ORNITOLOGIA NEOTROPICAL 23: 251–260, 2012

ALARM CALLS OF NESTING SOUTHERN HOUSE WRENS (*TROGLODYTES MUSCULUS*)

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Resumen. – Llamados de alarma de la Ratona Común *(Troglodytes musculus)* durante el período de nidificación. – Examinamos la estructura y características de los llamados de alarma emitidos por individuos de Ratona Común (*Troglodytes musculus*) durante las temporadas de cría 2007–2008. Tomamos múltiples medidas estructurales de 221 llamados emitidos por individuos en cría y se realizaron análisis multivariados para clasificarlos. Reconocimos 2 llamados de alarma distintivos, denominados Tipo I y Tipo II. Los llamados Tipo I resultaron de mayor duración y presentaron frecuencias más altas que los llamados de Tipo II, sin embargo la tasa de llamados fue más alta para éste último. Dadas las diferencias estructurales encontradas entre los tipos de llamados, proponemos que cada tipo tiene una función diferente que aun no se ha probado.

Abstract. – We examined the structure and characteristics of alarm calls uttered by nesting Southern House Wrens (*Troglodytes musculus*) during the 2007–2008 breeding seasons. We took multiple structural measures of 221 calls uttered by breeding individuals and used multivariate analyses to classify them. We recognized two distinctive alarm calls, named Type I and Type II. Type I calls were longer in duration and had higher frequencies than Type II calls; however, birds used Type II calls at a higher rate. Given the structural differences found between both call types; we propose that each call type has a different function, which remains to be tested. *Accepted 25 June 2012.*

Keywords: Southern House Wren, *Troglodytes musculus*, Troglodytidae, communication, calling rate, call structure.

INTRODUCTION

Birds generally use vocalizations when faced with a predator or a threat (e.g., Klump & Shalter 1984, Marler 2004, Zuberbühler 2009). These vocalizations are known as alarm calls, and could meet different functions. For example, some calls are uttered to warn conspecifics or close relatives the presence of a predator ("warning calls"; Taylor *et al.* 1990, Högstad 1995, Kleindorfer *et al.* 1996, Platzen & Magrath 2004, Krams *et al.* 2006, Suzuki 2011), to attract the predator's attention ("distraction calls"; Curio 1978, Greig-Smith 1980, Högstedt 1983), or to deter or mob the predator ("defensive or mobbing calls"; Hasson 1991, Haftorn 1999, Grim 2008, Kennedy *et al.* 2009).

Due to the different functions that alarm calls could have, it would be expected that structural characteristics of alarm calls have evolved to meet these specific functions (Marler 1955). For example, when alarm calls are emitted to alert conspecifics, it must be detectable for congeners, while the caller must remain undetected by the predator (e.g., Ryan *et al.* 1982, Sordahl 1990, Bayly & Evans 2003, Caro 2005). On the other hand, calls directed primarily to the predator (either to deter or threat) should be both detectable and localizable by the predator and the conspecifics if the main function is to mob the predator and to drive away the threat from the nest (Curio 1978, Greig-Smith 1980, Klump & Shalter 1984, Grim 2008, Kennedy *et al.* 2009).

In this study, we examined the structure of alarm calls uttered by nesting Southern House Wrens, *Troglodytes musculus.* These calls were elicited approaching the nest when wrens were rearing nestlings. The main purpose of this paper is to present a detailed acoustical analysis of call variants uttered during the nestling rearing stage. The analysis of its structure will allow us to infer about the function that these alarm calls could have, and to understand the potential costs and benefits for the uttering parents.

METHODS

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

Southern House Wrens are year-round residents that defend all-purpose territories. The predominant social mating system is monogamy with biparental care of nestlings (Llambías & Fernández 2009, LaBarbera *et al.* 2010). Incubation period in this species lasts 13–14 days whereas nestlings remain in the nest for 16–17 days (Llambías & Fernández 2009).

The study site comprised of 45 and 35 wren territories defended by males during 2007 and 2008 respectively. Each territory had at least one nest-box that individuals usually used to breed. Nest-boxes were checked periodically during the breeding season to register the nesting attempts. Once a nesting attempt was noted, we visited the nest-box to register the nesting stage and identify the adults. Most adults (87%) were color-ringed.

