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ARTICLE

Burrowing Owls *Athene cunicularia* (Strigidae) respond with increased vigilance to calls of the Curl-crested Jay *Cyanocorax cristatellus* (Corvidae) in the Paraguayan Cerrado

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ABSTRACT: Nesting Burrowing Owls (*Athene cunicularia*) in the Cerrado of northeastern Paraguay were observed to show increased vigilance in response to Curl-crested Jay (*Cyanocorax cristatellus*) calls. To test whether this reaction was species specific, a playback experiment was conducted using jay calls, a native passerine and three exotic passerines, and responses of the owls to the recordings were measured. The results indicated that the owls responded with increased vigilance only to calls of the Curl-crested Jay. It is hypothesized that the interaction between the two species may be related to competition for dietary resources initiating a greater aggressive response in the diurnal jay due to its more limited foraging time, compared to the nocturnal and diurnal owls. The vigilant response of the owls may thus be related to avoidance of potentially costly aggressive interactions with jays.

KEY-WORDS: behavior, corvid, interspecies, Laguna Blanca, playback.

INTRODUCTION

Heterospecific species interactions have become an increasingly popular focus of animal behavioral studies in recent years, but their functions remain poorly understood. Interspecies interactions are often energy demanding with evolutionary benefits that are not immediately apparent, making their role difficult to understand. Despite this, they appear to be quite common in nature (Peiman & Robinson 2010). Such interactions vary widely in relation to trophic levels, taxonomy, ecology, time and space (Laiolo 2013) and may be indicative of ecological symbioses or direct competition (Martin & Martin 2001), or simply a result of misdirected interspecies aggression (Murray-Jr. 1971, Martin & Martin 2001).

To date, much of the research in avian interspecies reactions has focused on mixed species flocks (Morse 1970, Krebs 1973, Ragusa-Netto 2002, Harrison & Whitehouse 2011, Sridhar *et al.* 2013, Goodale *et al.* 2015). Studies examining non-flocking species have looked largely at interactions in which the relationship between species is well understood; *i.e.* predators interacting with known prey species or competitive interactions where the dominant species was easily identifiable (Pravosudov & Grubb 1999, Robinette & Crockett 1999). However, more subtle species interactions can also occur but are not as frequently documented, perhaps due to difficulties associated with quantifying them. The ongoing investigation of interspecies interactions, whether overt or subtle, in a variety of species and ecological contexts, remains important in revealing information about species and the environment they inhabit.

In the Cerrado of Reserva Natural Laguna Blanca, San Pedro Department, eastern Paraguay (56°17'W; 23°46'S), previously undocumented direct and indirect heterospecific interactions were observed between the Cerrado endemic Curl-crested Jay *Cyanocorax cristatellus* (Corvidae) and the widespread Burrowing Owl *Athene cunicularia* (Strigidae). The Curl-crested Jay is an intelligent, highly mobile, social corvid (Amaral & Macedo 2003), and a generalist feeder (Amaral & Macedo 2003) which has expanded its range in recent decades (Lopes 2008). The non-melodic call of the Curl-crested Jay is capable of travelling considerable distances across the open terrain that typifies its habitat (Amaral & Macedo 2003), and is easily audible to other species that reside in close proximity. However, the vocal repertoire is poorly understood and differences between calls have yet to be

formally identified. The Burrowing Owl is a widespread terrestrial owl distributed throughout the Americas in open habitats from grasslands and deserts to cattle ranches and farmlands (Berardelli *et al.* 2010). This small raptor nests in burrows in the ground which it constructs itself, but will also utilize abandoned burrows of other animals (Crowe & Longshore 2013). In addition to building burrows, Burrowing Owls have been shown to exhibit numerous interesting behaviors including eavesdropping (Bryan & Wunder 2014) and the utilization of dung as a tool to attract insects to their burrows (Levey *et al.* 2004).

