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Territory defense of nesting Burrowing Owls: responses to simulated conspecific intrusion

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ABSTRACT. To investigate the potential expression of territorial behavior of Burrowing Owls (*Athene cunicularia*) in southwestern Idaho, we used a playback protocol to determine if Burrowing Owls actively defended their nesting site from conspecifics, and if so, to determine the extent of their territorial boundaries. Eighty-eight percent of male Burrowing Owls responded to the broadcast of conspecific primary calls. All responsive males uttered primary calls, and many owls approached the broadcast speaker, exhibited white-and-tall stances, and bobbed. Females responded less frequently than males, but one female whose mate was presumably dead exhibited an intense response to the playback trial. There were no differences in number of primary calls uttered, number of white-and-tall stances performed, or number of bobs of focal males among three broadcast distances: (0 m, 50 m, and 100 m) from the active nest burrows. However, focal owls approached the broadcast speaker more closely at broadcast distances of 0 m and 50 m than at 100 m. These findings suggest that owls actively defended their nesting site from conspecifics and that they defended an area larger than that immediately surrounding the nest burrow. Although they continued to vocalize at distances of at least 100 m, they did not physically approach an intruder at this distance as frequently as at shorter distances. Therefore, Burrowing Owls appear to defend a territory that encompasses some, but not all, of the foraging area used during nesting.

SINOPSIS. **Defenza territorial de individuos nidificantes de *Athene cunicularia*: respuesta a la presencia simulada de congéneres**

Para investigar el potencial de expresión de la conducta territorial del buho *Athene cunicularia* en el suroeste de Idalho, utilizamos el protocolo de voces grabadas para determinar si los buhos defendían sus territorios activamente de otros congeneres y para determinar los límites territoriales de la especie. El 88% de los machos respondieron a la grabación de la llamada primaria de congéneres. Todos los machos respondieron con su llamada principal y hubo individuos que se acercaron a las bocinas y frente a estas exhibieron patrones de conducta de defenza territorial. Las hembras respondieron con menor frecuencia que los machos, pero una hembra, que aparentemenete había perdido a su pareja, exhibió una intensa respuesta a la grabación. No hubo diferencias en el número de llamadas primarias producidas, en los patrones de conducta asociados al territorialismo o a diferentes distancias a las cuales se colocaron bocinas (0, 50 y 100 m) de las cavidades en donde se encontraban los buhos. Sin embargo, la tendencia de acercarse a las bocinas fue mayor entre más cerca se colocaron las mismas de las guaridas. Los hallazgos sugieren que los buhos defienden activamene sus guaridas de congéneres y que defiende un área mayor que las inmediaciones del hueco en que viven. Aunque vocalizan como respuesta a la grabación de la voz de un congénere colocada a 100 m de distancia, fisicamente no se acercan al aparente intruso de la misma manera que cuando el artefacto es colocado a menor distancia. Por lo tanto, los buhos estudiados aparentan defender un territorio que incluye, pero no en su totalidad, toda el área que utilizian para forrajear durante el periodo de anidamiento.

Key words: *Athene cunicularia*, Burrowing Owl, Idaho, playback experiment, territory defense

Territorial defense is an important aspect of the breeding behavior of many birds (Brown 1964; Dhondt and Schillemans 1983; Bosakowski and Smith 1998). A territory can be simply defined as any defended area, which may be defended by threat, song, or any other behavior that results in avoidance by other individuals (Hinde 1956). Individuals that are able to defend territories that contain superior resources (e.g., food and nesting sites) ensure a greater chance of successful reproduction. Although many studies have documented the territorial behavior of birds and factors contributing to this behavior (Krebs 1971; Evans 1980; Galeotti 1994), most aspects of territoriality in Burrowing Owls (*Athene cunicularia*) are poorly understood. Previous research has provided anecdotal information regarding aggressiveness in Burrowing Owls that biologists presume is indicative of territoriality (e.g., Thomsen 1971; Martin 1973), but to our knowledge no experimental investigations have confirmed this notion.