During visits to 24 nests where parents were rearing nestlings during the 2007–2008 breeding seasons, we recorded calling bouts (a continuous series of alarm calls) uttered by the parents when one of us approached the nest. Recordings were made *ad libitum* with a digital Fostex FR–2LE CF field recorder (Fostex Electric Co, Ltd, Japan) attached to 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 between 2–10 m, under varying climatic conditions (but not during rainy days) and recordings were digitalized at a sample rate of 44.1 kHz with 16-bit resolution (mono format). In 18 cases we were able to measure call amplitude (A-weighting) at 1–2 m from the bird with a TES-1350A sound level meter (TES Electrical Electronic Corp., Taiwan, accuracy ±2 dB at 94 dB).

For each subject, we analyzed a short sequence of calls that had the greatest signal-to-noise ratio and did not overlap with other vocalizations or bird sounds. A total of 39 calling bouts uttered by 36 individuals (19 males and 17 females) were recorded from field. We collected 212 calls from these recordings for the analysis (mean: 5.8 calls per bout; three bouts were discarded as they were performed by individuals previously recorded). Recorded alarm calls were high-pass filtered at 0.3 kHz to reduce the low frequency noise, and analyzed using the program Canary 1.2.4 (Charif *et al.* 1995). We conducted a fast Fourier transformation to obtain spectrograms and average spectra of each sequence of calls (frame length of 512 points, time grid resolution 5.8 ms with 50 % overlap, FFT 1024 points, frequency resolution 43.07 Hz, Hamming window, and the default clipping level of -80 or -95 dB). We identified the calls as each sound unit detectable on spectrograms. We measured the length of each call and the call rate from the spectrogram. The acoustical structure of calls was evaluated from the power spectrum of each call. We measured (1) the peak frequency (the frequency with the highest peak amplitude), (2) the lowest frequency above -10 dB relative to the peak, (3) the highest frequency above -10 dB, (4) the highest frequency above -20 dB, (5) the lowest frequency above -20 dB, and (6) the bandwidth at -10 dB and -20 dB (Fig. 1). The 10 and 20 dB amplitude threshold were chosen arbitrarily in order to analyze differences in the bandwidth of frequencies with higher amplitudes.

Data analysis. Structural variables measured from calls were averaged for each individual and included into a principal component analysis (PCA) to determine groups of calls that differ in structure. We retained the principal components with eigenvalues > 1, and we extracted the variables that had contribution coefficients > 0.70 on these components. Visual inspection of the factors allowed us to identify groups. To validate the classification, groups of calls were included in a discrimination function analyses (DFA) to test if indeed these alarm calls were structurally different. For this analysis, call types (groups) were the response variable and the duration of the alarm call bout and all structural variables were included as predictors. The DFA provides a function based on predictor variables that best characterizes the difference between groups and produces *a posteriori* classification assigning each call to its appropriate group (correct assignment) or to other group (incorrect assignment) based on a discriminant function. Therefore, based on the percentage of correct assignment by the DFA, we can confirm our *a priori* classification of calls. For this analysis we used all samples of calls available. However, as we included 4–6 calls per subject, we could potentially obtain incorrect results due to the lack of independency of the calls (Mundry & Sommer 2007). Therefore, we repeated the analysis using a permuted DFA (pDFA) to control for individual effects. The pDFA was performed with an R routine provided by Roger Mundry. We included subject as a random factor nested into call type in the analysis. We used 4 randomly selected elements per subject for the initial calculation of the discriminant functions (total number of calls included = 140). Then, we used the remaining calls (n = 81) to cross-validate the analysis (hold-out sample; Mundry & Sommer 2007). A total of 100 random selections of the original data set were performed and data obtained was analyzed with a DFA and discriminant functions cross-validated. Results obtained from these analyses were compared with those obtained from calculation of discriminant functions resulting from the analysis of 1000 random permutations of the original data set. We considered that calls differed in their acoustical structure if the average number of correctly classified elements as well as correctly cross-classified elements from the original set differed from those estimated from the randomized data sets.

