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In the Danger Zone: Wrens Respond More Strongly to Experimentally Simulated Predators Near Their Nest

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ABSTRACT

Animals routinely face predation risk, and the behaviors that animals exhibit in the face of danger have life and death fitness consequences. When encountering predators, animals may exhibit divergent responses depending on perceived risk to themselves and their offspring. We used a predator presentation experiment to study the vocal responses of breeding rufous-and-white wrens (*Thryophilus rufalbus*) to simulated ferruginous pygmy-owls (*Glaucidium brasilianum*) at different distances from their active nests. We hypothesized that wrens' responses would vary with perceived predation risk, and we predicted that closer distances between the predator and wrens' nests would elicit stronger responses. We used lifelike 3D-printed models and acoustic playback to simulate owls at two distances from the nests (5 and 20 m) simulating high and low predation risk, respectively, as well as a non-predatory songbird as a control stimulus. We found that rufous-and-white wrens were highly vocal in response to predator simulations, producing both songs and alarm calls, and exhibiting substantial variation in intensity of response. Males vocalized more quickly in response to predators near the nest than to predators far from the nest, whereas females showed similar latencies of response. Wrens approached near-nest predators more closely than far-from-nest predators. Together, males and females showed stronger calling responses to near-nest predators compared to far-from-nest predators. Song rate did not change in response to model presentations for both sexes, but males performed more songs than females across all treatments. Our results reveal that birds respond more strongly, and with higher calling rates, in the face of heightened predation risk. Therefore, breeding birds exhibit divergent responses in different scenarios, displaying higher intensity vocal responses to predators nearer to their nests.

1 | Introduction

Predation risk modifies animal behavior (Lima and Dill 1990). Most animals face predation risk across much of their lifetime, and individuals that modify their behavior according to predation risk may enhance their chances of survival and maximize the success of their breeding activities (Lima 2009; Menezes and Marini 2017). Survival-enhancing antipredator behaviors include increasing vigilance behavior (Lima and Dill 1990; Lendrem 1983; Jones et al. 2009), reducing overall activity (Cooper 2000; Whitham and Mathis 2000; Bonachea and Ryan 2011), changing parental behavior (Fontaine and Martin 2006; Zanette et al. 2011; de Moraes et al. 2020), and producing anti-predator vocalizations (Magrath et al. 2010; Curé et al. 2013). These behaviors have been documented across diverse taxa including terrestrial mammals (Périquet et al. 2012; Campos and Fedigan 2014), marine mammals (Curé et al. 2013), amphibians (Bonachea and Ryan 2011), and birds (Jones et al. 2009; Lourenço et al. 2013; Ellison and Ydenberg 2019). Across taxa, adults and offspring are particularly vulnerable to predation during the reproductive period, given that breeding animals are tied to a particular

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location and therefore have restricted opportunities to escape from predators (Lima 2009). This heightened vulnerability during the reproductive period has consequences for individuals and populations, given the impact of predation on individual fitness (Zanette et al. 2011; Eyck et al. 2019), social behavior (Carlson et al. 2017), and population growth (Allen et al. 2022).

Diverse animals produce antipredator signals to mitigate the risk of predation. Alarm calls evolved as a shared signal among many phylogenetically distant species (Marler 1957; Wheatcroft and Price 2015). In birds, alarm calls uttered in the presence of a predator elicit well-characterized agonistic behaviors from conspecifics or other nearby species, known as mobbing (Grava et al. 2012; Sandoval and Wilson 2012; Dutour et al. 2021). For example, black-capped chickadees (*Poecile atricapillus*) communicate alarm by uttering high-duty-cycle calling bouts—calls produced at high repetition rates with brief pauses between notes—of their namesake *chick-a-dee* call when reacting to small, high-threat predators and low-duty-cycle bouts—shorter, sparser, or less frequent calls—in response to large, lower-threat predators (Templeton et al. 2005; Wilson and Mennill 2011; Landsborough et al. 2020). Alarm calls produced in the face of danger provide social information to nearby conspecific and heterospecific animals, and responses to alarm calls are expected to vary based on the perception of risk by nearby receivers (Lima 2009). The collective response to a predator is adaptive if it affords individuals a higher chance of survival or an opportunity to learn about threatening predators.

