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How great tits respond to urgency-based information in allopatric Southern house wren mobbing calls

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Abstract

Many species of birds use alarm calls to signal information about predators, including the level of threat. Previous playback experiments suggest that the urgency response towards heterospecific calls is phylogenetically conserved, notably in the Paridae family. Using playback experiments conducted on European great tits (*Parus major*), we tested whether this species perceives information about urgency in mobbing calls produced by an allopatric non-Paridae species, the Southern house wren (*Troglodytes aedon bonariae*), by broadcasting calls with high-calling rate (high threat) and calls with low-calling rate (low threat). We found that great tits tend to approach the loudspeaker during playbacks of calls with high-calling rate more often than during playbacks of calls with low-calling rate. Female great tits gave more calls during playbacks of calls with high-calling rate than during playbacks of calls with low-calling rate, whereas there was no significant difference in the number of calls given by males between playbacks of calls with high- and low-calling rates. Thus, our results suggested that great tits perceived the urgency message encoded in calls given by an allopatric non-Paridae species.

KEYWORDS
allopatric call, calling rate, great tit, playback, Southern house wren, urgency

1 | INTRODUCTION

Many species of birds and mammals use alarm calls to warn others of the presence of danger. These calls can also convey information about the type and the degree of danger (Leavesley & Magrath, 2005; Manser et al., 2002). The level of urgency can be encoded by differences in call structure, repetition or composition, and the way of encoding such information varies between species. In birds, high-urgency alarm calls often have a higher repetition rate than low-urgency alarm calls in both fleeing and mobbing contexts (Dutour, Walsh, & Ridley, 2021; Suzuki, 2016). Flee alarm calls are associated with the caller fleeing to cover while motivating other individuals to freeze or flee, whereas mobbing calls are associated with the caller approaching and vocalizing or displaying towards the predator while recruiting others behaviourally to join it (Curio, 1978; Magrath et al., 2015).

In fleeing contexts, playback experiments have revealed that birds are more likely to flee in response to both conspecific and heterospecific high-urgency alarm calls than low-urgency alarm calls (Fallow & Magrath, 2010). In mobbing contexts, receivers rapidly approached call variants that were associated with high threat (Ellis, 2008; Templeton & Greene, 2007). Mobbing is an ideal

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situation to test how individuals respond to risk-based information in heterospecific calls because appropriately responding to other species mobbing calls has a survival function (Caro, 2005).

Three mechanisms have been suggested to explain the development of responsiveness to urgency in heterospecific alarm calls (Fallow & Magrath, 2010; Magrath et al., 2015). First, birds learn the signalling system of other species. In particular, birds may learn to associate a particular type of alarm call with a particular event through social interactions. Mobbing events offer probable opportunities for learning since they involve repetitive alarm calling from multiple callers which perform stereotyped behaviours (Curio et al., 1978). Second, birds may use information in heterospecific calls by generalizing from their own urgency-encoding system (Ghirlanda & Enquist, 2003). Heterospecific call recognition may be facilitated by a similar structure of different species' mobbing calls (Fallow et al., 2011). Finally, birds may innately respond more strongly to greater call repetition (Randler, 2012). Previous playback experiments suggest that the urgency response towards heterospecific mobbing calls is phylogenetically conserved. Indeed, European great tits (*Parus major*) responded stronger than the playbacks of an allopatric American species (black-capped chickadee, *Poecile atricapillus*) broadcasting high-urgency mobbing calls compared with low-urgency mobbing calls (Randler, 2012), suggesting that this response is a phylogenetically conserved recognition mechanism within the family Paridae (Langham et al., 2006).

