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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).

by *O. beecheyi* activity (e.g., Tule Elk, *Cervus canadensis nannodes*) or consistently avail themselves of the above-ground 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,

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).

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.

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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