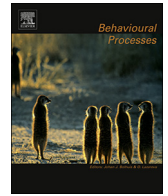




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Burrowing owls eavesdrop on southern lapwings' alarm calls to enhance their antipredatory behaviour



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ARTICLE INFO

Keywords:

Alert behaviour
Alarm calls
Athene cunicularia
Pampas
Predation risk
Vanellus chilensis

ABSTRACT

Eavesdropping is a widespread behaviour among animals, providing the receiver with valuable information to assess the habitat, resources or threats. This kind of behaviour has been reported for the burrowing owl (*Athene cunicularia*), which in its northern range lives in close association with fossorial mammals and eavesdrops on their alarm calls as indicators of risk. In their southernmost range, burrowing owls do not associate with mammals, but they are often found sharing foraging and nesting patches with the southern lapwing (*Vanellus chilensis*), a noisy, territorial and aggressive plover species. We designed a field experimental study aimed at determining if burrowing owls are able to use lapwing calls as indicator of potential risk. We exposed focal owls to a sequence of sounds including lapwing alarm calls, and biological and non-biological controls, and registered their response as alert or relax behaviours. Linear mixed modeling showed that owls increased their alert behaviour in response to lapwing alarm calls but not in response to control treatments. In addition, owls' response was consistent between habitats (rural and urban) and seasons (breeding and non-breeding). Our results suggest that eavesdropping is a generalized strategy of burrowing owls to acquire environmental information throughout its distribution range.

1. Introduction

Animals gather information from the environment actively as a result of their experience, from signals that came from conspecific or other species that occupy and share the same habitats. Such information is often inadvertently shared from one species to another and gives adaptive rewards to those that can take advantage from it (e.g. Danchin et al., 2004). This information usually referred to as public information can be obtained from many sensorial sources, including chemical, visual, and aural, among others (Jones et al., 2011). In particular, alarm vocalizations emitted by individuals of the same or different species that share the same predators may provide information about the presence or closeness of a threat, thus allowing the receiver to avoid unexpected attacks, increase the vigilance rate, shelter or hide to avoid being captured (Magrath et al., 2014). Another advantage underlying the use of alarm calls is a reduction of the time invested in vigilance and, consequently, an increase in the time devoted to other activities like foraging. In this way, animals able to use the public information provided by other animals can obtain valuable data about what is happening in the environment at a relatively low cost (Magrath et al., 2014).

Antipredatory associations are frequent between species that live in proximity to each other (Quinn and Ueta, 2008). This is the case, for example, of burrowing owls and fossorial mammals. The burrowing owl is a small raptor distributed across the Americas, which shows the particularity of locating its nest in subterranean burrows (Marks et al., 1994). In North America, this owl species lives in close association with fossorial mammals (e.g. prairie dogs *Cynomys* sp., squirrels *Spermophilus* sp.), given that it depends on abandoned burrows of these mammals for nesting (Poulin et al., 2011). Previous studies have shown that burrowing owls eavesdrop on the alarm calls of associated mammals using these signals as indicators of risk (Columbe, 1971; Martin, 1973), which allow them to optimize their vigilance rate (Bryan and Wunder, 2013; Henderson, 2013). In southern South America, burrowing owls have become independent of fossorial mammals and dig their own burrows (Hudson, 1920). This is related to the fact that the once abundant plains viscacha (*Lagostomus maximus*), a large fossorial mammal that has been historically associated with burrowing owls in this part of its distribution, experienced a drastic population decrease in the last century after they were labeled as agricultural pests (Jackson et al., 1996; Machicote et al., 2004). Alternatively, the burrowing owl seems to have developed an association with the southern lapwing

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<https://doi.org/10.1016/j.beproc.2018.10.002>

Received 24 May 2018; Received in revised form 3 September 2018; Accepted 7 October 2018

Available online 09 October 2018

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(*Vanellus chilensis*), a common and conspicuous plover species that inhabits open habitats of the Neotropics. The southern lapwing is considered as a “sentinel species”, given that it is noisy, territorial, and aggressive against intruders (Gallegos Luque, 1984; Canevari et al., 1991). This species spends a large portion of its daily time in vigilance and defensive behaviours (Costa, 2002; Maruyama et al., 2010). The aggressive behaviour of this species attracted the attention of the renowned ornithologist W. H. Hudson, who wrote about the southern lapwing “... In defense of its territory it wages perpetual war against most living creatures, the objects of its special abhorrence being men, dogs, Rheas, and birds of prey generally. Its noisy cry and irascible temper are spoken of by most travelers and naturalists; for no person riding across the pampas could possibly overlook the bird, with its screaming protests against all trespassers perpetually ringing in his ears...” (Hudson, 1920).