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

RESULTS

We retained only the first factor from the PCA as it accounted for 81.6 % of the

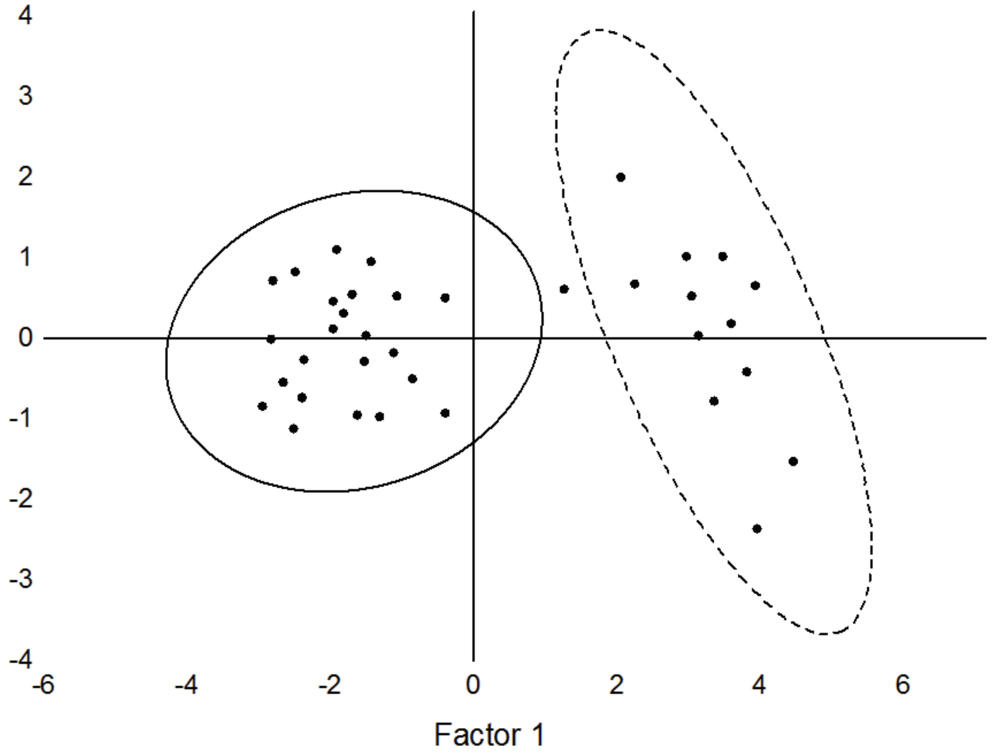

FIG. 1. Plot of the alarm calls uttered by nesting Southern House Wrens according to a Principal Component Analysis of the structural characteristic of these calls. Ellipses denote the two groups of calls (Type I and Type II calls) identified based on structural similarities of calls. We included spectrograms and power spectra for these calls.

variance (Table 1). All variables included in the analysis contributed to explain variation along factor 1 (Table 1). Scores at the negative end of the axis corresponded to longer calls with higher frequency peaks and higher maximum and minimum frequencies above -10 dB and -20 dB, and a broader frequency band. Therefore, alarm calls given by nesting house wrens could be grouped in two types that we named as Type I and Type II alarm calls (Fig. 1). Females contribute to most of Type I alarm calls (15/24), whereas males uttered most of Type II calls (9/11). The first call is a harsh hissing sound – a *buzz* – that is usually uttered in a repetitive manner in response. Type II calls are significantly shorter low-pitched calls – a highly repetitive *trrr* call that, in our experience, is less frequently uttered by the birds during nesting (Fig. 2). The sound pressure level for Type I alarm calls averaged 58.75 dB (range: 56–64 dB, n = 11) at 1–2 m, whereas Type II calls had a sound pressure level of 56.48 dB (range 54–59 dB, n = 7).

DFA conducted to corroborate this classification showed that Type I and Type II calls can be easily distinguished ($F_{(8,212)}$ = 217.95, p < 0.001, Fig. 3). The correct assignment of calls to the *a priori* classification made based on PCA analysis was 99.54 %. Only one call that was classified as Type II was assigned

TABLE 1. Factor loadings for the three first principal components resulting from the analysis of the structure of alarm calls uttered by nesting Southern House Wrens.

