J. Raptor Res. 53(2):172–179

CAN CALIFORNIA GROUND SQUIRRELS REDUCE PREDATION RISK TO BURROWING OWLS?

LISA A. HENDERSON[1] AND LYNNE A. TRULIO[2]
Department of Environmental Studies, San José State University, One Washington Square, San José, CA 95192 USA

ABSTRACT.—In northern California, USA, western Burrowing Owls (*Athene cunicularia*) use burrows in active California ground squirrel (*Otospermophilus beecheyi*) colonies for nesting and protection. Ground squirrels have well-developed, anti-predator alarm-calling behavior, but the potential benefits of such alarm calling to Burrowing Owls have not been examined. The objective of this study was to assess the rate and types of predator interactions experienced by Burrowing Owls and the extent to which they may benefit from alarm calls given by California ground squirrels. We studied interactions of California ground squirrels and Burrowing Owls at Moffett Federal Airfield in urban Santa Clara County, California, during two Burrowing Owl breeding seasons, in 2012 and 2013, using cameras and direct observations. We detected 177 approaches by predators, four of which resulted in predation events on owls. The rate of predator approach during diurnal periods, as determined by direct observation, was 0.93/hr. Ground squirrels called in response to predator approaches before owls did 66% of the time, which was approximately proportional to the abundance of ground squirrels and Burrowing Owls. When squirrels called first, an estimated 75% of owls exhibited alert responses, including alarm calling, running to the burrow, and scanning, indicating that owls benefited from ground squirrel alarm calls in response to approaching predators. Our research suggests that healthy ground squirrel populations may provide important predator alert services to Burrowing Owls, especially in the context of increasing populations of urban predator species.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *California ground squirrel*; Otospermophilus beecheyi; *alarm calling*; *California*; *predation risk*; *photo-trapping*; *urban*.

¿PUEDEN LAS ARDILLAS TERRESTRES DE CALIFORNIA REDUCIR EL RIESGO DE DEPREDACIÓN DE *ATHENE CUNICULARIA*?

RESUMEN.—En el norte de California, EEUU, *Athene cunicularia* usa las madrigueras de las colonias activas de la ardilla terrestre de California *Otospermophilus beecheyi,* tanto para anidar como para su protección. Las ardillas terrestres tienen comportamientos de gritos de alarma anti-depredadores bien desarrollados, pero los beneficios potenciales de este grito de alarma para *A. cunicularia* no han sido aún examinados. El objetivo de este estudio fue evaluar la tasa y los tipos de interacciones con depredadores que experimentan los individuos de *A. cunicularia* y el grado con el que pueden beneficiarse de los gritos de alarma dados por las ardillas terrestres de California. Estudiamos las interacciones entre las ardillas terrestres de California y *A. cunicularia* en el aeródromo federal de Moffett en el área urbana del Condado de Santa Clara, California, durante dos estaciones reproductivas de *A. cunicularia* en 2012 y 2013, usando cámaras y observaciones directas. Detectamos 177 acercamientos de depredadores, cuatro de los cuales resultaron en eventos de depredación sobre los búhos. La tasa de acercamiento de depredadores durante los períodos diurnos, determinada a partir de las observaciones directas, fue 0.93/h. Las ardillas terrestres gritaron en respuesta a los acercamientos de los depredadores antes que los búhos un 66% de las veces, lo que fue aproximadamente proporcional a la abundancia de ardillas terrestres e individuos de *A. cunicularia.* Cuando las ardillas gritaron primero, aproximadamente un 75% de los búhos exhibieron respuestas de alerta, incluyendo gritos de alarma, carreras a las madrigueras y oteos, indicando que los búhos se benefician de los gritos de alarma de las ardillas terrestres en respuesta al acercamiento de los depredadores. Nuestra investigación sugiere que las poblaciones saludables de ardillas terrestres pueden proporcionar importantes servicios al alertar sobre la presencia de depredadores a *A. cunicularia*, especialmente en el contexto del aumento de las poblaciones de especies de depredadores urbanos.

[Traducción del equipo editorial]

---

[1] Present address: Olberding Environmental, Inc., 3170 Crow Canyon Place, Suite 260, San Ramon, CA 94583 USA.