As part of a broader project aimed to study the ecology of burrowing owls in the southeastern Pampas region of Argentina, we found that up to 70% of owl nests were located in patches where southern lapwings were also present (Authors' unpubl. data). This percentage of co-occurrence between these species, in appearance quite high for a raptor and a potential prey, may reflect the fact that owls and lapwings share many ecological preferences. First, both species inhabit open habitats (including rural and urban areas) and are abundant and conspicuous species in the Pampas region (Codesido et al., 2011). Second, they consume the same type of prey (mostly insects; Isacch, 2001; Gantz et al., 2009, 2016; Cavalli et al., 2014) and they are often found foraging in the same short-grass patches. Third and more importantly, they share the same type of predators, like grisons (*Galictis cuja*), foxes (*Pseudalopex gymnocercus*), harriers (*Circus cinereus*, *C. buffoni*), caracaras (*Milvago chimango*, *Caracara plancus*), man and domestic animals (Delibes et al., 2003; Vargas et al., 2007; Idoeta and Roesler, 2012; Sade et al., 2012; Cavalli et al., 2016a; Rebolo-Ifrán et al., 2017). Thus, it seems likely that the association between burrowing owls and southern lapwings would respond to an antipredatory strategy. In absence of associated mammals, owls may take advantage of lapwing alarm calls as an early warning of the closeness or approach of a threat. If owls respond to alarm calls by optimizing their vigilance behaviour (i.e. better protection of themselves or their brood) this would increase their fitness; hence we expect that the burrowing owl - southern lapwing association has evolved as an adaptive strategy to diminish predation risk.

In this study, we evaluated the use of southern lapwings' alarm call by the burrowing owl in rural and urban habitats in order to determine if owls recognize this interspecific stimulus as indicator of a threat. Our main hypothesis is that burrowing owls improve their vigilance behaviour by eavesdropping on lapwing alarm calls. In addition, we questioned whether owls' responses varied between habitats (urban and rural) and seasons (breeding and non-breeding). Previous studies showed that urban burrowing owls show lower fear responses than rural owls when facing a potential threat (Cavalli et al., 2016a, 2016b), thus suggesting that the antipredatory behaviour of this species would be context-dependent. In this sense, we expected to find lower response of owls to lapwing alarm calls in urban habitat. In addition, it has been reported that burrowing owls, like many other birds, usually increase their vigilance behaviour during the breeding season to prevent nest predation (Newton, 1998; Cavalli et al., 2016b). We also expected to find that owls show a higher response to lapwing calls during the breeding season than during the non-breeding season.

2. Methods

2.1. Study area

The study was conducted in the southeastern portion of the Pampas region (Buenos Aires Province, Argentina). The landscape of the Pampas was historically dominated by grasslands (Soriano et al., 1991), but the original gramineous vegetation community has been highly

modified by agriculture (Bilenca and Miñarro, 2004). Thus, the study area comprises a mosaic of different land-uses, including a diverse array of natural vegetation, such as native grasslands, marshes, coastal dunes, and native forests, and modified environments, such as grazing fields, croplands and urban zones (Isacch et al., 2016). The dominance of one or another of these land-uses depends on soil conditions. Livestock raising has been traditionally the main productive activity in this sector of the Pampas, and most of the land is devoted to grazing fields, whereas croplands (mainly soybean, maize, and wheat) are limited to best-quality upland soils. Urbanizations are mostly represented by periurban areas (small touristic villages with < 800 inhabitants and scattered houses) and suburban areas of larger cities to a lesser extent (Zelaya et al., 2016).

2.2. Sampling design

During 2014 and 2015, we looked for burrowing owls by vehicle through paved and unpaved roads in urban and rural areas of the study area. Burrowing owls are active in the daylight, and individuals remain at burrow entrances most of the day (Cavalli, 2017). Thus their nesting sites are easily located (Marks et al., 1994). Once a nest was located, we conducted a broadcast trial following the experimental design described by Bryan and Wunder (2013). We exposed owls to three treatments: Lapwing (L), which consisted of a series of lapwing's alarm calls, used as experimental treatment; Mooing (M), which consisted of a series of sounds of cattle mooing, used as biological control; and Engine (E), which consisted of motorcycle engine sounds, used as non-biological control. A fourth treatment, which consisted of ambient sound (Silence; S) was used to separate M-L-E treatments and considered a silence control treatment. In most cases, we performed the tests in sites where only one individual was present at the time of the experiment (76.6% of cases), or two individuals (i.e. the mating pair) in the remaining cases (n = 111). We didn't perform trials in sites with more than two individuals present.