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Playbacks are commonly used to census birds and address territoriality (Johnson et al. 1981). This is done by broadcasting tape-recorded vocalizations of either conspecifics (Carpenter 1987; Mosher et al. 1990; Galeotti et al. 1997) or heterospecifics (Bosakowski and Smith 1998; Boal and Bibles 2001) that typically simulate a territorial intrusion to which residents respond. As a censusing technique, playbacks have been valuable in detecting the presence of many owl species (Clark 1988; Morrell et al. 1991; Salvati et al. 2000; Gosse and Montevecchi 2001), including Burrowing Owls (Haug and Didiuk 1993; Fahler 1998), and other secretive or elusive taxa (Conway et al. 1993; Glahn 1974; Repking and Ohmart 1977). The playback technique also has been used to study the territorial behavior and ecology of owls (e.g., Gerhardt 1991; Galeotti and Pavan 1993; Boal and Bibles 2001).

Although previous research (Haug and Didiuk 1993; Conway and Simon 2003) has established the general effectiveness of playbacks for detecting nesting Burrowing Owls, this method has not been used to investigate the expression and intensity of territorial behavior in this species. Therefore, we conducted a field experiment using playback protocols and previous information on Burrowing Owl vocalizations (Thomsen 1971; Haug et al. 1993) to determine whether Burrowing Owls actively defend their nesting site from conspecifics, and if so, their response to simulated conspecific instrusion at differing distances from the nest. Based on observations in Thomsen (1971) and Martin (1973), we anticipated that Burrowing Owls would actively defend their nesting site, and that they would defend more than the area immediately surrounding the nest burrow. Thus, we hypothesized that owls would defend an area corresponding with the distance from the nest at which the owls were not likely to encounter another nesting Burrowing Owl. To test this hypothesis and to determine the extent of Burrowing Owl territorial boundaries, we designed a playback experiment that broadcast Burrowing Owl primary calls at various distances from active nests.

STUDY AREA AND METHODS

We studied Burrowing Owls nesting within and near the Snake River Birds of Prey National Conservation Area (NCA) located in southwestern Idaho. We focused on several areas situated approximately 8–20 km north northeast of Grand View (Elmore County) and 3 km south of Kuna (Ada County). This study area was once representative of a typical shrub-steppe community dominated by large expanses of big sagebrush (*Artemesia tridentata wyomingensis*; Hironaka et al. 1983). Disturbances, such as range fires, have converted the majority of this shrubland to exotic annual grasslands dominated by cheatgrass (*Bromus tectorum*) and tumble mustard (*Sisymbrium altissimum*). Surrounding areas also contained irrigated agricultural fields (primarily alfalfa, sugar beets, and mint), scattered residential homes, paved and dirt roads, a military training area, and public lands managed by the Bureau of Land Management.

We conducted playback experiments at active owl nests during the 2001 and 2002 breeding seasons. We chose to focus mainly on the responses of males, as we expected them to be more visible and more likely to respond than females. To control for effects of nesting period, all playback experiments took place during the first week after young hatched (mid-May to early June; Marler and Moore 1991; Herting and Belthoff 1997).

To help determine how large an area Burrowing Owls defended, we conducted playback experiments at 0 m, 50 m, and 100 m from active nest burrows. The interval of 100 m represented a distance at which we thought the owls would be unlikely to respond, as it is quite possible for an owl to encounter another nesting owl within 100 m of its own nest (J.R. Belthoff, unpubl. data). However, at a distance of 50 m an owl would be less likely to encounter another nesting owl, and we expected the focal male to consider an owl at this distance to be a potential intruder. Finally, a distance of 0 m from the nest burrow represented a serious encroachment on the focal male's territory, and should have elicited an intense territorial response.

Playback recordings. We used previously tape-recorded Burrowing Owl vocalizations, broadcast from a Johnny Stewart Bird and Animal Caller® (JS Caller), to potentially elicit territorial responses during systematic trials. To control for the potential effects of the presence of the speaker and sound being broadcast from

the speaker, we also used recordings of Western Meadowlarks (*Sturnella neglecta*). Because Western Meadowlarks are common in our study area, the Burrowing Owls likely were familiar with this particular species' song.

