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Short Communication

Variation in the alarm calls of Southern House Wrens (*Troglodytes musculus*)

Gustavo J. Fernández[A,B], *M. Gabriela Corral*[A] *and Mariana E. Carro*[A]

[A]Laboratorio de Ecología y Comportamiento Animal, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EHA, Buenos Aires, Argentina.

[B]Corresponding author. Email: gjf@ege.fcen.uba.ar

Abstract. We examined variation in the structure and characteristics of alarm calls of nesting Southern House Wrens (*Troglodytes musculus*) during the 2007 and 2008 breeding seasons. We took multiple measures of 221 calls of 21 males and 18 females and analysed them for individual and sexual differences. We recognised two distinctive alarm calls, named Type I (TI) and Type II (TII). Sexes did not differ in rates of calling or call structure. However, females produced TI calls more frequently and TII calls less frequently than males. Rate and acoustical structure of TI calls varied with the age of nestlings, but there was no relationship between this factor and TII calls. Individuals increased the emission of TI calls with nestling age, but these calls had lower frequencies when nestlings were older. Given the differences we found across call types, we propose that each call type has a different function, which remains to be tested.

Additional keywords: calling rate, call structure, communication, signal function.

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Introduction

In birds, alarm calls have been suggested to perform a number of functions. Birds generally use alarm or warning calls to communicate the presence of a predator (e.g. Klump and Shalter 1984; Marler 2004; Zuberbühler 2009), for example, during the nestling stage, adults can give alarm calls in order to silent nestlings in presence of a predator (Greig-Smith 1980; Kleindorfer *et al.* 1996; Platzen and Magrath 2004; Madden *et al.* 2005; Suzuki 2011) or to alert mates (Högstad 1995; Haftorn 2000; Krams *et al.* 2006). Alarm calls may also function to distract or deter predators (Greig-Smith 1980; Högstedt 1983), or to attract mates, and other conspecifics or even other species, to help the caller in mobbing a predator (Curio 1978; Grim 2008).

Individual variation in alarm calls has been found in several studies, particularly in socially living mammals (e.g. Cheney and Seyfarth 1988; McCowan and Hooper 2002; Blumstein and Munos 2005). This individual variation is presumed to give information about the caller, such as age, sex or kinship, which could affect the reliability of the signal (Blumstein *et al.* 2004). In birds, far fewer studies have assessed the possibility that alarm calls vary among callers, with implications for the study of potential benefits of caller identification (Kennedy *et al.* 2009; Colombelli-Négrel *et al.* 2011). Individual variation in alarm calls could lead to adaptive outcomes when calling is performed to alert kin or mates. However, if calls are given to deter a predator, no specific selective pressure could be expected to favour individual distinctiveness of calls. Sexual and age-related differences in alarm calls have also been found in some studies and have been related to the different benefits obtained by the callers, such as differences in terms of mate investment and reproductive success (Högstad 1995; Rajala *et al.* 2003).

In this study, we examined variation in the structure of alarm calls of individual Southern House Wrens. This species has two types of general alarm call, known as Type I and Type II (Fasanella and Fernández 2009; TI and TII hereafter). T1calls are a harsh hissing sound – a *buzz* –usually uttered in a repetitive manner in response to the presence of predators (Fig. 1). TII calls are much shorter and low-pitched calls – a highly repetitive *trrr* – that is given by birds during nesting but overall less frequently than TI calls. The use of TI calls by breeding birds increases with progressive nesting stages, with more frequent calls made during the rearing of older nestlings (Fasanella and Fernández 2009). Also nestlings reduce their activity and vocalisations when they hear the calls of their parents (Serra and Fernández 2011). The use of TII calls does not vary with nesting stage and its function is not known. The main objective of this study was to explore individual (sex, breeding experience) and contextual (nestling age) variation in calls. If calls are emitted to alert nestlings or mates, individual or sex differences in call structure should be evident. If calls are performed as a deterrent or mobbing signal directed to a predator, we would not expect individual or sex differences, but we would expect variation with experience (age) or nesting stage. The analyses of this study will allow us to understand the sound properties of the calls and develop new hypotheses to test their function.

