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

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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 (Coloumbe, 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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(*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 (*Galictus 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 sounds 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