During our field studies the two species were observed interacting in four different ways. The most common interaction was Burrowing Owls responding with increased vigilance to Curl-crested Jay calls. This response suggested that the owls were able to recognize the calls of the jays and responded to them as though they indicated a threat. The other interactions we observed, however, made it difficult to deduce exactly why the owls would respond defensively. One interaction that would suggest there is a direct antagonistic relationship between species was a mobbing event. A group of seven jays were observed mobbing an owl away from its nest while two members of the jay's flock occupied the ground directly surrounding the entrance to a burrow. On the other hand, despite frequent observations over three months, this mobbing behavior was only observed once. In the majority of the direct interactions between species, no antagonistic response was elicited from either species, with the jays foraging within 50 m of the owl burrow on multiple occasions without the owls responding. One other indirect interaction was captured by a camera trap set up to watch the entrance of a burrow. The video shows a jay consuming a small unidentified white object taken from the sand at the very entrance of an owl burrow. These observations suggest that the Burrowing Owls and the Curl-crested Jays interact frequently and in a diverse number of ways. The vigilant response of semi-terrestrial owls to the vocalizations of the largely arboreal jays is noteworthy as no obvious link between the ecology of the two species is described in the literature. To test whether the call of the Curl-crested Jay alone was indeed the trigger for the increased vigilance of the Burrowing Owls, we designed an audio playback study. This paper describes the results of this field experiment and suggests possible hypotheses for how the two species may interact.

METHODS

Study Site

The Cerrado is South America's second largest biome (Ab'Saber 1977, Lopes 2008), covering 1.5–1.8 million ha (Cardoso-da-Silva 1995) from central Brazil, west into eastern Bolivia and south to northeastern Paraguay. Studies of the avifauna of the Cerrado are few, and the habitat has been largely overlooked by researchers in Paraguay (Robbins *et al.* 1999) despite the recognized conservation concern of this biodiversity hotspot and the imminent conservation threats that it faces (Cardoso-da-Silva & Bates 2002).

This study was carried out within the Important Bird Area Cerrados of Laguna Blanca (Cartes *et al.* 2008) which is located in San Pedro Department of Paraguay (Figure 1). The area is a large island of Cerrado habitat that was historically bordered on all sides by the Upper Parana Atlantic Forest. The Cerrado of Laguna Blanca is one of only a few places in Paraguay that has been intensively surveyed in terms of its avifauna. It is home to over 319 bird species (Smith *et al.* 2016) 10 of which are of global conservation value (Smith *et al.* 2012). The IBA has recently been classified as an "IBA in danger" as a result of habitat fragmentation due to transformation to agricultural land (BirdLife 2015).

The study site was located across two neighboring properties: Rancho Laguna Blanca, an 1145 ha property home to an eco-tourism business that held private reserve status during the time of the study (the protection elapsed in April 2015); and Agroforestal Rio Verde, a >2000 ha eucalyptus plantation with large tracts of untransformed Cerrado. While neither property currently has formal protection, all the Burrowing Owls observed were found in areas of well-preserved Cerrado habitat alongside internal roads.

Recordings

All recordings were obtained from the XC online data base (www.xeno-canto.org). The recordings fell into one of three categories; 1) target species call; Curl-crested Jay (*Cyanocorax cristatellus*) (Smith 2008, da Silva 2011) 2) familiar local-species call; White-rumped Tanager (*Cypsnagra hirundinacea*) (Velazquez 2008), and 3) exotic species call; Willie-Wagtail (*Rhipidura leucophrys*) (Jacobson 2008), Noisy Myna (*Manorina melanocephala*) (Woodall 2010) or Satin Bowerbird (*Ptilonorhynchus violaceus*) (Deroussen 2011). White-rumped Tanager calls and Curl-crested Jay calls were chosen based on their clarity, and recordings from Paraguay were used to minimize any potential differences in response that may occur due to different unreported vocal dialects in these species. For the category 'exotic species call', we chose three different species' calls to ensure that responses to the unknown calls were not impacted by gradual habituation across the experiment period (Groves & Thompson 1970, Dong & Clayton 2009) and to eliminate pseudo-replication (Catchpole 1989). As all recordings were a maximum of 30 s, they were played placed on a loop so as to run for 60 s during each trial.