This study investigated whether the great tit could perceive information about urgency in mobbing calls given by an allopatric non-Paridae species, the Southern house wren (*Troglodytes aedon bonariae*, Figure 1). Southern house wrens encode urgency information in their mobbing calls by increasing the rate of alarm calling in response to closer threats, to which conspecifics and sympatric heterospecifics respond appropriately (Fernández & Carro, 2022). Great tits encoded urgency in a similar way to that of wrens, by increasing the rate of alarm calling according to the level of the threat (Carlson et al., 2017; Kalb et al., 2019). Thus, the higher call rate is in both species related to higher threat. Importantly, recent experimental work on great tits indicated that their vigilance behaviour towards conspecific mobbing calls depend on the calling rate broadcast, but their approaching behaviour towards conspecific mobbing calls does not (Salis et al., 2022). Here, we used playback experiments to test whether higher calling rates triggered a stronger mobbing response from great tits. Among the three mechanisms explaining the development of responsiveness to urgency in heterospecific alarm calls in the context of our experiment, the first is not an option because house wrens are allopatric. For the second hypothesis, great tit can generalize from their own calls and some sympatric species can also encode urgency in a similar way to that of house wrens that the great tits may be familiar with and therefore generalize from. Finally, great tits can also have an innate recognition of urgency encoding via call rate. In such case, one would expect that they would respond to any similar sound at an appropriate level, regardless of species. To discriminate between these hypotheses, we analysed acoustic properties of the mobbing calls given by the Southern house wren, the great tit and the only species of wren present in the study site, the Eurasian wren (*Troglodytes troglodytes*). We also compared the urgency-encoding system of these three species. If the acoustic properties of the mobbing calls and the calling rate in high-risky situation of these three species are different and if great tits respond more during playbacks of high-urgency calls than during playbacks of low-urgency calls, these would suggest that great tits have an innate recognition of urgency encoding via call rate.

2 | METHODS

2.1 | General experimental design, study site and species

To assess the responses of great tits to variation in the calling rates of house wrens, we performed a playback experiment by broadcasting calls with high-calling rate (high threat) and calls with low-calling rate (low threat). The song of the house wren was used to control for novelty (i.e. to ensure that the great tits do not simply respond to any novel sound). Experiments were conducted in mixed deciduous-coniferous forests near Lyon (France) between December 2021 and January 2022 during the non-breeding season. We conducted this experiment with 72 adult great tits (24 individuals for each

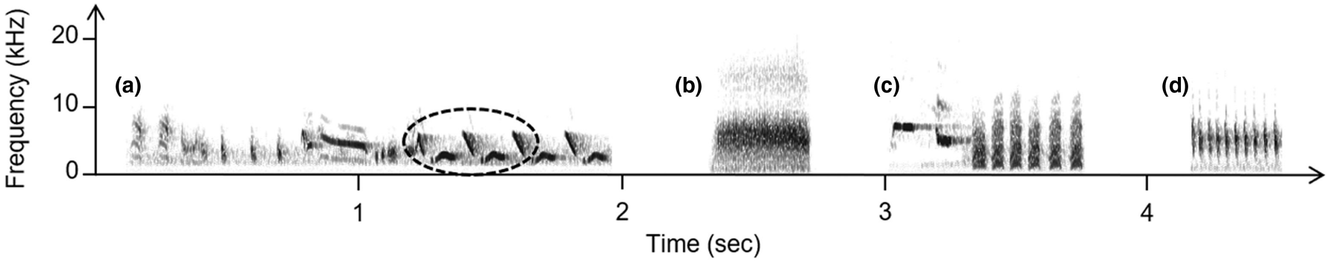

FIGURE 1 Spectrogram of (a) a song uttered by Southern house wrens, and typical mobbing calls uttered by (b) Southern house wrens, (c) great tits, and (d) Eurasian wrens. Mobbing calls of the house wrens are composed of a single note. The mobbing call of the great tit is made of the combination of 2 introductory notes followed by 6 broadband frequency notes (D notes). Eurasian wrens produce mobbing calls composed of 11 notes on average in high-risky situation. For playbacks, the 5 notes of the terminal part of the song (circled section) were used to keep the total sound duration similar between Southern house wren call and song segment (~0.5 s).

treatment, 42 males and 30 females). Sex can be assigned by plumage: Female great tits are less intensively coloured yellow, the ventral black band is fading around the belly in females but pronounced in males. Further, the black is more jet black, and the borders are usually more clearly marked. All data have been collected by the same trained observer with an experience in the field of about 10 years (MD). These birds were not ringed for individual recognition. We kept a minimum distance of at least 200 m between experimental sites to minimize the chance of testing the same individuals more than once (Salis et al., 2022).

