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Western Burrowing Owls (*Athene cunicularia hypugaea*) Eavesdrop on Alarm Calls of Black-Tailed Prairie Dogs (*Cynomys ludovicianus*)

Rebecca D. Bryan & Michael B. Wunder

Department of Integrative Biology, University of Colorado, Denver, Colorado, USA

Correspondence

Rebecca Bryan, Department of Integrative Biology, University of Colorado, Denver, 1250 14th Street, Denver, Colorado 80217, USA. E-mail: Rebecca.Bryan@ucdenver.edu

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Introduction

180

Animals sharing a common habitat and common predators can indirectly receive information about their environment by observing information exchanges between other animals, a process known as eavesdropping. When an individual animal gathers information about the environment it may produce a vocal cue in response to that information for the benefit of other group members or kin. When an alarm call is

Abstract

Animals sharing a common habitat can indirectly receive information about their environment by observing information exchanges between other animals, a process known as eavesdropping. Animals that use an auditory alarm calling system are an important indirect information source for eavesdropping individuals in their environments. We investigated whether Western burrowing owls (Athene cunicularia hypugaea) nesting on black-tailed prairie dog (Cynomys ludovicianus) colonies responded to broadcasts of prairie dog alarm calls. Western burrowing owls are closely associated with black-tailed prairie dogs in Colorado and neighboring states on the Great Plains of the United States. Prairie dog burrows in active colonies can serve as nesting sites for Western burrowing owls, and prairie dogs may act as an alternative prey source for predators, potentially decreasing the burrowing owls' risk of predation through the dilution effect. Burrowing owls nesting on prairie dog colonies may also eavesdrop on prairie dog alarm calls, enhancing their survival and nesting success on prairie dog colonies. We performed broadcast experiments with three different sounds: a prairie dog alarm call, a biological control (cattle mooing), and a non-biological control (an airplane engine), and characterized burrowing owl responses as either alert or relaxed. For each sound stimulus, we recorded the time to first alert response to broadcast sounds (latency) and also how frequently the target burrowing owl exhibited an alert response within the first ten seconds of the broadcast (intensity). Burrowing owls reacted more quickly to the prairie dog alarm than to the biological control. They significantly increased the intensity of alert behaviors in response to broadcasts of the alarm, but did not show an increased reaction to either the biological or the non-biological control. Our results suggest that burrowing owls nesting on prairie dog colonies eavesdrop on, and increase their alert behaviors in response to, prairie dog alarm calls.

sent out, there is also the potential for unintentional recipients (<u>Goodale et al. 2010</u>). Animals that use an auditory antipredator alarm calling system are an important indirect information source for eavesdropping individuals in their environments.

Eavesdropping behavior is common between species of birds and between species of mammals, but interorder and even interclass eavesdropping is effective in many systems as well. Though they may be from different taxa, animals that share a habitat and have similar predators are likely to pay attention to alarms because doing so can increase their fitness (Templeton & Greene 2007; Carrasco & Blumstein 2012). Evidence of interorder and interclass eavesdropping on avian alarm calls has been documented in mammalian and reptilian species (Randler 2005; Vitousek et al. 2007; Lea et al. 2008; Mueller & Manser 2008; Schmidt et al. 2008; Ito & Mori 2010). In the studies listed above, the eavesdropper is attending an avian alarm call. Rainey et al. (2004) found evidence of a more unusual interclass eavesdropper: a bird eavesdropping on a mammalian alarm call. Yellow-casqued hornbills (Ceratogymna elata) eavesdrop on alarm calls of Diana monkeys (Cercopithecus diana), and are able to differentiate between the monkeys' alarm signals (Rainey et al. 2004).

