

Effect of conspecific alarm calls in the parental behaviour of nesting southern house wrens

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Abstract Alarm calls are usually used to signal the presence of a threat to members of the same species and have been studied broadly in social foraging species. We analysed the effects of conspecific alarm calls on the parental behaviour of a territorial species, the southern house wrens (*Troglodytes aedon musculus*), during nestling stage. We compared the parental response of adults feeding 9–11-day-old nestlings when faced with conspecific alarm calls and with a control non-sympatric species' song broadcast from a neighbouring territory. We measured the time required by parents to return to the nest (latency) when exposed to the stimuli and estimated parent's nest visitation rate and mean visit duration. Parents took longer to resume parental activities when we broadcast a conspecific alarm call, but they did not modify their nest visitation rate or the mean visit duration. Heterospecific songs did not seem to affect parental behaviour. Our results suggest that nesting southern house wrens can use alarm calls uttered from neighbouring territories to assess the presence of a threat and adjust their parental behaviour accordingly.

Keywords Acoustic cues · Information networks · Parental care · Risk assessment · Southern house wren

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Introduction

Predation is an ecological factor that severely affects individual fitness; hence, natural selection should favour anti-predator behaviours that will make detection, attack and capture less likely (reviewed in Caro (2005)). The risk of encountering a predator greatly depends on the individual ability to detect cues of its presence (Curio 1993). In birds and mammals, visual detection is one of the most frequent mechanisms to locate a predator (Blumstein et al. 2000; van der Veen 2002), although other signals produced by predators such as vocalizations and odour are also used (Hauser and Caffrey 1994; Zuberbühler et al. 1997; Amo et al. 2008; Barrera et al. 2011). Prey can also avoid predators by using environmental indicators that provide information about the likelihood of encountering a predator (e.g. vegetation structure, weather and daytime; Thorson et al. 1998; Orrock et al. 2004). Alternatively, alarm calls uttered by individuals of the same or different species can be used to assess environmental risk (e.g. Seyfarth et al. 1980; Rainey et al. 2004; Magrath et al. 2007, 2009; Templeton and Greene 2007) even in the absence of a visual stimuli (Seyfarth and Cheney 1990; Evans et al. 1993; van der Veen 2002; Lind et al. 2005).

There is increased evidence that individuals who are not directly involved in a given signalling interaction can obtain information without direct participation in the communication network (McGregor 1993; McGregor and Peake 2000; Peake et al. 2002; Magrath et al. 2009). This behaviour can provide valuable, low-cost information for the incidental receiver, and it has been shown to be a significant component of the communication environment in territorial species (McGregor 1993). In this study, we used a playback experiment to investigate if nesting pairs of the southern house wren (*Troglodytes aedon musculus*) use alarm calls played

from a neighbouring territory as acoustic cues of predation risk during the nestling stage. We broadcast conspecific alarm calls from neighbours' territories and measured the behavioural response of the breeding pair. We compared this response to the one obtained when broadcasting an unfamiliar non-threatening heterospecific song. We chose these songs as control over unfamiliar alarm calls because bird calls could present some similar structural characteristics and birds can respond to these in spite of being non-familiar (Marler 1955; Fallow et al. 2011). Response to an unfamiliar song could instead reveal an unspecific response to a strange sound emitted from a neighbouring territory. Nesting birds reduce the threat to themselves and to the eggs or nestlings in response to an increase in the perceived risk by increasing the time taken to resume parental activities after the stimulus and by reducing the rate and duration of the nest visits (Burhans 2000; Martin et al. 2000; Eggers et al. 2005). Therefore, if southern house wren breeding pairs can obtain information about the environmental risk from alarm calls uttered from a neighbour's territory, parents will increase the time to resume parental activities and reduce the number of nest visits and their duration when exposed to conspecific alarm calls but not when exposed to an unfamiliar non-threatening heterospecific song.

Methods

The southern house wren is a small (11–13 g) territorial insectivorous passerine distributed from Eastern Mexico to Tierra del Fuego, Argentina (Brewer 2001). In our study area, wrens are socially monogamous and resident all year around (Llambías and Fernández 2009).

The study was carried out in an 8-ha deciduous woodland at General Lavalle (36°20' S, 56°54' W), Buenos Aires, Argentina, during the 2005 and 2007 breeding seasons (October–January). The woodland is composed mainly of *Celtis tala* and *Scutia buxifolia* and contains 93 wooden nest-boxes attached at a height of 1.5 m above the ground to trees that wrens use regularly to breed. We determined nesting territories considering the area surrounding the nest as the core area and determining boundaries using song playback and recording the bird response to playback. We also performed observations ad libitum of animal movements near the nest considering that the maximum distance travelled by nesting birds corresponded to the most external limit of the territory.