FIGURE 1. Location of study site at Reserva Natura Laguna Blanca in San Pedro Department, Paraguay. The study site was located across two neighboring properties: Rancho Laguna Blanca, an 1145 ha property home to an eco-tourism business that held private reserve status during the time of the study and Agroforestal Rio Verde: a >2000 ha eucalyptus plantation with large tracts of untransformed *Cerrado*.

Playback design

For the playback experiment, we utilized a single speaker design (Douglas & Mennill 2010) using an EcoExtreme Speaker (EcoXGear). Nine nest sites were chosen based on accessibility and the site fidelity of the owls. Over the three day study period, we visited each nest three times a day: morning (6 AM–8 AM), mid-day (11 AM–1 PM), and late afternoon (4:30 PM–6:30 PM) (Table 1). The call category remained consistent across each time slot, but the order was changed every day. This was done so that owls were exposed to each call type across the three time frames, eliminating effects of time of day.

Due to the predictable behavior of the owls and their preference to sentinel on bare perches, the researchers were able to approach consistently on the same course for each nest. The owls were easy to locate in all trials except one where the birds were absent from the site. The birds were clearly visible throughout playback trials.

For each trial, nesting areas were approached slowly in a vehicle until the observers reached 60 m from the nearest Burrowing Owl (which were always within 10–20 m of their nests). The use of a vehicle in this experiment as an observation point did not appear to adversely affect behaviors of the owls. As vehicles are used frequently on the properties the birds in this experiment were habituated to their presence prior to the experiment being conducted. Additionally, the distance maintained by observers away from nests appeared sufficient to prevent vigilance responses to the observers themselves. In pilot studies, if researchers exited the vehicle to perform observations, owls showed obvious vigilance behaviors that did not resolve quickly. In this study, conducting observations from a vehicle proved the most efficient unobtrusive means of observing the birds. The angles of nest entries varied for each site, but were either parallel or perpendicular to the vehicle. Due to the terrain, we were limited in the angle we could approach the nests without adversely affecting the owls behavior and thus the results of the experiment.

On arrival, each observer was assigned a single bird to observe and each individual bird was treated as an independent sample. The Burrowing Owls were observed for 120 s to ensure that a vigilant response would not be

an artifact of our presence or the presence of some other threat. Playback trials were cancelled if the owls displayed any vigilant response within that 120 s time frame. Trials were also abandoned if some other factor that would cause an external vigilant response (*e.g.* presence of a bird of prey was apparent to observers). The recordings were played from the speaker placed on top of the car directed towards the owls while the observers watched from within the vehicle.

During each trial the same 60 s long recording was played twice at each site. There was a 30 s latent period of silence between each playback. In trials of the familiar local-species call and exotic species call; if the owls remained undisturbed throughout both playbacks, a third recording, that of the target species (the Curl-crested Jay), was played at the end of the trial. This was done to take advantage of the opportunity to test the target call against the two controls in the same time and setting.

Responses of owls were observed using binoculars and behaviors categorized and ranked in order of the intensity of reaction from 0 to 3 (Table 2). Category 0 behaviors showed no obvious response to the playback and birds continued natural behaviors such as preening and sleeping. Category 1 indicated that the playback had been heard, *e.g.* birds would glance in the direction of the playback or cock their head, but no obvious change in behavior or posture indicated an alarmed response. In these cases, owls would often look in the direction of the playback, but then look away almost immediately. A definite increase in vigilance behavior was categorized as a class 2 response and included 360º scan of surroundings, glancing up at the sky, stiffened posture, widened eyes and head bobbing. Finally, category 3 behaviors displayed an active defensive response, *e.g.* taking flight, assuming higher perch or alarm calling. Observers were trained prior to the experiment using videos to ensure that categorization of behaviors remained consistent between observers. The responses were then further categorized as "non-alarmed" (0 or 1) or "alarmed" (2 or 3) for statistical analysis (Table 2). In our analysis, we used a Fisher's Exact Test to test the significance of responses between playback categories. The data was further analyzed using odds-ratio tests to test for observer bias. We used R software, version 2.11.1 for all statistical analyses.