Avoiding predation is energetically costly, but the reward is survival. There is a trade-off between behaviors that are fundamental for acquiring resources and reproducing versus behaviors that minimize the chances of predation (Harvey and Greenwood 1978; Lima and Dill 1990; Lima and Bednekoff 1999). Songbirds, for example, reduce their food intake or the number of visits to a food source when they perceive the presence of a predator (Lima 1985; Moiron et al. 2018; Arteaga-Torres et al. 2020). Offspring care in songbirds involves a trade-off between parents feeding their nestlings and the potential of revealing their nest location to would-be predators. In many tropical songbirds, parents reduce the number of times they provision food to their young when a potential predator is nearby (Ghalambor et al. 2013; Martin 2015; de Moraes et al. 2020). In both temperate and tropical regions, mortality risk is heightened at nest sites during the reproductive season, which shapes life history traits such as clutch size and food provisioning behavior, with a general pattern of higher predation risk in the tropics (McKinnon et al. 2010; Martin 2015). Considering the contrast between the survival and reproductive costs of responding to predators, it is clear that animal behaviors have been shaped by predation risk. We may better understand antipredator behavior by exploring how animals assess and respond to variable levels of predation risk, where individuals that exhibit context-appropriate nest defense responses have a selective advantage (Kleindorfer et al. 2005).

In this study, we conducted a field-based experiment that involved simulating predators and assessing the responses of rufous-and-white wrens (*Thryophilus rufalbus*) during the breeding season. Male and female rufous-and-white wrens are involved in parental care behaviors (nest construction and food provisioning), and females incubate the eggs (Topp and Mennill 2008). We presented simulated predators to pairs of wrens in two scenarios: a close distance between the predator and an active nest (a higher risk scenario) and a farther distance between the predator and an active nest (a lower risk scenario). Risk assessment has been tested in three species of *Acrocephalus* warblers and in the house wren (*Troglodytes aedon bonariae*), revealing stronger anti-predator responses (i.e., higher calling rates) when predators were closer to the nest (Kleindorfer et al. 2005; Fernández and Carro 2022). We created a multi-modal simulation of a predator, including a life-like 3D-printed representation of a diurnal owl predator, the ferruginous pygmy-owl (*Glaucidium brasilianum*), coupled with a playback of the predator's call. We simulated the predator at a distance of 5 m (higher risk) and 20 m (lower risk) from the active nests of breeding rufous-and-white wrens. Ferruginous pygmy-owls consume both adult songbirds (Proudfoot and Beasom 1997; Carrera et al. 2008) and nestling songbirds (Proudfoot et al. 2020), and therefore we reasoned that an owl nearer the nest was a higher-risk scenario than an owl farther from the nest. We hypothesized that responses would vary with the perceived predation risk, and we predicted that the distance between the predator and the nest would influence the reactions of rufous-and-white wrens, where closer distances would elicit stronger responses. Given the propensity of birds to vocalize in response to predators, we expected higher call output and shorter latencies to vocalize in the higher risk scenario. Finally, we sought to characterize variation between individuals' responses when reacting to predators, to gain insight into flexibility under different predation risk scenarios.

2 | Methods

2.1 | Study Site

We performed the predator simulation experiment from May to June 2023 in the world's largest remaining stand of tropical dry forest, Sector Santa Rosa (10°52′ N, 85°36′ W) in the Área de Conservación Guanacaste in northwestern Costa Rica (Janzen 1988). Santa Rosa National Park has two defined seasons: a dry season characterized by scant rainfall and high temperatures (December–May) and a wet season characterized by abundant rainfall and warm temperatures (May–November; Sánchez-Azofeifa et al. 2005). In the year of this investigation, the rainy season was delayed; therefore, all pairs experienced similar weather conditions associated with the end of the dry season during our May to June study period.

