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REPETITIVE CALLS IN SOUTHERN HOUSE WRENS: INFORMATION ENCODED IN THE NUMBER AND RATE OF ALARM CALLS

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ABSTRACT: Birds often use acoustic alarm signals to alert co- and heterospecifics about nearby threats. Callers can use single calls or longer sequences of repetitive calls, which can produce a sustained effect on the behavior of the signal targets. The rate at which the alarm calls are given can also reveal the 'urgency' or level of risk perceived by the caller. In Southern House Wrens, *Troglodytes musculus*, breeding individuals give repetitive alarm signals when a threat is detected near the nest. To understand the information that encodes the number and calling rate of alarm signals produced by Southern House Wrens, we tested the individuals' responses to experimentally manipulated signals. We broadcast alarm calls that differed in calling rate and length (i.e., the number of calling notes) and recorded the response probability, response latency, minimum approach distance to the speaker, and the time spent near the speaker by conspecifics. Wrens responded more frequently and quickly to alarm calls repeated at higher rates. Furthermore, individuals spent more time near the speaker when we played back calls at a high rate and when we played back longer sequences of calls. However, individuals also got closer to the speaker when we broadcast long call sequences at a low rate. We propose that the repetition of calls could reveal the persistence of the stimulus, whereas the calling rate could encode information about the risk level detected. These findings contribute to the understanding of how receivers extract the information from conspecific alarm signals.

KEYWORDS: *calling rate, communication, mobbing call, Troglodytes musculus*

Acoustic alarm signals are a simple and widely used anti-predator strategy used by birds and mammals, which can alert co- and heterospecifics of the presence of danger in the vicinity (Klump & Shalter 1984, Caro 2005). Understanding the elements of vocalization that trigger a response in signal receptors is important for understanding the biological significance and design evolution of alarm calls (Guilford & Dawkins 1991, Rowe 2013).

Alarm calls vary widely both between and within species. Call structure can vary with the predator type or risk level, providing contextual information about the threat detected (e.g., Leavesley & Magrath 2005, Templeton et al. 2005, Suzuki 2011, 2016, Sommer et al. 2012, Kalb et al. 2019, Fernández & Carro 2022). Furthermore, alarm vocalizations can consist of a unique or a short series of discrete elements (or calls), or a longer repetitive sequence of calls separated by varying periods of silence (Le Roux et al. 2001). Sometimes, callers can use single alarm calls to signal to group members the close presence of a threat, but in other cases, they can use longer sequences of repetitive calls. Leavesley and Magrath (2005), for example, found that White-browed Scrubwrens, *Sericornis frontalis*, used signals with a higher number of elements when the distance to a predator was shorter to prompt a more immediate response from listeners. In contrast, when the predator was further away, individuals uttered vocalizations with fewer elements. Sciurids also show variation in their alarm vocalizations, using a repetition of a few calls when they detect a nearby threat, which trigger a rapid escape response

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in listeners, and longer vocalizations, with a greater repetition of calls, to stimulate vigilance in receivers (Loughry & McDonough 1988, Sloan & Hare 2004).

The repetition of signals in acoustic alarm systems has been puzzling. At first glance, the repetition of a signal may attract the attention of a predator to the caller and increase its detectability and risk of predation. Then, there should be some functional meaning to the repetition of signals when the alarm call is given. Schleidt (1973) suggested that frequent repetition of signals can produce a sustained effect on the behavior of the targets of the signals. In that sense, the repetition of a signal ('tonic signaling') might reinforce the meaning of the signal produced. Thus, repetition does not act as multiple discrete signals but rather generates a continuous or sustained effect on the receiver's state. In some cases, call repetition maintain an increased alertness in receivers for a longer period than single calls (e.g., Harris et al. 1983, Loughry & McDonough 1988, Le Roux et al. 2001). McLachlan and Magrath (2020) found that New Holland Honeyeaters, *Phylidonyris novaehollandiae*, responded to the first element of conspecific alarm calls to assess risk level. However, they were more likely to flee when alarm calls had more elements. Then, the repetition of elements within an alarm signal can be thought of as a mechanism to ensure that receivers have detected the signal, making turn it more reliable and error-resistant (McLachlan & Magrath 2020).

Alternatively, signal repetition rate can inform the degree of urgency or immediate danger detected (Morton 1977). This urgency hypothesis postulates that calling sequences can signal the nature or location of a threat in a risky situation. This can be achieved by altering the structure of calls, combining different calls, or changing the timing patterns of calls (Manser 2001, Leavesley & Magrath 2005, Schlenker et al. 2016). For example, Baker and Becker (2002) found that Black-capped Chickadees (*Poecile atricapillus*) signaled the immediacy of threat or proximity of a predator mainly by altering the rate of calling. In American Crows (*Corvus brachyrhynchos*) calls with a longer duration and a higher call rate reflect a higher degree of danger (Yorzinski & Vehrencamp 2009). Shah et al. (2015) also found that Herring Gulls (*Larus argentatus*) increased the rate of alarm calling with perceived threat level, and receivers responded most urgently to high-threat calls broadcast at a high calling rate.

In Southern House Wrens, *Troglodytes musculus*, nesting individuals have been found to give alarm calls at high rates when a predator model was placed near the nest or when a threat (e.g., a human) approaches the nest (Fasanella & Fernández 2009, Fernández et al. 2012, Fernández & Carro 2022). In addition to vocalizing, they perform conspicuous actions, including approaching and moving away from the detected predator or threat, and occasionally carrying out a physical attack (Fernández et al. 2024). Although these calls are not specifically warning signals, as they are directed at the predator, they are capable of attracting the attention of con- and heterospecifics, promoting a community mobbing response (Carro & Fernández 2021). Also, in previous field playback experiments, we found that listening House Wrens approached the speaker more frequently during playback of alarm calls at higher rates than during playback of calls at lower rates (Carro & Fernández 2021, Fernández et al. 2023). This response seems to indicate that the simple repetition of calls is not enough to trigger a response in receivers and that this response depends on the temporal pattern of the utterance. However, a signal emitted at a higher rate has a larger number of calls and a shorter inter-call interval, so it is not easy to identify the specific structural element in the calls that triggers the response.