	Factor 1	**Factor 2**	**Factor 3**
Eigenvalue	6.52	0.76	0.38
Percentage of variance	81.58	9.51	4.84
Duration of call	-0.92	-0.11	-0.19
Bandwidth at -10 dB	-0.81	0.39	-0.42
Minimum frequency above -10 dB	-0.93	-0.23	0.26
Maximum frequency above -10 dB	-0.99	0.01	0.002
Bandwidth at -20 dB	-0.84	0.47	0.25
Minimum frequency above -20 dB	-0.79	-0.54	-0.14
Maximum frequency above -20 dB	-0.97	0.12	0.13
Peak frequency	-0.96	-0.09	0.06

by the discriminant function as Type I. This call had an unusual high peak frequency (4.65 kHz) but was short in duration (79 ms). The pDFA analysis produced a similar result. The average number of correctly classified cases of the original data was 139.4 (99.6 %), and the average number of correctly cross-classified elements was 74.7 (99.2 %). These values differed significantly from those estimated from the randomized data sets (p = 0.001 for originally included elements and cross-classified elements). All variables included in the analyses contributed significantly to differentiate the calls. Table 2 shows the mean values (± SE) for the acoustical variables of Type I and Type II calls analyzed in this study.

Besides structural differences between calls, alarm calling rate also was different for Type I and Type II calls. Calling rate of Type II calls was higher than that for Type I calls (8.48 calls/s ± 8.55, n = 13, range: 1.98–29.47 calls/s vs 1.22 calls/s ± 0.17, n = 26, range: 0.34–3.87 calls/s, respectively; Mann-Whitney test, $U = 9, p < 0.01$). There is a high variation in calling rates for each call type and we also detected that this variation in calling rate was related to variation in call structure within each call type. Therefore, Type I calls uttered at a high calling rate were shorter in duration (Pearson-moment product tests, $r = -0.47, p = 0.02$). Also, short and fast-uttered Type I calls (high calling rate) showed a non-significant tendency to have a lower frequency above -10 db ($p = 0.05$), and a lower frequency peak ($p = 0.08$) than calls emitted at a slower rate. In a similar way, the calling rates of Type II calls were negatively correlated with the frequency band above -20 dB ($r = -0.7$, $p = 0.008$) and highest frequency above -10 dB ($r = -0.57, p = 0.04$) of calls.

DISCUSSION

Observations we made revealed that southern house wrens emit two general alarm call types, named respectively as Type I and Type II calls. These calls are relatively easy to distinguish and clearly differ in structural components of the call characteristics. Both alarm types are noisy calls, but Type I calls had a higher frequency peak, broader frequency band, lower rate and longer duration than Type II calls.

Type I alarm calls were the most common call response when we approached the nest, and it has been also observed in response to potential predators in the vicinity of the nest, such as skunks, opossums, and domestic dogs (GJF pers. observ.). Type I calls have a relative broad frequency band and long duration make