TABLE 1: Schedule of playback experiments. Observers visited each of the nine nest sites, three times a day: morning (6 AM–8 AM), mid-day (11 AM–1 PM), and late afternoon (4:30 PM–6:30 PM). The time period between trials was approximately 3 h. The time period between repeated trials was at least one day. During each time period, focal animals were exposed to one of three categories of call: target species, exotic species or familiar local species. The call category remained consistent across all nests during each time slot. To eliminate effects of time of day, owls were exposed to each call type once in every time period.

Time Slot	Day 1	Day 2	Day 3
Morning	Target	Exotic	Familiar local
Mid-day	Familiar local	Target	Exotic
Afternoon	Exotic	Familiar local	Target

TABLE 2: Burrowing Owls (*Athene cunicularia*) response levels in reaction to various playback experiments. The playbacks fell into three categories: Target species call – Curl-crested Jay (CCJ) (n = 76); familiar local species call – White-rumped Tanager (WRT) (n = 38); and exotic species call (EXS) (n = 42). Response levels were categorized on an ordinal scale of 0–3; 0 = no reaction, 1= interest or curiosity, *e.g.* staring in the direction of the call or a cocking of the head, 2 = definite reaction with increased vigilance, *e.g.* 360º scan of surroundings, glancing up at the sky, stiffened neck, widened eyes and head bobbing, 3 = active defensive response, *e.g.* taking flight, assuming higher perch or alarm calling. During the playback experiment and then further categorized as either "Non-alarmed Response" or "Alarmed Response" for data analysis.

Call Type	Non-Alarmed Responses			Alarmed Responses		
	No. of 0 Responses	No. of 1 Responses	Total Non-Alarmed Responses	No. of 2 Responses	No. of 3 Responses	Total Alarmed Responses
CCJ	8	13	21	51	4	55
WRT	35	2	37	1	0	1
EXS	16	24	40	2	0	2

RESULTS

Overall, behavioral categories were relatively easy for observers to define as alarmed responses were pronounced. When owls responded with increased vigilance, their gazes were largely directed upward at the sky or in a 360° scan of their surroundings. These scans were repeated during the duration of the playback. Postures also became upright and stiffened. Alarm calls were often accompanied with foot stamping and claw clenching which did not appear to be made in any particular direction. On 3 occasions trials had to be abandoned as owls were showing vigilant behaviors prior to arrival at the sites.

There was a significant difference in the reaction level of the Burrowing Owl to the Curl-crested Jay call when compared to both of the other two categories: familiar species call (Fisher's Exact Test, $p < 0.001$) and exotic species call (Fisher's Exact Test, $p < 0.001$), meaning Burrowing Owls responded with increased vigilance to calls of the Curl-crested Jay more than all other trials (Figure 2). There was no significant difference in reaction levels of the Burrowing Owl between the local species call and the unfamiliar exotic species call (Fisher's Exact Test, $p = 0.538$). Vigilance responses to these calls occurred infrequently. An odds-ratio test showed no significant difference between observers (O-R 1.736, 95% CI: 0.844–3.409).