[2] Corresponding author: Lynne.Trulio@sjsu.edu

The Burrowing Owl (*Athene cunicularia*) is a bird of open grasslands that nests underground. In northern California, Burrowing Owls (hereafter "owls") use burrows dug by California ground squirrels (*Otospermophilus beecheyi*; "ground squirrels" or "squirrels") for nesting and protection (Thomsen 1971, Trulio and Chromczak 2007). Although once prevalent in the western United States, this owl is declining due to anthropogenic impacts (Gervais et al. 2008), especially in areas undergoing rapid urbanization (DeSante and Scalf 2007, Wilkerson and Siegel 2010). In urban settings, Burrowing Owls are vulnerable to habitat loss and degradation, prey limitation, loss of ground squirrels and increasing populations of urban predators (Gervais et al. 2008).

Adult Burrowing Owls are small, 19–25 cm tall, and weigh approximately 150 g. They are visible during the day standing near their burrows; at dawn, at dusk and at night Burrowing Owls actively hunt. Adults, juveniles, and eggs are all highly vulnerable to predation. Predators of Burrowing Owls include Red-tailed Hawks (*Buteo jamaicensis*), American Crows (*Corvus brachyrhynchos*), Common Ravens (*Corvus corax*), coyotes (*Canis latrans*), striped skunks *(Mephitis mephitis),* gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), domestic cats (*Felis catus*), gopher snakes *(Pituophis catenifer),* and rattlesnakes (*Crotalus* spp.; Coulombe 1971, Green and Anthony 1989).

Nest predation is a major source of reproductive failure in bird species (Ricklefs 1969), including Burrowing Owls, and greatly reduces owl productivity (Thomsen 1971, Green and Anthony 1989, Martell 1990, Millsap and Bear 2000). Although there is much information on nestling survivorship, there are no specific data on rates or sources of predation faced by adult and young Burrowing Owls during the breeding season. One factor that may affect and potentially reduce the predation rate faced by Burrowing Owls is the presence of California ground squirrels. California ground squirrels are semi-fossorial, colonial rodents that dig extensive burrow systems and share a similar complement of predators with Burrowing Owls. Although both species have well-developed alarm-calling behavior (Owings and Virginia 1978, Owings et al. 2002, Bryan and Wunder 2013), little is known about how alarm calling by California ground squirrels may affect the predation risk of Burrowing Owls.

Burrowing Owls living in colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) increased their alert behavior in response to prairie dog alarm calls as compared to non-alarm call sounds, and thus may use prairie dog calls to alert themselves to approaching predators (Bryan and Wunder 2013). As in prairie dog colonies, Burrowing Owls may also benefit from nesting near California ground squirrels, as coloniality is associated with enhanced detection of predators (Pulliam 1973). The predation risk for Burrowing Owls living with squirrels could decrease due to "selfish herd" effects (an individual's risk of capture decreases when the predator chooses the closest prey; Hamilton 1971, Mooring and Hart 1992) or dilution effects (an individual's risk is reduced because the predator has many choices of individual prey; Dehn 1990). Living in larger groups may also allow an individual owl to be less vigilant (detection effect; Dehn 1990), thereby allowing owls more opportunities to engage in other activities, such as foraging.

This study quantified the rate of predator approaches to Burrowing Owls and their nests in urban Santa Clara County, California, and tested the extent to which Burrowing Owls and California ground squirrels responded to each other's alarm calls. We expected a significant number of Burrowing Owls and ground squirrels to respond to the other species' alarm calls. We also tested whether owl responses differed between predator and non-predator approaches, and examined whether the predator approach rate was related to the number of ground squirrels or differed between the daytime and nighttime periods.

Methods

We studied Burrowing Owls at Moffett Federal Airfield, approximately 60 km southeast of San Francisco, California (37°24.849′N, 122°2.916′W). Moffett Federal Airfield, an area of approximately 405 ha, included three large aircraft hangers, an active airfield, administrative and research buildings, roads, an irrigated golf course, and open grassland habitat. Open grasslands were dominated by nonnative grasses (predominantly *Avena* spp. and *Hordeum* spp.) and nonnative annuals, especially *Salsola kali, Brassica* spp., *Helminthotheca echioides*, and *Dittrichia graveolens* (Trulio and Higgins 2012). Burrowing Owl habitat on the site was restricted to the golf course, fragmented fields, roadside embankments, airfield edges, and ornamental landscaping (Trulio and Chromczak 2007). Between 1992 and 2000, 18–27 pairs of owls nested there each year (Trulio and Chromczak 2007).