2.2 | Call collection and stimuli preparation for playbacks

For all playbacks, we used "Type I" mobbing calls that were previously recorded from house wrens between 2013 and 2015 near General Lavalle, Buenos Aires province, Argentina (36°20′S, 56°54′W) (*N* = 4, Figure 1; Fernández & Carro, 2022). These calls are produced when house wrens are confronted with threats during nesting and have a frequency that varies from 1 to 9 kHz (reaching a peak frequency at 4–6 kHz) and a duration of between 0.4 and 0.6 s (Fernández & Carro, 2022). The "Type I" calls were elicited by exposure to a human at different distances from the nest boxes. Calls were recorded using a Fostex FR-2 LE solid-state recorder (Fostex Company; sampling rate: 44.1 kHz; accuracy: 16-bit; file format: WAV) with a Sennheiser K6/ME66 shotgun microphone (Sennheiser Electronic GmbH & Co. KG; see Fernández & Carro, 2022 for more details). We selected for playback four calls from each of four individuals. We built 1-min sound files by repeating these calls at either 60 calls/min for 4 high-calling rate files or at 20 calls/min for 4 low-calling rate files (one individual's call per file). These calling rates roughly corresponded to the maximum rates per minute observed in the high-risk (with the predator model at <0.3 m from the nest) and low-risk (with the model at 3 m from the nest) experiments (see Fernández & Carro, 2022 for more details).

The house wrens' songs (*N* = 4) were recorded with a Marantz PMD660 portable solid-state audio recorder (Marantz™) (sampling rate: 44.1 kHz; accuracy: 16-bit; file format: WAV) with a Sennheiser K6/ME66 shotgun microphone (Sennheiser Electronic GmbH & Co. KG) at the same site where the alarm calls were obtained. We edited the songs using Audacity 2.0.5 (Audacity Team, 2013) and took a section of the terminal part of the song to elaborate the files for playback (Figure 1) to keep the total sound duration similar between Southern house wren call and song segment (mean duration of each song or call is ~0.5 s). In addition, we kept the calling rate similar between song segments playbacks and high-calling rate playbacks (60 calls or songs/min). Sound files were saved as WAV files and transferred to a Shopinnov 20 W loudspeaker (frequency response 100 Hz–15 kHz) for playback. To prevent a possible effect of sound intensity on the responses of great tits, all signals were broadcast with the same intensity (~70 dB [SPL], measured at 1 m from the loudspeaker).

2.3 | Playback experiments

Playbacks were conducted between 10:00 and 16:00 under calm and dry weather. The playback treatment of the stimuli was randomized at each study site. Each playback was conducted by two experimenters (MD and a field assistant). The field assistant was assigned to the soundtrack preparation, while behavioural responses were collected by the experienced ornithologist who participated in the whole study (MD). On finding an individual, the loudspeaker was hung from a tree at 1.5 m from the ground and placed 30 m away from the bird. Before the beginning of the playback, the baseline behaviour of the focal great tit was observed during 1 min. If the great tit showed alarm behaviour or move towards the loudspeaker during this pre-playback period, the test was abandoned. To determine the tits' responses to different treatments, we recorded the two following behavioural variables during 1 min of playbacks: (1) approaching the loudspeaker: we recorded whether birds approached within 15 m of the loudspeaker during the playback and (2) number of mobbing vocalizations: we counted the number of calls that focal birds produced the during the playback (Dutour, Kalb, et al., 2021). We set the approach distance to 15 m since this approach distance was previously found to be a relevant measure of mobbing propensity in great tits (see Dutour et al., 2017 for more details). To control for the reliability of calling scoring, a subset of these playbacks including another observer independently collecting data was conducted. Results revealed a very high concordance between observers (*N* = 9 playbacks: 8 out of 9 scores were similar; see Table S1; Supplementary Material 1). The observations were carried out with binoculars (Argonne, 10×42, Europe Nature Optik) at 10 m from the loudspeaker, a distance from which the tit's behaviour was not disturbed (Dutour et al., 2016, 2020).