Western burrowing owls (Athene cunicularia hypugaea) are listed as a species of special concern in several states in the U.S. Great Plains, including Montana, Oklahoma, Utah, and Wyoming (Klute et al. 2003), and are listed as a state-threatened species in Colorado (Colorado Division of Wildlife 2013). Western burrowing owls (hereafter, burrowing owls) are closely associated with black-tailed prairie dogs (Cynomys ludovicianus) (hereafter, prairie dogs), and the decline in prairie dog populations due to management and sylvatic plague has been correlated with declines in burrowing owl populations (Desmond et al. 2000). Burrowing owls are and have historically been found more often on than off active prairie dog colonies in the Western Great Plains (Butts & Lewis 1982; Agnew et al. 1986; Barko et al. 1999; Tipton et al. 2008). Burrowing owls commonly nest on prairie dog colonies with high burrow densities (Plumpton & Lutz 1993), and show a preference for active prairie dog colonies over abandoned colonies (Butts & Lewis 1982; Sidle et al. 2001). Multiple hypotheses have been put forth to explain this association between burrowing owls and prairie dog colonies. The disturbances prairie dogs create provide nest sites, and the short grass provides foraging habitat and visibility of predators (MacCracken et al. 1985; Green & Anthony 1989; Plumpton & Lutz 1993). Also, having prairie dogs nearby may cause a dilution effect if prairie dogs act as an alternative prey source for predators (Desmond et al. 2000). Desmond et al. (2000) and Beradelli et al. (2010) suggested that burrowing owls nesting on black-tailed prairie dog colonies may eavesdrop on the prairie dogs as well. This could enhance the birds' survival on colonies and offer a further explanation of burrowing owl presence on active prairie dog colonies.

Burrowing owls use vocal alarm signals to alert each other to dangers, and those alerted (young or a nearby member of a pair) will retreat in response (Coulombe 1971). Burrowing owls sharing a habitat with another species that uses an alarm calling behavior (e.g. prairie dogs or ground squirrels) may increase their vigilance when they hear an alarm from that species. Black-tailed prairie dogs emit alarm calls in the presence of predatory threats to alert relatives and distant kin of danger (Hoogland 1995). Burrowing owls share predators with prairie dogs: American badgers (Taxidea taxus), coyotes (Canis latrans), red-tailed hawks (Buteo jamaicensis), and possibly prairie rattlesnakes (Crotalus viridis) and bullsnakes (Pituophis catenifer) predate both prairie dog and burrowing owl young (Coulombe 1971; Halpin 1983). Burrowing owl adults that eavesdrop on alarming prairie dogs could potentially learn when predators are approaching. If they increase their vigilance so they can respond appropriately to protect their young, they may enhance their fitness. In this study, we tested whether burrowing owls would respond differently to a prairie dog alarm call than to a non-alarm sound.

Methods

With permission from the Central Plains Experimental Range (CPER) and the U.S. Forest Service, we conducted broadcast experiments on nesting burrowing owls on 14 different prairie dog colonies on the CPER and the Pawnee National Grasslands (PNG) (40°49' 24"N 103°58'10"W, elevation 1594 m), located in Weld County, Colorado. We conducted experiments during June and July 2011. The PNG is an arid shortgrass steppe ecosystem characterized by a monsoonal precipitation pattern (SGS-LTER. 2007). We conducted our experiments on prairie dog colonies on actively grazed rangeland, where vegetation included buffalo grass (Buchloe dactyloides), blue grama (Bouteloua gracilis), prickly pear cactus (Opuntia polyacantha), scarlet globemallow (Sphaeralcea coccinea), saltbush (Atriplex canescens), and field bindweed (Convolvulus arvensis).

We conducted audio broadcasts to burrowing owls nesting at 20 different locations on 14 active prairie dog colonies; five of the colonies had >1 nesting burrowing owl pair present, and on these colonies, we performed broadcasts near different nests on different days. We broadcasted 5-min recordings of a randomized sequence of sounds to each bird: a prairie dog alarm call (the experimental treatment), a small airplane engine (a non-biological control treatment), and cattle mooing (a biological control treatment). We reasoned that there might be sound quality differences between what was played on the speaker and natural sound, so we included ambient noise (intermittent birdsong, insect chatter, and other typical prairie sounds) before and between sound broadcasts. This allowed consistency between the sound quality of normal ambient sound and our broadcasts.