We collected data during two Burrowing Owl breeding seasons, from 25 June to 18 August 2012 and 8 May to 13 July 2013. We located 41 adult Burrowing Owls (20 pairs and one solitary owl) in 2012 and 26 adults (12 pairs and two solitary owls) in 2013.

We obtained information on predator approaches using cameras and direct observations. For camera placements, factors such as accessibility and presence of human activity dictated which burrows were most appropriate. Bushnell 8MP Trophy cameras, operated by infrared beam, were mounted on stakes and directed at the burrow from a distance of no closer than 5 m, which resulted in a field of view of approximately 2.25 m × 2.25 m around each burrow. Anti-perching spikes placed on cameras prevented owls and their predators from perching on them. We divided the 24-hr period of camera operation into "daytime," from 0700 to 1800 H, and "nighttime" which was the remainder of the day. One of us (LAH) downloaded the photos from the cameras each week and reviewed all photos to identify species that approached owls and/or burrows and to ascertain if owls, nestlings, or eggs were taken. All photos had a date- and time-stamp associated with predator and non-predator approaches.

We used direct observations to collect data at all accessible nests; most of these also had cameras near them. A single observer conducted observations from an automobile at a distance of 30–60 m to ensure that owls were not disturbed (Bryan and Wunder 2013). Observations included thoroughly scanning the sky and terrain around focal nest sites for as far as reliably practical. Thus, a much greater field of observation was possible for direct observations compared to cameras, although direct observations were limited to daylight hours. We observed each nest approximately every other week for approximately 2 hr using Swift Reliant 10 × 42 binoculars and a Nikon Spotter XLII spotting scope (16 × 48). Times of day for viewing systematically rotated among three time periods (0600–1100 H, 1100–1600 H, and 1600–2100 H) to ensure observations occurred throughout the day. During each observation period, we conducted scan samples (Altmann 1974) by counting the number of squirrels and owls (adults and young) within 25 m of the focal owl nest at 15-min intervals. We then calculated the average number of squirrels and owls present near a nest burrow when predators were not present.

We defined potential predators as species documented in the literature as Burrowing Owl predators as well as animals to which squirrels or owls gave alarm calls. When potential predators were seen, we recorded: (1) the number of ground squirrels and owls present, (2) whether ground squirrels or owls responded first to predators entering the nesting areas, (3) ground squirrel and owl behavior in response to the species first calling (responses by squirrels or owls were classified by the animal's first response behavior; see Table 1), (4) the species, number, and behavior of potential predators, (5) the time of the approach, and (6) the length of time until owls returned to the burrow entrance if they went underground or flew away, to provide an index of predator effects on adults and nestlings. The longer adults stay underground or away from nestlings, the less time they have to feed their young, which could affect nestling health. In addition, birds that flee their burrow may risk increased exposure to predators.

For all observations (both breeding seasons combined) in which owls gave alarm calls first, we summed the number of squirrels (adults and young) exhibiting each type of behavior and divided by the total number of squirrels we observed in all observations to determine the percent of squirrels responding to owls by response behavior. This represented an overall response rate of squirrels to owl alarm calling, as some squirrels may have been observed more than once. Similarly, we calculated an overall response rate for owls when squirrels called first. Because we observed some burrows and thus probably some birds multiple times, we also calculated owl response to squirrels using no more than two observations per burrow per season. In this case, we used the earliest and latest observations in the season when there were more than two observations for a particular burrow, as this decreased multiple sampling of the same birds and provided the greatest chance of sampling different birds.

We classified each predator approach as one of four mutually exclusive categories: (1) "transit," defined as walking or flying near but not approaching nests or owls, (2) "move toward," defined as moving clearly toward the nest or owls, (3) "hunt," defined as attempting to enter the nest for terrestrial predators or as plunging downward toward the nest or owls by aerial predators, and (4) "predation," defined as an attack resulting in owl mortality or egg loss. The predator approach rate to each burrow per hour was calculated by summing all approaches for the season for each burrow and dividing by the total

Table 1. Behaviors of Burrowing Owls and California ground squirrels in response to alarm calling by the other species. Response behaviors are divided into two categories, alert behaviors and non-alert behaviors.

