Otospermophilus beecheyi (Rodentia: Sciuridae)

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Abstract: *Otospermophilus beecheyi* (Richardson, 1829), the California ground squirrel (formerly, Beechey ground squirrel), is dorsally brown with silver spotting. This facultatively social and ecologically flexible species occurs at a range of elevations, has a wide dietary niche, and is common in California grasslands and oak woodlands. Although listed as "Least Concern," it has a tenuous relationship with humans. It contributes to crop and infrastructure damage and is associated with the spread of zoonoses, including plague. Nonetheless, it is an important prey species for mammalian carnivores, snakes, and birds and an ecosystem engineer that constructs burrows that benefit commensals. Ongoing study of its behavioral ecology continues to advance our understanding of mammalian antipredator behavior, disease transmission, behavioral plasticity, and social evolution.

Key words: antipredator, California, ground squirrel, herbivory, rodent

Otospermophilus beecheyi (Richardson, 1829)

California Ground Squirrel

Arctomys (Spermophilus) beecheyi Richardson, 1829:170, plate XII. Type locality "neighbourhood of San Francisco and Monterey, in California [USA];" restricted to Monterey, Monterey Co., California, United States by Grinnell (1933:120).

Spermophilus beecheyi: Cuvier, 1831. Name combination.

Spermophilus grammurus atricapillus Bryant, 1889:26. Type locality "Comondu, lower California [Baja California Sur, México]."

Spermophilus beecheyi fisheri Merriam, 1893:133. Type locality "Kern Valley, California (25 km above Kernville)."

Citellus nesioticus Elliot, 1904:263. Type locality "Santa Catalina Island, [near Avalon] California, [USA]."

Otospermophilus beecheyi: Mearns, 1907:324. First use of current name combination.

Citellus beecheyi parvulus Howell, 1931:160. Type locality "Shepherd canyon, Argus Mountains, California [USA]."

Fig. 1.—An adult male *Otospermophilus beecheyi* from Berkeley Marina, Berkeley, Alameda County, California, United States. Photograph by D. J. Long.

Citellus beecheyi rupinarum Huey, 1931:17. Type locality: "Cataviña, lower California [México], lat. 29° 54′ north, 114° 57′ west."

Citellus beecheyi nudipes Huey, 1931:18. Type locality "Laguna Hanson, Sierra Juàrez, lower California [México], altitude 5,200 feet. Lat. 31° 58′ north, long, 115° 53′ west."

Citellus beecheyi sierrae Howell, 1938:153. Type locality "Emerald Bay, Lake Tahoe, El Dorado Co., California [USA]."

CONTEXT AND CONTENT. Order Rodentia, suborder Sciuromorpha, family Sciuridae, tribe Marmotini (Howell 1938; Hall 1981; Helgen et al. 2009). Eight subspecies of *Otospermophilus beecheyi* were recognized by Howell (1938), Hall (1981), Thorington and Hoffmann (2005), and Helgen et al. (2009). However, recent genetic studies support elevation of *O. b. douglasii* to a full species as *O. douglasii* and inclusion of *O. atricapillus* as a subspecies of *O. beecheyi* (Álvarez-Castañeda and Cortés-Calva 2011; Phuong et al. 2014). Thus, the 3 species of *Otospermophilus* are *O. beecheyi* (Richardson, 1829), *O. douglasii* (Richardson, 1829), and *O. variegatus* (Erxleben, 1777). To reflect this, we have made every effort to exclude information on *O. douglasii* (formerly *O. b. douglasii*) from this account. Our revised distribution for *O. beecheyi* follows the traditional subspecific distribution of *O. beecheyi* from previous workers, with the Sacramento River assumed to be the biogeographic barrier between *O. beecheyi* and *O. douglasii* (Grinnell and Dixon 1918; Howell 1938; Hall 1981). However, the taxonomic delineation of *Otospermophilus* living in southeastern Yolo and Solano counties, along the northwestern margin of Sacramento–San Joaquin Delta, remains undecided (Phuong et al. 2014). Given that current uncertainty, we have included information about those squirrels but have noted the county of origin of those data. For brevity, we also excluded information about *O. b. atricapillus* (formerly *O. atricapillus*) because information about its distribution has been previously summarized (Álvarez-Castañeda et al. 1996). We follow this revised taxonomy of *O. beecheyi* and recognize the following subspecies:

O. b. atricapillus (Bryant, 1889:26). See above.
O. b. beecheyi (Richardson, 1829:170). See above.
O. b. fisheri (Merriam, 1893:133). See above.
O. b. nesioticus (Elliot, 1904:263). See above.
O. b. nudipes (Huey, 1931:18). See above.
O. b. parvulus (Howell, 1931:160). See above.
O. b. rupinarum (Huey, 1931:17). See above.
O. b. sierrae (Howell, 1938:153). See above.

NOMENCLATURAL NOTES. Formerly placed in *Spermophilus*, as *S. beecheyi*, Helgen et al. (2009) reclassified this species as *O. beecheyi* in the genus *Otospermophilus*. Taxonomy follows Helgen et al. (2009). The type specimen was collected by Alexander Collie, ship surgeon and naturalist aboard the H.M.S. Blossom, captained by Frederick William Beechey, whom *O. beecheyi* was named to honor (Grinnell 1933; Linsdale 1946).

Otospermophilus beecheyi belongs to the genus *Otospermophilus*, a name derived from Greek and attributed to the animal's relatively large ears and its dietary preference for eating seeds. Specifically, "*Otos*" means ear, "*spermatos*" means seed, and "*phileo*" means love (Jaegar 1955). *Otospermophilus* is a sister lineage of *Callospermophilus* (Helgen et al. 2009). Members of both genera have crescent markers over the shoulders and relatively large ears for their body sizes (Helgen et al. 2009).

DIAGNOSIS

The pelage of *Otospermophilus beecheyi* is laterally and dorsally grayish brown speckled with white spots (Fig. 1). Its distinguishing traits include a yellowish white to light brown venter, a bushy tail, and white rings around the eyes. *O. beecheyi* is distinct from other ground squirrels in California because of its bushy tail edged with white fur (Eder and Ross 2005).

Multiple characteristics distinguish *O. beecheyi* from its congeners (reviewed by Thorington et al. 2012). *O. beecheyi* differs from *O. variegatus*, the rock squirrel, in that *O. variegatus* has a dark grayish dorsum mixed with cinnamon buff. The dorsum of *O. variegatus* may also be light brown to bone brown to dark blackish brown; its head and shoulders are often black. The eye ring of *O. variegatus* is sometimes white like that of *O. beecheyi*, but *O. variegatus* has a buff or tawny dorsum and a grayish white to cinnamon buff venter (Thorington et al. 2012). *O. beecheyi* and *O. douglasii* possess similar color variation, but the medial stripe of *O. douglasii* is darker (Allen 1974).

O. b. beecheyi is less pale and has less silver-gray fur on the sides of neck and shoulders than *O. b. fisheri* (Thorington et al. 2012). *O. b. beecheyi* is less dark and has more yellowish brown on the venter than *Otospermophilus b. nesioticus* (von Bloeker 1967). *O. b. beecheyi* may be distinguished from *O. b. nesioticus*, because *O. b. beecheyi* lacks any black on the top of its head and ears as well as the mixed black and tawny ochraceous patch that is typical between the shoulders of *O. b. nesioticus*. *O. b. beecheyi* is generally darker than *O. b. rupinarum* and lacks the silver-white mantle found in *O. b. nudipes*. *O. b. beecheyi* lacks the blackish- to pinkish-buff doral and lateral color typical of *O. b. atricapillus* (Álvarez-Castañeda and Cortés-Calva 2011). *O. b. beecheyi* is generally paler overall than *O. b. parvulus* (Álvarez-Castañeda et al. 1996). *O. b. beecheyi* closely resembles *O. b. sierra* in its appearance, but *O. b. beecheyi* is more buffy, has less gray on sides of the head, and has a darker venter than *O. b. sierra* (Grinnell and Dixon 1918; Álvarez-Castañeda and Cortés-Calva 2011).

GENERAL CHARACTERS

Otospermophilus beecheyi is widely identified in California by a crescent shape of light brown or peppered fur beginning at the back of the neck and draping down over its shoulders (Eder and Ross 2005). This grayish white collar is usually present on the

back, the neck, and the sides. Although mainly brown with white-peppered fur on its back, albinistic, melanistic, and xanthic forms have been reported (Grinnell and Dixon 1918; Ryckman and Lindt 1953). The pelage coloration of *O. beecheyi* varies with season and land-use type across its range (Jachowski and Hubbart 2012). Specifically, *O. beecheyi* on unmanaged grasslands has lighter pelage in the autumn and darker pelage in the winter than those on agricultural and pasture lands (Jachowski and Hubbart 2012). These site-specific differences apparently increase the efficiency in thermoregulation and reduce the predation risk for squirrels.