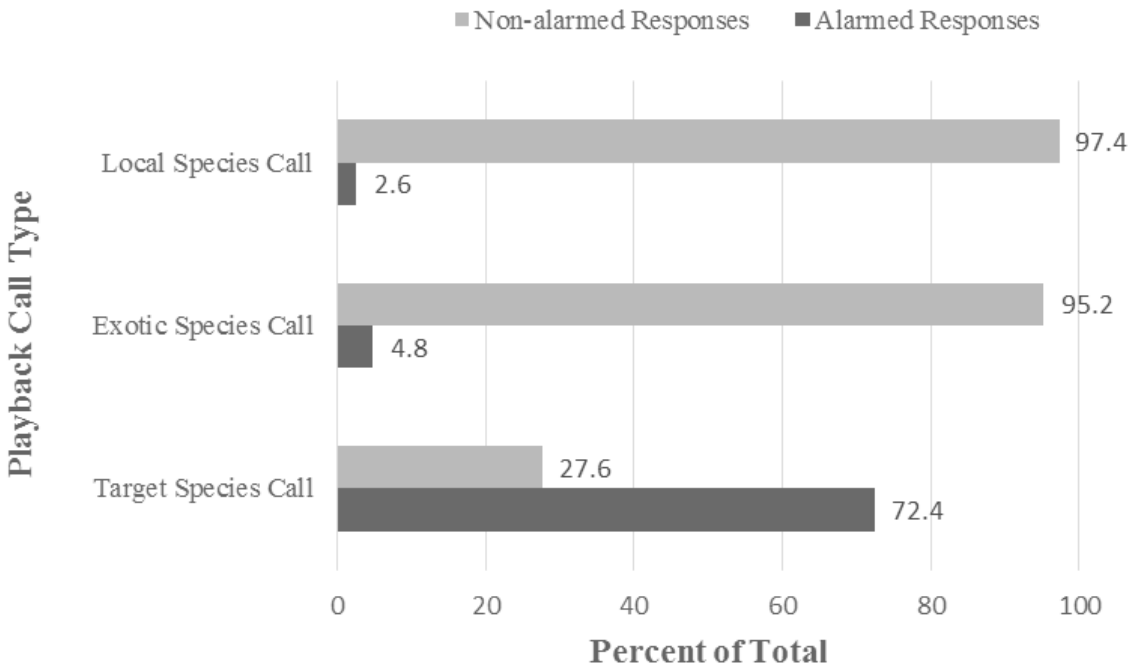

FIGURE 2. Comparison of the percentage of alarmed reactions displayed by burrowing owls in response to different playback experiments. The playbacks fell into three categories: Target species call – Curl-crested Jay (CCJ) (n = 76); local species call – White-rumped Tanager (WRT) (n = 38); and Exotic species call (EXS) (n = 42). Response levels were categorized on an ordinal scale of 0–3 during the playback experiment and then further categorized as either "Non- alarmed Response" or "Alarmed Response" for data analysis.

DISCUSSION

Results confirm that Burrowing Owls of the Paraguayan Cerrado respond to calls of the Curl-crested Jay with increased vigilance. Upon hearing calls of the Curl-crested Jay, Burrowing Owls would scan their entire surroundings, particularly the sky, widen their eyes and straighten their necks, adopting a more upright posture. In many cases a flight or alarm call response was initiated. However, the reason for these vigilant responses and the nature of their interactions remains unclear. Perhaps the simplest explanation is that the owl's response reflects a potential threat posed by the jays. As generalist omnivores it is feasible that jays might predate eggs or small chicks as many corvids do (Andrén 1992, França *et al.* 2009, Němec & Fuchs 2014), although the burrow nests of owls would make these difficult to obtain. However, in order for this to be the most parsimonious explanation, jays would need to be significant predators on owl nests, and such behavior has never been previously reported. It thus seems unlikely that predation by jays on owls is a contributing factor.

Jays, like many corvids, are known to mob species that they see as a potential threat (Yorzinski & Vehrencamp 2009, Marzluff *et al.* 2015) in order to drive them from their immediate vicinity (Krama & Krams 2005, Krams *et al.* 2009). Despite this being an energetically costly practice (Poiani & Yorke 1989, Krama & Krams 2005,

Bērziņš *et al.* 2010) "erroneous" mobbing of species that are not actual threats at all does occur (Peiman & Robinson 2010), and it seems that such behavior may have evolved to be directed at a predetermined "search image" of a threat rather than an actual threat (Dawkins 1971). In birds, this "threat image" is particularly associated with members of the families Accipitridae, Falconidae and Strigidae and on two occasions during our field work Curl-crested Jays were observed to mob the falconid American Kestrel (*Falco sparverius*). The largely insectivorous Burrowing Owl (Vieira & Teixeira 2008, Andrade *et al.* 2010) is unlikely to pose any direct threat to adult jays. However, such a mobbing response may be elicited by the fact that other species of owl are potential predators as has been witnessed in another species of corvid, the Western American Crow (*Corvus brachyrhynchos hesperis*) (Caffrey 2000). This would have an interesting side effect in that the vigilant behavior of the owls was elicited in response to a potential aggressive reaction from the jays toward them. Such a reaction by the jays, a non-vulnerable species, would thus be based on a falsely-perceived threat. Though such encounters would involve unnecessary energetic costs in both species, they may have evolved as a byproduct of the eminently useful "search image" of an owl threat to jays.