In this study, we aim to evaluate whether the response of receivers in the Southern House Wren (hereafter House Wren) depends on the number of calls or the temporal pattern of emission of these calls. Based on a field playback experiment, we compared the response of individual House Wrens when we played back short and long call sequences broadcast at high and low rates. According to the tonic hypothesis, we expect receivers to respond more frequently, and their response to be more sustained over time in experiments with long call sequences than with short sequences, regardless of the call rate. On the other hand, if the rate at which the calls are uttered has informative value, we expect that the receiver's response will be more related to the calling rate than to the number of calls issued.

METHODS

We carried out this study at a site near San Martín de los Andes, Neuquén, Argentina (40°7'S, 71°18'W) during the 2022, 2023, and 2025 breeding seasons (November-December). The study site comprises a 14-ha woodland composed mainly of *Nothofagus antarctica* and *N. obliqua* (Supplementary Material, Fig. S1). We performed regular censuses (2-3 days/week) from late September to late December of each year, which allowed us to identify between 25 and 35 territories defended by singing males during these breeding seasons (GJF, personal observation).

Experimental design

To evaluate the effect of repetition rate and call number on the response of House Wren, we conducted a field experiment in which we manipulated both parameters within a calling sequence (Table 1). We used Type I calls, which have a peak frequency of 4–6 kHz and a duration of 200–600 ms (Fig. 1). These calls are produced during mobbing events and typically attract the attention of both hetero- and conspecifics (Carro & Fernández 2021, Fernández & Carro 2022, Fernández et al. 2023). First, we used long-duration (3-min) playback treatments that differed in the calling rate. For these treatments, we prepared sequences of alarm calls based on calls recorded in the field from three different individuals that were subsequently manipulated in the lab. We used calls from only three individuals to minimize potential variability in the response caused by using different calls, even though this might limit the response's generality. We recorded calling individuals in the field using a Marantz PMD-660 digital recorder (Marantz, Japan; sampling rate: 44.1 kHz; accuracy: 16-bit; file format: *.wav*) with a Sennheiser K6/ME66 shotgun microphone (Sennheiser Electronic GmbH and Co. KG, Wedemark, Germany). From each individual's recording we selected six calls with similar spectral characteristics and constructed three-min playback files by repeating that sequence. We created three playback files, each with calls recorded from a single individual using a high calling rate (~95 calls/min; thereafter High), and another three files using a low calling rate (30 calls/min; thereafter Low). These recordings that were similar in duration but differed in their calling rate constituted the treatments. Call rates in House Wrens vary with the perceived risk

Table 1. Experimental design of field tests. The treatments consisted of playbacks of Southern House Wren (*Troglodytes musculus*) alarm call playbacks that varied in call rate and the number of calls. High represent 3-min sequences of calls broadcast at a high calling rate (~95 calls/min); Low represent 3-min sequences of calls broadcast at a low calling rate (30 calls/min); Hshort represent the broadcasting of 30 calls played back at a high rate (~95 calls/min); Lshort represent the broadcasting of 30 calls played back at a low rate (30 calls/min).

Treatment	Duration (s)	Number of calls	Calling rate (calls/min)	Number of trials	Calling rate	Calling length
High	180	285	95	17	High	Long
Low	180	90	30	17	Low	Long
Hshort	19	30	95	18	High	Short
Lshort	60	30	30	17	Low	Short

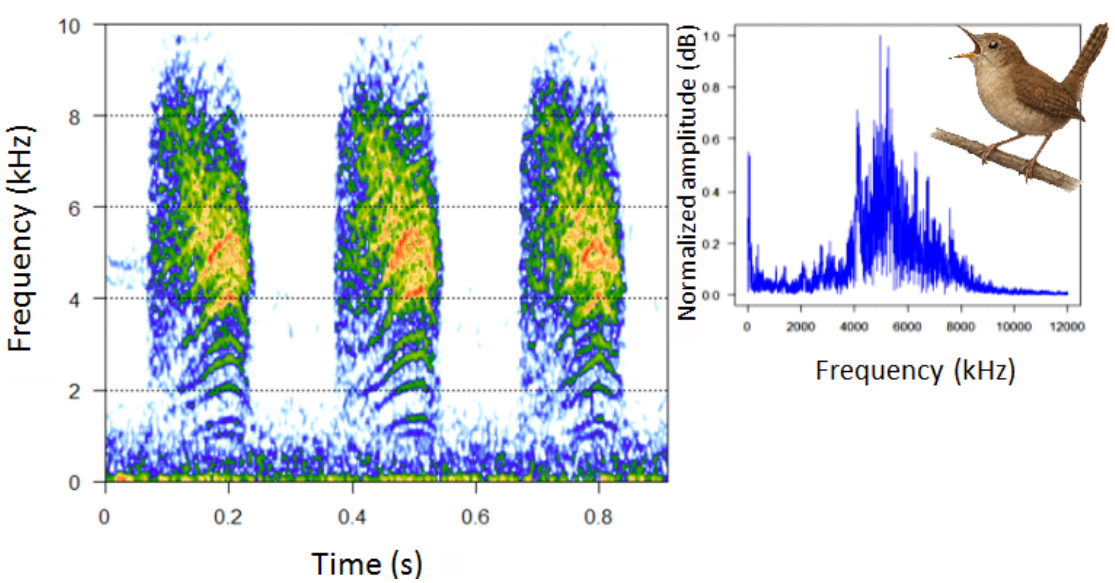

Figure 1. Spectrogram (left) and power spectrum (right) of the Type I call of the Southern House Wren (*Troglodytes musculus*). We obtained the spectrogram using the '*seewave*' package (Sueur et al. 2008) in R, using a fast Fourier transformation (FFT, 512 points; overlap, 75%; Hanning window).

(Fernández & Carro 2022), ranging from a few calls (0 - ~30 calls/min) when risk is very low to many calls at very high rates (~90 >120 calls/min) when risk is higher. Therefore, we considered the rates of 30 calls/min and 90 calls/min to be representative of low-risk and high-risk situations, respectively.