Otospermophilus beecheyi varies in body size as a function of temporal, spatial, and latitudinal factors (reviewed by Thorington et al. 2012). These patterns are generally consistent with the predictions of Bergmann's cline, with the smallest animals occurring in the southern part of the range in xeric environments with reduced precipitation and resource availability (Blois et al. 2008). For example, Blois et al. (2008) found that adult body size of *O. beecheyi* varies geographically and climatically but was generally largest in wet and cold (northern) regions. Interestingly, measures of skull length and maxillary toothrow length indicate that body sizes of *O. beecheyi* at low elevations in the Sierra Nevada Mountains were stable over the past century (Eastman et al. 2012). Specimens collected from 2000 to 2008 were not significantly larger than those collected from 1902 to 1950 (Eastman et al. 2012).

Mass of adult *O. beecheyi* typically ranges from 280 to 738 g, height from 145 to 225 mm, body length from 330 to 510 mm, and tail length from 127 to 229 mm (Eder and Ross 2005). Fat accumulation accounts for one-third of body mass during the growing seasons (summer and autumn), giving rise to the heaviest annual body mass during this period (Tomich 1962). As such, masses vary seasonally and across ontogeny (Holekamp and Nunes 1989; for details on mass variation see "Ontogeny" section). Despite size variation across its range, adult males are always larger than adult females in body and cranial morphometrics (Howell 1938). Specifically, body dimensions (mm) for adult males ($n = 10$) and females ($n = 10$), respectively, were: total length 434 (410–460), 401 (370–442); tail length 177 (156–190), 158 (137–180); hind foot length 59 (57–61), 56 (53–59); and ear length from notch 19.9 (18–21), 20.7 (19–22—Howell 1938). Skull morphology of *O. beecheyi* (Fig. 2) is nearly identical to its congener *O. variegatus* (Hall 1926; Oaks et al. 1987). Cranial dimensions (mm) for adult males ($n = 20$) and females ($n = 20$), respectively, were: greatest skull length 59.4 (57–62.4), 57.1 (53.9–60.4); palatilar length 28.8 (27–30.5), 27.5 (26–30); zygomatic breadth 38.3 (36.3–40.5), 36 (33.6–38.6); cranial breadth 24.5 (23.4–25.9), 23.6 (22.7–25.2); interorbital breadth 14.7 (13.2–15.8), 13.8 (12.9–15.4); postorbital constriction 15.6 (14.8–16.9), 15.6 (13.7–16.7); length of nasals 22.1 (20–24), 21 (19.7–22.4); maxillary toothrow 12 (11.2–12.9), 11.9 (10.6–12.7—Howell 1938).

DISTRIBUTION

The 8 recognized subspecies of *Otospermophilus beecheyi* are distributed from north-central California and west-central Nevada (United States) to Baja California Norte (México—Hall 1981;
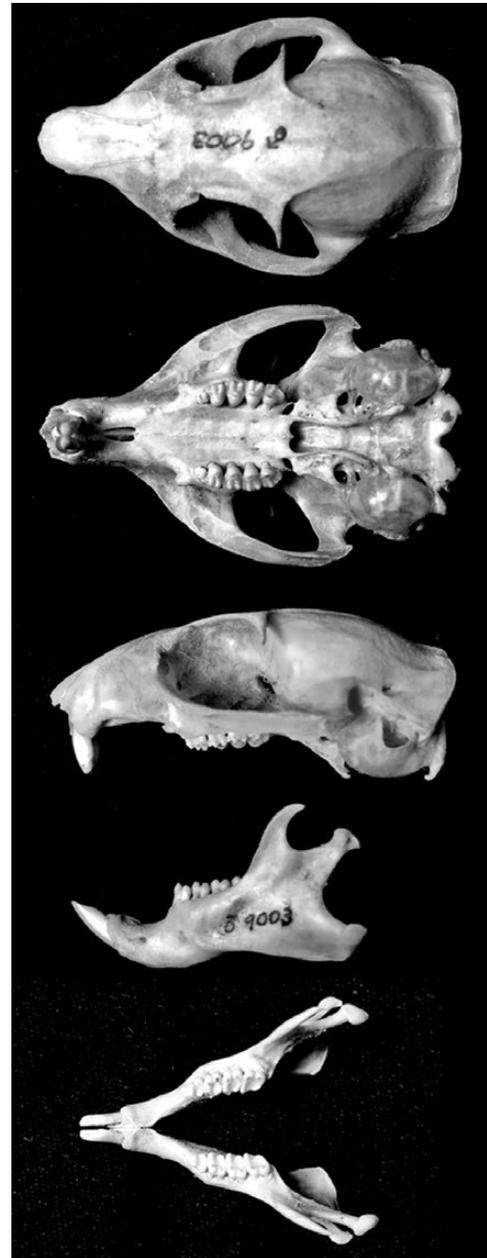
Fig. 2.—Dorsal, ventral, and lateral views of the skull and lateral and dorsal views of the mandible from an adult male *Otospermophilus beecheyi* (California Academy of Sciences Mammalogy Collections 9003) collected by K. Staeger on 11 July 1940, Calaveras Dam, Alameda Co., California, United States; 59.2 mm total skull length. Greatest skull length is 59.2 mm.

modified by Álvarez-Castañeda and Cortés-Calva 2011 and Phuong et al. 2014; Fig. 3). In the state of California, *O. beecheyi* is distributed from the intertidal zone along the coast (Roest 1993; Carlton and Hodder 2003) and vertically to at least 3,000–3,200 m elevation in the Sierra Nevada Range (e.g., Mt. Whitney, Little Cottonwood Creek) and in Riverside County at Mt. San Jacinto (Grinnell and Dixon 1918).

Otospermophilus b. fisheri is distributed throughout the Central Valley of California and into northeastern California
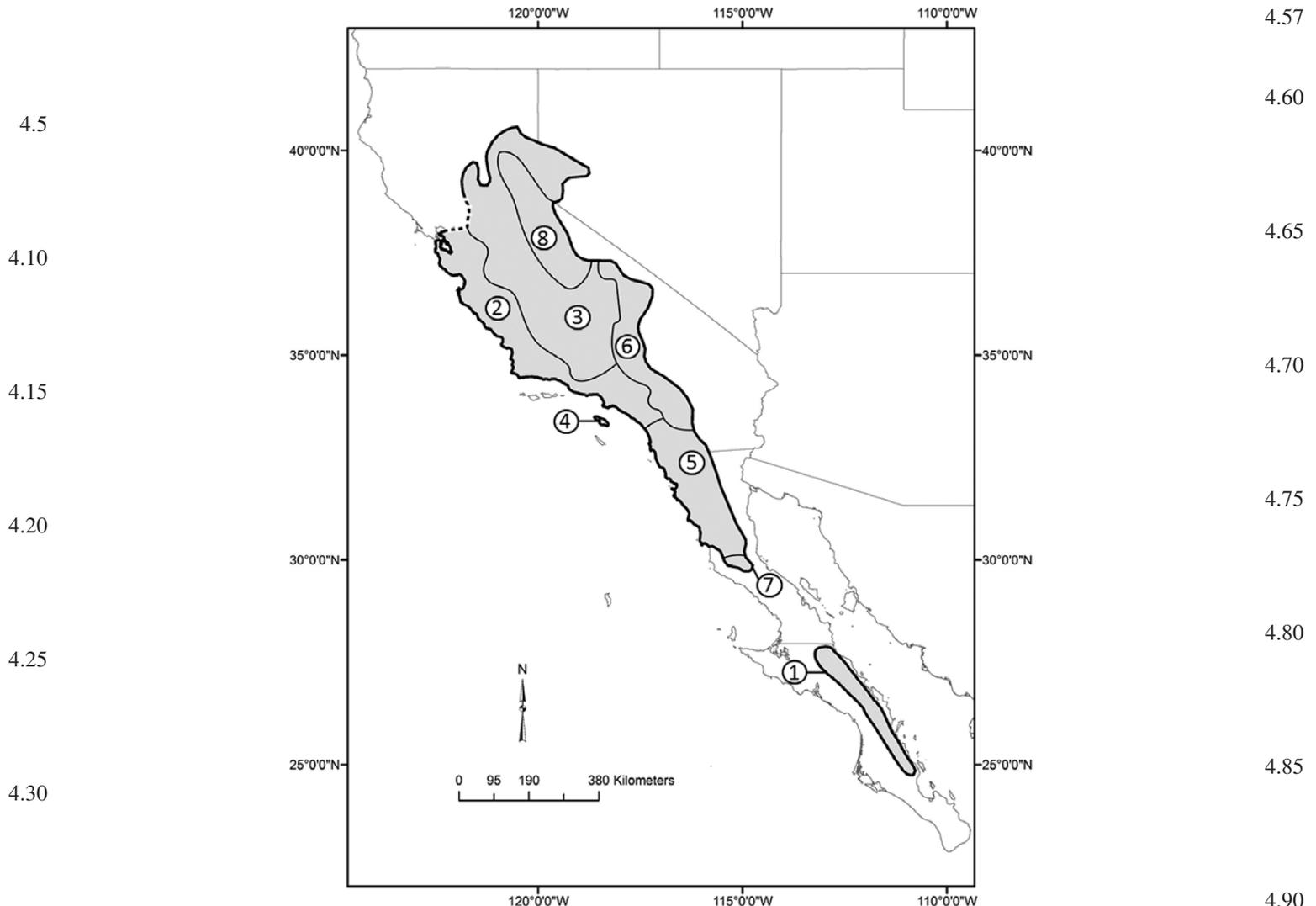
Fig. 3.— Geographic distribution of the 8 subspecies of *Otospermophilus beecheyi*: 1, *O. b. atricapillus*; 2, *O. b. beecheyi*; 3, *O. b. fisheri*; 4, *O. b. nesioticus*; 5, *O. b. nudipes*; 6, *O. b. parvulus*; 7, *O. b. rupinarum*; 8, *O. b. sierrae* (modified from Hall 1981 and Álvarez-Castañeda et al. 1996, and Phuong et al. 2014). The dotted line in the northwest edge of the *O. beecheyi* range represents an imprecise boundary between *O. b. beecheyi* and *O. douglasii* due to genetic uncertainty about the specific geographic division between these 2 species (Phuong et al. 2014). This map should therefore serve as a tentative boundary for *O. beecheyi* until further genetic data confirm a species division in that region.

