle Population
- **3rd: Ian Axsom—**Spatial Distribution of Temperatures Linked to an Ectotherm's Thermoregulation and Movement

POSTER:

- **1st: Tess McIntyre—**Watery Going To Do About Drought Impacts on Lizards?: Osmoregulation of Blunt-Nosed Leopard Lizards
- **2nd: Sophie Preckler-Quisquater—**Preliminary Comparison of Genetic Diversity in the Endangered San Joaquin Kit Fox (*Vulpes macrotis mutica*) Before Versus After a Mange Outbreak
- **3rd: Tali Caspi—**DNA Metabarcoding Identifies Urban Dietary Patterns of Coyotes in San Francisco

2023 Western Section Workshops

- **California Condors**, October 7-11, 2023, Central Coast
- **Bumble Bee Field Course**, July 21-23, 2023, Markleeville
- **Interest-Based Negotiation**, May 15-17, 2023, Sacramento
- **Vernal Pool Branchiopods**, January 15-21, 2023, Davis and Sacramento

2023 Western Section Membership

Retired - 46
Regular - 735
Lifetime-full - 50
Lifetime-partial - 4
Student - 173
New Professional - 130
Contributing - 3
Supporting - 8
Youth - 0
Honorary - 2
Total (excluding Honorary) - 1,150

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McCormick Biological

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WESTERN WILDLIFE
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