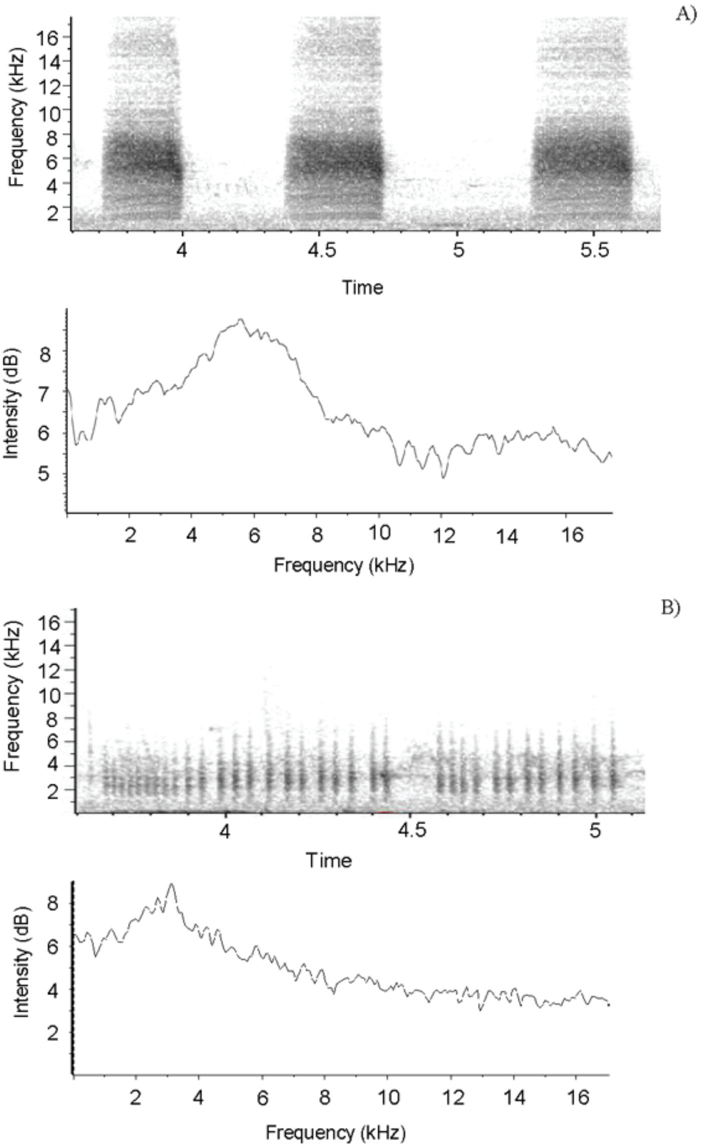

FIG. 2. Spectrogram and power spectra of typical Type I (A) and Type II (B) calls emitted by Southern House Wrens. The amplitude has been scaled relative to the highest energy overtone (dB = 0).

the caller easily localizable. Therefore, we presume that this call might be uttered, either, as a distraction-mobbing response, attracting the predator's attention away from the nest or attracting the mate (and perhaps other birds) to the location of the predator, or well, as a "pursuit-deterrent" signal informing the predator that it has been detected and

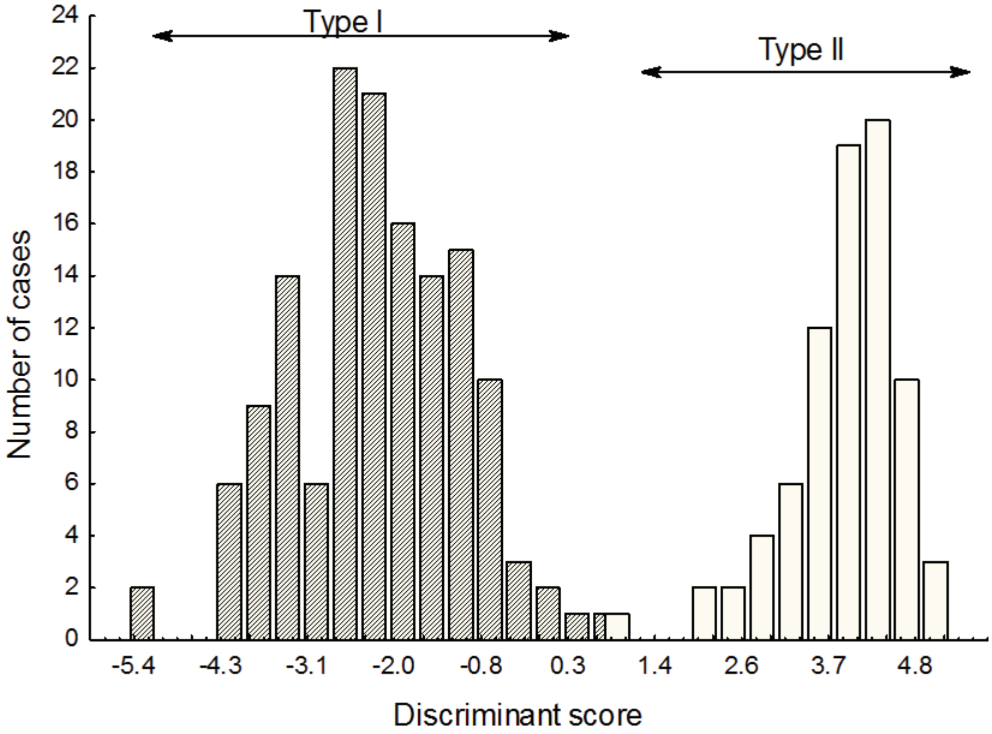

FIG. 3. Distribution of discriminant scores for alarm calls uttered by Southern House Wrens when a human visited the nest. Hatched bars: Type I alarm calls, open bars: Type II alarm calls. Calls at each extreme of the x-axis can be assigned easily to their actual category. Calls in the overlapping region have a low probability of assignment to the actual category according to the classification function used.

encouraging it to depart (Curio 1978, Klump & Shalter 1984, Hasson 1991, Kennedy *et al.* 2009). The evidence favoring this hypothesis is not conclusive, but when researchers visit the nests, birds make Type I alarm calls, approaching the visitor in constant movement; in some cases (very rarely), the birds attempt to physically deter the intruder with an over flight attack (GJF pers. observ.). In contrast to the wren behavior when they uttered Type I alarm calls, individuals emitting Type II calls remained hidden and evasive. This behavior, together with the short duration, low frequency, and relatively narrow bandwidth of the Type II call, makes it difficult to localize the caller. The function of this call remains elusive but it may be uttered to alert mates or nestlings about the presence of a threat, or may differ based on predator type. It is necessary to test experimentally the context in that this call is uttered, and the mate and nestling responses to elucidate its function.