2.4 | Acoustic analysis: comparison of house wren mobbing calls with great tit and Eurasian wren mobbing calls

Mobbing calls of the house wrens are composed of a single note (Figure 1, Fernández & Carro, 2022), whereas mobbing calls produced by the great tits and the Eurasian wrens are more complex (Figure 1). Great tits produce mobbing calls made of two parts: a few frequency-modulated elements, which are then followed by a string of broadband frequency notes (D notes, Figure 1, Dutour et al., 2019). Eurasian wrens produce mobbing call composed of several notes (Figure 1). In mobbing calls of great tits and Eurasian wrens, the number of notes within each call increase with the level of risk (Carlson et al., 2017; Kalb et al., 2019).

We compared house wren mobbing calls with (1) the D notes of the great tit mobbing calls (Figure 1) and (2) the mobbing calls of Eurasian wren. Six acoustic properties were measured for each call or note (only one note for each species): (1) duration of the first note; (2) peak frequency (the frequency for which amplitude [Hz] is maximum); (3) mean frequency (Hz); (4) maximum frequency (highest frequency in Hz); (5) minimum frequency (lowest frequency in Hz) and (6) frequency bandwidth (differences in Hz between maximum frequency and minimum frequency measure on a linear amplitude spectrum); maximum and minimum frequencies were identified as the frequencies at which the sound amplitude drops 20 dB below the sound peak amplitude (amplitude of the loudest frequency), which captures the vast majority of sound energy in songs/mobbing calls while being generally robust to interference by background noise in our recordings. Recordings were analysed with Avisoft SASLab software (Avisoft Bioacoustics, Berlin, Germany). To obtain these measurements, we marked individual calls/notes on spectrograms and then used automatic measurement tools. We analysed the mobbing calls produced by 10 adult great tits, four house wrens (calls used in our playback experiment, see above) and 10 Eurasian wrens (one call per individual for each species). Finally, we analysed the recordings of the great tits and the Eurasian wrens to count the number of calls per min (calling rate) and the number of notes per call (only D notes for great tits, Figure 1).

We used adult great tits mobbing calls previously recorded in responses to sparrowhawk (*Accipiter nisus*, *N* = 3, Kalb et al., 2019) and playbacks of conspecific mobbing calls. Moreover, we used mobbing calls given by four adult Eurasian wrens previously recorded in responses to playbacks of calls given by Eurasian pygmy owls (*Glaucidium passerinum*, Dutour et al., 2016) and during a natural encounter with a European pine marten (*Martes martes*). These two predators are high-threat predators for Eurasian wrens. In addition, we used mobbing calls produced by six individuals obtained from the Xeno-Canto online database (www.xeno-canto.org), selected with A quality and under the denomination “alarm call” (files names: XC707281, XC663481, XC717601, XC670169, XC715486, XC691506).

2.5 | Statistical analyses

Analyses were performed using R (version 4.0.3; R Core Team, 2020). To compare the acoustic similarity of house wren mobbing calls to those of the great tit and the Eurasian wren, we used non-parametric Fligner-Policello tests.

Since playback soundtracks were each used 6 times, we first assessed whether the sound file identity had an effect on individuals' responses. We used generalized linear models with individuals' response as the response variable and the identity of the sound file as predictor. We assumed a negative binomial distribution to analyse the number of calls since a preliminary analysis using the Poisson distribution for the error term indicated a substantial overdispersion in the data set. We used a binomial error distribution and logit-link function for the analysis of approaching behaviour (dichotomous variable: approach within 15 m of the loudspeaker = 1; no approach the loudspeaker = 0).