We tested 22 breeding pairs, 12 during 2005 and ten during 2007 breeding seasons that were rearing 9–11-day old nestlings. Each experimental nest was tested once in each of two treatments to avoid habituation. Treatments involved the exposure of nests to: (1) playback of a conspecific alarm call and (2) playback of a rose-breasted grosbeak

(*Pheucticus ludovicianus*) song as a control. This last species is absent in the neotropical region and it has no closely related species in southern temperate areas; therefore, the song was presumably different from the song of any species present in the area. The treatments for a given pair were conducted on consecutive days and the order of the treatments was alternated between nests. We used type I alarm calls of southern house wrens as it is the most common call uttered by breeding birds when faced with a threat (Fasanella and Fernández 2009). When birds uttered this call, they approach the threat, moving constantly, and sometimes physically attacking the intruder (Fernández et al. 2012).

We recorded type I calls during the 2004 breeding season at the study site and at a nearby population (≈ 3 km away). Type I call duration is 400–600 ms and its frequency ranges from 1 to 9 kHz with an intensity peak at 6 kHz. Calls were recorded at a 22.05-kHz sample rate with a Marantz PMD222 recorder and a Sennheiser K6-ME66 directional microphone 1–2 m from the adults when a researcher visited the nests. We arbitrarily selected six calls that were similar in frequency and amplitude from six different individuals to build the sound files. We used the song of four rose-breasted grosbeaks obtained from the bird sound collection of the Museo de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina) to build control files.

Calls and songs were bandpass-filtered (with cutoff frequencies at 500 and 11,025 Hz) and edited at the lab using Canary 1.2 software (Charif et al. 1995). We built six different 20-min sound files of alarm calls at a rate that mimicked the natural bouts of calls uttered by house wrens when faced with an owl model (1 call/s; Fasanella and Fernández 2009). We also built four 20-min control files alternating 3-s rose-breasted grosbeak song with 5-s silence. Each tape contained the song of only one individual.

Playbacks were broadcast using a laptop Powerbook Macintosh 3400c placed ≈ 30 m away from the experimental nest, at a peak sound pressure of 52–58 dB measured with a TES-1350A sound level meter (TES Electrical Electronic Corp., Taiwan; accuracy ± 2 dB at 94 dB) located 1 m in front of the laptop. The intensity of the broadcast signal was similar to that of natural signals (56.4–59.6 dB at ≈ 1 m in front of the bird; GJF, unpublished data).

We conducted all trials between 6:00 and 11:00 and we randomly chose the files of both heterospecifics' and conspecifics' calls for playback. Every file was played back one to six times (mean, four nests per conspecific call file and 4.3 nests per heterospecific call file). The effect of tape broadcast on parental behaviour was tested by comparing the responses of parents to the playback of each tape of alarm calls and heterospecific song with Kruskal–Wallis tests. These tests were performed for each experimental period and parental behaviour variables we defined (see the following text discussion).

Each treatment was video-recorded using a Hi8 video-camera CCD TR940 (Sony Corp., Tokyo) focused to the nest-box entrance. Thirty minutes before nest recording started, cameras were placed >10 m from the nest to habituate the parents to its presence. Treatments consisted of: (1) a 60-min pre-exposure period, prior to the exposure of the nest to the playback stimuli and (2) a 20-min exposure period, where playback was activated.

We evaluated parental response to stimuli exposure from videotapes. We excluded from analyses five trials where parents took more than 5 min to resume parental care after the pre-exposure trial began; therefore, some nests were tested with only one treatment. We measured: (1) the time a parent took to enter the nest (latency) once the stimulus was activated, (2) the total nest visits by parents to the nest (visitation rate) in each treatment and (3) the mean duration of the visits. A visit was recorded when the adult entered the nest and its duration was calculated as the time elapsed since the wren entered the box until it flew away. Visitation rate was estimated as the number of parent's visits to the nest per hour, excluding the time taken to resume activity after the start of a trial (latency). Since birds might become habituated to the stimulus towards the end of the trial, we divided the exposure period into 10-min intervals (E_{10} and E_{20}). We used generalized linear mixed models to analyse bird response to the stimulus because it incorporates repeated measures over the same individual nests (Galway 2006). We included the model latency, nest visitation rates, and mean duration of visits as response variables, the nest identity as a random factor and experimental periods (pre-exposure, E_{10} and E_{20}), stimulus (alarm call or heterospecific song) and the interaction (stimulus \times period) as the predictive variables, assuming a normal error distribution and an identity link function (Galway 2006). The response variables were squared root (latency, nest visitation rates) or log-transformed (mean duration of visits). For latency, we only included stimulus as the predictive factor.