We used several tapes to minimize unidentified biases potentially present in the recordings and to increase the external validity of the experiment (Kroodsma 1989). Burrowing Owl tapes contained the primary call of males, and each tape consisted of vocalizations from one of three different individual owls. Control tapes contained Western Meadowlark songs, and each tape consisted of vocalizations from one of three different individual meadowlarks. Each tape consisted of a 5-min recording, which included two bouts of 2.25 min of Burrowing Owl or meadowlark vocalizations separated by 30 s of silence.

Initial playback trial design. In 2001, we exposed 14 owls to a single playback trial consisting of one Burrowing Owl recording and one Western Meadowlark recording broadcast from a speaker placed on the ground at either 0 m, 50 m, or 100 m from the nest burrow entrance. We randomly selected the playback tapes used for each trial from the collection of pre-recorded Burrowing Owl and Western Meadowlark vocalization tapes. All trials occurred in early evening (18:00–21:00 MST) on days of no precipitation and maximum wind speeds less than 16 km/h.

For each nest, in advance we randomly selected one of three broadcast distances, as well as the order in which the owls were exposed to the Burrowing Owl and meadowlark vocalizations. Each trial consisted of a 5-min pre-playback period and two 5-min playback periods (one Burrowing Owl playback period and one meadowlark playback period). During both trial periods, we made observations of focal owls from a portable blind (camouflage tarp draped over an observer seated on the ground) or from a parked vehicle, depending on location of the nest, from a distance of 50 m (the length of wire from the speaker to the JS Caller) from the broadcast speaker. Throughout the trial, the JS Caller remained with the observer, who manually controlled the start and end of playbacks.

After placement of the speaker and subsequent retreat to the observation blind, pre-playback periods began once focal owls appeared to resume to their normal behavior (approx. 5–7 min). During the pre-playback and playback periods, we recorded 1) distance of the focal owl from the speaker at the beginning of the trial, 2) distance from the speaker at each 1-min interval, 3) number and type of vocalizations uttered, and 4) behavioral actions, such as bobbing, flying, and the white-and-tall stance (standing erect with white throat and facial patches exposed; see Coulombe 1971; Thomsen 1971; and Martin 1973). We set 100 calls as a cut-off limit for primary call vocalizations to reduce skewing of data (although several individuals did exceed this limit).

Revised playback trial design. None of the 14 owls that were exposed to a Western Meadowlark recording in 2001 responded to the recording with any vocalizations or movements towards the speaker. This result suggested that any responses to the Burrowing Owl recording would be a result of the broadcast call and not the presence of the speaker itself or any other sound emanating from the speaker. Therefore, to complete a greater number of trials, we removed the meadowlark control from subsequent playback trials in 2001 and 2002. Each subsequent playback trial consisted of a 5-min pre-playback period and one 5-min playback period, which consisted of only Burrowing Owl vocalizations. All other procedures described in the initial design remained unchanged. We used these results to assess whether Burrowing Owls responded in a territorial manner, whether they defended more than just the immediate area around the nest burrow, and how large an area (up to 100 m) they defended.

Assessment of responses. We considered an owl to have responded to the playback in a territorial manner if it uttered primary calls, performed white-and-tall stances, bobbed, flew towards the speaker, approached the speaker closely while assuming a territorial posture (i.e., standing erect with white throat patches exposed), or attacked the speaker. These behaviors were previously described in Burrowing Owls when they were reportedly involved in territorial disputes with other owls (Coulombe 1971; Thomsen 1971; Martin 1973; Haug and Didiuk 1993).

Statistical analysis. We examined the effects of distance (0 m, 50 m, and 100 m) and playback period (pre-playback vs. playback) on