Next, we built short calling sequences using the same field-recorded calls. These files contained only 30 Wren alarm calls but varied in their calling rate. We built three files containing 30 calls repeated at a high rate (~95 calls/min; thereafter Hshort), and three other files with 30 calls repeated at a low rate (30 calls/min; thereafter Lshort). Then, the files of the calls uttered at a high rate had a length of 19 sec, whereas those built at a low rate lasted 60 sec, both shorter than the first set of treatments previously described.

Field tests followed the general procedures described in Fernández et al. (2023). We performed tests at sites where we located one or more individuals (usually male and female) nearby. We hung a speaker (Stromberg Bent, frequency response: ~100 Hz - 15 kHz) from a tree at 1.0-1.5 m above the ground and ~20 m away from the birds. We used a tape to delimit the 10 m distance from the sound source on either speaker side before the experiment. One observer was positioned at ~10 m from the speaker. Practical issues did not allow us to record the data blindly. However, the observer had no a priori expectation about which hypothesis would be supported, making any bias unlikely. We randomly selected the files that were played back in an attempt to balance the different treatments. Before initiating the playback, the experimenter waited for one min to ensure that the focal bird was not giving alarm calls or was not engaged in a mobbing event. We played back the calls at a maximum sound pressure level of ~60 dB (A) (measured at one m with a TES-1350A sound level meter; TES Electrical Electronic Corp., Taiwan), similar to levels measured in the field for wrens (mean = 58.75 dB, range: 56–64 dB; Corral et al. 2012). Once the playback started, we conducted a three-min focal observation of the first individual that approached within 10 m of the speaker. The trials were recorded using a Tascam Dr-05 digital recorder (Tascam Co.) and transcribed in the lab.

We conducted a total of 69 trials at 35 sites (Supplementary Material Fig. S1): 34 trials used long calling sequences with high (n = 17) and low (n = 17) repetition rates, 17 trials used short sequences at a low repetition rate, and 18 trials used short sequences at a high repetition rate. Then, the duration of the call sequence reflected the number of calls played back. We sampled most sites more than once (modal number of trials per site = 1, range = 1-6), and therefore, it is likely that an individual could have been sampled more than once. In an attempt to avoid this, we never repeated the same treatment at the same site and left at least one week between trials at the same site or nearby places (< 200m). The sampling sites used on each sampling date were separated by more than 100 m.

Data recording

We took behavioral measurements of a focal individual, the first to come within < 10 m of the speaker. In only four trials, two individuals approached the speaker. Although the presence of another individual may affect the first individual's response, the low frequency of this occurrence in our experiments did not allow us to include it in the analyses.

We measured the approach latency of the focal individual by recording the time it took from the start of the trial for the individual to approach within 10 m of the active speaker. In cases where individuals did not approach within < 10 m of the speaker, latency was considered maximum (180 s) and the data censored. Once the individual approached, we recorded the time the individual remained within < 10 m of the speaker, the time that it remained near the speaker (< 5 m), and the minimum estimated distance to the speaker. We measured this distance using a tape measure after playback and only estimated for individuals that approached within < 10 m from the speaker (n = 44). Likewise, we only estimated the time spent within 5 m and 10 m for individuals that responded to the playback (n = 44).

Data analyses

We assessed the responses of focal House Wrens using generalized linear mixed models (GLMMs) with calling rate (High or Low), calling sequence length (long or short), and the interaction (calling rate × calling length) as predictors. We also included the playback file identity as a predictor, and the trial date nested within the year to control for temporal variation in the response behavior of House Wrens (Fernández et al. 2023). The trial date was estimated arbitrarily as the number of days elapsed since October 1st. We used October 1 as a reference date because by that time many of the breeding territories had already been established. In addition, to account for the use of sites in more than one trial, we also included the site as a random effect in all models.

We tested whether the probability that the

response of House Wrens differed between treatments using a GLMM assuming a binomial distribution and a logit link function. The response variable was one if at least one House Wren approached < 10 m of the speaker during the trial, or zero if no individual responded.

We used a Cox proportional hazards mixed regression model to compare approach latency to the speaker among treatments (see Fernández et al. 2023). The absence of a response from an individual was considered a censored response (undefined latency). Therefore, we included in the model a dichotomous variable defining whether or not the House Wren had responded to the playback. The global model supported the proportional hazards hypothesis ($\chi^2_5 = 5.61$, $p = 0.35$) indicating that the hazards in the groups were proportional.

To compare the minimum approach distance and the time the focal individual remained within 10 m and within 5 m of the speaker between treatments, we used linear mixed models (LMM), including only trials in which at least one individual responded to the playback. The differences in the time the focal individual remained within 10 m of the speaker were evaluated assuming a Gaussian error distribution and using a log link function. The time the focal individual remained within 5 m of the speaker and the minimum approach distance to the speaker were evaluated assuming a Gaussian error and using an identity link function. As the models were based on a subset of the original data, we also fitted inverse-probability weighted (IPW) models for these variables (Hernán & Robins 2020). For the weighted model testing the time that House Wrens remained less than 5m from the speaker, we removed the site as a random factor due to model convergence problems when we removed the interaction term (calling rate × calling length). Variance contribution of the site variable in the full model was ~0.

We tested for spatial autocorrelation in model residuals using Moran's I on site-level aggregated residuals and found no evidence of spatial structure ($p > 0.05$; see Supplementary Information). Accordingly, spatial correlation structures were not included in the final models.

We performed all statistical analyses in the R environment (version 4.1.3; R Core Team 2020), and we ran the GLMM models using the '*glmmTMB*' package (Brooks et al. 2017). We ran the Cox proportional hazards mixed-effect regression model using the '*COXME*' package (version 2.7.1; Therneau 2015). We compared nested models with and without the predictor using a likelihood ratio test to assess the significance of the predictor variables. To account for multiple testing on the same sample of individuals, we applied a Benjamini-Hochberg correction (FDR) to the *p*-value of each model (Benjamini & Hochberg 1995). We further compared significant effects between treatments by calculating the estimated marginal means using the '*emmeans*' package for R (Lenth 2020). We performed model diagnostics using the '*car*' (Fox & Weisberg 2019), '*performance*' (Lüdecke et al. 2021), '*DHARMa*' (Hartig 2020) and '*spdep*' (Bivand 2022) packages. All *p*-values quoted are two-tailed, and we considered differences significant at $p < 0.05$. We report here both, raw (p) and adjusted-p values (p_{adj}) when terms were significant.