Our study site is a mosaic of old-growth forest patches surrounded by secondary forest in different successional stages (Hilje et al. 2020). Since 2003, our research group has studied the population of rufous-and-white wrens that inhabit the old-growth forests and the late-successional second-growth forests. The vegetation and forest structure are similar in the late-successional second-growth forests and the old-growth forests in our study site (Hilje et al. 2020). In April 2023 we followed protocols we have established during our long-term studies, capturing birds in mist nets and banding them with individually distinctive combinations of color bands, mapping the birds' breeding territories, recording focal pairs, and observing nest-building behavior (Mennill 2006). Across the years, the number of neighbors in the study population varies from zero to four (Owen and Mennill 2021), with one or two neighbors being the most common for a given pair (Sánchez et al. 2024). We differentiated between males and females based on subtle body size differences and differences in the acoustic features of their songs (Mennill and Vehrencamp 2005). Wrens are difficult to capture, and not all birds were banded; at least one individual was color-banded for each of the subject pairs in this study, facilitating sex determination during playback trials.

2.2 | Study Species

Rufous-and-white wrens are tropical songbirds that inhabit foothills and lowlands from southwest Mexico to the north of Colombia and Venezuela (Stiles and Skutch 1989). In Costa Rica, the reproductive season of rufous-and-white wrens lasts from approximately April to August (Stiles and Skutch 1989). Both males and females contribute to nest construction, although males do more extensive nest building of secondary and tertiary nests after females commence incubation (D.J.M personal observation). The species is socially monogamous with low rates of extra-pair paternity (2% of nestlings across 6% of nests are extra-pair young; Douglas et al. 2012). Nests are typically placed on a branch or the fork of a bullhorn acacia tree (*Vachellia collinsii*) at 2–3 m height (Stiles and Skutch 1989). Females alone incubate the eggs and males provision females during the laying and incubation period, which lasts for approximately 2 weeks (Topp and Mennill 2008). Both parents provision offspring after hatch (Topp and Mennill 2008). For all subjects in this experiment, birds were in the late nest building phase or the early incubation phase; none of the subjects' nests showed indication of hatching (i.e., we never observed females bringing food to the nest).

Both male and female rufous-and-white wrens sing complex, flute-like songs which they learn from conspecific animals (Graham et al. 2018). They have a complex repertoire that consists of an average of 10.8 song types for males and 8.5 song types for females (Harris et al. 2016). Males and females often combine their voices to produce vocal duets, consisting of one or more songs performed by both members of the pair, either with overlapping songs or songs produced in direct succession (Mennill and Vehrencamp 2005). Calls are also part of the vocal repertoire of the species, and four different call types have been described (Topp and Mennill 2008). Chatter calls are commonplace in wrens, and they are considered antipredator alarm calls, mobbing calls, and pursuit-deterrent calls (Mennill and Vehrencamp 2005; Greig et al. 2010; Fernández and Carro 2022).

Rufous-and-white wrens have diverse predators. We chose to simulate a ferruginous pygmy-owl, a widespread neotropical predator which preys on insects, reptiles, and birds (Proudfoot et al. 2020). Ferruginous pygmy-owls are diurnal predators, known to consume adults of diverse bird species, including species as large as, and larger than, rufous-and-white wrens (Sazima 2015; Proudfoot et al. 2020). Pygmy-owls are also known to consume nestlings (Proudfoot and Beasom 1997; Proudfoot et al. 2020). As a control stimulus, we chose the chestnut-capped warbler (*Basileuterus delattrii*). Chestnut-capped warblers are common at our study site and throughout much of Central America (Demko et al. 2020). They are similar in size to the ferruginous pygmy-owl (Curson and García 2021). We have studied the resident chestnut-capped warblers at our study site between 2013 and 2015 (Demko and Mennill 2018, 2019). Chestnut-capped warblers are omnivores, consuming invertebrates and berries, and do not consume birds. We chose them as a control stimulus for the pygmy-owl experiment because of their similar body size and the lack of predation threat or competition threat to rufous-and-white wrens.