To test the effect of the playback treatments on response, we ran generalized linear models (GLMMs), with the approach and the number of calls emitted by the tits as response variables and the treatment (high rate, low rate and song), the sex of the individuals and the interaction between these two terms, as predictors. We used a negative binomial error distribution and log-link function for the analysis of number of calls and a binomial error distribution and logit-link function for the analysis of approaching behaviour.

GLMMs were run using the glmmTMB package (Brooks et al., 2017). Statistical significance of the predictor variable was evaluated by comparing the deviance of nested models (i.e. with and without the predictor) with a likelihood ratio test. Significant effects between treatments were further compared by calculating the estimated marginal means using the emmeans package for R (Lenth, 2020). Model diagnostics were performed using the DHARMa (Hartig, 2020) and performance (Lüdecke et al., 2021) packages.

2.6 | Ethical note and STRANGE statement

All tested great tits returned to normal activity relatively quickly following playbacks, so we were confident that they were not unduly stressful. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. We believe that there is little scope for bias in our research based on the STRANGE framework (Webster & Rutz, 2020). We used only unringed adult birds (both males and females). We did not know the exact age of animals, as all subjects were haphazardly selected in the wild. It is unlikely that there was extensive pseudoreplication. We kept a minimum distance of at least 200 m between experimental sites. However, it is possible that some resampling occurred since great tits were not marked (but see Salis et al., 2022).

3 | RESULTS

Acoustic analysis revealed that the calls produced by house wrens and great tits are distinguishable by three acoustic parameters: House wrens had a significantly higher peak frequency ($p < .001$) and higher mean frequency ($p = .01$) than great tits (Figure 1). The calls of the house wrens are longer than the D notes of the great tits ($p < .001$, Figure 1). We found no detectable differences between the house wren and the great tit for the minimal frequency, the maximum frequency and the frequency bandwidth ($p > .05$). Great tits produced on average 31 calls ±9 SD per min and 6 notes ±2 SD per calls. For the comparison of house wren mobbing calls with Eurasian wren mobbing calls, we found that house wrens had a significantly lower minimal frequency ($p < .001$) and larger frequency bandwidth ($p < .001$) than Eurasian wrens. The calls of the house wrens are longer than the first notes of the Eurasian wrens ($p < .001$). We found no detectable differences between the house wren and the Eurasian wren for the mean frequency, the peak frequency and the maximum bandwidth ($p > .05$). Finally, Eurasian wrens produced on average 35 calls ±11 SD per min and 10 notes ±7 SD per calls during high-risk situations.

There was no effect of file sound identity on either the number of calls given nor on the probability of approaching behaviour (all $p > .05$; see Table S2 Supplementary Material 2 for details). A significant interaction between treatment and sex of the focal individual was found for the number of calls given by great tits (generalized linear model: $\chi^2 = 7.14$; df = 2; $p = .03$; Figure 2). Females tended to give more calls during playbacks of high-urgency calls than during playback of low-urgency calls, whereas there was no significant difference in the number of calls given by males between high-urgency calls and low-urgency calls (Table 1; Figure 2). Both females and males produced more calls during playbacks of high-urgency calls than during playback of song segments (Table 1; Figure 2). Males gave more calls during playbacks of low-urgency calls than during playback of songs, whereas there was no significant difference in the number of calls given by females between low-urgency calls and song segments (Table 1; Figure 2).

There was a significant effect of playback treatments on the probability of approaching behaviour within 15 m of the loudspeaker (generalized linear model: $\chi^2 = 10.2$; df = 2; $p < .01$; Figure 3), whereas sex of the focal birds had no significant effect ($\chi^2 = 1.8$; df = 1; $p = .17$). More individuals approached the loudspeaker during playbacks of high-urgency calls than during playback of the house wren song (Table 1; Figure 3). Great tits tended to approach the loudspeaker during playbacks of high-urgency calls more often than during playbacks of low-urgency calls (45.8% vs. 16.7%; Figure 3), although we found a marginally non-significant difference between these two treatments in the approaching behaviour of focal individuals (Table 1). There was no significant difference in approaching response between low-urgency calls and house wren song segments (Table 1; Figure 3).