RESULTS

The probability of House Wrens responding differed between trials with stimuli that differed in calling rate ($\chi^2_1 = 14.20$, $p < 0.01$, $p_{adj} < 0.01$) and in their duration ($\chi^2_1 = 5.19$, $p = 0.02$, $p_{adj} = 0.05$). We detected no interaction effect between calling rate and call length ($\chi^2_1 = 0.03$, $p = 0.86$). House Wrens approached the speaker more frequently when we broadcast alarm calls at a high rate than when we played back calls at a low rate ($z = 3.34$, $p < 0.01$; Fig. 2). Also, House Wrens responded more frequently when we broadcast longer call sequences than when we played back short files ($z = 2.18$, $p = 0.03$; Fig. 2). House Wrens responded in 16 out of 17 trials performed with long call sequences at a high rate, whereas they responded in 14 out of 18 Hshort playbacks, 10 out of 17 Low trials, and 4 out of 17 Lshort trials (Fig. 2).

Latency to respond to conspecific alarm call playbacks also varied with the calling rate of the stimulus ($\chi^2_1 = 16.95$, $p < 0.01$, $p_{adj} < 0.01$), but there was no effect of calling sequence length ($\chi^2_1 = 0.63$, $p < 0.43$), nor was there an interaction between call rate and calling sequence length ($\chi^2_1 = 2.41$, $p = 0.13$). House Wrens approached the speaker more quickly when we broadcast files with a high calling rate (both, long and short sequences of calls) than when we played back short sequences of calls at a low rate ($z = 4.04$, $p < 0.01$; Fig. 3). The propensity of House Wrens to respond was higher when we played back calls at high rates than at low rates, as reflected by its hazard ratio (HR = 4.6).

The time that responding individuals remained within 10 m varied with the calling rate ($\chi^2_1 = 10.85$, $p < 0.01$, $p_{adj} < 0.01$) and the calling sequence length ($\chi^2_1 = 4.95$, $p = 0.03$, $p_{adj} = 0.05$). We detected no interaction between calling rate and sequence length ($\chi^2_1 = 0.24$, $p = 0.63$). The time individuals remained within 10 m

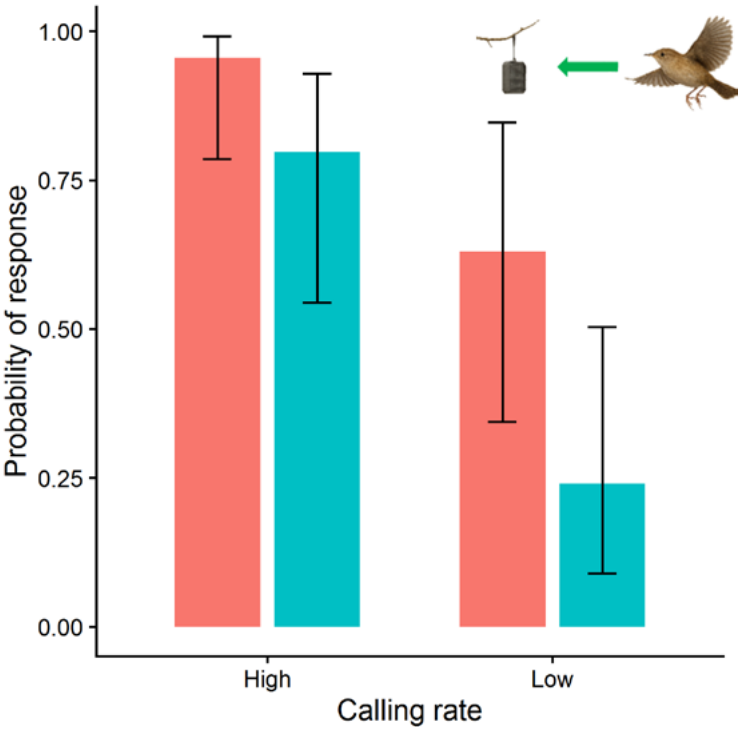

Figure 2. Predicted probability of response by Southern House Wrens (*Troglodytes musculus*) to playback of alarm call sequences that differed in duration and call rates. High: corresponds to call sequences played back at a high call rate (~95 calls/min); Low: corresponds to call sequences broadcast at a low call rate (30 calls/min). Blue bars correspond to the predicted probability of response to sequences of 30 calls played back at a high rate (~95 calls/min) or at a low call rate (30 calls/min). Red bars correspond to predicted probability of response to call sequences broadcast for 3 min at a high rate (~95 calls/min) or at a low rate (30 calls/min). Standard error is also represented for each treatment on the bars.

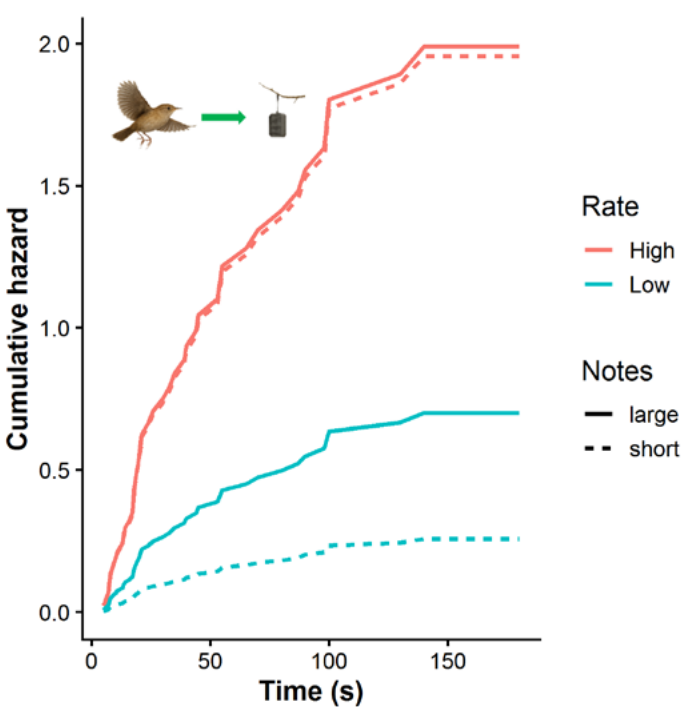

Figure 3. The propensity of Southern House Wrens (*Troglodytes musculus*) to approach a speaker when we played back sequences of alarm calls that varied in calling rate and number of calls. High: corresponds to call sequences played back at a high call rate (~95 calls/min); Low: corresponds to call sequences broadcast at a low call rate (30 calls/min); Short: corresponds to sequences of 30 calls; Large: corresponds to sequences of calls played back for 3 min.