and west-central Nevada; *O. b. sierra* lives throughout the northern Sierra Nevada range; *O. b. parvulus* extends from the southern Sierra Nevada Range into the Panamint, Argus, San Bernardino, and Peninsular ranges of south-central California; *O. b. beecheyi* occurs from the coast east to the western edge of the Central Valley, and south along the Coast Ranges into southern California; *O. b. nudipes* is distributed from southernmost coastal California into the coast ranges of Baja California Norte; *O. b. rupinarum* occurs in a relatively restricted region of the desert of Baja California Norte desert adjacent to the southern end of the range of *O. b. nudipes* (Hall 1946, 1981). *O. b. nesioticus* is endemic to the Santa Catalina Island, located off of the shore of southern California (Hall 1946, 1981).

There are no known successful introductions of *O. beecheyi* outside of its native range; 2 individuals were released in

Dunedin, New Zealand in 1906 but their introduction ultimately failed when they did not reproduce and died out 3 years later (Thomson 1922).

FOSSIL RECORD

Thorington et al. (2012) proposed 2 hypotheses concerning the possible ancestors of *Otospermophilus*: 1) *Miospermophilus* (late Oligocene to middle Miocene, about 24–12 million years ago) and 2) *Spermophilus* (middle Miocene, 16 million years ago in North America). It has been suggested by Black (1963) that *O. beecheyi* likely arose from this early Miocene *Miospermophilus* ancestor and Savage and Russell (1983) reported that numerous *Otospermophilus* occurred as early as the

beginning of the Barstovian late Miocene. More precisely, Savage (1949) documented the occurrence of *O. bensoni*, a close relative of *O. beecheyi*, from the early Pleistocene (Irvingtonian age) Irvington Quarry located near Mission San Jose, California. Fossil records of *O. beecheyi* are known from several late Pleistocene (Rancholabrean age) sites throughout California (Miller 1978; Kurten and Anderson 1980), including the La Brea tar pits where active tar seeps still trap ground squirrels (Stock 1972). Pajak et al. (1996) documented *O. beecheyi* fossils in the Elsinore Fault Zone in Riverside County, California from the lower to middle Pleistocene (Irvingtonian age). Fossils of *O. beecheyi* were cataloged at numerous late Pleistocene (Rancholabrean age) throughout southwestern California (Jefferson 1991). In most of these localities, early forms of *O. beecheyi* were historically associated with large grazing mammals, and extant *O. beecheyi* continues to live in close association with large grazing mammals, including domesticated cattle (e.g., Howard and Bentley 1959; Fehmi et al. 2005).

ONTOGENY AND REPRODUCTION

Ontogeny.—*Otospermophilus beecheyi* observed above ground may be categorized into 3 ontogenetic stages: newly emerged young (45–60 days of age), juveniles (> 60–364 days), and adults (> 364 days; young adults of ages 365–729 days are referred to as "yearlings"—Hanson and Coss 2001). Over 800 *O. beecheyi* from Yolo and Solano counties were examined by Tomich (1962) to document the ontogeny of *O. beecheyi*. Young are altricial, born hairless with their eyes closed; their skin is red at birth and gradually turns pink as they age (Tomich 1962). Vibrissae are 2 mm long at 3 days; by 3–7 days, young typically only weigh 9.3 g (range: 7.7–12.6 g—Tomich 1962). By day 13, the head has short silky fur, by day 27, young have their full pelage. By 21–28 days, young are usually able to crawl and have fully erupted incisors by 28 days; by around 1 month, the eyelids start to open (Tomich 1962). The 1st molt provides young with yellow, fluffy fur and the 2nd molt occurs prior to emergence from the natal burrow and changes fur to a shiny brown with white patches on the shoulders (Grinnell and Dixon 1918).

At around 6–7 weeks, young are weaned and start to emerge from their burrows and spend time above ground, a phenomenon that may occur as early as in late April, but the precise timing strongly depends upon the specific location of the population (Tomich 1962). For example, intensive study of *O. beecheyi* in Yolo County, California indicated that most young emerged in May, but that a small proportion of young emerged from burrows as late as June and July (Owings and Coss 2007). Similarly, young consistently emerged in May for 3 different years during a study on the University of California Santa Cruz campus (Holekamp et al. 1988). Regardless of the precise timing of independence, the fur pattern and color of newly emerged young resemble that of adults (Eder and Ross 2005). Juveniles molt at least twice (Grinnell and Dixon 1918).

Adult members of most described populations of *O. beecheyi* typically estivate or hibernate at some point in the year; this results in above-ground absences by adults for many months of each year (Fitch 1948; Tomich 1962; Dobson 1979; Holekamp et al. 1988; Holekamp and Nunes 1989). In contrast, there are no documented accounts of young of the year hibernating or estivating (Grinnell and Dixon 1918; Holekamp and Nunes 1989). Instead, they spend most of their 1st year foraging, maturing, and building up body fat for the mating season (Tomich 1962). *O. beecheyi* is capable of breeding by the end of its 1st year (Grinnell and Dixon 1918; Tomich 1962). The typical lifespan is up to 4 years in the wild and up to 9 years in captivity (Tomich 1962; Ranck et al. 2008).

The precise timing of seasonal changes in surface activity by adult *O. beecheyi* varies with climate. In cold areas, *O. beecheyi* may hibernate for several months, whereas squirrels living in warm areas often estivate to avoid excessive heat in the summer (Grinnell and Dixon 1918). When adults hibernate during unfavorably cold weather, they may do so for up to 6 months at high elevations (Grinnell and Dixon 1918; Hall 1946). For example, in areas where adults hibernate, males are typically dormant by late July to early August (after the breeding season), but adult females remain active until late September, presumably to put on fat stores for reproduction (Tomich 1962). At warmer elevations, such as the Central Valley or Mojave Desert, ground squirrels tend to stay in their burrows to escape hot temperatures in the late summer and emerge in mid-winter (Grinnell and Dixon 1918). On the campus of the University of California at Santa Cruz, *O. beecheyi* adults disappear from the surface for 3–4 months each year; males estivate from May or June to October or November whereas most females estivate from late July to December or January (Holekamp et al. 1988).

The mass of young at initial emergence is typically 100–150 g; young gain weight rapidly in the days following emergence (Holekamp and Nunes 1989). Juveniles typically reach their adult size after 7–8 months (Grinnell and Dixon 1918), attaining sex-specific masses resembling those of adults emerging from estivation (males: about 600 g in October or November; females: about 450 g in December or January—Holekamp and Nunes 1989). Annual mass maxima of adults peaked around June before estivation (males: about 1,000 g, females: about 700 g—Holekamp and Nunes 1989).

Reproduction.—*Otospermophilus beecheyi* likely follows a promiscuous mating system (Fitch 1948; Boellstorff et al. 1994). Periods of behavioral estrus last only an average ± S.D. of 6.7 ± 3 h (Boellstorff et al. 1994) or 3–5 h each year (Holekamp et al. 1988). Despite this short duration, females mate with an average of 6–7 males during this period (Boellstorff et al. 1994). Preliminary data are consistent with multiple paternity; polyacrylamide gel electrophoresis confirmed that 8 of 9 litters were fathered by multiple sires (Boellstorff et al. 1994).

The reproductive season is quite variable geographically and is linked to regional differences in climate (Thorington et al. 2012). In Yolo and Solano counties where squirrels hibernate, reproduction occurs soon after emergence from the burrow,

often starting in February, and lasting only a few weeks (Tomich 1962). In the San Francisco Bay region, the breeding season often lasts from February through April (Grinnell and Dixon 1918; Evans and Holdenried 1943). For populations located farther south in California, pregnant females were found throughout the year (Storer 1930). Additionally, adults living at high elevations in relatively cold climates tend to emerge from hibernation and mate later in the year (Grinnell and Dixon 1918). Although young are often born during June or July at high elevations, they are born around mid-April in many parts of California (Grinnell and Dixon 1918). Testicles enlarge during autumn and winter months in preparation for mating and regress by about 10% of maximal mass by July long after the breeding season has ceased (Tomich 1962).

Overall, observations based on field studies indicate that most females initiate their breeding careers as yearlings (Evans and Holdenried 1943; Fitch 1948; Tomich 1962; Dobson 1979; Holekamp et al. 1988). After mating, gestation is 25–30 days (Grinnell and Dixon 1918). Levels of circulating hormones vary with reproductive condition of pregnant and lactating females during the spring breeding season (Holekamp et al. 1988). Plasma progesterone peaks during pregnancy and then again during lactation. Prolactin peaks during lactation between the 2 peaks in progesterone (Holekamp et al. 1988).