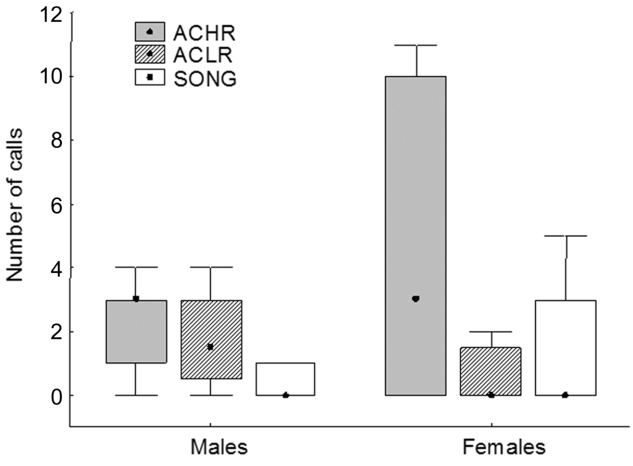

FIGURE 2 Number of calls produced by great tits during 1 min of playbacks of house wren song segments and mobbing calls (ACHR: high rate; ACLR: low rate) ($N = 72$ individuals, 24 per treatment). Median values (black dots within boxes), 25%–75% interquartile ranges (boxes) and value ranges (whisker caps) of the observed values are represented.

4 | DISCUSSION

In this study, we tested whether alarm intensity is correctly interpreted by birds of an allopatric and distantly related species. Our playback experiments revealed that great tits responded more to calls with high-calling rate (high threat) than to calls with low-calling rate (low threat) given by the Southern house wren. Females produced more calls and both females and males tended to approach more during the high-calling rate than during the low-calling rate. Although the calling rates are low overall, this is not atypical and is in line with previous findings when great tits responded to sympatric heterospecifics mobbing calls (Dutour & Randler, 2021).

This study adds to the increasing evidence that birds respond to heterospecific mobbing calls of allopatric taxa (Dutour et al., 2017, 2020, 2022; Johnson et al., 2003; Randler, 2012) and is in line with previous findings showing that great tits responded more to the playbacks of an allopatric Paridae species, the black-capped chickadee, broadcasting high-urgency mobbing calls compared with low-urgency mobbing calls (Randler, 2012). The mechanisms are still unclear. Call repetition rate may constitute an innate or early learned cue that can be used to predict the degree of risk in a given situation (Wheatcroft, 2015). The results of this study indicate that vocal rate cannot be the only cue used by great tits to guide their mobbing responses since the high-urgency mobbing call and the song had same repletion rates in our study (60 calls or songs/min), yet the birds responded more strongly towards the high-urgency mobbing calls than towards the songs. Instead, structural characteristics of calls could provide additional cues that may allow individuals to recognize risky situations and allopatric calls as alarm calls. Our results indicate that great tits do not simply respond to any novel sound with a high-calling rate and they perceive high-rate mobbing calls of house wrens as mobbing calls. Fallow et al. (2013) found that superb fairy-wrens (*Malurus cyaneus*) respond more frequently to synthetic calls with peak frequencies more similar to those of conspecific calls, even if other acoustic features differed. Although structurally different, some similarity in terms of the frequencies used in house wrens "Type I" mobbing calls and great tits D notes (terminal part of the call, Figure 1) could explain the response observed in the tits. Great tits would respond to house wren calls because we found no detectable differences between the house wren and the great tit for the minimal frequency, the maximum frequency and the frequency bandwidth. However, comparison of both calls revealed differences in peak frequency, mean frequency and duration of the calls. In addition, the natural calling rate of the great tits in risky situations is lower than those of the house wrens (31 ± 9 calls vs. 60 calls). Since the high-urgency mobbing calls of the great tits and the house wrens are overall dissimilar, this suggests that great tits do not generalize from their own calls. The overall dissimilarity between the calls in both species does not probably explain the behavioural response to house wren mobbing calls in the great tit. Furthermore, some sympatric species can also encode urgency in a similar way to that of house wrens that the great tits may be familiar with and therefore generalize from. For instance, great tits would respond to

TABLE 1 Comparison of the behavioural responses of the great tits (number of calls given during playbacks and approaching behaviour) during playbacks of house wren song segments and calls (ACHR: high rate; ACLR: low rate).