of the speaker when we broadcast long call sequences was higher than that recorded from individuals responding to short calling sequences (z = 2.27, p = 0.03; Fig. 4). Also, when we broadcast sequences at a higher calling rate, focal individuals remained for longer than when we played back calling sequences at a lower rate (z = 3.20, p < 0.01; Fig. 4). The weighted model produced similar results (Supplementary Material Table S1) but the effect of the length of the calling sequence was non-significant when we adjusted the p-values for multiple testing (p_{adj} = 0.08).

The time that responding individuals remained within < 5 m of the speaker did not vary with the calling rate (χ^2_1 = 1.61, p = 0.20; Fig. 5) but individuals tended (although it was not statistically significant) to remain near the speaker for longer when we broadcast long calling sequences than when we played back short sequences (χ^2_1 = 3.22, p = 0.07; Fig. 5). No effect of the interaction between the calling rate and the calling sequence length was detected (χ^2_1 = 0.01, p = 0.77). Similar results were found when we tested the effect of calling rate and calling sequence length using the weighted model (Supplementary Information Table S1).

House Wrens did not differ in the minimum approaching distances to the speaker among treatments. We detected no effects of calling rate and calling sequence length on the approach distance to the speaker was detected (χ^2_1 = 3.00, p = 0.08, and χ^2_1 = 1.29, p = 0.26, respectively; Fig. 6). A statistically non-significant effect was detected when considering the interaction between the call rate and the call sequence length (χ^2_1 = 3.09, p = 0.08). The weighted model supported an interaction effect between the calling rate and calling sequence length of the broadcast files (Supplementary Information Table S1). *A posteriori* contrasts revealed that House Wrens approached more closely to the speaker when we played calls at low rates for prolonged periods compared with short and long sequences of calls broadcast at a higher calling rate (z = 2.62, p = 0.04, and z = 3.16, p = 0.02, respectively; Fig. 6).

DISCUSSION

House Wrens responses to alarm call playback depended on the calling rate and the calling sequence length. House Wrens approached the speaker more frequently when we played back sequences of calls at high rates than at low rates, and when we played long calling sequences compared to short calling sequences. However, the approach was quicker when we played back call sequences at a higher rate. The time that responding House Wrens remained near the speaker (< 10 m and < 5 m) was also greater when we broadcast calling sequences at a high rate and for a longer duration than when we broadcast shorter and

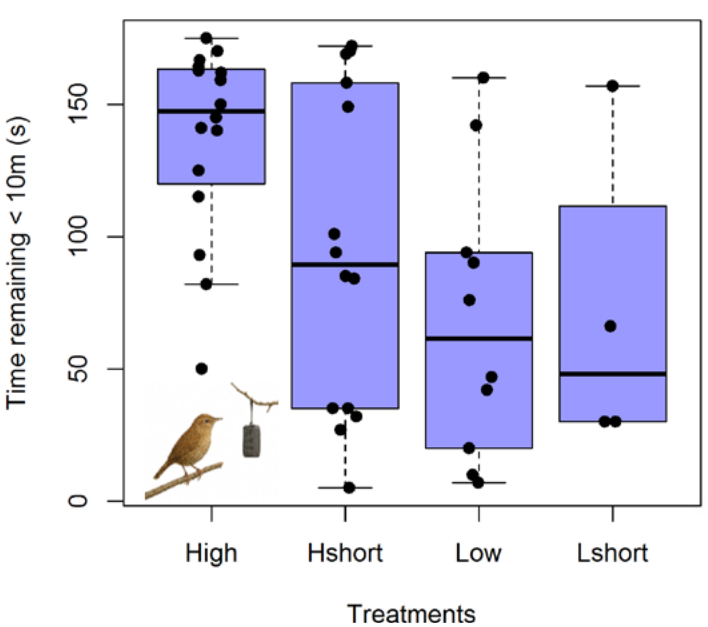

Figure 4. Time spent less than 10 m from the speaker by Southern House Wrens (*Troglodytes musculus*) when we played back sequences of alarm calls that varied in calling rate and number of calls. High: corresponds to call sequences played back for 3 min at a high call rate (~95 calls/min); Low: corresponds to call sequences broadcast for 3 min at a low call rate (30 calls/min); Hshort: corresponds to sequences of 30 calls played back at a high rate (~95 calls/min); Lshort: corresponds to sequences of 30 calls played back at a low call rate (30 calls/min). Median values (black lines), 25-75% interquartile range (boxes), and extreme values (lines) are presented. Black dots represent raw data. House wrens spent more time less than 10 m from the speaker when calls were played back at higher calling rates (90 calls/min), but also when the calling sequence was longer (3 min).