Adrenal glands of mammals mediate an individual's physiological response to stressors. Study of these glands allows for an understanding of how each sex copes with the demands of reproduction. For *O. beecheyi*, adrenals are largest for adult females during pregnancy, but adult males typically have larger adrenal glands than do adult females (Tomich 1962). In fact, adrenal glands of males in Yolo and Solano counties are largest directly after the mating season, suggesting that males experience more stressors during the mating season than do females (Tomich 1962).

Most adult females are monestrous, producing only a single litter each year of 4–11 young (Grinnell and Dixon 1918). Although the average litter size is 5 offspring per reproductive bout (Tomich 1962), litter sizes may vary seasonally for some populations. For one population, peak litter sizes documented in April averaged 8 young per litter (Grinnell and Dixon 1918). Female *O. beecheyi* are capable of giving birth to a 2nd litter if the individuals of the 1st litter fail to survive (Grinnell and Dixon 1918). Because some females have more than 1 reproductive bout per year, each adult female produces, on average, roughly 6.1 young per year, a value that exceeds the average litter size for a single reproductive bout for the species (Tomich 1962). If a female does produce a 2nd litter, then this 2nd litter is typically born late in the season (Grinnell and Dixon 1918). For example, in southern Tulare County, California, 20% of reproductively active females bred a 2nd time within a single breeding season (Simpson and Lamunyon 1980). In this population, excess embryos were sometimes resorbed in utero, lowering the mean litter sizes birthed by females; older adult females were more likely than younger females to produce a 2nd litter within the same breeding season (Simpson and Lamunyon 1980).

ECOLOGY

Population characteristics.—Population densities of adult *Otospermophilus beecheyi* are reported to be about 1.2–6.8 individuals/ha (Evans and Holdenried 1943), but densities may be as high as 8.4 individuals/ha (Schitoskey and Woodmansee 1978), 11.1 individuals/ha (Loredo-Prendeville et al. 1994), and even 70.4–92.5 individuals/ha in old orchards with abundant food in Yolo County (Owings et al. 1977; Boellstorff and Owings 1995). The annual rate of increase for 2 populations of *O. beecheyi* in Yolo and Solano counties is moderate compared to other grassland herbivores (Tomich 1962).

Otospermophilus beecheyi is primarily terrestrial and semifossorial but may occasionally also climb trees (Grinnell and Dixon 1918; Ingles 1945; Hall 1946). The species tends to avoid water but can swim if necessary (Grinnell and Dixon 1918; Olson 1950; Roest 1993). Although *O. beecheyi* occupies a wide variety of physical habitats and ecological communities, it most often occurs in open grasslands, oak savanna, oak woodland, nearshore rocky outcrops, and on agricultural lands; the openness of these habitats permits individuals to detect predators (Grinnell and Dixon 1918; Evans and Holdenried 1943; Linsdale 1946; Fitch 1948; Owings et al. 1977). In response to experimental burns in the Sierra Nevada Mountains, *O. beecheyi* was captured at higher rates in burned forests with low oak tree cover than in nonburned forests with high oak tree cover (Roberts et al. 2015). Nonetheless, *O. beecheyi* has also been documented on occasion in coniferous forest, riparian areas, and desert scrub (Grinnell and Storer 1924; Miller and Stebbins 1964; Ryan 1968; Roest 1993; Patten 1997). At low elevations, *O. beecheyi* largely occupies oak savanna, grasslands, and meadows but may also reside in tule marsh, riparian willow-cottonwood, and chaparral. In montane habitats, *O. beecheyi* mainly resides in mixed conifer forests (Grinnell and Storer 1924; Ryan 1968; Coppeto et al. 2006).

Space use.—Statistically similar home range sizes for adult males ($n = 2$; 5,466 m^2) and females ($n = 5$; 4,217 m^2) as well as extensive home range overlap within the sexes were reported by Owings et al. (1977); male home ranges overlapped by 45% and female home ranges overlapped by 87% in Yolo County. However, a subsequent study by Boellstorff and Owings (1995) in the same area based on larger sample sizes (1987: $n = 10$ females, $n = 13$ males; 1988: $n = 12$ females, $n = 11$ males) was able to detect significantly larger home ranges for females (616–902 m^2) than for males (313–376 m^2). Multi-year data collected from squirrels residing at different sites across various seasons are required to make additional generalizations about home range in this species.

Surprisingly, little is known about the patterns of dispersal in *Otospermophilus beecheyi*. Evans and Holdenried (1943) reported a relatively high incidence of movement among young males, suggesting that natal dispersal might be male-biased for this species. The longest distances of recorded movements were by 3 males; there is only 1 record of a young female dispersing

a long distance (1.0–1.2 km). Other data are consistent with this pattern, suggesting that females tend to establish home ranges adjacent to or overlapping with those occupied by their mothers and thus remain at their burrow system for multiple years (Boellstorff and Owings 1995). The results of a food addition study suggested that clumped food promotes squirrels to aggregate (Dobson 1979). Specifically, adult males permanently dispersed to the site of the food addition colony, whereas females only made exploratory trips to forage at the site of the food addition colony. Clearly, additional study of the causes and consequences of dispersal for *O. beecheyi* is warranted.

Otospermophilus beecheyi digs tunnels in the ground and resides in burrows to avoid danger and to raise young (Grinnell and Dixon 1918). Its eye morphology is specialized to achieve adequate vision under the low-light conditions of these burrows (Kryger et al. 1998). Soil excavation from burrow construction often results in the accumulation of large piles of dirt at burrow entrances (Grinnell and Dixon 1918). This dirt is often deposited in a fan shape directly in front of or to the side of the tunnel entrance. This excavation likely aerates the soil (Grinnell and Dixon 1918). Feces are often scattered around burrow entrances and along foraging paths; fecal pellets are cylinder-shaped with rounded ends (Grinnell and Dixon 1918). Soil type and squirrel density influence the length and complexity of burrow systems (Grinnell and Dixon 1918). Grinnell and Dixon (1918) reported tunnel lengths of 0.9–70 m, but Van Vuren and Ordeñana (2012) found a mean burrow length of only 7.5 m and a median burrow length of only 4.6 m because 79% of burrows sampled were less than 10 m long. Short burrows often lack connections to other burrows, but most burrows have interconnected tunnels and multiple openings (e.g., 6–20 openings) at the surface (Grinnell and Dixon 1918). The average diameter of burrow openings is 11 cm (range: 7–15 cm—Grinnell and Dixon 1918).

Diet.—The diet of *Otospermophilus beecheyi* is primarily based on seeds, particularly those of grasses and oaks (Linsdale 1946). Nonetheless, *O. beecheyi* relies almost exclusively on green herbaceous vegetation during growing seasons, consuming a variety of plant parts (including fruits and flowers) whenever available (Fitch 1948). Individuals typically forage standing up on their hind legs in a bipedal posture to collect seeds or clip grass when in tall grass over 10 cm (Owings et al. 1977). In vegetation shorter than 10 cm, such as in a mowed or grazed area, one of us (JES) often has observed individuals foraging in a quadrupedal posture with all 4 paws on the ground. As in other ground squirrels (e.g., Bednekoff and Blumstein 2009), *O. beecheyi* has been observed (JES) moving its head from side to side in a sequence of "looks" to scan the environment for potential danger.

Otospermophilus beecheyi often carries seeds in its extensive cheek pouches, which allow for considerable caching for a rodent of its body size (Grinnell and Dixon 1918). For instance, the cheek pouches of *O. beecheyi* are larger in relative and absolute size than those of Belding's ground squirrel (*Urocitellus beldingi*—Grinnell and Dixon 1918; Fig. 4). Cheek pouches of *O. beecheyi* open into each side of the mouth cavity; these
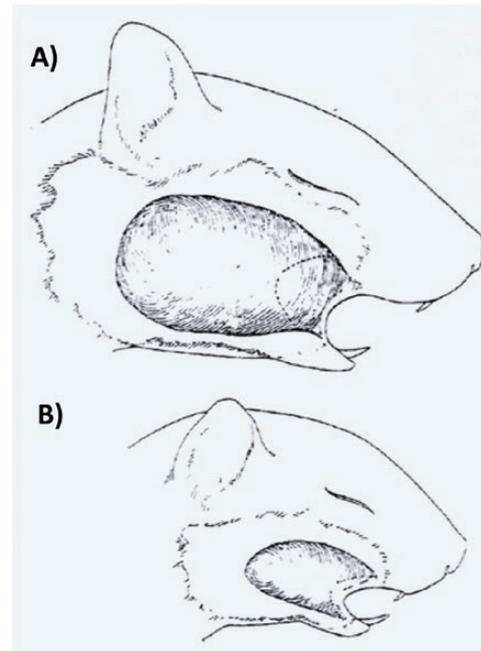

Fig. 4.—Drawings from dissections of the cheek pouches of A) *Otospermophilus beecheyi* and B) Belding's ground squirrel (*Urocitellus beldingi*) from non-copyrighted material of Grinnell and Dixon (1918) demonstrate the enhanced capacity for *O. beecheyi* cache seeds in its cheek pouches.

expansive pouches allow squirrels to efficiently carry seeds and bulbs to their burrows for caching (Grinnell and Dixon 1918). Seed caches are a means of storing food that is seasonally abundant or abundant for just a short time, such as acorns or grass seeds, to be eaten later (Grinnell and Dixon 1918; Linsdale 1946). For example, Grinnell and Dixon (1918) captured an adult female carrying 212 seeds of bur clover and 12 seeds from a wild grass in her cheek pouches. They also recorded an adult male carrying 97 grains of barley and 3 bur clover seeds. *O. beecheyi* occasionally disperses seeds, including acorns, when uneaten caches of seeds germinate (Sork 2016).