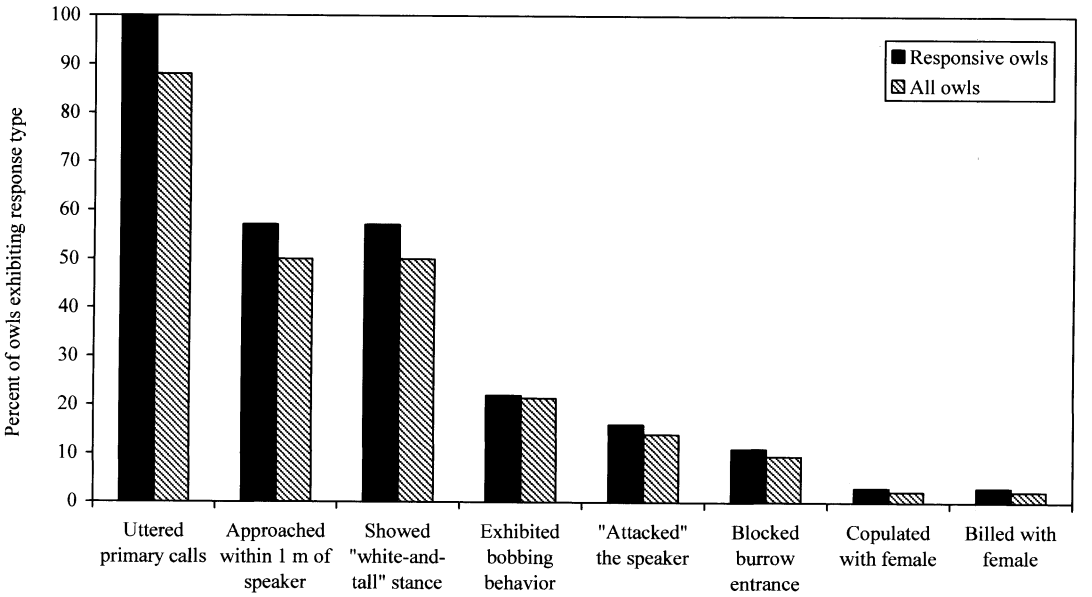

Fig. 1. Responses to playbacks of Burrowing Owl primary calls by all focal male ($N = 42$) and all responsive focal male Burrowing Owls ($N = 37$) in southwestern Idaho, 2001–2002.

the total number of primary calls uttered and the total number of individual behavioral responses (e.g, white-and-tall stances) using a two-factor ANOVA in which the second factor (playback period) was a repeated measure (JMPIN, SAS Institute, Inc., Cary, NC). Because we made comparisons of five dependent variables (closest approach to speaker, number of primary calls, white-and-tall stances, bobs, and flights), we adjusted alpha levels using sequential Bonferroni corrections (Rice 1989). Throughout we present means ±1 SE.

RESULTS

We conducted 47 playback trials during the 2001 and 2002 breeding seasons (31 in 2001, 16 in 2002). All but five focal males were visible during the pre-playback period. We later determined that one of these males was missing. These five males were not included in any calculations of response rates or statistical comparisons. Only three males were closer than 10 m from the speaker (2, 3, and 5 m) when the broadcast of the Burrowing Owl call began, whereas 75% of focal males were ≥50 m away at the start of the playback period.

Response rate and types of responses. Eighty-eight percent of the focal males responded to the Burrowing Owl calls. All owls that responded uttered primary calls, while 57% also approached within 1 m of the speaker while either standing tall or in a bent-over posture uttering primary calls (Fig. 1). Other common responses were white-and-tall stances, bobbing, and physical contact with the speaker (i.e., "attacking"). Less common responses were blocking the burrow entrance, copulating with the female, and billing with the female.

Of the owls that responded to the playback trials, response intensities varied (Table 1). While the mean number of primary calls uttered during the 5-min playback period was 40.8 (±4.2), the range was from seven to 100 calls uttered. The change in distance of the focal owl from the speaker between the beginning and the end of the playback ranged from 30 m to −295 m (positive numbers indicate moving away from the speaker, while negative numbers indicate moving closer to the speaker), with a mean of −64.5 (±11.0 m).

Females responded in eight of the 47 trials. One female, whose mate was missing and presumably dead, exhibited strong responses to the playback by bobbing repeatedly (75 times during the 5-min playback period), and uttering a long series of 77 "chuck-and-chatter" calls. Of the remaining seven females, five responded

Table 1. Intensity of responses to playback of male Burrowing Owl primary calls by focal male Burrowing Owls ($N = 37$) nesting in southwestern Idaho, 2001–2002. Closest approach to speaker is given as a median because of its skewed distribution.