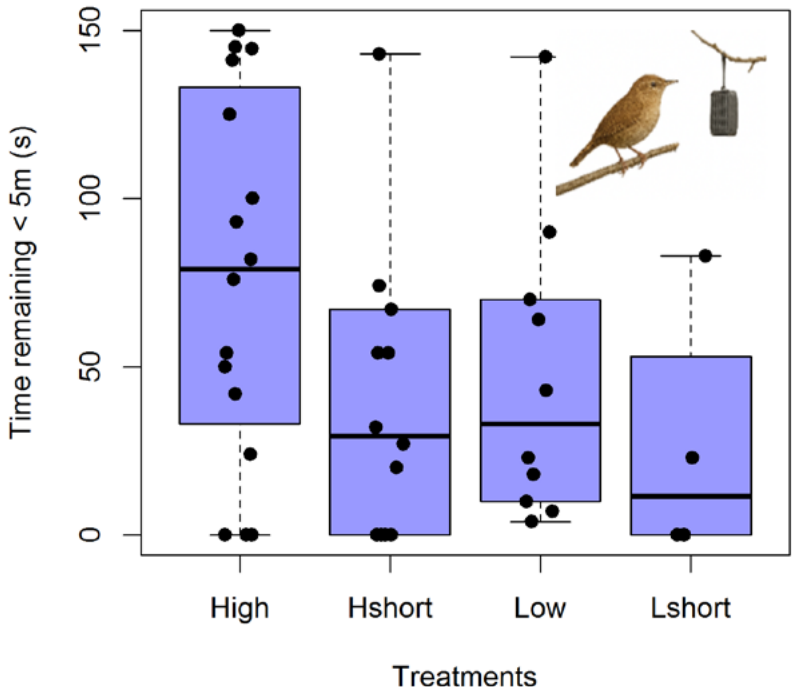

Figure 5. Time remaining < 5 m from the speaker by Southern House Wrens (*Troglodytes musculus*) when we played back sequences of alarm calls that varied in calling rate and number of calls. High: corresponds to call sequences played back for 3 min at a high call rate (~95 calls/min); Low: corresponds to call sequences broadcast for 3 min at a low call rate (30 calls/min); Hshort: corresponds to sequences of 30 calls played back at a high rate (~95 calls/min); Lshort: corresponds to sequences of 30 calls played back at a low call rate (30 calls/min). Median values (black lines), 25-75% interquartile range (boxes), and extreme values (lines) are presented. Black dots represent raw data. No differences in the time that individuals remained < 5 m from the speaker between treatments was detected.

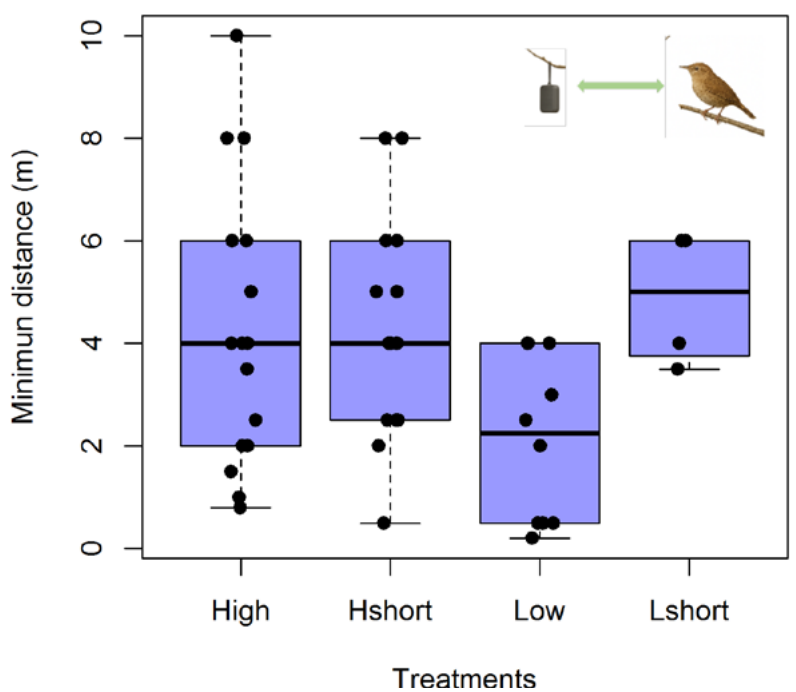

Figure 6. Minimum distance from the speaker to Southern House Wrens (*Troglodytes musculus*) approached when we played back sequences of alarm calls that varied in calling rate and number of calls. High: corresponds to call sequences played back for 3 min at a high call rate (~95 calls/min); Low: corresponds to call sequences broadcast for 3 min at a low call rate (30 calls/min); Hshort: corresponds to sequences of 30 calls played back at a high rate (~95 calls/min); Lshort: corresponds to sequences of 30 calls played back at a low call rate (30 calls/min). Median values (black lines), 25-75% interquartile range (boxes), and extreme values (lines) are presented. Black dots represent raw data. House wrens approached the speaker more closely when long sequences of calls at a low rate (30 calls/min) were broadcast.

lower call rate sequences. Regardless of the length of time spent near the speaker, the minimum approach distance of House Wrens to the speaker was shorter when we played back long sequence calls at a low rate.

Calling rate appears to be the main characteristic of alarm vocalization that triggers a response in House Wren receivers. The calling rate is a characteristic that receivers can directly relate to the arousal level of individuals and, therefore, to the risk perceived by the sender (e.g., Owings & Virginia 1978, Harris et al. 1983, Manser 2001, Baker & Becker 2002, Yorzinski & Vehrencamp 2009, Shah et al. 2015, Wheatcroft 2015, Common et al. 2025). In House Wrens, the calling rate increases with the level of risk, probably reflecting a state of greater excitement, supporting the urgency hypothesis (Fernández & Carro 2022). The differences found between responses to calls emitted at different rates could imply that calls produced at high rates generate greater excitement in listeners, leading them to search more intensely for the source of the signal. Previous results have also shown that these calls can attract conspecifics, particularly when they are played back at a high rate (Carro & Fernández 2021, Fernández et al. 2023). So, although the calls seem to be aimed at deterring predator, conspecifics seem to obtain information from and respond to the temporal structure of the call.

In addition to the effect of calling rate on the frequency and speed of the receivers' responses to the calling rate in House Wrens, we also found an effect of calling sequence duration on the response and the time receivers remained near the speaker. House Wrens also responded to long alarm sequences regardless of their rate and remained near the speaker for longer. In other species of both birds and mammals, it has also been observed that receivers can respond to the number of elements or duration of calls. In these cases, recipients often respond to longer calls or calls with a greater number of elements by remaining hidden longer or increasing their vigilance when the risk is greater or the threat is more immediate (Leger et al. 1979, Warkentin et al. 2001, Leavesley & Magrath 2005, Fallow & Magrath 2010, McLachlan & Magrath 2020). Repeating a signal can help the call be detected by receivers, but it can also provide information about the degree or level of a threat as well as increase the accuracy of the detection of the threat (Johnstone 1997, Wiley 2006, Yorzinski & Vehrencamp 2009). In this way, the receiver can reduce the costs of responding to a false alarm and the costs of failing to detect a threat (Wiley 1994, 2006). Therefore, the repetition of alarm calls can be interpreted as a mechanism for continuously transmitting information about risk, allowing recipients to detect, update, and integrate danger signals over time, enabling them to respond appropriately to both the level and duration of the threat (McLachlan & Magrath 2020).