We collected digital recordings of all sounds using a Marantz[®] PMD661 digital recorder (Mahwah, NJ, USA) and AudioTechnica[®] shotgun microphone (Stow, OH, USA). With the exception of the airplane sound, which we collected near the Rocky Mountain Metropolitan Airport in Broomfield, Colorado, we recorded all sound stimuli on the PNG or the CPER. We recorded a herd of mooing cattle on open range on the PNG. We recorded prairie dog alarm call responses to a simulated snake predator (a toy snake pulled through the colony on a fishing line) on the CPER. We edited and combined the sounds using RavenPro 1.4[®] sound analysis software (Ithaca, NY, USA). To minimize the chance that the order of the sound broadcasts affected burrowing owl responses, we created three different treatment orders: Order 1 - prairie dog alarm (A), cattle mooing (biological control - B), airplane (non-biological control - N); Order 2 – B, N, A; and Order 3 – N, A, B. Because of the potential for differences in sound qualities of natural and broadcast sounds, we started every trial with 2 min of pre-recorded ambient noise, and broadcasted all stimulus sounds at 80 dB. Each stimulus sound lasted 30 s, and the stimulus sounds were separated from each other by 1 min of pre-recorded ambient noise. We video recorded all trials using a JVC[®] Everio HD camcorder (Wayne, NJ, USA). The time frame over which we ran trials coincided with the burrowing owls' nesting and chick-rearing stages. We did not know if this would affect adult vigilance patterns, so we divided all trials into two categories: 'early' (when eggs had not yet hatched or had hatched but chicks had not yet surfaced) and 'late' (when nestlings had surfaced and were beginning to disperse to nearby burrows).

Field Methods

For each trial, we placed a SME-AFS portable field speaker (Elmont, NY, USA) within 10 m of an active nest burrow. Burrowing owls usually flushed or ducked into the nest or a nearby burrow upon our arrival. Before beginning any broadcast experiments, we waited in a blind (either a truck or camouflaged pop-up hunting blind) for the bird to return to the vicinity of the speaker. For most trials the target

182

burrowing owl was between 10 and 20 m of the speaker. The blind was 25 to 50 m from the nest burrow and target burrowing owl for all trials. We used the pop-up hunting blind when it was not possible to use the truck as a blind. Manning & Kaler (2011) found less displacement of burrowing owls when conducting surveys from inside of a vehicle, and we further reasoned that the burrowing owls might be more accustomed to trucks because of ranching activities on the PNG. We therefore used the truck as a blind as much as possible. We tested for differences in burrowing owl responses based on blind type when running analyses. Burrowing owls in our study were unmarked, so it was not possible to determine if broadcast trials were repeated on the same bird on different days. We rotated nest sites visited daily to ensure that we did not subject the same burrowing owl to the same broadcast trial on consecutive days. All observations and recordings were made by the same individual observer (RB). All work was approved by the University of Colorado Institutional Animal Care and Use Committee protocol number100961.

We conducted a total of 93, 3-sound broadcast experiment trials on 16 different adult burrowing owl nesting pairs on 14 active prairie dog colonies over the 2-month period. We analyzed burrowing owl responses from 55 total prairie dog alarm broadcasts (truck blind n = 42, pop-up blind n = 13), 52 total cattle moo broadcasts (truck blind n = 35, pop-up blind n = 17), and 50 total airplane engine broadcasts (truck blind n = 35, pop-up blind n = 15). We censored the remaining broadcasts for various reasons, including excessive background noise: high winds; interruptions such as vehicles, prairie dogs, or cattle; burrowing owls leaving the experimental trial area; or too much distance between the video camera and the target burrowing owl for accurate behavioral scoring.

Data Analysis

We watched the recorded videos and assigned burrowing owl behavioral responses as described in the ethogram in Table 1. We used JWatcher[®] 1.0 software (Blumstein et al. 2006) to track the number and rate of responses we saw in each video. If a target burrowing owl moved ≥ 30 m from the speaker during the broadcast or ducked underground and did not re-emerge, we included only those parts of the trial where the bird was ≤ 30 m from the speaker in analyses. If there were prairie dogs vocalizing during the broadcast, we did not include the trial in analyses.

We classified responses as either 'alert' or 'relaxed.' Alert responses included head turns, bobbing,

Alert behaviors	Description	Relaxed behaviors	Description
Head turn	Standing or perching and turning head in any direction other than down	Sleeping	Eyes closed or heavily lidded
Stretching up tall		Preening	Actively preening feathers or stretching wings
Squatting low		Yawning	
Vocalizing Bobbing	Chattering or screeching Full body or head bob	Foraging	Looking at the ground or following insects

Table	1:	Ethogram	of	scored	burrowing	owl	behaviors
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We tracked the number and rate of burrowing owl responses using J-Watcher 1.0 software (Blumstein et al. 2006). We scored each of the listed behaviors individually, and then classified them as 'alert' or 'relaxed' for data analysis.