Contrast	Effect size	SE	df	CI	*t*	*p*
Number of calls						
Females						
ACHR-ACLR	1.44	0.48	65	0.47 to 2.41	3.07	**<.01**
ACHR-Song	1.03	0.46	65	0.12 to 1.95	2.29	**.06**
ACLR-Song	−0.41	0.46	65	−1.34 to 0.52	−0.88	.65
Males						
ACHR-ACLR	0.02	0.35	65	−0.67 to 0.73	0.08	.99
ACHR-Song	1.14	0.44	65	0.26 to 2.01	2.67	**.02**
ACLR-Song	1.11	0.46	65	0.19 to 2.03	2.46	**.04**
Approaching behaviour						
ACHR-ACLR	1.44	0.69	69	0.05 to 2.83	2.11	.09
ACHR-Song	2.23	0.87	69	0.50 to 3.96	2.64	**.03**
ACLR-Song	0.79	0.9	69	−1.05 to 2.63	0.86	.67

Significant differences are indicated in bold.

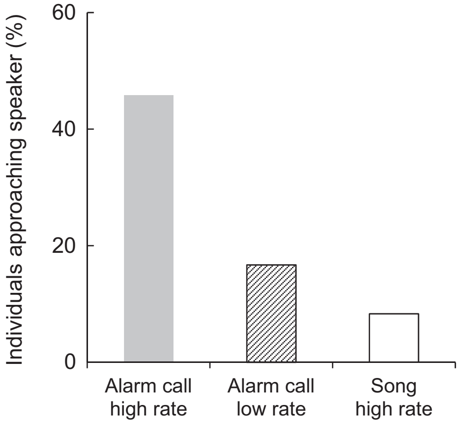

FIGURE 3 Percentage in which great tits approached within 15 m of the loudspeaker playbacks of house wren song segments and mobbing calls (*N* = 72 individuals, 24 per treatment).

house wren calls because there are similar to the calls of the Eurasian wren, a phylogenetically closely related species to the house wren. We found no detectable differences between the house wren and the Eurasian wren for the mean frequency, the peak frequency and the maximum bandwidth. However, we found differences in minimal frequency, frequency bandwidth and duration of the calls between calls of house wrens and calls of Eurasian wrens. In addition, the natural calling rate of the Eurasian wrens in risky situations is lower than those of the house wrens (35 calls vs. 60 calls) and the number of notes per calls of the Eurasian wrens is higher than those of the house wrens (10 notes vs. 1 note per call). Our acoustic analyses revealed that a calling rate of 60 calls per minute is an unfamiliar calling rate for the great tits. These results suggest that the tits do not generalize from the calls given by Eurasian wrens. To our knowledge, no other sympatric species have similar calls to that of the house wren that the great tits may be familiar with and therefore generalize from. However, acoustic analysis of the calls given by sympatric species would be necessary to confirm this hypothesis. Importantly, further studies are needed to investigate which acoustic parameters great tits use to recognize sounds as mobbing calls and to know much more about the perception and generalization processes in great tits. Our results suggest that social interspecific learning and calls similarity between house wrens and great tits are not the main recognition mechanisms explaining the responses of great tits to house wren calls. Another explanation is that great tits have a mental representation/or abstract concept of urgency following a simple rule "higher calling rate, higher threat" and respond accordingly (Randler, 2012; Suzuki, 2018). Finally, additional experimental work, particularly responses of young birds to playbacks of heterospecific calls with high- and low-calling rates, is required to explore the developmental mechanisms of responsiveness to urgency in heterospecific alarm calls.