In addition to its affinity for seeds, *O. beecheyi* eats a range of food items which vary spatially and temporally. Although seeds provide more overall energy content and increased assimilation efficiency than foliage, seeds are generally less abundant and contain less water content than foliage. *O. beecheyi* therefore also consumes a variety of plant parts from more than 20 species of grasses, legumes, and forbs (Grinnell and Dixon 1918; Schitoskey 1975; Owings et al. 1977). This opportunistic rodent consumes leaves, flowers, buds, stems, shoots, roots, tubers, twigs, and bark (Grinnell and Dixon 1918; Evans and Holdenried 1943; Linsdale 1946; Fitch 1948). *O. beecheyi* has been observed eating leaves of alfilaria (*Erodium*), leaves of star thistle (*Centaurea*), heads of foxtail (*Hordeum*), chilicothe (*Echinocystis macrocarpa*), elderberry (*Sambucus*), jimson weed (*Datura*), wild nightshade (*Solanum*), turkey mullein (*Eremocarpus*), tarweed (*Madia*), and prickly pear (*Opuntia*—Grinnell and Dixon 1918). In all, there are accounts of *O. beecheyi* consuming over 100 different

species of native and naturalized plant species (Merriam 1910; Grinnell and Dixon 1918; Hall 1927, 1946; Howell 1938; Evans and Holdenried 1943; Stanton 1944; Linsdale 1946; Fitch 1948; Olson 1950; Miller and Stebbins 1964; Baker 1984; Tietje et al. 1991; Roest 1993; Clark 1994).

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Otospermophilus beecheyi occasionally consumes animal prey and carrion. For example, it has been observed preying on various invertebrates (Evans and Holdenried 1943; Stanton 1944; Baker 1984; Carlton and Hodder 2003). Avian prey includes the eggs and nestlings of killdeer (*Charadrius vociferus*), California quail (*Lophortyx californica*), bobwhite quail (*Colinus virginianus*), ring-necked pheasant (*Phasianus colchicus*), mourning dove (*Zenaida macroura*), dark-eyed junco (*Junco hyemalis*), and American robin (*Turdus migratorius*—Grinnell and Storer 1924; Emlen and Glading 1938; Stanton 1944; Linsdale 1946; Fitch 1948; Leopold 1977; Baker 1984; Purcell and Verner 1999; de Szalay et al. 2003; Yeh et al. 2007). Captive *O. beecheyi* have killed and eaten side-blotched lizards (*Uta stansburiana*) and western fence lizards (*Sceloporus occidentalis*), but predation of lizards by *O. beecheyi* has not been observed in the wild (Sandberg and Banta 1973). Killing of young gopher snakes (*Pituophis catenifer*) and destruction of their eggs by *O. beecheyi* has been documented in the wild and captivity (Fitch 1949). Fitch (1948) observed *O. beecheyi* feeding on young desert cottontails (*Sylvilagus audubonii*), adult pocket gophers (*Thomomys*), and kangaroo rats (*Dipodomys*). There are rare reports of scavenging on trapped fish, meat, woodrats (*Neotoma*), songbirds, and, in 1 case, another *O. beecheyi* (Grinnell and Dixon 1918; Fitch 1948; Miller and Stebbins 1964). *O. beecheyi* may eat eggs of California grunion (*Leuresthes tenuis*—Olson 1950) or chickens (*Gallus domesticus*—Grinnell and Dixon 1918; Howell 1938).

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Given its broad diet, *O. beecheyi* can be a serious agricultural pest and is responsible for an estimated annual losses of around 12–16 million dollars to the state of California (Marsh 1998). Crops most at risk include apple (*Malus domestica*), carrot (*Daucus carota*), avocado (*Persea americana*), fig (*Ficus carica*), grape (*Vitis vinifera*), olive (*Olea europaea*), almond (*Amygdalus communis*), pistachio (*Pistacia*), macadamia (*Proteaceae ternifolia*), walnut (*Juglans*), several types of citrus (*Citrus*) and melons (*Cucumis* and *Citrullus*), potato (*Solanum*), sugar beet (*Beta vulgaris*), strawberry (*Fragaria ananassa*), alfalfa (*Medicago sativa*), barley (*Hordeum vulgare*), wheat (*Triticum*), cotton (*Gossypium hirsutum*), and certain types of *Prunus* (peach, nectarine, apricot, and prune—Grinnell and Dixon 1918; Stanton 1944; Baker 1984; Schramm and Bullard 2004). In facilities with poultry and livestock, *O. beecheyi* frequently steals feed grains, pellets, and molasses lick blocks (Baker 1984). Coprophagy has been reported (Fitch 1948); expelled fecal pellets from rabbits and squirrels were documented in the stomach contents of *O. beecheyi*.

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Diseases and parasites.—*Otospermophilus beecheyi* can harbor diseases, most of which are spread by the ectoparasites it carries and some of which pose a public health threat

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to humans. Marion et al. (1987) also detected relatively high levels of hepatitis B virus in squirrels trapped on the San Francisco Peninsula; over 50% of these infected adults suffered from hepatocellular carcinoma, a form of cancer in the liver. Ticks and fleas of *O. beecheyi* are of great interest because they can carry bacteria that cause Lyme disease, plague, tularemia, or relapsing fever (Holdenried et al. 1951). These ectoparasites may be transmitted to conspecifics and heterospecifics, including humans. *O. beecheyi* also carries mites (*Demodex*), the epizootic vectors of mange (Waggie and Marion 1997) and, possibly, of Chagas disease (Navin et al. 1985). Mainly recognized for carrying ectoparasites, *O. beecheyi* also carries several endoparasites. Its endoparasites include protozoa (*Leucocytozoon citellicola* and *Trypanozoon otospermophili*), flatworms (*Cysticercus portolae*), and mites (*Cytoleichus banksi*—Wellman and Wherry 1910). *O. beecheyi* is also an important reservoir host of *Cryptosporidium parvum* and of *Bartonella washoensis*, the human bacterial pathogen (Thorington et al. 2012).

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Furman and Loomis (1984) present the most comprehensive account to date of the species of ticks associated with *O. beecheyi* and the burrows they occupy. Their account includes reports of the Pacific coast tick (*Dermacentor occidentalis*), the deer tick (*Ixodes sculptus*), the Western black-legged tick (*I. pacificus*), and the relapsing fever tick (*Ornithodoros turicata*) on *O. beecheyi*. The Pacific coast tick is generally the most abundant tick species found on *O. beecheyi*, carrying a member of the spotted fever group rickettsiae, designated 364D, known to infect humans in the United States (Shapiro et al. 2010). The Pacific coast tick and the Western black-legged tick both serve as vectors for tularemia.

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Otospermophilus beecheyi serves as host for several flea species including *Hoplopsyllus anomalus*, *Oropsylla montana* (formerly *Diamanus montana*), and *Echidnophaga gallinacea*; all 3 species of fleas are known vectors of sylvatic plague (Furman and Loomis 1984; Bursten et al. 1997; Lang 2004; Nieto et al. 2007; Hubbart et al. 2011). In addition, *Oropsylla montana* and *H. anomalus* can spread trypanosomiasis or sleeping sickness. *O. beecheyi* has triggered outbreaks of sylvatic plague in California as a result of hosting fleas containing the plague bacterium, *Yersinia pestis* (Wherry 1908; Rutledge et al. 1979; Hubbart et al. 2011). Squirrels with fleas carrying plague have been documented in suburban areas close to human dwellings and in recreational facilities near wild areas (Lang and Willis 1991; Mian et al. 1996; Townzen et al. 1996). Outbreaks of plague are obvious because they result in a large number of dead squirrels (Spano 1994). Poisoning and gassing are most widely used to suppress squirrel populations and, thus, reduce the size of the potential plague reservoir (Wobeser 1994). However, the liberal use of flea powder at bait stations or at burrow entrances is an extremely effective method to suppress fleas, and, accordingly, the potential risk for plague outbreaks without the direct killing of *O. beecheyi* hosts (Spano 1994).

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Flea densities on *O. beecheyi* vary seasonally. *H. anomalus* is the most prevalent species year round and is most abundant in spring and summer (Hubbart et al. 2011). Of the 2 less abundant species, *O. montana*, is found most often in the winter, especially on adult *O. beecheyi*, although *E. gallinacea* is most abundant in autumn on juvenile squirrels (Hubbart et al. 2011).