SPECIES AND RESPONSE BEHAVIOR CATEGORIES	BEHAVIOR AND DEFINITION	BEHAVIORS OBSERVED IN RESPONSE TO THE OTHER SPECIES' ALARM CALLING: NUMBER	BEHAVIORS OBSERVED IN RESPONSE TO THE OTHER SPECIES' ALARM CALLING: PERCENT OF TOTAL
Burrowing Owl			
Alert behaviors	Scan: Head movements to watch area	40	43
	Fly: Fly toward or away from burrow	4	5
	Alarm call: Rattles, clucks, and chatter	8	9
	Bob: Body and head up and down	2	2
	Run: Move quickly to burrow on foot	3	3
	Go underground: enter burrow	12	13
	Mob: Repeated flights toward predator	0	0
Non-alert behaviors	Stand: Stationary at burrow entrance	16	17
	Underground: Know to be in burrow	2	2
	Forage: Look for prey	0	0
	Preen: Nibble feathers with beak	1	1
	Rasp: Begging call	1	1
	No reaction: No change in behavior compared to before predator approach	4	4
TOTAL		93	100
California ground squirrel			
Alert behaviors	Stand up: Go from all-fours to standing on hind legs	14	18
	Run: Move quickly toward the burrow	13	17
	Dive: Quick move to go underground	1	1
	Whistle/chirp: Loud, single-note alarm call	3	4
	Chatter: Three- to four-note alarm call	0	0
	Tonic call: Continuous, repetitive chirp	0	0
Non-alert behaviors	Forage: Gathering/eating food	25	32
	Stand: Stand stationary	3	4
	Transit: Non-running movement between locations	5	7
	No reaction: No change in behavior compared to before predator approach	13	17
TOTAL		77	100

number of observation hours. We also measured the length of time owls took to return to the entrance of their burrow if they went underground or flew away in response to predators compared to non-predator species.

We used SYSTAT 13 for our statistical analyses. To test whether predator approach rates differed between daytime and nighttime periods, we summed the number of approaches recorded for each of the 16 burrows with cameras during the daytime period and the nighttime period over the season. We then divided by the total number of daytime or nighttime hours, respectively, recorded by each camera, to determine the daytime and nighttime predator approach rates per hour at each burrow. Using a paired *t*-test, we compared the daytime to the nighttime predator approach rates recorded per hour at each burrow ($n = 16$; log [x + 0.001] transformation). To compare the length of time owls took to return to the entrance of their burrows when approached by potential predators versus non-predator species, we used a Mann-Whitney *U*-test, as these data were not normal. For this second comparison, birds that did not reappear within 24 hr after the disturbance were not included, as we could not determine the length of time birds were underground or away from the burrow. We used a chi-square test to evaluate whether the ratio of squirrels and owls calling first was in proportion to their relative abundance. We used regression analysis to examine the relationship between the average number of ground squirrels near owl burrows (log [x

Table 2. Number of approaches by potential predators to Burrowing Owls and/or their nests (in order of greatest to fewest approaches), classified by observation type (direct observation, daytime camera, or nighttime camera) and by approach behavior category.

	OBSERVATION TYPE			APPROACH BEHAVIOR			
POTENTIAL PREDATOR	DIRECT	DAYTIME CAMERA	NIGHTTIME CAMERA	TRANSIT	MOVE TOWARD	HUNT	PREDATION
Red-tailed Hawk	60	5	1	15	24	26	1 (1 adult owl)
Common Raven	21	32	0	12	25	15	1 (1 egg)
Striped skunk	0	0	20	2	0	17	1 (1 clutch of eggs)
Coyote	0	0	14	2	7	5	0
Red fox	0	0	7	0	2	4	1 (4 juvenile owls)
Domestic cat	4	2	0	0	4	2	0
Peregrine Falcon	4	0	0	1	3	0	0
American Kestrel	2	0	0	0	1	1	0
Great Blue Heron	1	1	0	2	0	0	0
Gray fox	0	0	1	0	1	0	0
Egret spp.	1	0	0	1	0	0	0
Snake spp.	0	1	0	1	0	0	0
TOTAL	93	41	43	36	67	70	4

+ 1] transformation) and the rate of predator approach to each burrow per hour (log [x + 1] transformation).

RESULTS

We conducted 78 direct observations at 19 nests (10 nests in 2012 and nine in 2013), with a combined direct observation time of 100 hr over two seasons. Two of the nests were active in both years, and were included in the analysis; it was unknown whether the attendant owls were the same individuals in both years. The maximum number of ground squirrels near Burrowing Owl burrows during 15-min interval samples ranged from 0–21 squirrels ($\bar{x} = 6.05$, SE ± 0.278). On average, squirrels were more numerous than owls, as the ratio of the average number of squirrels to owls was approximately 2.8:1. Over the two seasons, we observed young at 12 of 19 nests.