Results

We did not find any effect of tape broadcast on any of parental responses for both control and conspecific call treatments (Kruskal–Wallis tests, $P > 0.05$). Latency to return to the nest was affected by conspecific alarm calls; breeding adults showed significantly greater latencies when exposed to a conspecific alarm call than to a heterospecific song (Wald test=5.77, $df=1$, 21.7, $P=0.02$; Fig. 1).

Nest visitation rates did not significantly differ between the experimental periods nor between stimuli played back (Wald test=0.67, $df=1$, 103, $P=0.41$, and Wald test=1.12, $df=2$, 94.3, $P=0.57$, respectively). Also, we did not detect an interaction effect of stimulus played back and the

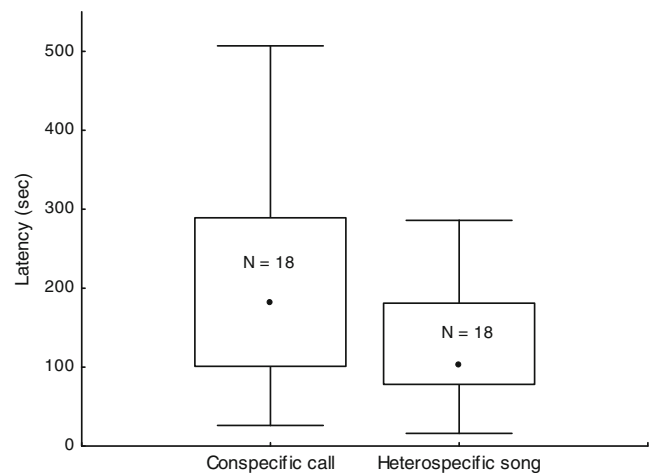


Fig. 1 Latency of parents to enter the nest when exposed to an acoustic stimulus (conspecific alarm call or heterospecific song). Dots represent median values; boxes are the 25 and 75 percentiles, and whiskers denote the range of values measured

periods on the response of birds (Wald test=0.30, $df=2$, 94.3, $P=0.57$).

The mean duration of parents' visits decreased when we broadcast the stimulus (Wald test=6.03, $df=2$, 84.3, $P=0.05$), but no differences were found when we compared the response to conspecific alarm calls and to heterospecific songs (Wald test=1.41, $df=1$, 91, $P=0.24$). We did not detect an interaction effect between stimulus played back and periods (Wald test=0.93, $df=2$, 90.3, $P=0.93$). Duration of parent's visits was shorter during both E_{10} and E_{20} periods than during the pre-exposure.

Discussion

Nesting southern house wrens responded to conspecific alarm calls broadcast from a neighbour's territory by increasing the time to re-enter the nest. Furthermore, parental activity at the nest was not affected when we broadcast a heterospecific song from a non-sympatric species. The fact that house wrens did not respond similarly to heterospecific songs but changed their parental behaviour when exposed to specific alarm calls strongly suggests that they were able to recognize and exploit vocal information that was released in a neighbouring territory.

Parents did not alter the nest visitation rate during the broadcasting of conspecific alarm calls but increase the returning time to the nest, suggesting that wrens might spend more time outside the cavity to detect, evaluate or anticipate the threat when being alerted of a predator's presence. Therefore, although a threat at a neighbours' territory may not be perceived as an immediate threat, wrens seem to change their behaviour by anticipating a possible danger inside their territory.

Several studies have shown that nesting birds usually respond to the placement of a predator model near the nest by modifying their activity (Martin et al. 2000; Eggers et al. 2005), strongly suggesting that parents are able to respond to a direct threat. Studies evaluating the importance of acoustic information in assessing predation risk in birds reported that acoustic cues provided incomplete information, and therefore animals respond differently than when receivers have a direct, visual cue (van der Veen 2002; Lind et al. 2005). A possible explanation is that visual detection of a predator gives direct information about the nature of the predator and the threat that it represents (Lind et al. 2005). When individuals have access only to indirect information such as that provided by alarm calls, it is more difficult for receivers to assess the risk unless calls carry information about the nature of risk (van der Veen 2002; Lind et al. 2005; Barrera et al. 2011). The response of receivers lies therefore on the reliability of the signal and the information that it can carry (Lind et al. 2005; Magrath et al. 2009). An experiment manipulating both acoustical and visual signals of a predation threat would be necessary to assess the relative value of direct and indirect information.

Our results suggest that, although alarm calls are not directed to neighbours, they can still use this information to adjust their parental investment and risk taking behaviour. Similar use of information has been described for other behaviours in birds, such as fighting ability assessment (e.g. Peake et al. 2002), mating partner selection (Mennill et al. 2002) and predation risk assessment through the use of heterospecific alarm calls (Rainey et al. 2004; Goodale and Kotagama 2008; Bell et al. 2009). We believe that our results emphasize the importance of social environment and information networks in the assessment of predation risk in nesting birds.

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