Interspecific interactions.—*Otospermophilus beecheyi* provides an important food source for a diverse assemblage of predators and is an important ecosystem engineer that generates valuable habitat for commensal species. Venomous snakes occur throughout the range of *O. beecheyi* and regularly depredate young and, occasionally, juvenile and adult *O. beecheyi*; adults are largely resistant to rattlesnake venom (Poran et al. 1987; Biardi et al. 1999, 2005). The major snake predators of *O. beecheyi* are the venomous Northern Pacific rattlesnake (*Crotalus oreganus oreganus*) and Southern Pacific rattlesnake (*C. o. helleri*); other snake predators include the nonvenomous Pacific gopher snake (*Pituophis catenifer catenifer*) as well as the venomous speckled rattlesnake (*C. mitchelli*), and red diamond rattlesnake (*C. ruber*—Grinnell and Dixon 1918; Fitch 1949; Klauber 1972; Hanson and Coss 1997; Rodriguez-Robles 2002). The strength in venom resistance is most intense in populations where venomous snakes are abundant (Coss et al. 1993). Because venom resistance increases with squirrel age, rattlesnakes are largely limited to killing young during the first 45 days of life; the small body volume of immature *O. beecheyi* limits its capacity to neutralize snake venom (Owings and Coss 2007).

Mammalian predators of *O. beecheyi* include coyote (*Canis latrans*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), island fox (*U. littoralis*), kit fox (*V. macrotis*), long-tailed weasel (*Mustela frenata*), mink (*Mustela vison*), fisher (*Martes pennanti*), badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and feral cats (*Felis catus*) and dogs (*C. lupus familiaris*—Grinnell and Dixon 1918; Grinnell et al. 1937; Linsdale 1946; Nussbaum and Maser 1975; Orloff et al. 1986; Weintraub 1986; Towell and Anthony 1988; Golightly et al. 1994; Loredo-Prendeville et al. 1994; Moore and Collins 1995; White et al. 1995; Cypher et al. 1996; Hanson and Coss 1997; Kuenzi 1997; Zielinski et al. 1999; Murdoch et al. 2004). *O. beecheyi* attracts coyotes, increasing the risk of human–coyote encounters in rural and suburban areas (Timm et al. 2004).

Avian predators include the prairie falcon (*Falco mexicanus*), white-tailed kite (*Elanus leucurus*), golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), red-shouldered hawk (*B. lineatus*), Swainson's hawk (*B. swainsoni*), great horned owl (*Bubo virginianus*), spotted owl (*Strix occidentalis*), barn owl (*Tyto alba*), burrowing owl (*Athene cunicularia*), and loggerhead shrike (*Lanius ludovicianus*—Evermann 1882; Fisher 1893; Dixon 1906; Grinnell and Dixon 1918; Fowler 1931; Saylor 1937; Fitch et al. 1946; Fitch 1947; Stoner 1949; Carnie 1954; Boyce 1985; Weintraub 1986; Laymon 1988; Estep 1989; Loredo-Prendeville et al. 1994; DAAR/IPM 2006; Rabin et al. 2006). *O. beecheyi* is often directly killed by vehicular traffic (Warren-Allen 2004). In response, the California condor (*Gymnogyps californianus*) and turkey vulture (*Cathartes aura*) regularly scavenge on carcasses of *O. beecheyi* (Grinnell and Dixon 1918; Linsdale 1931; Koford 1953; Collins et al. 2000).

Otospermophilus beecheyi competes for food with the western gray squirrel (*Sciurus griseus*), mule deer (*Odocoileus hemionus*), California quail, western scrub jay (*Aphelocoma californica*), yellow-billed magpie (*Pica nuttalli*), Lewis woodpecker (*Melanerpes lewis*), and acorn woodpecker (*Melanerpes formicivorus*); it may also compete for both food and space with the antelope ground squirrel (*Ammospermophilus leucurus*) and Botta's pocket gopher (*Thomomys bottae*—Hall 1927; Evans and Holdenried 1943; Linsdale 1946; Miller and Stebbins 1964; Ryan 1968; Koenig and Mumme 1987; Vander Haegan et al. 2005).

Like many burrowing mammals (Davidson et al. 2012), *O. beecheyi* increases biodiversity and habitat heterogeneity by generating habitat for many commensal species that occupy active or abandoned burrows (Lenihan 2007). Species that benefit from the burrows produced by *O. beecheyi* include the burrowing owl, screech owl (*Otus asio*), California tiger salamander (*Ambystoma californica*), Pacific tree frog (*Pseudacris regilla*), western toad (*Bufo boreas*), giant garter snake (*Thamnophis gigas*), San Francisco garter snake (*T. sirtalis tetrataenia*), California whipsnake (*Masticophis lateralis euryxanthus*), Pacific rattlesnake, gopher snake, pocket gopher, black rat (*Rattus rattus*), and house mouse (*Mus musculus*—Grinnell and Dixon 1918; von Bloeker and Rudd 1937; Linsdale 1946; Fitch 1949; Baker 1984; Littrell 1990; Winchell 1994; Loredo et al. 1996; Trenham and Shaffer 2005; DAAR/IPM 2006).

BEHAVIOR

Grouping behavior.—The social organization of *Otospermophilus beecheyi* remains poorly understood. Trapping data clearly document a range of densities at which squirrels persist (see "Population characteristics") and available information on space use by *O. beecheyi* (e.g., Owings et al. 1977; Boellstorff and Owings 1995) and our observations (JES) of predominantly amicable social interactions among burrow mates suggest that their social organization may resemble that of their close relative, the yellow-bellied marmot (*Marmota flaviventris*, a well-studied facultatively social rodent—e.g., Johns and Armitage 1979; Nowicki and Armitage 1979). Early field work by Owings et al. (1977) in Yolo County documented the occurrence of amicable behaviors in *O. spermophilus* that they called, "greetings," "cheek rubs," and "nose-to-cheek." Greetings involve the initiator (greeter) touching noses with the recipient squirrel (Owings et al. 1977). A cheek rub is similarly amicable but occurs when a squirrel rubs its cheek on another squirrel (Owings et al. 1977). Finally, nose-to-check combines patterns of behavior from a greeting and a cheek rub; it occurs when one squirrel approaches another head-on and noses near the corner of the other squirrel's mouth (Owings et al. 1977). Owings et al. (1977) documented

that these amicable behaviors largely involved members of the same sex, suggesting these are sociopositive behaviors that promote social cohesion rather than serve a sexual function. Clearly, exploring the functions of these behaviors should prove to be a fruitful avenue for future field research.

Although play behavior is poorly understood for *O. beecheyi*, our observations (JES) suggest that it is primarily limited to juveniles involving play biting, boxing, chasing, slapping, mounting, pouncing, and wrestling much in the same ways as has been well documented for yellow-bellied marmots (e.g., Nowicki and Armitage 1979; Blumstein et al. 2013). Although a single play bout ends when one animal moves apart from its play partner, partners are likely to remain in close proximity after play ends. Juvenile squirrels as well as adults also maintain spatial proximity with each other, presumably as a form of sociopositive behavior. For example, a squirrel may walk less than 1 m behind another squirrel to maintain spatial proximity during foraging or in nonforaging contexts. One of us (JES) observed that a squirrel may also maintain spatial proximity with another squirrel by sitting less than 1 m from it or by sitting in direct body contact with it.

Agonistic interactions among adult *O. beecheyi* involve simple displacements, chases, and direct contact involving biting and pushing (Owings et al. 1977). After an aggressive interaction, former opponents often separate from each other and one or both of these individuals may vocalize. A "lateral approach" is a low level of threat during which the aggressor orients so its body is parallel to the recipient (Owings et al. 1977). The backs of both squirrels are slightly arched and tail hairs are erect. The tail is oriented towards the opponent and the mouth is open. Lateral approaches may result in "displacement behavior" in which one squirrel displaces another by just approaching within < 1 m of other squirrel without making physical contact with the recipient (e.g., no pushing or biting). A "flank push" occurs when the aggressor touches its flank (rear) against that of its opponent (recipient of aggression—Owings et al. 1977). The aggressor shoves the other animal side-ways with its own body. This often starts with squirrels tooth-chattering at each other at 1–2 m away and then the aggressor approaching the recipient. This may escalate into a "flank slam" during which the attacker slams its body at a 180° angle against the recipient or include "chases" during which the aggressor runs after the target of aggression or "pouncing" during which the aggressor pounces on the target in an aggressive manner (Owings et al. 1977). "Bites" occur when the attacker snaps its mouth at the receiver in an aggressive manner. "Mouth spars" involve 2 squirrels lunging at each other with open mouths in an aggressive manner (Owings et al. 1977). "Snapping, snarling, hissing" occurs when the initiating squirrel vocalizes in an aggressive way towards a target squirrel (Owings et al. 1977). "Wrestling" involves both parties locking forearms and struggling to push the other squirrel onto the ground (Owings et al. 1977). "Dusting" occurs between adult males; one squirrel rapidly pushes substrate with its hind limbs or slides on its side or dorsal region during agonism (Owings et al. 1977).

Individuals often take dust baths and autogroom (self-groom) to cope with ectoparasites (Owings et al 1977). Cephalocaudal autogrooming is a highly stereotyped form of grooming, characterized by up to 25 grooming actions that together make up a syntactic chain; the face and head are first groomed and then the torso following a sequence of stereotyped movements (Bursten et al. 2000). Cephalocaudal autogrooming in nonsocial contexts presumably reduces ectoparasite loads; whether it functions to reduce conflict, remove parasites, or is simply part of the fight sequence itself during agonistic interactions remains unclear (Durant et al. 1988; Bursten et al. 2000).