Further evidence that these calls are emitted to immediate listeners (mates, nestlings, or predators) is provided by the low emission intensity of the sound. Both Type I and Type II calls are uttered at a low intensity (54–65 dB at c. 1 m away from caller), and presumably they would attenuate quickly when emitted. From geometric spreading of sound, it would be estimated that the amplitude of the

TABLE 2. Mean values (SE) of the variables measured from calls uttered by Southern House Wrens. Values estimated from 212 alarm calls emitted by 36 individuals. [1]n = 11; [2]n = 7.

Variables	**Type I call** (n = 142)	**Type II call** (n = 70)
Duration of call (ms)	399.27 (8.69)	52.02 (7.54)
Bandwidth at -10 dB (kHz)	3.52 (0.06)	2.33 (0.09)
Highest frequency above -10 dB (kHz)	7.53 (0.05)	4.10 (0.08)
Lowest frequency above -10 dB (kHz)	4.05 (0.05)	1.77 (0.06)
Bandwidth at -20 dB (kHz)	6.82 (0.07)	4.65 (0.13)
Highest frequency above -20 dB (kHz)	8.68 (0.06)	5.44 (0.11)
Lowest frequency above -20 dB (kHz)	1.83 (0.05)	0.79 (0.04)
Peak frequency (kHz)	5.80 (0.06)	2.74 (0.06)
Intensity (dB)	58.75 (0.15) [1]	56.48 (0.11) [2]

sound at the nearest neighbor (wren's territory size averaged c. 60 m in diameter, Llambías *et al.* unpubl. data) would be about 20–28 dB, which could be difficult to detect in background noise. Hence, assuming that the maximum distances over which a species can use an acoustic signal to communicate are equivalent to the distances over which components of that signal are physically detectable (McComb *et al.* 2003), both calls types uttered by nesting Southern House Wrens appear to be used in short-distance communication, supporting the hypotheses of within-pair or prey-predator communication. Also, there is experimental evidence that nestlings would benefit from parents' alarm calls. Serra & Fernández (2011) found that nestlings reduce their activity at the nests and cease begging when Type I calls are presented. However, the authors failed to show that these calls are uttered by the parents to meet this function.

Call structure also varied with the calling rate for both calling types. This variation could be the result of differences in individual motivation or personality (Hollander *et al.* 2008), or due to the existence of mechanical constraints imposed by morphological or physical limits. Such a constraint occurs because of the existence of limits on the performance capacity of the beak and respiratory musculature, which have been shown to affect sound production (Podos 1997). A high call repetition rate requires rapid and brief respiratory movements, which could affect the sound structure (Podos 1997). Further mechanistic analyses are required to assess that there are physical constraints to sound production in this species or whether effectively the variation of call structure respond to motivational differences associated to the context. Also, experimental and observational studies are necessary to determine the functions of the calls we identified, and if it encode information about the level of the threat.

ACKNOWLEDGMENTS

We thank Paulo E. Llambías and Myriam E. Mermoz for helping in the field, the Whisky-Michelli family and Luis Martinez for allowing us to work on their ranches at Buenos Aires, and Mario Beade for logistical support. We specially thank R. Mundry for facilitating the software to perform the pDFA analyses and C. Battagliese for checking the English grammar. We also thank to A. Weller, L. S. Johnson, and an anonymous reviewer for the comments on an earlier version of this paper. This work was supported by the Buenos Aires (grant X434 and UBACyT 20020090200117) and CONICET (PIP112-200901-00011) grants to GJF. All methods used in the present study meet the ethical requirements for science research and comply with the current laws of the country in which they were performed.

REFERENCES

Bayly, K. L., & C. S. Evans. 2003. Dynamic changes in alarm call structure: a strategy for reducing conspicuousness to avian predators? Behaviour 140: 353–369.

Caro, T. 2005. Anti-predator defenses in birds and mammals. Univ. of Chicago Press, Chicago, Illinois, USA.