2.3 | Owl Stimuli and Control Stimuli

We created three lifelike 3D-printed models to simulate ferruginous pygmy owls (*Glaucidium brasilianum*, hereafter “owl”; Figure 1A). The owl models were modeled, printed, and hand-painted by L. Savi of SaviMade animal models (savimade.ca), showing only subtle differences in plumage color, while still maintaining the species-typical color pattern. The three control models were hand-carved wooden models of chestnut-capped warblers (hereafter “warblers”) created in the course of a different project (A. D. Demko; pers. comm.; Figure 1B). The warbler models were created by wood carvers at the Windsor Wood Carving Museum and were similar in size to the ferruginous pygmy owls. Both models were made following morphological measurements reported in the literature (Stiles and Skutch 1989; Proudfoot 1996) and the Birds of Costa Rica field guide (Stiles and Skutch 1989). Models were painted using reference photos, including photographs of museum specimens and photographs of wild animals taken in the field.

We designed five playback stimuli using five different vocalizations of pygmy-owls. We selected five recordings from five different individuals from the Macaulay Library online repository at the Cornell Lab of Ornithology (ML105563, ML193099, ML165040, ML212869, and ML167792). We selected only one call from each pygmy-owl recording to create the stimuli, which consisted of a repetition of notes defined as territorial “toots” (Proudfoot and Beasom 1996, Figure 1C). We first removed the background noise and other sounds present in the recording using the selection tool in Adobe Audition (v 23.3; Adobe Systems Inc.). Each stimulus consisted of 9 notes of the pygmy-owl forming a call of 12 s total followed by a silence of 4 s, and we repeated the call and the silence to create a stimulus of 4 min, using Adobe Audition. Similarly, for the control stimuli, we selected one warbler song from five different individuals provided by the Macaulay Library (ML370775581, ML170855511, ML260936IAVH-CSA11140, ML110747681, and ML32183921) and removed the background noise following the same procedure as the owl stimuli (Figure 1D). Each control stimulus consisted of 10 repetitions of the same song within 1 min, separated by 4-s silences, and was repeated to create a stimulus of 4 min. We broadcast all stimuli from a FoxPro Scorpion loudspeaker (FoxPro Inc., Lewiston, PA, U.S.A.).

To minimize pseudoreplication, we randomly selected one of three owl models or one of three warbler models, and we randomly selected one of five owl or warbler playback tracks. We used random selection without replacement, sequentially, until each stimulus had been used.