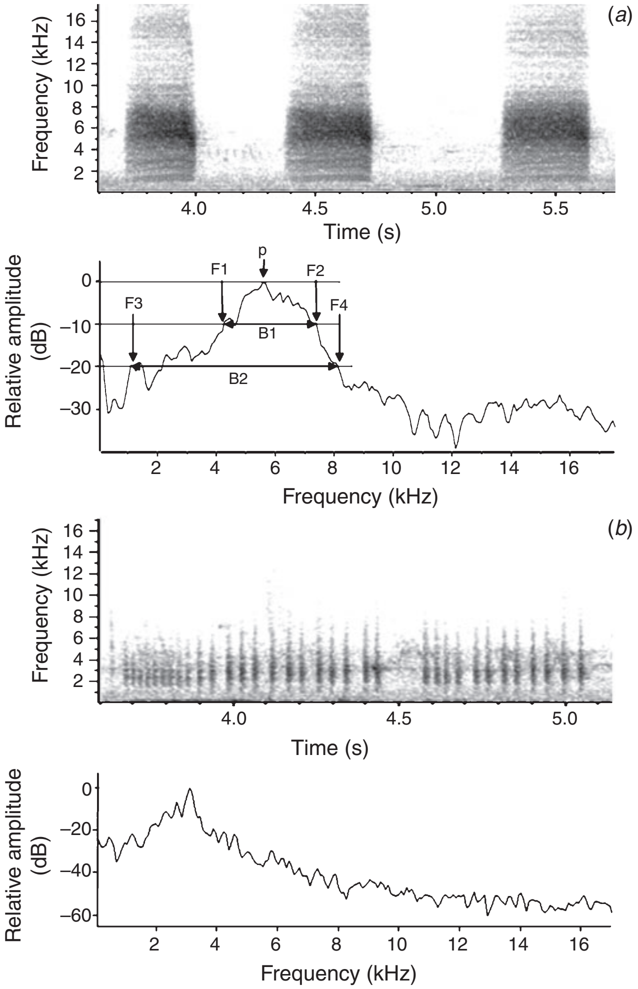

Fig. 1. Spectrogram and power spectra of typical alarm calls of Southern House Wrens: (*a*) Type I (TI) calls and (*b*) Type II (TII) calls. Amplitude has been scaled relative to the highest energy overtone (dB = 0). Acoustic variables measured were: peak frequency (p); lower and upper frequencies above –10 dB (F1 and F2); and lower and upper frequencies above –20 dB (F3 and F4). The bandwidth at –10 dB was calculated by subtracting F1 from F2 (B1), and the bandwidth at –20 dB was calculated by subtracting F3 from F4 (B2).

Materials and methods

The study was carried out in an 8-ha native woodland at General Lavalle (36°20′S, 56°54′W), Buenos Aires, Argentina. Vegetation was mainly *Celtis tala*, *Scutia buxifolia* and *Schinus longifolius*. This site contained 93 wooden nest-boxes attached to trees, 1.5 m above the ground, that Wrens used regularly for nesting since 2004.

Southern House Wrens are resident and socially monogamous, with males defending all-purpose territories year-round (Llambías and Fernández 2009). The study site held 45 Wren territories during 2007 and 35 during 2008. Territories and nest-boxes were checked periodically during the breeding season. Most adults (87%) were colour-banded before or during the first nesting attempt. On each visit we recorded the stage of nesting (number of days after the first egg was laid), identified the adults and noted if males or females gave alarm calls. In 36 cases we were able to determine if the caller was either an experienced (at least their second year as a breeder; $n = 19$) or inexperienced (in their first year as a breeder; $n = 17$) breeder. As Wrens are able to breed when they are 10–11 months old, inexperienced birds were mostly ~1 year old and experienced birds mostly 2–3 years old.

We recorded calling bouts (a continuous series of alarm calls) of 36 individuals (19 males and 17 females during visits to the nests *ad libitum* with a digital Fostex FR-2 LE CF field recorder (Fostex Electric Co. Ltd, Tokyo, Japan) and a Sennheiser shotgun microphone (K6 power module and ME66 recording head with MZW66 pro windscreen, frequency response 20 Hz–20 kHz, ±2.5 dB; Sennheiser Electronic, Wedemark, Germany). We recorded alarm calls at distances of 2–10 m, under varying climatic conditions (except rainy days) and at a sample rate of 44.1 kHz with 16-bit resolution (mono format). For each individual recorded, we analysed calls that had the greatest signal-to-noise ratio and did not overlap with other vocalisations or bird sounds. A total of 221 calls were collected for analysis (4–6 calls per individual): 118 from 19 males and 103 from 17 females.