Reproductive behavior.—Mate-guarding likely occurs in *Otospermophilus beecheyi*; males chase away intruding males from the area in which the female he is courting lives and males also chase females as part of the courtship ritual (Owings et al. 1977). Courtship typically starts with an adult sniffing the anogenital region of another squirrel of the opposite sex (Owings et al. 1977). The male will engage in a "foot to cheek behavior" after approaching a female head-on and holding her head between his forepaw and muzzle (Owings et al. 1977). This behavior may lead to a nose-to-perineum posture during which the female turns, raises her tail, and allows the male to sniff her perineum (Owings et al. 1977). Mating itself involves lordosis displays by the female and mounting by the male; the male bites the skin in between the female's scapulae during ejaculation and then the female typically runs into her burrow and produces a high-pitched vocalization (Owings et al. 1977).

Communication.—*Otospermophilus beecheyi* has evolved a myriad of modes of communication to cope with threats, much of which has been documented in Yolo County, California. In response to danger, *O. beecheyi* often vocalizes, producing long-lasting bouts of alarm calls that consist of up to 3 distinct components: whistles, chatter, and chats (Owings et al. 1977; Leger and Owings 1978). Firstly, whistles contain little noise and have a fundamental frequency of about 3–10 Hz (Owings et al. 1977). Secondly, chatters are characterized by a rapid sequence of chat-like vocalizations, each of which contains 2–7 components (Owings et al. 1977). Finally, chatter-chat calls are more structurally variable than pure chatters (Leger and Owings 1978). Chatter-chat calls include both chatters and a 1-note call with a high noise content, called a chat; as a result, chatter-chat calls are structurally variable and always characterized by noise (Leger and Owings 1978).

Alarm calls influence the behavioral repertoire of *O. beecheyi*. In the absence of threats, *O. beecheyi* typically allocates most of its daily above-ground activity budget to feeding, sunning, dust-bathing, grooming, and socializing with conspecifics (Owings et al. 1977). *O. beecheyi* often lies on its venter and extends it forearms on the ground with its head raised to bathe in the sun. It also rests sitting straight up and motionless with its forelegs hanging down across its chest and its paws resting one upon the other (Owings et al. 1977). In both resting positions, it often watches its surroundings. When presented with the alarm call of a conspecific, receivers generally increase the height of their posture, allocating more time to running and less time to feeding, walking, and nonlocomotion movements (Leger
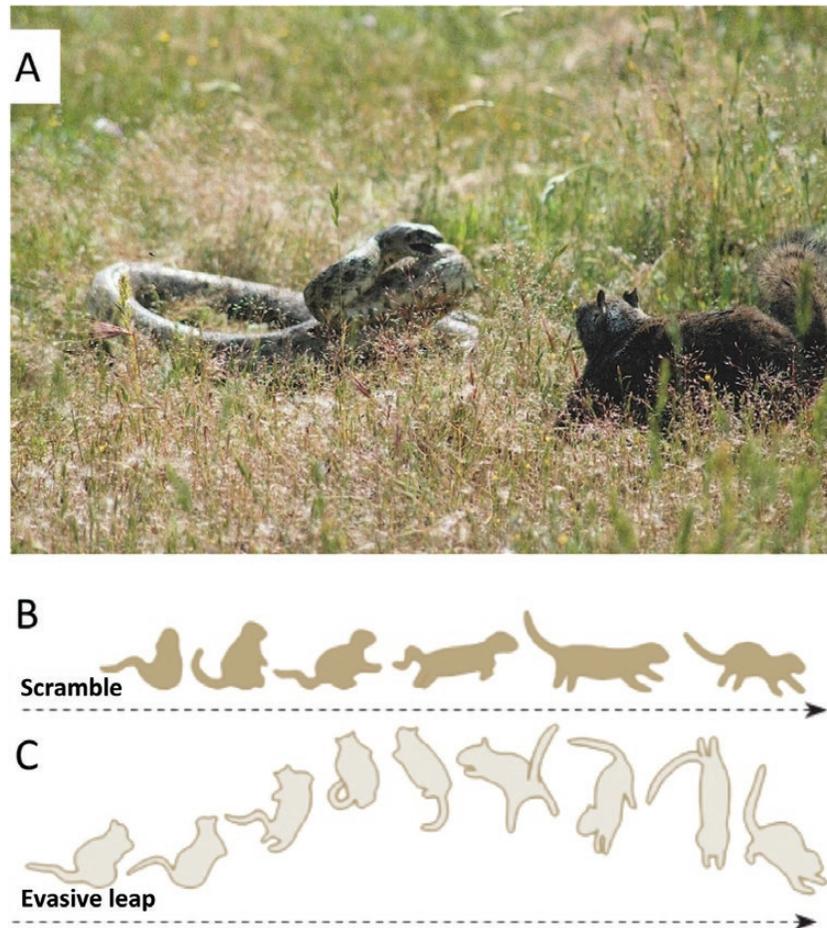
Fig. 5.— *Otospermophilus beecheyi* interactions with rattlesnakes may include: A) harassing snakes by mobbing, and throwing or kicking sand at it and B) responding by scrambling away when surprised, and engaging in an evasive leap if the squirrel perceives increased danger of the snake. Photograph, taken by Jerry Kirkhart, is a freely available image licensed under the Creative Commons Attribution 2.0 Generic (CC by 2) license. Schematic reprinted with permission from Putman and Clark (2015).

and Owings 1978). Each call type elicits a consistent response, suggesting alarm calls are referential signals (Leger and Owings 1978). For example, chatters signal a terrestrial predator is near; receivers immediately respond to chatters by producing a series of chatter-chats, displaying an upright posture, and suppressing feeding (Leger and Owings 1978). In contrast, whistles signal that an aerial predator is near; receivers typically respond by running or standing upright (Leger and Owings 1978). Chats evoke less response from receivers than do other components of alarm calls (Leger and Owings 1978).

Rates of calling also vary based on the state and environmental context of callers. For example, the adult *O. beecheyi* calls more often in response to exposure to rattlesnakes, domestic dogs, coyotes, and bobcats after its young reach the age of 1st emergence from natal burrows than prior to offspring emergence (Owings et al. 1986). This finding is consistent with the finding that parous females are generally more reactive to threats than nonparous females (Leger and Owings 1978). *O. beecheyi* is also more responsive to alarm calls at noisy sites with electricity-generating wind turbines than at sites lacking turbines (Rabin et al. 2006).

Otospermophilus beecheyi has evolved a number of adaptive behavioral responses to the predatory threats of snakes, including a combination of innate and learned auditory, olfactory, and visual responses (Coss and Owings 1978; Hennessy and Owings 1978; Poran and Coss 1990; Coss 1991). These include snake-specific warning calls (Owings and Leger 1980). Squirrels assess the potential danger based on the size, temperature, and posture of the snake (Rowe and Owings 1978, 1990, 1996; Swaisgood et al. 1999, 2003). Responses of *O. beecheyi* varies based on the threat posed by the snake (Hennessy and Owings 1978) and the sex, reproductive state, and other individual traits of the squirrel at risk, and whether the squirrel at risk recently encountered a snake (Coss and Biardi 1997; Swaisgood et al. 2003; Putman and Clark 2015). For example, squirrels often visit and sniff areas where snakes were recently encountered, presumably in search of olfactory cues from snakes (Owings and Coss 1977). Young are also more vulnerable than adults because they are not as good at detecting hidden snakes and their reaction time to snake strikes is not as fast as adult squirrels (Putman and Clark 2015).

Otospermophilus beecheyi uses a novel form of chemical defense by directly applying heterospecific substances to its

body; it chews skins shed from rattlesnakes and then licks its fur to apply the scent (Clucas et al. 2008a). Female squirrels with young also lick their vulnerable young to apply the scent (Clucas et al. 2008b). Juveniles and adult females engage in longer bouts of application than do adult males, a finding that Clucas et al. (2008b) suggest is likely attributed to the fact that young are more vulnerable than juveniles to predation, and adult females actively protect young.

Because *O. beecheyi* is diurnal and has an acute visual system, it primarily relies upon the production of visual pursuit-deterrent signals when coping with snakes (Owings and Coss 1977). Squirrels often assume the bipedal alert posture after climbing a "promontory," such as a log or stone; increased height presumably allows for increased visibility of the surroundings (Owings et al. 1977). Upon detecting a snake predator, a squirrel increases its vigilance and often rears up on alert as a defense mechanism (Putman and Clark 2015). *O. beecheyi* is most vigilant if it recently encountered a predator and, on average, a vigilant squirrel reacts more quickly and escapes more effectively in response to simulated snake strikes than does a nonvigilant squirrel (Putman and Clark 2015).

Otospermophilus beecheyi also engages in a number of stereotyped visual displays when it encounters a live snake, presumably to gain information about the snake and to attempt to remove it from the area. It often directly harasses and approaches snakes by elongating its body to taunt the snake and then quickly jumping back to avoid capture (Fig. 5A; Owings and Coss 1977). Field experiments in San Diego County, California using snake replicas (made of plasticine) suggest that *O. beecheyi* distinguishes between the risks associated with snakes, directing the most intense and frequent aggression towards the heads of small snake replicas, but only mild aggression towards the tail of large snake replicas (Mitrovich and Cotroneo 2006). Confrontational behaviors are used especially to distract snakes away from burrows containing young; these include squirrels kicking sand towards, pouncing on, or even biting the snake (Fig. 5A; Owings and Coss 1977). Squirrels may also plug tunnels or burrow entrances to deter snakes (Coss and Owings 1978).