Response variable	Mean ± SE	Range
Vocalizations		
Number of primary calls	40.8 ± 4.2	7–100
Number of alarm calls	0.1 ± 0.1	0–2
Behaviors		
Number of bobs	0.2 ± 0.1	0–3
Number of white-and-tall stances	0.9 ± 0.2	0–3
Number of flights	2.8 ± 0.4	0–8
Closest approach to speaker (m)	1.0 ± 3.1	0–150

simply by emerging from the burrow and remaining at the entrance, one copulated with the male and then flew above the speaker while uttering alarm calls, and one bobbed and rasped from the ground while facing the speaker. Females that did not respond to the playbacks presumably were inside the nest burrows brooding recently hatched young.

Finally, on five occasions owls other than the focal owl responded to the broadcast from distances of 150–300 m. We had already conducted playbacks on these owls, and therefore the results for them should not have been affected by hearing and responding to the playback at another nest.

Effect of playback period and broadcast distance. The two-factor ANOVA revealed no significant interactions between playback period and broadcast distance on closest approach to the broadcast speaker ($F_{2,39} = 1.24$, $P = 0.30$), number of primary calls ($F_{2,39} = 0.27$, $P = 0.76$), white-and-tall stances ($F_{2,39} = 0.31$, $P = 0.74$), bobs ($F_{2,39} = 0.75$, $P = 0.48$), or flights ($F_{2,39} = 0.20$, $P = 0.82$). Therefore, we interpreted the main effects of playback period and broadcast distance.

Pre-playback period vs. playback period. Vocalizations and behavior of focal males were significantly different between the playback and pre-playback periods. Scanning from various perches was the most common (76%) behavior of focal males during the pre-playback period, while only 19% of males exhibited scanning behavior during the playback period. No males uttered primary calls during the pre-playback period, whereas 88% of males uttered primary calls during the playback period (Fig. 1). During the playback period, males made more flights and performed more white-and-tall stances than during the pre-playback period (Table 2). There was no difference in bobbing behavior between pre-playback and playback periods. Finally, owls were significantly closer to the speaker by the end of the playback period than they were at the end of the pre-playback period.

Table 2. Mean (± SE) number of behavioral responses to the playback by focal male Burrowing Owls ($N = 42$) during the pre-playback and playback periods in southwestern Idaho, 2001–2002.

Variable	Playback period		*F*-ratio	*P*-value
	Pre-playback	Playback		
Vocalizations				
Number of primary calls	0.0 ± 3.1	34.9 ± 3.1	65.00	<0.0001[a]
Behavior				
Number of white-and-tall stances	0.1 ± 0.1	0.8 ± 0.11	17.48	0.0002[a]
Number of flights	0.5 ± 0.3	2.5 ± 0.3	24.35	<0.0001[a]
Number of bobs	0.2 ± 0.1	0.3 ± 0.1	0.31	0.58
Closest approach to speaker (m)	96.6 ± 7.4	34.8 ± 7.4	34.69	<0.0001[a]

[a] Significant based on sequential Bonferoni corrections adjusted from an original alpha level of 0.05.

Table 3. Mean (± SE) number of behavioral responses of each focal male Burrowing Owl at broadcast distances of 0 m (N = 16), 50 m (N = 14), and 100 m (N = 12) from the active nest burrow.

Variable	Broadcast distance			F-ratio	P-value
	0 m	50 m	100 m		
Vocalizations					
Number of primary calls	16.8 ± 3.5	19.7 ± 3.7	15.9 ± 4.0	0.27	0.76
Behaviors					
Number of "white-and-tall" stances	0.8 ± 0.2	0.3 ± 0.2	0.4 ± 0.2	1.89	0.16
Number of flights	1.4 ± 0.3	1.7 ± 0.3	1.5 ± 0.3	0.33	0.72
Number of bobs	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.56	0.57

Effect of distance. Focal males responded to broadcasts of Burrowing Owl primary calls from all three broadcast distances. However, we found a significant effect of distance on the closest approach of focal owls to the broadcast speaker ($F_{2,39}$ = 7.77, P = 0.001). Focal owls exposed to broadcast distances of 0 m (N = 16) and 50 m (N = 14) from the nest burrow approached closer to the broadcast speaker than owls exposed to the broadcast distance of 100 m (N = 12). On average, owls exposed to 0 and 50 m broadcast distances had nearest approach distances of 43.8 (±10.22) m and 51.4 (±10.9) m from the speaker, respectively. Owls exposed to the 100 m broadcast distance had a nearest approach distance of 102.0 (±11.8) m from the speaker. We found no significant differences in number of primary calls, white-and-tall stances, bobs, or flights of male Burrowing Owls between the three broadcast distances (Table 3).