All sounds used for treatments were obtained in the field using a parabolic antenna and a digital recorder. Later in the laboratory, we used the free software Audacity (Audacity Team, 2014), to edit and combine the sounds and create the final sound sequences. Lapwing treatment consisted of alarm calls of a bird on the ground (first 15 s) and calls of other two birds in flight (last 15 s). Mooing treatment consisted of three cows mooing, broadcasted at a rate of 1 moo every 4–5 s. Engine treatment consisted of the noise of a motorcycle passing by and occurred for the entire 30 s broadcast. During each trial we exposed the focal owl to a randomized sequence of the L-M-E treatments (duration of each treatment: 30 s), separated one from each other by a S treatment (60 s). Thus, the final broadcast followed the general order: Treatment 1 (30 s) – S1 (60 s) – Treatment 2 (30 s) – S2 (60 s) – Treatment 3 (30 s). All sound treatments were broadcast at 80–85 db (measured 1 m from the speaker). Simultaneously, we registered the behaviour of focal individuals (female and males) using a HD portable camcorder (Bryan and Wunder, 2013). All these procedures were performed from the vehicle at a distance of approximately 50 m (Manning and Kaler, 2011).

2.3. Data processing and statistical analysis

We watched video files using a portable computer and registered the behaviour of owls during experimental trials. We performed an ethogram to characterize owl behaviours (Table 1) and quantified type and duration of all activities using the software BORIS v.2.2 (Friard and Gamba, 2016). Then we calculated the total time that owls devoted to “relax” and “alert” activities during each trial (Table 1) and expressed as the proportion of time owls devoted to such activities. We assumed that during foraging activity (i.e. when the individual search for prey by walking near the nest with eyes oriented downward) owls' vigilance was directed toward prey and not toward potential predators, thus

Table 1

Ethogram showing the states and activities used to describe the behaviour of the burrowing owl during playback trials.

State	Activity	Definition
Relax	Resting	The individual rests or remains inactive with closed eyes.
	Comfort	The individual performs maintenance activities (cleaning, grooming, preening).
	Foraging	The individual search for prey on the ground (walking, looking downward, catching prey).
Alert	Watching/vigilance	The individual regularly scan the area, open eyes.
	Standing	The individual stretches and stands to get taller.
	Vocalizing	The individual makes alarm calls.
	Bowing	The individual moves up and down in the same place.
	Moving	The individual moves toward the nest, enters the nest, or flies away.

foraging behaviours were categorized as relax responses (see Bryan and Wunder, 2003).

We fitted Generalized Linear Mixed Models with a binomial error distribution and a logit link function (lmer function in library lme4; Bates et al., 2013) to evaluate the effect of explanatory variables on the proportion of time that the focal individual was alert (response variable). The global model included sex (male, female), season (breeding, non-breeding), habitat (urban, rural), treatment sequence (L-E-M, E-M-L, M-E-L) and treatment (L, E, M, S) as explanatory variables, and identity of each focal individual was included as random factor. Because the percent of time that owls remain alert during silence periods after L treatment was longer than during silences after M or E treatments ($\beta = 1.240$, $SE = 0.328$, $Z = 3.783$, $P < 0.001$), we excluded silence after L treatment from silence control data set. We also tested if number of owls (one or two) had an effect on the alert response before performing further analyses; we found no significant effect of this variable ($\chi^2_{14,1} = 0.406$, $P = 0.523$).

Model comparisons and selection of the variables that best explain response variability were performed by likelihood ratio tests. We followed a backward stepwise procedure starting from a full model which included the main effects. Each variable was tested for statistical significance comparing the most general model including the variable with a simplified model without it. Significance was tested using a chi-squared function and only significant effects ($P < 0.05$) were retained in the final model. Statistical analyses were carried out using R software (R Development Core Team, 2018). Values are reported as mean \pm SE except where noted.

3. Results

We performed a total of 111 broadcast experiment trials on different adult burrowing owls throughout the sampling period. Sixty trials were performed in rural areas (43 and 17 during the non-breeding and breeding seasons, respectively) and 51 trials were performed in urban areas (17 and 34 during the non-breeding and breeding seasons, respectively).