Our research revealed that sexes respond differently because female great tits gave more calls during playbacks of calls with high-calling rate than during playback of calls with low-calling rate, whereas there was no significant difference in the number of calls given by males between high-urgency calls and low-urgency calls. This deserves further study, because most previous work did not assess sex differences and in most studies, responses to playbacks were pooled irrespective whether those were male or female calls. Differences between sexes may be a consequence of different perceptual abilities of males and females. In red-winged blackbirds (*Agelaius phoeniceus*), females are able to recognize and discriminate against imitation male songs, which cannot be discriminated by males (Searcy & Brenowitz, 1988). Similarly, male Bengalese finches (*Lonchura striata*) are unable to discriminate between songs of other males, which can be discriminated by females (Ikebuchi et al., 2003). Female cowbirds (*Molothrus ater*) are also more acoustically sensitive and have a higher capability of discrimination of heterospecific songs (particularly at low frequencies) than cowbird males (Gall & Lucas, 2010). Thus, the differences observed between male and female great tits may be due to differences in acoustic sensitivity and ability to discriminate heterospecific alarm calls. This aspect deserves further study in future research. Furthermore, as the playbacks were made during the winter season, potential reproductive aspects can be neglected. In the breeding and nest defence context, males were found to be more engaged in mobbing in blackbirds (*Turdus merula*; Kryštofková et al., 2011), while no sex differences in antipredator responses between male and female pied flycatchers (*Ficedula hypoleuca*) were found (Krams et al., 2014). However, females calling at a higher rate compared with males have been found by Randler (2013) in the Cyprus wheatear (*Oenanthe cypriaca*). Here, differences between the sexes in type I calls were found with females calling at higher rate. In great tits, nest defence was higher in males (Curio et al., 1983; Regelmann & Curio, 1986) and was adjusted to brood size and sex ratio of the offspring (Radford & Blakey, 2000). Kalb and Randler (2019) also found that male great tits tended to take higher risks in a mobbing experiment; they tended to approach the loudspeaker broadcasting conspecific mobbing calls faster and closer than females. In this study, we found no significant effect of sex on approaching behaviour. Future studies might compare the different sexes of the same species during the breeding and the non-breeding season. The current studies showed that females may be more receptive towards allopatric or heterospecific alarm calls, which may result from the fact that males invest more time in territorial defence, and females may have more time to listen.

Importantly, future studies are needed to investigate (a) if great tits respond as strongly as to high-urgency calls of Southern house wrens as they do to high-urgency calls of conspecifics and (b) if the response difference between high-urgency and low-urgency calls is similar for conspecific playbacks versus the house wren playbacks. Interestingly, a recent study found that the approaching behaviour of great tits towards conspecific mobbing calls does not depend on the calling rate broadcast (Salis et al., 2022). However, since different calling rates were used in both studies (present study: high-calling rate: 60 calls per min vs. low-calling rate 20 calls per min; Salis et al., 2022: high-calling rate: 30 calls per min vs. low-calling rate 15 calls per min), and different populations may respond differently to calls even of their own species, depending on their ecological community, future studies in the present study population are needed. Specifically, future playback experiments investigating the responses of great tits to conspecific calls should use a high-calling rate with 40 calls per min since our results suggest that this calling rate is given during very high-risky situations.

As a conclusion, the allopatric response to mobbing calls of Southern house wrens by great tits suggested that a Paridae species perceived the urgency message encoded in calls given by an allopatric non-Paridae species. These findings raise some questions about how birds encode and perceive information about urgency of threat in alarm calls of heterospecifics.

AUTHOR CONTRIBUTIONS

M.D., G.J.F. and C.R. designed the experiment; M.D. collected the field data; M.D. and G.J.F. did the statistical analysis. All authors contributed to the writing of the paper and approved its final stage.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data sets generated are available as supplementary material.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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