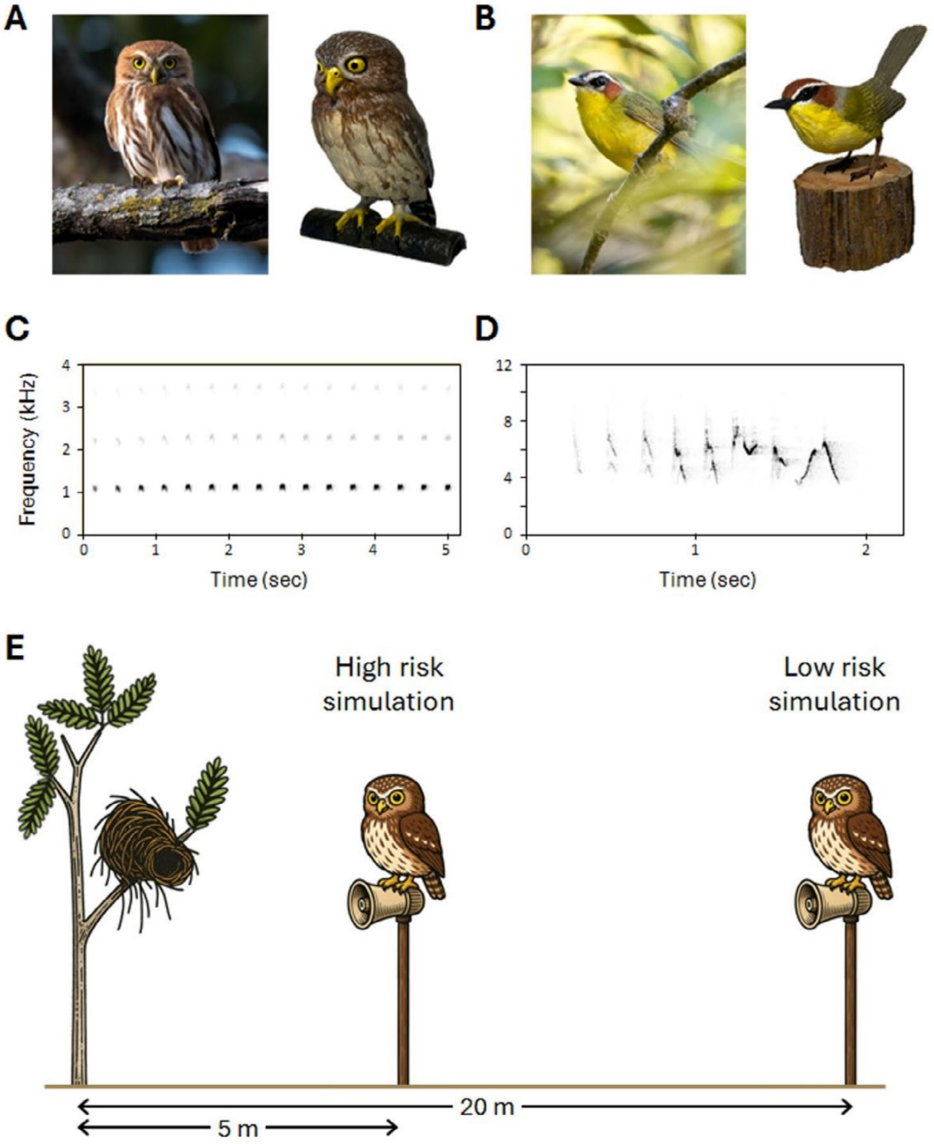

FIGURE 1 | (A) A ferruginous pygmy-owl (*Glaucidium brasilianum*) photo and 3D model. (B) A chestnut-capped warbler (*Basileuterus delattrii*) photo and 3D model for control treatment. (C) A ferruginous pygmy owl call spectrogram. (D) A chestnut-capped warbler song spectrogram. (E) Stylized representation of the multi-modal predator simulation (model owl + call playback) with two levels of predation risk: A predator at 5 m or 20 m from a rufous-and-white wren nest. Bird photographs by Adrian Delgado.

2.4 | Experimental Design and Response Measures

We presented the two owl simulations and one warbler simulation to each of ten pairs of rufous-and-white wrens (20 individuals; 10 males and 10 females). The experiment consisted of an owl model plus owl calls at a far distance from a nest, an owl model plus owl calls at a close distance to a nest, and a warbler model plus warbler songs at a close distance to a nest, over a 3-day period. On Day 1 of all trials, we presented the control stimulus, the warbler model plus the warbler song broadcast from a loudspeaker. We placed the model and the speaker on a 1.5 m pole at a distance of 5 m from the rufous-and-white wren nest and played the stimulus for 4 min (Figure 1). After the 4 min, we stopped the playback using a remote control and removed the model from the pole. The warbler species is typically vocally active at the same time as the rufous-and-white wren, and we observed both species in close proximity without showing aggressive behavior; therefore, we only performed the control treatment at 5 m from the nest. On Day 2, we randomly selected one of two distances from the nest (5 m or 20 m) for each pair. We placed an owl model and the speaker on a 1.5 m pole and played the stimulus for 4 min (Figure 1). When the 4 min experimental playback was completed, we stopped the playback and removed the model from view. On Day 3, we performed the same experiment using the owl model and the owl calls at the remaining distance from the nest. Although we always presented the control stimulus on Day 1 and randomized the order of the experimental stimuli on Days 2 and 3, a better design for future experiments might involve randomization of all three stimuli across all 3 days. In all trials, we removed the model from view after the predator presentation phase, following the protocol used by Tilgar and Moks (2015): one observer silently approached the model, removed it from the pole, and returned to a concealed location to reduce the stress of the birds when they discovered the owl model.