The cameras placed at seven of the 10 nest burrows in 2012 and all nine burrows in 2013 collected a total of 14,540 hr of recordings and 317,531 photographs. Combining both direct and camera observations, we recorded 177 predator approaches by 12 taxa over both seasons (Table 2), 93 directly observed and 84 captured on camera. Red-tailed Hawks were the most frequently recorded predator and were most often seen during direct observations. The next most common predators were Common Ravens, striped skunks, and coyotes, all of which were detected more often with cameras than with direct observations. Most transits and approaches involved Red-tailed Hawks and Common Ravens, and most hunting behavior involved Red-tailed Hawk, striped skunk, coyote and red fox (Table 2). The predator approach rate during diurnal periods, as determined by direct observation, was 0.93/hr.

Four of 177 approaches resulted in predation (Table 2). One predation event, involving Red-tailed Hawks, was directly observed; the other predators were captured on camera and included a striped skunk, red fox, and Common Raven. The owls remaining after each of these four attacks abandoned their nests immediately or within a week of the predation event. Birds at four additional nests abandoned their burrows within a week after predator approaches; five of the eight abandonments occurred after nocturnal predator approaches. Thus, we recorded predation at 4 of 19 nests (21%) and nest abandonment at 8 of 19 nests (42%) after predator activity during the 2-yr period.

The predation by the Red-tailed Hawks was a collaborative effort by four hawks that mobbed owls at a burrow before one hawk captured an adult owl and flew away with it. The other daytime predation event involved a Common Raven taking an egg away from the entrance to a burrow. Predation by the red fox took most of a night beginning at midnight and involved the fox digging up the burrow and eventually taking four nestlings. The striped skunk was recorded entering a nest, and the next day we saw eggshells outside of the burrow.

There were 71 predator approaches during which both ground squirrels and owls were present and one or the other species gave alarm calls. Ground squirrels responded to predators before owls 66% of the time (47 approaches), and Burrowing Owls responded first 34% of the time (24 approaches). The ratio of squirrels to owls calling first was proportional to their relative abundance ($\chi^2 = 1.82$, df = 1, $P = 0.177$).

Of 93 owls observed at 19 burrows during predator approaches when squirrels called first, 75% of the owls exhibited alert behaviors (Table 1). Using data from no more than two observations per burrow in a season, we observed 33 owls at 12 different burrows over the two seasons and 84% percent of these owls exhibited alert behavior in response to squirrel alarm calls. Of 77 squirrels observed during predator approaches when owls called first, 40% exhibited alert behavior (Table 1).

The average length of time for owls to return to the entrance of their burrow differed significantly between approaches by potential predator species ($n = 44$) and approaches by non-predator species ($n = 24$), which included black-tailed jack rabbits (*Lepus californicus*), California Gulls (*Larus californicus*) and goats (*Capra* spp.; U-test = 239.0, df = 1, $P < 0.001$). Owls returned to burrow entrances after a non-predator approach in an average of 79.9 ± 35.1 min (range = 0–647 min), compared to 174.6 ± 31.1 min (range = 0–876 min) for predator approaches.

The rate of predator approach per burrow per hour was positively correlated to the average numbers of squirrels present ($R^2 = 0.567$, $P = 0.011$, $n = 19$), based on direct observations. At 16 burrows where we had cameras, the average rate of predator approach was 0.004 ± 0.001/hr during the daytime period, significantly lower than during the nighttime period (0.007 ± 0.002/hr; $t = -2.492$, df = 15, $P = 0.025$).

Discussion

In the urban setting at Moffett Federal Airfield in northern California, the most commonly recorded potential predators of Burrowing Owls (in order of greater to lesser frequency) were Red-tailed Hawks, Common Ravens, striped skunks, coyotes, red foxes, and domestic cats. The red fox, responsible for the loss of four young in a clutch, is a nonnative species in the South San Francisco Bay known to prey on ground-nesting bird species (Meckstroth et al. 2007). The frequency of Common Ravens, the second most common potential predator species, is of concern as the abundance of this species is increasing rapidly in urban areas (Webb et al. 2011) and may be affecting Burrowing Owl populations (Liebezeit and George 2002).