vocalization, or stretching tall or squatting low with eyes open and focused on any area other than the ground. Relaxed responses included preening, yawning, or sleeping (Table 1). For the purposes of this study, we also categorized foraging or looking straight down at the ground or feet as relaxed responses, because we assumed the burrowing owls' vigilance was directed toward prey and not toward external threats such as predators. We did not include locomotion such as walking, running, or flying in our ethogram, as these ended in censorship because the owl went off-camera. We were not able to differentiate whether alert responses were a result of vigilance or mating behaviors. We calculated (1) latency: the time to first alert response to broadcast sounds (how quickly the burrowing owl reacted to the sound broadcast), and (2) intensity: how frequently the target burrowing owl exhibited an alert response within the first 10 s of the broadcast. We used R[®] version 2.11.1 (©2010: The R foundation for statistical computing) for all statistical analyses.

Latency

We measured how quickly burrowing owls responded to each sound stimulus, and compared these measurements among broadcast types. To determine the response times in seconds, we subtracted the start time of a broadcast from the start time of the first alert response of the focal burrowing owl after that broadcast began. Because we ran the experiment multiple times on the same nest, and did not know if we were testing the same individual each time, we had to determine if we could look at trials independently. We fit a mixed effects model for time to response with broadcast type as a fixed effect and nest identity as a random effect. From that analysis, we computed the proportion of the variance that could be explained by nest identity. Of the variability that was explained, less than 2 \times 10⁻⁷ was explained by nest id. Thus we decided to treat each experiment as an individual trial

and interpreted fixed effects from the model directly. After censoring trials for reasons described above, we were left with 61 trials that used the AMP order, 52 that used the MPA order, and 41 that used the PAM order. Because this censoring resulted in an experimental design that was imbalanced across broadcast order, we quantified the proportion of variance explained by broadcast order. A mixed effects model with broadcast type as a fixed effect and order as a random effect showed that 0% of the variability was explained by order. To determine if nesting stage affected latency to response, we conducted a 2-way ANOVA to test interaction between these two variables. Similarly, we used 2-way ANOVAs to test whether there was an interaction between 1) blind type and latency and 2) between latency and the order we presented the sound cues. We used a Kruskal–Wallis rank sum test to determine whether there were differences in median time to response in each of the broadcast categories: alarm, biological control, and non-biological control. To determine which of the burrowing owls' responses were different from one another, we conducted Bonferroni-adjusted Wilcoxon matched-pairs signed-ranks tests.

Intensity

We counted the number of alert responses the focal burrowing owl showed during the first 10 s following a broadcast. To determine whether we could look at trials independently, we fit a mixed effects model to determine the proportion of variance explained by nest identity as with latency models. From that analysis, we computed that approximately 15% of the variability was explained by nest id, whereas 85% of the variability could be explained by the sound treatment. As with latency, we had to censor some responses in our intensity measurements. After censoring, we were left with 23 using the AMP order, 24 using the MPA order, and 21 that used the PAM order. Because this censoring again resulted in an imbalanced

experimental design, we quantified the proportion of variance explained by broadcast order for these trials. A mixed effects model with broadcast type as a fixed effect and order as a random effect again showed that 0% of the variability was explained by order. We decided to treat each broadcast as an individual trial, and assigned the response to one of three categories. We categorized intensity as low: 0–2 alert behavioral responses, moderate: 3–4 alert behavioral responses, or high: 5 or more alert behavioral responses. We used a Fisher's exact test to determine whether nesting stage or blind type affected the distribution of burrowing owls' categorical responses. We used a Fisher's exact test to compare the distributions of categorical responses among sound types.

Results

Latency

We fit two different mixed effects models to compare median response times to the alarm, plane, and moo stimuli. Both models included the nest id as random effect. One included stimulus as an explanatory factor and the other did not. We computed the likelihood ratio for our model that included stimulus as an explanatory factor for response time and compared it to the null model that did not include stimulus as an explanatory factor. The likelihood ratio for the model response time with the stimulus as a factor suggested that the broadcast stimulus had a non-zero effect on the difference in time to response ($\chi^2 = 5.525$, p = 0.063). There were no significant differences in the median latency to response based on the order in which we broadcast the sounds (2-way ANOVA stimulus by order interaction: $F_{2,148} = 0.76$, p = 0.63), the birds' nesting stage (2-way ANOVA stimulus by phenology interaction: $F_{2,151} = 0.62$, p = 0.54), or by blind type (2-way ANOVA stimulus by blind interaction: $F_{2,151} = 0.32$, p = 0.72), so we pooled data over these variables in subsequent analyses. Median latency to response times differed significantly among broadcasts (Kruskal–Wallace $\chi^2_2 = 8.697$, p = 0.013). The median latency to response to the prairie dog alarm broadcast (\tilde{x} : 1.3 s, range: 0.22–32.9 s) and to the non-biological control broadcast (\tilde{x} : 0.75 s, range: 0.28-35.42 s) were less than the median latency to response to the biological control broadcast (\tilde{x} : 2.62 s, range: 0.25-125.82 s) (Wilcoxon tests with Bonferroni adjustment: Biological control vs. Non-biological control W = 1691, p = 0.045, Alarm vs. Biological control W = 971, p = 0.028) (Fig. 1). There was,