On the day prior to commencing a playback experiment for each pair (i.e., Day 0), we surveyed a rufous-and-white wren territory to determine where birds were actively breeding and to choose playback locations a distance of 5 m and 20 m from their nest. We placed a metal pole at each of the locations (defined with a measuring tape), thereby reducing the set-up time during Days 1, 2, and 3 of the experiment. On the days of an experiment, we arrived at the territory of the focal pair, approached the nest area quietly, and waited 10 min to place the model and loudspeaker on the pole. One observer turned on the loudspeaker and turned it off after 4 min of playback using a remote control. A second observer was located 15 m from the model and recorded the vocalizations of the pairs before, during, and after the experiment. Before starting each trial, we confirmed the presence of both members of the focal pair near the breeding nest. We performed the experiments between 05:15 and 07:30 h, a time period of high vocal output in this population (Mennill and Vehrencamp 2005). We recorded all the experiments with a handheld Marantz recorder PMD661 connected to a shotgun microphone Sennheiser MKH70 (WAV format; 44,100 Hz sampling rate; 16 bit depth). In all trials, we recorded the responses of birds during the simulation and for 4 min after the simulation was complete. During the recording, the second observer described behaviors such as approaches to the model, duets, and positions of the male and the female related to the nest and the model. Finally, we also recorded the distance of closest approach as the minimum distance that the pair approached the model during the presentation. We used as distance references the positions of the two poles at 5 m and 20 m from the nest, and a natural landmark (e.g., a shrub, a rock, or a fallen tree) at a location of 10 m distance from the nest. In some instances, the field observer was able to identify the responding male or female rufous-and-white wren by looking at their leg bands; in other cases, the thick vegetation at this study site made visual identity confirmation impossible. When birds sang, we were able to differentiate between males and females based on their voice, but when birds called, we were not able to differentiate between males and females. It was common to hear and record the males singing