California ground squirrels were a regular part of the environment for the owls we studied and owls appeared to benefit from squirrel alarm-calling behavior. Squirrels called first in response to detection of predators 66% of the time. Because alarm calling is risky, as it may draw attention to the caller (Hoogland 1996), the owls likely benefited from the fact that alarm calls were given by squirrels most of the time. Also, because squirrels were more numerous than owls, the owls may benefit from dilution or "selfish herd" effects. In addition, over 75% of owls responded to squirrel alarm calls with alert behavior. This high response rate suggests owls used squirrels to alert themselves to predators, as has been documented for Burrowing Owls living within prairie dog colonies (Bryan and Wunder 2013). Owls seem to respond to the well-developed alarm-calling behavior of squirrels, which is known to reduce successful predator attacks on squirrels (Leger and Owings 1978, Hoogland 1996) and would be expected to have the same benefit for owls.

The frequency of the species that responded first to approaches matched the relative abundance of the two species at our study site. Because there were fewer owls than squirrels, the squirrels may have gained less from owl alarm calling. Also, only 40% of squirrels exhibited alert behaviors in response to owl alarm calls. Leger and Owings (1978) found that squirrels only call after a predator has been confirmed. Thus, the squirrels may not have responded to the owl alarm calls until the squirrels themselves detected the approaching predator.

The rate of predator approaches may have increased with increasing numbers of squirrels around owl burrows, although other factors not included in this analysis (e.g., relative predator density at different spatial scales) and the small sample size ($n = 19$) make this a preliminary result. Even if this was the case, Desmond et al. (2000) found predation rates for Burrowing Owls were lower in higher-density prairie dog colonies and Nisbet (1975) and Hoogland (1981), studying colony-nesting species, reported reduced rates of predation with increasing colony size.

Because predation was rare, we could not test whether squirrel alarm calling reduced predation of owls. Camera data indicated a higher rate of predator approaches and predation at night compared to daytime. Although there may be a number of reasons for this result (i.e., more effective predators), one factor might be that no squirrels were present at night. More data are needed to determine whether the predation rate is truly lower during the day and whether the presence of squirrels is a contributing factor.

When owls either went underground or flew from their burrows as a predator approached, they were gone much longer in comparison to approaches by non-predators. If the presence of squirrels decreases predator approaches that cause owls to flee, then owls would benefit from the reduction in the time they are displaced from the protection of their burrows or prevented from foraging by being underground.

Our results suggest that Burrowing Owls likely benefit from the alarm-calling behavior of California ground squirrels. Reductions in California ground squirrel populations, whether natural or human-caused, can inhibit the effective conservation of Burrowing Owl populations (Gervais et al. 2008). Loss of ground squirrels not only removes potential burrows for the owls, but also reduces the predator-detection service provided by the alarm calls of squirrels. This study underscores the value of maintaining large and healthy colonies of ground squirrels at sites where managers seek to protect and increase Burrowing Owl populations.

ACKNOWLEDGMENTS

We thank the following people for their assistance throughout this study: Chris Alderete at NASA Ames Research Center for his help and access to Moffett Federal Airfield; Debra Chromczak for her field assistance; Rachel O'Malley from the Department of Environmental Studies, San José State University, and Philip Higgins, City of Mountain View, for their review of this research; and Miranda Melen, Marissa Ponder, and Robert Olds for their content review and moral support. The College of Social Sciences at San José State University supported this work with a research grant. Our research was conducted with the approval of the San José State University Institutional Animal Care and Use Committee (Protocol # 2012-D). This paper was improved by the comments of the journal editors and reviewers and we thank them.

LITERATURE CITED

Altmann, J. (1974). Observational study of behavior: sampling methods. Behavior 48:227–265.

Bryan, R. D., and M. B. Wunder (2013). Western Burrowing Owls (*Athene cunicularia hypugaea*) eavesdrop on alarm calls of black-tailed prairie dogs (*Cynomys ludovicianus*). Ethology 120:180–188.

Coulombe, H. N. (1971). Behavior and population ecology of the Burrowing Owl, *Speotyto cunicularia*, in the Imperial Valley of California. The Condor 73:162–176.

Dehn, M. M. (1990). Vigilance for predators: detection and dilution effects. Behavioral Ecology and Sociobiology 26:337–342.