Fig. 1: Latency of response of burrowing owls to sound broadcasts. Burrowing owls had shorter median latency to response times to the prairie dog alarm broadcast and the non-biological control broadcast than to the biological control sound (Pairwise Wilcoxon test with Bonferroni adjustment: Alarm vs. Non-biological control cue p = 0.045, Alarm vs. Biological control cue p = 0.028). Responses to the biological sound broadcast showed more variance in the length of time from sound cue to first alert response.

however, no statistically significant difference in the median response time to the non-biological control sound and the prairie dog alarm sound (W = 1424.5, p = 1.0).

Intensity

There were no significant differences in frequency distributions of response intensity categories (low, moderate, high) based on the order in which we broadcasted the sounds (Fisher's exact test on each stimulus by position in order: Alarm: p = 0.31, Biological Control: p = 0.20, Non-biological control: p = 0.32) or based on nesting stage of the target burrowing owl (Fisher's exact test p = 0.30). When we compared distributions by blind type, we found fewer high intensity responses (n = 3) than expected with the pop-up blind (Fisher's exact test p < 0.01). Because of this discrepancy, we analyzed the data collected in each blind type separately.

In experiments conducted from the truck, burrowing owls showed more high intensity responses and fewer low intensity responses than expected when we broadcasted the prairie dog alarm sound. In response to the biological control sound, we found burrowing owls showed fewer high intensity responses and more low intensity responses than expected. Burrowing owl responses were not different than expected in response to the non-biological sound (Fisher's Exact test p = 0.024; Fig. 2). In experiments conducted from the pop-up blind, we found no significant differences in the burrowing owls' observed and expected response categories for all sound types (Fisher's Exact test p = 0.15). However, we recorded only three high intensity responses to broadcasts played from the popup blind, and all of those were in response to the prairie dog alarm cue.

Discussion

Our study provides an example of cross-taxa eavesdropping that may alert the eavesdroppers to potential threats in their environment. We found that burrowing owls living on prairie dog colonies increased their alert behaviors when we broadcasted recorded prairie dog alarm calls. Burrowing owls reacted more quickly to the prairie dog alarm broadcast than to a non-alarm biological sound broadcast (cattle mooing), and sustained an increase in alert behaviors after their initial response.

We used a prairie dog alarm call in response to a simulated snake predator. Burrowing owl eggs are prey for snakes. Although we found no documentation



Fig. 2: Intensity of response of burrowing owls to sound broadcasts. We presented owls with three different sound stimuli: our experimental treatment ('Alarm') - a prairie dog barking in response to a snake predator, a Biological Control – cattle mooing, and a Non-biological Control – a low-flying airplane engine. Intensity of responses are categorized as 'low' (0-2 alert behaviors within the first 10 s of playback), or 'high' (5 or more alert behaviors within the first 10 s of playback).

of snakes predating adult burrowing owls, all of our experimental trials took place during the nesting season, and we reasoned that snakes would be seen as a threat by nesting burrowing owls. We also chose to use the snake because we wanted to ensure that the prairie dog alarm was in direct response to a predator, and we could control the presentation timing of the snake on the colony. It was important to record and broadcast an alarm call from prairie dogs currently living in the study area. There is evidence that prairie dogs may have different dialects depending on their location (<u>Slobodchikoff et al. 1998</u>), and we wanted to make certain that the burrowing owls receiving the broadcast sounds were hearing alarms in the dialect to which they were accustomed.