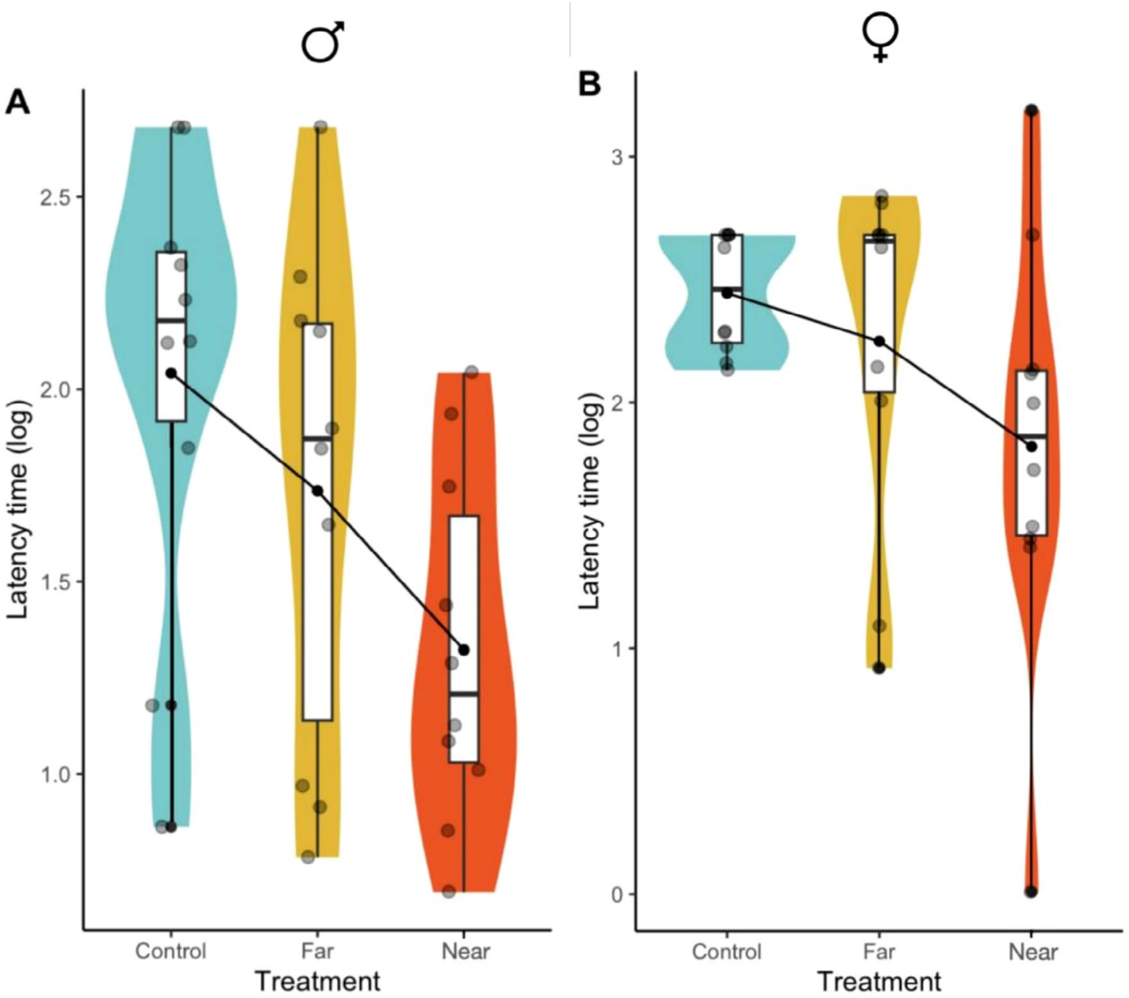

FIGURE 2 | The latency of response of rufous-and-white wrens to multi-modal simulations of a predator, a ferruginous pygmy owl (*Glaucidium brasilianum*), at two distances from the nest, far (20 m) and near (5 m), and a non-predator, a chestnut-capped warbler (*Basileuterus delattrii*). Data are shown for males (A) and females (B). Violin plots show the data distribution. Box plots show means (black dots connected by lines), and 25th, 50th, and 75th percentiles, with whiskers showing the full extent of the data. Observations over 4 min trials (240 s) are longer latency times during 4 additional recording minutes (480 s total).

before the experiment started. During the experiments, we quantified the approach distance to the model, and whether the subjects were within 5 m of the model, between 5 and 10 m of the model, or more than 10 m from the model. We recorded whether the male or the female made any movements towards the predator model during each 4 min trial.

2.5 | Statistical Analysis

We used linear mixed-effects models (LMM) to examine the effect of the playback treatment (i.e., predator versus non-predator at 5 m distance; predator at 5 m vs. 20 m distance) on three response variables: latency to respond (time from the first playback vocalization to the first song from the subject), song rate (total number of songs per minute), and calling time (total time in seconds of calling bouts in 4 min, each bout was separated by more than a second and males and females could be calling at the same time). For each linear mixed-effects model, we defined the following random effects: individual identity for the models including the response variable latency time or song rate, and pair identity for the model including the response variable calling time. We tested the interaction of Sex × Treatment for latency time and song rate. We used R package "lme4" to construct linear mixed-effects models, with normal distribution as the assumed error distribution, and parameter estimation method REML (Bates et al. 2015). To improve model fit, we log transformed the response variable latency time and square root transformed the response variable calling time (tested with qqplots and residuals plots). We compared the best model fit of the simple model versus the interaction model with the function "anova()" in R; a low p-value, below 0.05, for the interaction model indicates a better fit than the model without the interaction effect. We reported in the results ANOVA test output of the coefficients of the model to obtain p-values for the comparisons of the main effects (R package "car"), the Type II Wald Chi-square test and post hoc Tukey tests.

To compare distances of approach, we performed a Cumulative Link Mixed Model (CLMM) using the R package "ordinal" (Christensen 2023). Number of approaches at a given distance (1–5 m, 5> and <10, and more than 10 m) was defined as the response variable (categorical variable with three levels), the multi-model presentation treatments were the fixed effect, and pair identity was the random effect. This approach allowed estimation of treatment effects while accounting for repeated measures. We report the Wald p-value of the treatment effect and the likelihood ratio test (X^2, df, and p-value) of the owl presentation treatment model compared to the null model. We conducted all statistical analyses in R 4.3.0 (R Core Team 2023).