House Wrens came closer to the speaker when we played long call sequences at a low rate compared to when we broadcast both short and long sequences of calls at a higher rate. This fact is puzzling. House Wrens responded to all treatments by approaching the source (although the frequency and speed of their approach varied with the treatment; see above). Approaching the source of the vocalizations allows receivers to assess the risk and ultimately decide on an appropriate response. When calls are given at a low rate, individuals may approach the speaker more closely because they perceive a lower risk than when calls were produced at higher rates. This approach may result from the need to locate the source (emitter) and assess the factor that triggers the response. Conversely, when alarm calls occur at a high rate, this may signal a high-risk situation to listeners, who would adopt a more cautious strategy. This hypothesis requires further research and specific field experiments.

In sum, we provide evidence of the role of calling rate and call sequence duration as recruitment cues in the House Wren, attracting conspecifics to the caller's location. Our results show that both the encoding of urgency, primarily reflected in the calling rate, and tonic effects, driven by the duration of the calling sequence, appear to be present in this species' risk signaling. Repeated calls at a high repetition rate when an individual detects a predator come at a high cost to the caller, as they increase its detectability and expose it to greater risk, particularly when the signal is directed at a predator, as in the case of the House Wren (Marler 1955, 1957). Therefore, the call rate may indicate the caller's perception of greater risk, while the duration may indicate not only the perceived risk but also its persistence. These calling features can constitute simple, easily identifiable, and honest cues that can then be used by receivers to assess the perceived level of risk.

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USE OF ARTIFICIAL INTELLIGENCE

We used an AI-based grammar correction service (http://www.grammarly.com, free online version) to improve language editing. Codes for inverse-proportional weighted (IPW) models, and Southern House Wren illustrations included in the figures were obtained using AI (http://www.chatgpt.com).

SUPPLEMENTARY MATERIAL

You can access the supplementary material for this article by visiting the link https://doi.org/10.56178/eh.v41i2.1543.

REFERENCES

Baker MC, Becker AM (2002) Mobbing calls of black-capped chickadees: effects of urgency on call production. The Wilson Bulletin 114(4):510-516. https://doi.org/10.1676/0043-5643(2002)114[0510:MCOBCC]2.0.CO;2

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society: Series B 57(1):289-300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bivand R (2022) R packages for analyzing spatial data: A comparative case study with areal data. Geographical Analysis 54(3):488-518. https://doi.org/10.1111/gean.12319

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker B (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. The R Journal 9(2):378-400. https://doi.org/10.32614/RJ-2017-066

Caro T (2005) Antipredator Defenses in Birds and Mammals.University of Chicago Pres, Chicago

Carro ME, Fernández GJ (2021) Alarm calls of house wrens (*Troglodytes aedon bonariae*) elicit responses of conspecific and heterospecific species. Behaviour 158(10):829-847. https://doi.org/10.1163/1568539X-bja10097

Common LK, Yelimlieş A, Colombelli-Négrel D, Austin VI, Kleindorfer S (2025) The 'seet' danger call: an active nest warning in superb fairy-wrens. Royal Society Open Science 12(11):251100. https://doi.org/10.1098/rsos.251100

Corral MG, Carro ME, Fernández GJ (2012) Alarm calls of nesting Southern house wrens (*Troglodytes musculus*). Ornitología Neotropical 23(2):251-260

Curio E (1978) The adaptive significance of avian mobbing: I. Teleonomic hypotheses and predictions. Zeitschrift für Tierpsychologie 48(2):175-183. https://doi.org/10.1111/j.1439-0310.1978.tb00254.x

Fallow PM, Magrath RD (2010) Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. Animal Behaviour 79(2):411-417. https://doi.org/10.1016/j.anbehav.2009.11.018

Fasanella M, Fernández GJ (2009) Alarm calls of the Southern House Wren *Troglodytes musculus*: variation with nesting stage and predator model. Journal of Ornithology 150(4):853-863. https://doi.org/10.1007/s10336-009-0406-2

Fernández GJ, Corral MG, Carro ME (2012) Variation in the alarm calls of Southern House Wrens (*Troglodytes musculus*). Emu 112(1):71-75. https://doi.org/10.1071/MU11033

Fernández GJ, Carro ME (2022) Alarm calls of southern house wrens, *Troglodytes aedon bonariae*, convey information about the level of risk. Ethology 128(4):293-302. https://doi.org/10.1111/eth.13255

Fernández GJ, Dutour M, Carro ME (2023) Information transfer during mobbing: call rate is more important than the number of callers in a southern temperate passerine. Behavioral Ecology and Sociobiology 77(7):78. https://doi.org/10.1007/s00265-023-03357-z

Fernández GJ, Carro ME, Johnson LS (2024) Southern House Wren (*Troglodytes musculus*), version 1.0. In: Juárez R, Keeney BK, Billerman S M (eds.) Birds of the World. (Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.houwre4.01

Fishbein AR, Lawson SL, Dooling RJ, Ball GF (2019) How canaries listen to their song: Species-specific shape of auditory perception. Journal of the Acoustical Society of America 145(1):562-574. https://doi.org/10.1121/1.5087692

Fox J, Weisberg S (2019) An R Companion to Applied Regression. Sage, Thousand Oaks, California

Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of animal signals. Animal Behaviour 42(1):1-14. https://doi.org/10.1016/S0003-3472(05)80600-1

Harris MA, Murie JO, Duncan JA (1983) Responses of Columbian ground squirrels to playback of recorded calls. Zeitschrift für Tierpsychologie 63(4):318-330. https://doi.org/10.1111/j.1439-0310.1983.tb00747.x

Hartig F (2020) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package ver. 0.3.3.0. [URL: http://florianhartig.github.io/DHARMa/]