DISCUSSION

Male Burrowing Owls responded strongly to broadcast recordings of conspecifics. Haug and Didiuk (1993) reported a similar response rate by male Burrowing Owls nesting in Saskatchewan. In contrast, all of the responsive owls in our study uttered primary calls, compared to only 64% of owls in Saskatchewan (Haug and Didiuk 1993). This preponderance of primary calls suggests that vocalizations are an important component of communication among Burrowing Owl territory holders. Martin (1973), in his observations of territorial disputes between male Burrowing Owls, reported that owls would approach within 1 m of each other when primary calls and white and tall stances were not successful in repelling an intruder. The owls in our study exhibited similar behavior; 57% of males who responded approached within 1 m of the speaker during the playback period, and 16% made physical contact with the speaker.

Females were less responsive than males to the playback trials; only 17% of females emerged from the burrow, flew over the speaker, or uttered alarm calls. Haug and Didiuk (1993) reported that 29% of the females in their study responded to recorded calls. This slightly higher response rate may be a result of their study occurring during the period of nest initiation. During this period, females are more active above ground and perhaps participate more in territory establishment and defense. In our study, we conducted playback experiments during the first week after hatching, when the females brooded recently hatched young and were apparently less likely to participate in nest defense.

Although females responded less than males to the playback stimulus, their ability to take on the role of the male in defending the nest was apparent with the one female whose mate was presumably dead. Her aggressive response to the broadcast consisted of repetitive bobbing behavior and a long series of "chuck-and-chatter" calls. No other female in our study responded with the same intensity, and Haug and Didiuk (1993) did not report similar behavior by females in Saskatchewan. However, this female's nest defense in the absence of the male may have been costly. All of her nestlings died of either exposure or starvation within one week of hatching, during which time she spent the majority of the day scanning from the nest

perch, a behavior generally performed by the male during this period.

We found a significant effect of broadcast distance on how close focal males approached the broadcast speaker. Burrowing Owls exposed to calls nearer the nest burrow approached the speaker more closely than when the calls were farther away. In contrast, we found no effect of distance on any other response variable (e.g., number of primary calls). These results suggest that although males may continue to defend their territories vocally against intruders at least 100 m away from their nest, they are less likely to physically approach an intruder at this distance.

As in other work (e.g., Haug and Oliphant 1990), Burrowing Owls in our study frequently foraged within 100 m of the nest burrow for invertebrate prey and foraged farther away (up to 600 m) from the nest burrow for vertebrate prey. Our results suggest that although Burrowing Owls forage for prey from areas both adjacent to the nest and far removed from the nest, they actively defend an area less than 100 m in radius. Therefore, Burrowing Owls appear to defend relatively large nesting territories (larger than the nest area itself) that do not, however, encompass all foraging areas.

Whether territorial behavior of Burrowing Owls changes over the course of the breeding season remains unknown. Both Haug and Didiuk (1993) and Fahler (1998; study conducted in southeastern Idaho) noticed a decrease in response of Burrowing Owls to playbacks as the breeding season progressed but were unable to differentiate between habituation to the playback recordings and a change in territorial aggressiveness. Interestingly, while Haug and Didiuk's (1993) study was conducted from egg-laying through incubation on a weekly basis, we conducted playback experiments during the first week after hatching and found a response rate similar to that seen during the earlier playbacks of their study. Although further investigation is necessary, this suggests that the decrease in response rate that they observed may have been a result of habituation.

In summary, our results suggest that Burrowing Owls actively defend their nesting site, and they defend an area beyond their nest burrow. However, the type of defense Burrowing Owls use varies depending on the distance of the potential intruder from the nest. Male Burrowing Owls are unlikely to approach or defend against an intruder that is at least 100 m away, but they will respond vocally, by uttering primary calls, in response to an intruder at this distance. As several owls responded with primary calls to broadcasts from distances of up to 300 m, it appears that owls may respond vocally to the broadcast of a male Burrowing Owl call as long as it is audible from their location.

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