A third hypothesis involves the owls and jays acting as resource competitors. As both species are omnivorous, dietary overlap undoubtedly occurs, and with seasonal resources often limited in the arid Cerrado habitat (Ratter *et al.* 1997, Pinheiro *et al.* 2002) direct competition for food sources is feasible where the species come into close contact with each other. Jays may be attracted to the entrance of owls burrows by potential food resources such as remnant prey items and pellets (Hall *et al.* 2009) discarded by the owls, or seek to capitalize on the Burrowing Owls strategy of placing mammal dung near their nests to attract insect prey (Levey *et al.* 2004). Such "baiting" behavior also occurs in Burrowing Owls of the Cerrado, with dung found frequently near burrows as shown by a video footage showing a Burrowing Owl depositing dung at the entrance of its burrow (authors' unpub. data). It is possible that a kleptoparasitic relationship may have arisen in the Cerrado as has been observed in other corvids, *e.g.* House Crows (*Corvus splendens*) and Ospreys (*Pandion haliaetus*) (Yosef *et al.* 2012). However, if this was negatively affecting owls to the point of distantly calling jays eliciting a vigilant response, it is difficult to understand why the actual presence of jays actively kleptoparasitising their food sources does not result in any defensive reaction by the owls.

The value of a resource correlates positively with the willingness of an individual to engage in energy costly heterospecific interactions to obtain it (Peiman & Robinson 2010). As any such competition would be likely to negatively affect the diurnal jays (with more limited foraging time) more so than the diurnal or nocturnal owls (who can forage jay-free at night), it may be expected to elicit a stronger aggressive response from the jays and a more muted defensive/vigilant/avoidance response from the owls. That this mobbing behavior is resource-based rather than threat-based is circumstantially supported by observations of jays foraging on the ground close to owl burrows with no apparent fear of predation by the occupants. The lack of a defensive response to the jays by the breeding owls may also be understood to imply a lack of fear of nest predation on behalf of the owls. Indeed during three months of camera trap observations on active owl nests, no instances of jays entering owl burrows were recorded. Avoidance of the more aggressive jays as they forage by the more relaxed owls is thus most likely precautionary and aimed at energy conservation rather than through any real direct threat posed by the jays to the owls.

A final and potentially intriguing hypothesis for the consistent vigilant response of the owls to the jay calls, but the lack of a consistent response to the physical proximity of the jays, is that the owls are eavesdropping on jay calls and extracting some other information from them that was not discernible within the boundaries of this experiment (Schmidt *et al.* 2010). Unfortunately, the ability to make conclusions based on this hypothesis requires a better understanding of the vocal repertoire of the Curl-crested Jay. Though the vocabulary of the Curl-crested Jay appears superficially to be limited when compared to some other members of the genus (including the sympatric Plush-crested Jay, *Cyanocorax chrysops*) the complexity of information transfer should not be underestimated.

In order to fully understand interactions between Burrowing Owls and Curl-crested Jays, more research needs to be done into the ecology and general behavior of the understudied Curl-crested Jay. Research into the ecological interactions between animals within the highly threatened Cerrado habitat will greatly enhance current understanding of ecosystem complexity and function and hence contribute to a more effective conservation plan. More investigation of the potential lines of interaction suggested here is likely to be rewarding.

In conclusion, Burrowing Owls of the Paraguayan Cerrado respond with increased vigilance to calls of the Curl-crested Jay and our observations suggest that interactions between the Curl-crested Jay and Burrowing Owl may be more extensive than originally thought. The precise nature of the interaction between these two species cannot be determined without further study, but it may be hypothesized that resource competition is a contributing factor. With more limited foraging time, the diurnal jays place greater value on food resources in the

resource poor environment of the Cerrado than do the owls that can forage by both day and night. Further study exploring the feasibility of the hypotheses suggested here is desirable.

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