When we broadcasted the prairie dog alarm, burrowing owls showed fewer low intensity responses than expected based on chance alone, and they showed significantly more moderate and high intensity responses than expected. Although burrowing owls initially reacted quickly to both non-biological and alarm sound broadcasts, the alert responses following the non-biological sound broadcast were not sustained. The nonbiological sound broadcast was of a loud airplane engine and started suddenly without any build-up. Because of this, it may not have particularly resembled any sounds that the burrowing owls were accustomed to hearing at the study site. We suggest that this sudden sound may have startled the burrowing owls into a quick alert response, but it was likely not interpreted as an immediate threat. The burrowing owls did not sustain an increase in alert behaviors over the subsequent ten second interval.

Our study sites on the PNG and CPER provide summer grazing for cattle at 'moderate' rates (4 acres per animal unit month (AUM)) (M. Ashby, CPER, personal communication), though intensities vary because grazing pastures are leased to private cattle owners. During the time we conducted our experiments, burrowing owls were likely accustomed to cattle near their nests. Cattle communicate vocally with each other, and although some cow vocalizations may be in response to threats (Watts & Stookey 2000), cattle do not share predators with burrowing owls. Even if cattle respond to snakes in a way that burrowing owls could eavesdrop upon, that behavior may not have had time to develop. Burrowing owls and prairie dogs have shared habitat for thousands of years, whereas organized cattle ranching on the Great Plains did not begin until the late 1860s (ERS 2000). Burrowing owls historically shared this ecological niche with American Bison (Bison bison) as well as prairie dogs, and bison may serve in many ways as an ecological analog to cattle. However, bison do not moo to communicate with each other. Also, it may not be necessary for burrowing owls to become or to remain highly alert in the presence of cattle: it is possible that the presence of cattle deters potential predators and thus reduces predation risk to burrowing owls.

Burrowing owls in this area are strongly associated with prairie dogs; the owls live in abandoned or co-opted burrows on active colonies and occasionally interact with foraging or cover-seeking prairie dogs that approach their nests by flying at them or vocalizing toward them (R.D. Bryan, personal observation). Foraging black-tailed prairie dogs are generally quiet and intermittently vigilant, looking around or standing up and scanning the environment periodically during grazing (Hoogland 1979). Black-tailed prairie dogs do not rely on a single sentinel keeping watch for the entire group; instead all individuals regularly survey their surroundings, and when a threat is detected, the individual detecting the threat will alert others in the group with a bark alarm (Hoogland 1995). Like prairie dogs in the vicinity of the alarming animal, burrowing owls in the area also increase their alert behaviors in response to the alarm.

Our data suggest that burrowing owls nesting on prairie dog colonies may benefit from eavesdropping

on prairie dog alarm calls. Burrowing owls that increase alert behaviors in response to a prairie dog alarm may become aware of threats in their environment sooner than would otherwise be the case. However, whether the owls are reacting to the urgency of the alarm or to semantic information contained in the alarm is not known and deserves further exploration. In many eavesdropping species, eavesdroppers can differentiate alarm calls from non-alarm vocalizations (Vitousek et al. 2007; Goodale et al. 2010; Ito & Mori 2010), as well as distinguish predator-specific alarm calls (Rainey et al. 2004). Eavesdroppers that can differentiate among call types would have the advantage of investing less energy on increased vigilance by not responding to calls that do not indicate a threat to the eavesdropper. Rainey et al. (2004) demonstrated that yellow casqued hornbills are able to distinguish between predator-specific calls given by Diana monkeys, and only show increased antipredator behaviors when they hear the alarm for a shared predator. Prairie dogs also emit predator-specific calls that differ in response to predator type and mode of approach (Fredrickson & Slobodchikoff 2007). Burrowing owls may in turn differentiate among types of prairie dog alarm calls. In this study, we quantified reactions to only the snake predator alarm call. Further studies of owl reactions to a range of specific alarm and non-alarm calls would help determine whether owls are able to decipher the information coded in prairie dog alarms.

Regardless of whether burrowing owls can differentiate among the prairie dog alarm calls, our data demonstrate that burrowing owls respond to prairie dog alarm calls by increasing their alert behaviors. Burrowing owls in the Great Plains states prefer active prairie dog colonies (Desmond et al. 2000; Sidle et al. 2001). Our study demonstrates that aside from the available nesting sites and short-cropped grass on prairie dog colonies, there may be another benefit to burrowing owls nesting on active prairie dog colonies: reduced predation may derive from the *in situ* prairie dog alarm system.

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