Charif, R. A., S. Mitchell, & C. W. Clark. 1995. Canary 1.2 User's manual. Cornell Lab. of Ornithology, Ithaca, New York, USA.

Curio, E. 1978. The adaptive significance of avian mobbing: I. Teleonomic hypothesis and predictions. Z. Tierpsychol. 48: 175–183.

Greig-Smith, P. W. 1980. Parental investment in nest defence by stonechats (*Saxicola torquata*). Anim. Behav. 28: 604–619.

Grim, T. 2008. Are blackcaps (*Sylvia atricapilla*) defending their nests also calling for help from their neighbours? J. Ornithol. 149: 169–180.

Haftorn, S. 1999. Contexts and possible functions of alarm calling in the Willow Tit, *Parus montanus*: The principle of "better safe than sorry." Behaviour 137: 437–439.

Hasson, O. 1991. Pursuit-deterrent signals: Communication between prey and predator. Trends Ecol. Evol. 6: 325–329.

Högstad, O. 1995. Alarm calling by willow tits, *Parus montanus*, as mate investment. Anim. Behav. 49: 221–225.

Högstedt, G. 1983. Adaptation unto death: Function of fear screams. Am. Nat. 121: 562–570.

Hollander, J. L., T. Van Overveld, & E. Matthysen. 2008. Personality and nest defense in the Great Tit (*Parus major*). Ethology 114: 405–412.

Kennedy, R. A. W., C. S. Evans, & P. G. McDonald. 2009. Individual distinctiveness in the mobbing call of a cooperative bird, the Noisy Miner *Manorina melanocephala*. J. Avian Biol. 40: 481–490.

Kleindorfer, S., H. Hoi, & B. Fessl. 1996. Alarm calls and chick reactions in the Moustached Warbler, *Acrocephalus melanopogon*. Anim. Behav. 51: 1199–1206.

Klump, G. M., & M. D. Shalter. 1984. Acoustic behaviour of birds and mammals in the predator context. II. The functional significance and evolution of alarm signals. Z. Tierpsychol. 66: 206–226.

Krams, I., T. Krama, & K. Igaune. 2006. Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? J. Avian Biol. 37: 131–136.

LaBarbera K., P. E. Llambías, E. R. A. Cramer, T. D. Schaming, & I. J. Lovette. 2010. Synchrony does not explain extrapair paternity rate variation in northern or southern house wrens. Behav. Ecol. 21: 773–780.

Llambías, P. E., & G. J. Fernández. 2009. Effects of nest boxes on the breeding biology of southern house wrens *Troglodytes aedon bonariae* in the southern temperate zone. Ibis 151: 113–121.

Marler, P. 1955. Characteristics of some animal calls. Nature 176: 6–8.

Marler, P. 2004. Bird calls: Their potential for behavioral neurobiology. Ann. N. Y. Acad. Sci. 1016: 31–44.

McComb, K., D. Reby, L. Baker, C. Moss, & S. Sayialel. 2003. Long-distance communication of acoustic cues to social identity in African elephants. Anim. Behav. 65: 317–329.

Mundry, R. & C. Sommer. 2007. Discriminant function analysis with nonindependent data: consequences and an alternative. Anim. Behav. 74: 965–976.

Platzen, D., & R. D. Magrath. 2004. Parental alarm calls suppress nestling vocalization. Proc. R. Soc. Lond. B. 271: 1271–1276.

Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution 51: 537–551.

Ryan, M. J., M. D. Tuttle, & A. S. Rand. 1982. Bat predation and sexual advertisement in a Neotropical anuran. Am. Nat. 119: 136–139.

Serra, C., & G. J. Fernández. 2011. Reduction of nestlings' activity in response to parental alarm calls in the Southern House Wren, *Troglodytes musculus*. J. Ornithol. 152: 331–336.

Sordahl, T. 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. Wilson Bull. 102: 349–352.

Suzuki, T. N. 2011. Parental alarm calls warn nestlings about different predatory threats. Curr. Biol. 21: R15–R16.

Taylor, R. J., D. F. Balph, & M. H. Balph. 1990. The evolution of alarm calling: a cost-benefit analysis. Anim. Behav. 39: 860–868.

Zuberbühler, K. 2009. Survivor signals: the biology and psychology of animal alarm calling. Adv. Stud. Behav. 40: 277–322.