We found that treatment order had no effect on burrowing owls' alert behaviour. In addition, alert response was similar among sexes, habitat type and season. The model that best explained burrowing owls' alert behaviour included only Treatment as explanatory variable (Table 2). Owls spent more time being alert during L treatment than during control treatments (Fig. 1, Table 3).

4. Discussion

The use of public information to reduce predation risk is a common strategy in different groups of animals, but it is especially common

Table 2

Model results based on 111 broadcast surveys testing the effect of the sound treatments (lapwing alarm call, motorcycle engine, cattle mooing), habitat type (urban, rural), season (breeding, non-breeding), and sex (male, female) on the behavioural responses of burrowing owls (percent time alert). Text in bold denotes significant results.

Fixed factors	Chi-square	P
Habitat Treatment Season Sex Sequence		
Habitat Treatment Season Sex	$\chi^2_{14,4} = 6.21$	0.18
Habitat Treatment Season	$\chi^2_{10,2} = 0.55$	0.75
Habitat Treatment	$\chi^2_{8,1} = 1.29$	0.25
Treatment	$\chi^2_{7,1} = 1.68$	0.19
Null	$\chi^2_{6,4} = 103.23$	< 0.001

among birds and mammals (e.g. Rainey et al., 2004; Bryan and Wunder, 2013). The ability to recognize antipredatory signals emitted by heterospecifics is relatively common among species that live in close association and that share habitat and predators (Magrath et al., 2014). The burrowing owl seems to be particularly prone to this kind of association, as it has been reported that they may take advantage of alarm calls emitted by their associated fossorial mammals in North America (Bryan and Wunder, 2013; Henderson, 2013) and, in this study, we found that it has also the ability to respond to alarm calls of other birds (see also Austin et al., 2016).

Our results showed that burrowing owls use lapwings' alarm calls as a warning signal, switching to a defensive alert behaviour when (and after) they are exposed to such sound. In Colorado, where burrowing owls are strongly associated with prairie dogs (Poulin et al., 2011; Ray et al., 2016), previous studies demonstrated that burrowing owls respond to the alarms calls of this mammal, increasing their alert behaviour (Bryan and Wunder, 2013). Further, Henderson (2013) found that California ground squirrels help burrowing owls to reduce risk through alarm calling vocalizations and vigilance. In agreement with these reports, our results suggest that burrowing owls may optimize their vigilance behaviour at a relatively low cost using lapwings' alarm calls, by adopting a defensive behaviour when necessary (Magrath et al., 2014). This may also allow owls to devote more time to other activities (e.g. resting or foraging) when associate species are silent, which may represent a benefit in individuals' fitness.

A question that arises from our study is whether lapwings may obtain any reward from this association. Like other raptors, the burrowing owl may appear at a first sight as threatening for lapwings, however this owl rarely preys on birds (e.g. birds represent < 0.5% of total prey in the study area; Cavalli et al., 2014). It is likely that the association between southern lapwings and burrowing owls may be mutually beneficial. Owls may relax their vigilance behaviour by relying in lapwing calls if a threat appears and lapwings may benefit from having a protective association with a top predator. For instance, burrowing owls also prey on snakes and opossums (Bó et al., 2007), two potential predators of southern lapwing nests.

We postulated that the response of burrowing owls to southern lapwing alarm calls should be higher in urban than in rural areas and during the breeding season than during the non-breeding season, but none of these predictions was supported by our results. The fact that responsiveness was not influenced by spatial or seasonal variables evidences a close protective association between both species, which is a requisite to the evolving of the recognition to heterospecific alarm calls (Magrath et al., 2014). The recognizing of antipredatory signals may have innate but also learned components (Lind and Cresswell, 2005; Epp and Gabor, 2008; Haff and Magrath, 2012). Innate responses would allow animals to respond to interspecific alarm signals without having a previous experience, whereas learned responses would allow certain flexibility in the alert response (Magrath and Bennet, 2012). Despite the fact that our study design does not allow to determine the underlying processes behind the responses of owls to lapwing alarm