Recorded calls were high-pass filtered at 0.3 kHz, and analysed using the program Canary 1.2.4 (Cornell Laboratory of Ornithology, Ithaca, NY). We obtained spectrograms and power spectrums of each call using a fast Fourier transformation (frame length, 512 points; time-grid resolution, 5.8 ms; overlap, 50%; FFT, 1024 points; frequency resolution, 43.07 Hz; Hamming window; and the default clipping level, –80 or –95 dB). From these, we measured: call-length, call-rate (number of calls per second), peak frequency (the frequency with the highest peak amplitude), lowest frequency above –10 dB relative to the peak, the highest frequency above –10 dB, the highest frequency above –20 dB, the lowest frequency above –20 dB, and the bandwidth at –10 and –20 dB (Fig. 1). The 10- and 20-dB amplitude thresholds were chosen arbitrarily in order to characterise the bandwidth of frequencies with higher amplitudes.

Data analysis

We performed a variance component analysis to identify structural variables that showed higher inter-individual differences in each call type. These variables were included in a standard discriminant function analysis (DFA), with individual as the grouping variable. Correct assignment of calls in the classification matrix derived from this analysis allows us to assess the existence of consistent structural differences among calls uttered by different individuals.

Differences in the characteristics of alarm calls between sexes was tested on TI calls because females uttered few TII calls (only one recorded). To test for differences between sexes, we used a permuted DFA (pDFA) with sexes (male–female) as the grouping variable, and the call length and structural variables as predictor variables. pDFA controls for repeated sampling on the same individuals (we had 4–6 calls per individual; Mundry and Sommer 2007). We included subject as a control factor nested into call type in the analysis. We used four randomly selected elements per subject for the initial calculation of the discriminant functions (total number of calls included = 140). We then used the remaining calls ($n = 81$) to cross-validate the analysis (hold-out sample). A total of 100 random selections of the original dataset were performed and data obtained were analysed with a DFA and discriminant functions cross-validated. We considered that calls differed in their acoustical structure if the average number of correctly classified elements differs from those obtained from calculation of discriminant functions resulting from the analysis of 1000 random permutations of the original dataset.

We used generalised linear models to analyse the effect of sex, nesting stage, individual experience (first or subsequent breeding season) and the interaction among these factors on the rates of TI and TII alarm calls and over the structural characteristics of these calls. We assumed a gamma error distribution of the response variables (call rates) and used an identity link function for TI calls and a reciprocal link function for TII calls. We did not include the sex of caller as a factor in the analysis of TII call-rate because we had only one recording of a female uttering this type of call. To test the effect of these variables on structural characteristics of calls we first performed a principal components analysis (PCA) for each call type to reduce the number of structural variables to be included in the model. We retained the PC with eigenvalues >1, and we extracted the variables that had contribution coefficients >0.70 on these components. We used the mean values of PCA scores for each individual for each call type as the response variable with a normal distribution of the error in the GLMs, and sex, individual experience and nesting stage, and their 2- and 3-factor interactions as the predictive variables, with an identity link function. We performed backward elimination of fixed terms to obtain minimal models, checking the change in deviance of the model (Crawley 1993).

All *P*-values quoted are two-tailed and differences were considered significant at $P < 0.05$.

Results

On 154 visits to the nest during which parents called, individuals uttered TI calls on 119 occasions and TII calls on 66. Females gave TI calls more often than males but gave TII calls less often (Fisher Exact' test, $P < 0.001$; Table 1). Rate of TI calling did not differ between sexes or among individuals with different breeding experience, but it increased with nesting stage (deviance ratio, $Dr = 4.99$, d.f. = 1, 18, $P = 0.04$). Rate of TII calling did not differ with individual experience, nesting stage or the interaction of these ($Dr = 0.65$, d.f. = 3, 11, $P = 0.60$).

Sexes did not differ in the structure of TI calls. According to the pDFA simulations, the number of correctly classified calls and correctly cross-classified calls from the randomised datasets exceeded the average number of correctly classified calls and correctly cross-classified calls from the original datasets ($P = 0.57$ and 0.58).