Otospermophilus beecheyi regularly engages in a snake-directed pursuit-deterrent signal, called tail-flagging; this consists of side to side motions of the elevated, piloerected tail to signal to snakes that the squirrel has detected the snake's presence (Owings and Coss 1977; Hennessy et al. 1981). Tail-flagging serves as a warning signal to other squirrels in the area and communicates to the snake the squirrel's detection of the hidden predator along with its vigilance and readiness to leap away (Putman and Clark 2015). As in many other species of small animals that encounter snakes, *O. beecheyi* uses vertical or lateral evasive leaps to avoid snake strikes (Figs. 5B; Putman and Clark 2015).

Otospermophilus beecheyi also modulates its tail temperature when tail-flagging at rattlesnakes but not when tail-flagging at gopher snakes (Rundus et al. 2007). That is, *O. beecheyi* increases its tail temperature when interacting with rattlesnakes, which are able to detect thermal cues using a pair of facial heat-sensing pit organs, but not at gopher snakes lacking pit organs and thus the ability to physiologically detect thermal information produced by squirrels (Rundus et al. 2007). Barbour and Clark (2012) indicated that rattlesnakes are indeed less successful in striking tail-flagging squirrels, suggesting that the infrared tail-flagging by squirrels diverts the strike away from the body of the squirrel.

GENETICS

Otospermophilus beecheyi has a diploid number (2n) of 38 and a fundamental number of 72 (Nadler 1966; Oaks et al. 1987). Taxonomic placement is based on DNA sequence data from the mitochondrial cytochrome-*b* gene and extends historical classification by systematists based on anatomy by confirming that *O. beecheyi* belongs to the squirrel family, Sciuridae, and within the Tribe Marmotini (the marmots—Herron et al. 2004; Helgen et al. 2009). Herron et al. (2004) determined that the Holarctic ground squirrels are paraphyletic (GenBank Accession number: AF157918, sequence length = 1,140 base pairs). Importantly, phylogenetic analysis of the mitochondrial gene cytochrome-*b* provides strong evidence that *Otospermophilus* and *Callospermophilus* are sister lineages, both of which have members with crescent markers over the shoulders and relatively large ears for their body sizes (Helgen et al. 2009). Genetic data therefore confirm early morphological and chromosomal comparisons between these lineages. Skulls of *Otospermophilus* are generally much larger than and differ in shape from those of *Callospermophilus* (Helgen et al. 2009). The rosta, bullae, and teeth of *Otospermophilus* are proportionally larger and heavier than those of *Callospermophilus* (Howell 1938). Blood proteins from *O. beecheyi* can be used to assign paternity (Boellstorff et al. 1994).

CONSERVATION

The International Union for Conservation of Nature and Natural Resources *Red List of Threatened Species* lists *Otospermophilus beecheyi* as a species of "Least Concern" with a stable population trend and limited known threats (Thorington et al. 2012). It therefore is at the lowest risk of extinction and is considered widespread and abundant. As such, it has a long history with humans, originally as a food resource, and later as a competitor for agricultural crops, a vector of disease, and destroyer of human structures. *O. beecheyi* was commonly eaten by native peoples throughout its historic range and by the Spaniards and other settlers upon their arrival to California (Jacobsen 1918). In Beechey's (1941:80) account of his 1826–1827 visit to central California, he mentions that the squirrel is "…rather a pretty little animal, said to be good to eat." In the mid 1800s and continuing as late as the 1920s, commercial hunters harvested tens of thousands of squirrels annually for local markets and also shipped them to urban centers in San Francisco and Oakland (Jacobsen 1918; Leopold 1977).

Otospermophilus beecheyi persists in highly disturbed ecosystems including clear-cut forests, developed agricultural areas, and habitat fragments within suburban and urban areas (Gashwiler 1970). Within developed areas, excavation by *O. beecheyi* can weaken irrigation canals, aqueducts, levees, railroad grades, roadbeds, building foundations, and remove soil covering ammunition bunkers at weapons storage areas (Grinnell and Dixon 1918; Loredo-Prendeville et al. 1994; Bayoumi and Meguid 2011; Ordeñana et al. 2012). Damage to tree crops can include theft of fruit, eating of buds and flowers, and gnawing on bark that may cause girdling, and eventually death, of the tree (Grinnell and Dixon 1918). *O. beecheyi* is therefore a significant agricultural pest (Marsh 1998).

Whether *O. beecheyi* and cattle directly compete for forage remains controversial. For example, Howard and Bentley (1959) used rodenticides to manipulate the densities of *O. beecheyi* for 8 years. They found that the daily weight gain of heifers was lower in the presence than in the absence of *O. beecheyi* and that these effects were most pronounced during the growing season. In contrast, Schitoskey and Woodmansee (1978) found that *O. beecheyi* has very low daily maintenance requirements (only 92.40 cal g^{-1} day^{-1}) and feeds primarily on food that differs from that preferred by cattle. They estimated that a modest to high squirrel population density (8.4/ha) could only consume very little (e.g., 0.6%, 0.4%, and 0.2%) of the forage plants available during the growing season (February, March, and April, respectively). These data suggest that *O. beecheyi* should have little effect on the diet of cattle (Schitoskey and Woodmansee 1978).

The effects of cattle grazing on *O. beecheyi* density are also equivocal. For example, experimentally induced cattle grazing over a 3-year experiment failed to consistently increase or decrease the spatial distribution of *O. beecheyi* burrows (Fehmi et al. 2005). In contrast, *O. beecheyi* appears to benefit from grazing in other areas (e.g., Hastings Reservation in California—Linsdale 1946; San Joaquin Experimental Range near Fresno—Howard and Bentley 1959), presumably because of the increased ability for *O. beecheyi* to detect predators in open, grazed habitat.

There has been a century-long campaign to control *O. beecheyi* populations through trapping, application of poisoned bait, injection of toxic gasses into burrows, or physical destruction of burrows (Gilson and Salmon 1990; Marsh 1994; O'Connell 1994).

Rodenticide use should be approached with care. In the past, poison baits were used indiscriminately and often killed nontarget animals. For example, secondary ingestion of *O. beecheyi* killed by toxicants fatally poisoned and reduced the numbers of carnivores, including coyotes (Marsh et al. 1987) and endangered kit foxes (Schitoskey 1975). As a result, the use of these toxicants is now banned. Moreover, ingestion of squirrel carcasses containing lead shot or toxins from poisoning is a known source of mortality to California condor, turkey vulture, red-tailed hawk, golden eagle, and American raven (*Corvus corax*—Linsdale 1931; Koford 1953; Pattee et al. 1990; Collins et al. 2000). Similarly, although subsequent data are required to support these claims, some have argued that toxic fumigants in burrows may potentially kill commensal species, such as the California tiger salamander and burrowing owl (e.g., Loredo-Prendeville et al. 1994; Winchell 1994). To confront this issue, Whisson (1999) established ways to use poisons that minimize losses of nontarget species.

Nonlethal control such as habitat modification can be successful after the removal of squirrels from a site; destruction of burrows (to at least 18 inches deep) using a tractor-drawn ripper reduces the likelihood of reinvasion by squirrels (Gilson and Salmon 1990). McGrann et al. (2014) found that squirrel densities on levees increased with the percent cover of perennial nut crops on adjacent lands, suggesting that establishing crops least attractive to *O. beecheyi* is a viable tool for reducing damage to levees and thus reducing conflicts with humans.

Translocations also provide a nonlethal method that is successful, but only in cases where *O. beecheyi* are moved substantial distances from their original locations (Loredo-Prendeville et al. 1994; Van Vuren et al. 1997). Density reductions may prove largely ineffective because of continuous dispersal from outside areas and immigration into control areas (Fitch 1948; Stroud 1982). To cope with the extirpation of *O. beecheyi*, populations may be reestablished artificially through restoration efforts (Salmon 1981).

REMARKS

Despite its reputation for being a rangeland pest and for potentially harboring disease, *Otospermophilus beecheyi* plays an important dual role in grassland conservation as both a major prey source for avian, reptilian, and mammalian predators as well as a valuable ecosystem engineer that promotes ecosystem function in California grasslands and oak woodlands by generating burrows for use by commensal species. Moreover, its presence likely promotes biodiversity in California (e.g., Lenihan 2007). Numerous studies have provided insights into a suite of adaptive behavioral responses used by *O. beecheyi* to cope with a wide range of predators while foraging. Specifically, we know a great deal about the complex suite of antipredator behaviors used to evade rattlesnakes. Conversely, we know surprisingly little about the social and spatial organization of this species, including information about its timing and distance of dispersal. Because of its diurnal activity and preference for open habitats, tracking of its social behavior and patterns of space use should be straightforward. Thus, this species should provide an interesting model organism for future studies into the causes and consequences of mammalian sociality, disease transmission, and behavioral development in natural conditions.

ACKNOWLEDGMENTS

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