Hernán MA, Robins JM (2020) Causal inference: What if. Chapman & Hall/CRC, Boca Raton

Johnstone RA (1997) The evolution of animal signals. In: Krebs JR, Davies NB (eds.) Behavioural Ecology: An Evolutionary Approach. Pp. 155-178. Blackwell Publishing, Oxford, UK

Kalb N, Anger F, Randler C (2019) Subtle variations in mobbing calls are predator-specific in great tits (*Parus major*). Scientific Reports 9(1):6572. https://doi.org/10.1038/s41598-019-43087-9

Klump GM, Shalter MD (1984) Acoustic behaviour of birds and mammals in the predator context; I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. Zeitschrift für Tierpsychologie 66(3):189-226. https://doi.org/10.1111/j.1439-0310.1984.tb01365.x

Le Roux A, Jackson T, Cherry M (2001) The effect of changing call duration and calling bouts on

vigilance in Brants' whistling rat, *Parotomys brantsii*. Behaviour 138(10):1287-1302. https://doi.org/10.1163/15685390152822229

Leavesley AJ, Magrath RD (2005) Communicating about danger: urgency alarm calling in a bird. Animal Behaviour 70(2):365-373. https://doi.org/10.1016/j.anbehav.2004.10.017

Leger DW, Owings DH, Boal LM (1979) Contextual information and differential responses to alarm whistles in California ground squirrels. Zeitschrift für Tierpsychologie 49(2):142-155. https://doi.org/10.1111/j.1439-0310.1979.tb00283.x

Lenth R (2020) emmeans: Estimated marginal means, aka least-squares means. R package version 1.5.1. [URL: https://CRAN.R-project.org/package=emmeans]

Loughry WJ, McDonough CM (1988) Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis. Animal Behaviour 36(5):1533-1540. https://doi.org/10.1016/S0003-3472(88)80224-0

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D (2021) performance: An R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6(60):3139. https://doi.org/10.21105/joss.03139

Manser MB (2001) The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proceedings of the Royal Society, London 268(1483):2315-2324. https://doi.org/10.1098/rspb.2001.1773

Marler P (1955) Characteristics of some animal calls. Nature 176(4470):6-8. https://doi.org/10.1038/176006a0

Marler P (1957) Specific distinctiveness in the communication signals of birds. Behaviour 11(1):13-39. https://doi.org/10.1163/156853956X00066

McLachlan JR, Magrath RD (2020) Speedy revelations: how alarm calls can convey rapid, reliable information about urgent danger. Proceedings of the Royal Society of London B. 287(1921):20192772. https://doi.org/10.1098/rspb.2019.2772

Morton ES (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. The American Naturalist 111(981):855-869. https://doi.org/10.1086/283219

Owings H., Virginia RA (1978) Alarm calls of California ground squirrels (*Spermophilus beecheyi*). Zeitschrift für Tierpsychologie 46(1):58-70. https://doi.org/10.1111/j.1439-0310.1978.tb01438.x

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [URL: https://www.R-project.org/]

Rowe C (2013) Receiver psychology: a receiver's perspective. Animal Behaviour 85(3):517-523. https://doi.org/10.1016/j.anbehav.2013.01.004

Schleidt WM (1973) Tonic communication: continual effects of discrete signs in animal communication systems. Journal of Theoretical Biology 42(2):359-386. https://doi.org/10.1016/0022-5193(73)90095-7

Schlenker P, Chemla E, Schel AM, Fuller J, Gautier JP, Kuhn J, Veselinović D, Arnold K, Cäsar C, Keenan S, et al. (2016) Formal monkey linguistics. Theoretical Linguistics 42(1-2):1-90. https://doi.org/10.1515/tl-2016-0001

Shah SS, Greig EI, MacLean SA, Bonter DN (2015) Risk-based alarm calling in a nonpasserine bird. Animal Behaviour 106:129-136. https://doi.org/10.1016/j.anbehav.2015.05.011

Sloan JL, Hare JF (2004) Monotony and the information content of Richardson's ground squirrel (*Spermophilus richardsonii*) repeated calls: Tonic communication or signal certainty? Ethology 110(2):147-156. https://doi.org/10.1111/j.1439-0310.2003.00955.x

Sommer C, Todt D, Ostreiher R, Mundry R (2012) Urgency-related alarm calling in Arabian babblers, *Turdoides squamiceps*: predator distance matters in the use of alarm call types. Behaviour 149(7):755-773. https://doi.org/10.1163/1568539X-00003003

Sueur J, Aubin T, Simonis C (2008) Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics 18(2):213-226. https://doi.org/10.1080/09524622.2008.9753600

Suzuki TN (2011) Parental alarm calls warn nestlings about different predatory threats. Current Biology 21(1):R15-R16. https://doi.org/10.1016/j.cub.2010.11.027

Suzuki TN (2016) Semantic communication in birds: evidence from field research over the past two decades. Ecological Research 31(3):307-319. https://doi.org/10.1007/s11284-016-1339-x

Templeton CN, Greene E, Davis K (2005) Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308(5730):1934-1937. https://doi.org/10.1126/science.1108841

Therneau T (2015) Mixed effects Cox models. [URL: https://cran.r-project.org/web/packages/coxme/vignettes/coxme.pdf]

Warkentin KJ, Keeley AT, Hare JF (2001) Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. Canadian Journal of Zoology 79(4):569-573. https://doi.org/10.1139/z01-017

Wheatcroft D (2015) Repetition rate of calls used in multiple contexts communicates presence of predators to nestlings and adult birds. Animal Behaviour 103:35-44. https://doi.org/10.1016/j.anbehav.2015.02.009

Wiley RH (1994) Errors, exaggeration, and deception in animal communication. In Real LA (ed.) Behavioral Mechanisms in Evolutionary Ecology. Pp. 157-189. University of Chicago Press, Chicago

Wiley RH (2006) Signal detection and animal communication. Advances in the Study of Behaviour 36:217-247. https://doi.org/10.1016/s0065-3454(06)36005-6

Yorzinski J L, Vehrencamp SL (2009) The effect of predator type and danger level on the mob calls of the American Crow. Condor 111(1):159-168. https://doi.org/10.1525/cond.2009.080057