Table 1. Frequency of use of Type I and Type II calls uttered by nesting male and female Southern House Wrens (*n* = 137)

Only cases where we could identify the caller were included. Figures are numbers of calls, with percentage of total calls in parentheses

	Type I	Type II	Total
Males	29 (15.7)	53 (28.7)	82 (44.3)
Females	90 (48.6)	13 (7.0)	103 (55.7)
Total	119	66	185

Variance component analysis of TI calls showed that frequency bandwidth above –10 and –20 dB had the highest inter-individual differences. However, when included in the DFA, only 35.9% of calls were correctly assigned to the caller ($F_{72,344} = 6.34$, $P < 0.001$). A similar result was obtained when considering TII calls. Here, the length of the call, the minimum frequency above –10 dB, and the peak frequency showed the highest inter-individual differences. Given these differences, DFA only correctly classified 49.28% of calls ($F_{33,162} = 17.48$, $P < 0.001$).

Modelling methods also showed that sex did not significantly contribute to variation in the structure of TI calls ($\Delta Vr = 0.13$, d.f. = 1, 19, $P = 0.72$) but PCA scores of the factor 1 increased with the nesting stage ($\Delta Vr = 4.86$, d.f. = 1, 19, $P = 0.04$). Factor 1 correlated negatively with the maximum frequency above –10 and –20 dB, and the frequency peak of the call. Scores at the negative end of the axis corresponded to high-pitched calls with higher maximum frequencies above –10 and –20 dB and higher frequency peaks. No effects of sex, age or nesting stage on any other call characteristic were detected. Also, structural variation of Type II alarm calls did not appear to vary with individual experience or nesting stage, as these variables did not show a significant contribution to the model fit ($\Delta Vr = 0.09$, d.f. = 1, 10, $P = 0.78$ and $\Delta Vr = 1.71$, d.f. = 1, 10, $P = 0.23$).

Discussion

We found much variation in call structure both among and within individual Southern House Wrens. During our visits to the nests, males more often uttered TII calls, whereas females mainly uttered TI calls. We did not detect differences in call structure between sexes and, although statistical analyses revealed that individual calls could be differentiated, the *a posteriori* percentage of correct call assignment was low (<40% for TI calls, and ~50% for TII calls).

The use of TI alarm calls increased with nesting stage, being higher when nestlings were older (see also Fasanella and Fernández 2009). This is a common pattern in alarm calling behaviour, and is usually attributed to an increase in nest defence owing to the greater reproductive value of the brood (Curio 1987; Redondo and Carranza 1989) or to the higher detectability of the young (Burger *et al*. 1989; Weatherhead 1989). This pattern of calling and the lack of individual or sex differences in call structure appear to support the hypothesis that these alarm calls might be uttered to attract the predator's attention from the nest, or as a 'pursuit-deterrent' signal informing the predator that it has been detected and encouraging it to depart (Curio 1978; Klump and Shalter 1984; Hasson 1991; Kennedy *et al*. 2009). Our evidence for this hypothesis is not conclusive, but the broad frequency band of this call and the fairly long duration make TI calls noticeable. Also, when giving TI alarm calls, birds approach the threat, moving constantly, and also attempt to physically deter the intruder with attacking flights over the predator (G. J. Fernández, pers. obs.).

Alternatively, it has been suggested that alarm calls are directed to nestlings (Knight and Temple 1988; Kleindorfer *et al*. 1996; Platzen and Magrath 2004; Suzuki 2011) or mates (Yasukawa 1989; Haftorn 2000; Krams *et al*. 2006). In Southern House Wrens, Serra and Fernández (2011) found that nestlings reduced their vocalisations and activity inside the nest-box in response to TI alarm calls uttered by parents. However, they failed to show that parents produced the alarm calls to silence the nestlings. Furthermore, under this hypothesis, individual differences in call structure would be expected owing to natural selection and would increase the reliability of the signal. However, we did not detect differences in call structure that allow individual discrimination.

TII alarm calls did not vary with nestling stage, were emitted mainly by males, and were uttered much less frequently than TI calls (see also Fasanella and Fernández 2009). In contrast to the behaviour of Wrens when they uttered TI alarm calls, individuals emitting TII calls remained hidden and evasive. This behaviour, together with the short duration, low frequency and fairly narrow bandwidth of TII calls, makes it difficult to localise the caller. The function of this call is not known but it may be given to alert mates or nestlings to the presence of a threat, or may differ based on predator type (see Kleindorfer *et al*. 2005). Specific experiments assessing how are readily TI and TII calls can be detectable and located by predators, and the response of conspecifics to these calls are necessary to confirm these hypotheses.

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