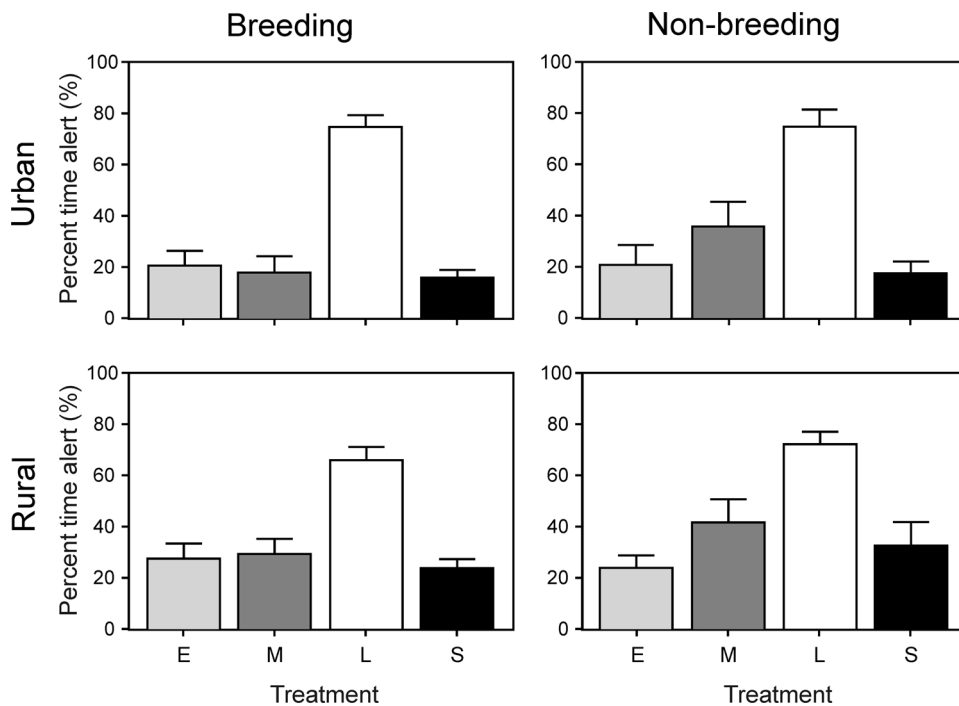


Fig. 1. Percent time that burrowing owls stay alert during playback treatments. Three sound treatments were presented to owls: the experimental treatment consisted of alarm calls of southern lapwing (L), the non-biological control consisted of the sound of a motorcycle engine (E), and the biological control consisted of cattle mooing (M). A silence (S; ambient noise) was intermingled between sound treatments. Experimental trials were performed during the breeding (left graphs) and non-breeding (right graphs) seasons, and in urban (upper graphs) and rural (lower graphs) habitats. Columns and bars represent mean \pm SE.

Table 3

Fixed factor contrasts from mixed effects models testing the effect of the sound treatments (lapwing alarm call, motorcycle engine, cattle mooing) on the behavioural responses of burrowing owls (percent time alert) based on 111 broadcast surveys. Text in bold denotes significant results.

Fixed Factor contrasts		$\beta \pm SE$	Z	P
Silence	Engine	0.313 \pm 0.296	1.057	0.290
	Mooing	0.515 \pm 0.288	1.787	0.074
	Lapwing	2.740 \pm 0.292	9.363	< 0.001
Engine	Mooing	0.202 \pm 0.326	0.620	0.535
	Lapwing	2.427 \pm 0.329	7.370	< 0.001
Mooing	Lapwing	2.225 \pm 0.322	6.909	< 0.001

calls, the uniformity of the owls' response behaviour between habitats and seasons suggests that innate components would be the primary explanation for burrowing owl – southern lapwing association. Notwithstanding, innate and learned mechanisms would not be mutually exclusive (Magrath and Bennet, 2012). In burrowing owls, nestlings frequently remain associated with the parental nest almost until the following breeding season (Cavalli, 2017), and it seems likely that this prolonged time residence in the natal area may favor the learning process within the familiar group.

As in their association with fossorial mammals in North America, burrowing owls in South America rely on southern lapwings to gather relevant environmental information. The existence of similar behavioural responses in northern and southern burrowing owl populations suggests that this is a widespread and probably adaptive strategy to reduce predation risk. Further studies are needed to understand and explain the processes modulating this behaviour and to advance our knowledge of convergent patterns in burrowing owl eavesdropping throughout the species' range.

Acknowledgements

We thank Aguas Brillantes, San José and Los Alemanes Ranches for their courtesy and permission to work on their properties. We are grateful to two anonymous reviewers who made valuable criticisms on an early version of this manuscript. We appreciate the improvements in

English usage made by Bruce Peterson through the Association of Field Ornithologists' program of editorial assistance. This study was funded by Universidad Nacional de Mar del Plata (EXA-745/15), Agencia Nacional de Promoción Científica y Técnica (PICT-0461) and CONICET (doctoral scholarship to MC).

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