DeSante, D. F., and R. Scalf (2007). Distribution and relative abundance of Burrowing Owls in California during 1991–1993: Evidence for a declining population and thoughts on its conservation. In Proceedings of the California Burrowing Owl Symposium, November 2003 (J. H. Barclay, K. W. Hunting, J. L. Lincer, J. Linthicum, and T. A. Roberts, Editors). Bird Populations Monographs No. 1. The Institute for Bird Populations and Albion Environmental, Inc., Point Reyes Station, CA, USA. pp. 1–41.

Desmond, M. J., J. A. Savidge, and K. M. Eskridge (2000). Correlations between Burrowing Owl and black-tailed prairie dog declines: a 7-year analysis. Journal of Wildlife Management 64:1067–1075.

Gervais, J. A., D. K. Rosenberg, and L. A. Comrack (2008). Species accounts: Burrowing Owl (*Athene cunicularia*). Studies of Western Birds 1:218–226.

Green, G. A., and R. G. Anthony (1989). Nesting success and habitat relationships of Burrowing Owls in the Columbia Basin, Oregon. The Condor 91:347–354.

Hamilton, W. D. (1971). Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hoogland, J. L. (1981). Evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). Ecology 62:252–272.

Hoogland, J. L. (1996). Why do Gunnison's prairie dogs give anti-predator calls? Animal Behaviour 51:871–880.

Leger, D. W., and D. H. Owings (1978). Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. Behavioral Ecology and Sociobiology 3:177–186.

Liebezeit, J. R., and T. L. George (2002). A Summary of Predation by Corvids on Threatened and Endangered Species in California and Management Recommendations to Reduce Corvid Predation. Species Conservation and Recovery Program Report 2002–02. California Department of Fish and Game, Sacramento, CA, USA.

Martell, M. S. (1990). Reintroduction of Burrowing Owls into Minnesota: a feasibility study. M.S. thesis, University Minnesota, Minneapolis, MN, USA.

Meckstroth, A. M., A. K. Miles, and S. Chandra. (2007). Diets of introduced predators using stable isotopes and stomach contents. Journal of Wildlife Management 71:2387–2392.

Millsap, B. A., and C. Bear (2000). Density and reproduction of Burrowing Owls along an urban development gradient. Journal of Wildlife Management 64:33–41.

Mooring, M. S., and B. L. Hart (1992). Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. Behavior 123:173–193.

Nisbet, I. C. T. (1975). Selective effects of predation in a tern colony. The Condor 77:221–226.

Owings, D. H., M. P. Rowe, and A. S. Rundus (2002). The rattling sound of rattlesnakes (*Crotalus viridis*) as a communicative resource for ground squirrels (*Spermophilus beecheyi*) and Burrowing Owls (*Athene cunicularia*). Journal of Comparative Psychology 116:197–206.

Owings, D. H., and R. Virginia (1978). Alarm calls of California ground squirrels (*Spermophilus beecheyi*). Ethology 46:58–70.

Pulliam, H. R. (1973). On the advantages of flocking. Journal of Theoretical Biology 38:419–422.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. Smithsonian Contribution to Zoology 9:1–48.

Thomsen, L. (1971). Behavior and ecology of Burrowing Owls on the Oakland Municipal Airport. The Condor 73:177–192.

Trulio, L. A., and D. A. Chromczak (2007). Burrowing Owl nesting success at urban and parkland sites in northern California. In Proceedings of the California Burrowing Owl Symposium, November 2003 (J. H. Barclay, K. W. Hunting, J. L. Lincer, J. Linthicum, and T. A. Roberts, Editors). Bird Populations Monographs No. 1. The Institute for Bird Populations and Albion Environmental, Inc., Point Reyes Station, CA, USA. pp. 115–122.

Trulio, L. A., and P. Higgins (2012). The diet of western Burrowing Owls in an urban landscape. Western North American Naturalist 72:348–356.

Webb, W. C., J. M. Marzluff, and J. Hepistall-Cymerman (2011). Linking resource use with demography in a synanthropic population of Common Ravens. Biological Conservation 144:2264–2273.

Wilkerson, R. L., and R. B. Siegel (2010). Assessing changes in the distribution and abundance of Burrowing Owls in California, 1993–2007. Bird Populations 10:1–36.

Received 31 August 2017; accepted 3 January 2019
Associate Editor: Joseph B. Buchanan