2.6 | Ethical Note

This research was approved by Área de Conservación Guanacaste (Research Permit R-SINAC-ACG-PI-014-2023) and the University of Windsor Animal Care Committee. Bird banding and playback were conducted by experienced ornithologists using techniques we have developed over two decades of research on this population of rufous-and-white wrens. We minimized stress during capture and handling by checking nets frequently and holding birds for the minimum amount of time possible before releasing birds at the site of capture. We

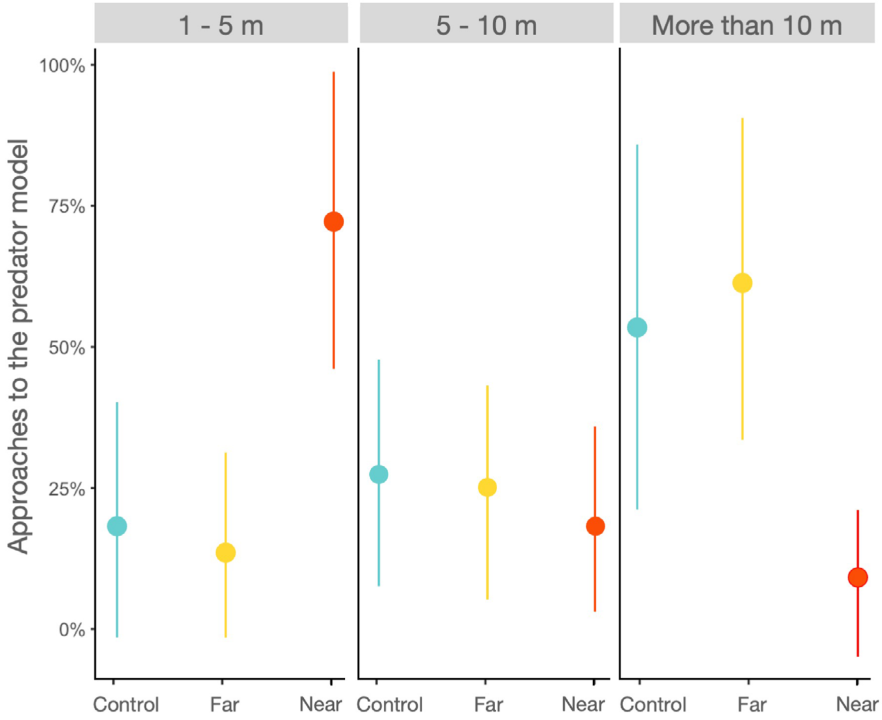

FIGURE 3 | Predicted probabilities of wren approaching the model at distance categories for male and female rufous-and-white wrens during multi-modal simulations of a predator, the ferruginous pygmy owl (*Glaucidium brasilianum*), at two distances from the nest, far (20 m) and close (5 m), and a non-predator, the chestnut-capped warblers (*Basileuterus delattrii*). The model predictions are generated from the Cumulative Link Mixed Model number of approaches explained by treatment with the random factor pair ID.

minimized stress during predator simulation by confirming that birds returned to nesting activities during preliminary trials and by designing an experiment with brief predator simulations.

3 | Results

In response to the simulation of a predator—a ferruginous pygmy-owl—rufous-and-white wrens always approached the site of the model presentation and playback and produced songs and calls. In response to the simulation of a non-predatory and non-competitive control animal—a chestnut-capped warbler—wrens showed little or no response. Birds exhibited substantial variation in their responses in the predator treatments near versus far to their nests, which may reflect both the features of the responding wrens and the features of the risk posed by the simulated predator.

Latency time of male and female wrens was shorter during response to near-nest predator (5 m) compared to far-from-nest predator (20 m) and control (Wald LMM $X^2 = 12.12$, df = 2, $p = 0.002$, Figure 2A,B). The interaction term among sex and treatment had no effect (Wald LMM $X^2 = 0.09$, df = 2, $p = 0.95$); both males and females showed lower latency to the near-nest predator treatment, and similar latency times across the far-from-nest predator and control. Males responded with shorter latency times than females (Wald LMM $X^2 = 8.76$, df = 1, $p = 0.003$, Figure 2A,B).

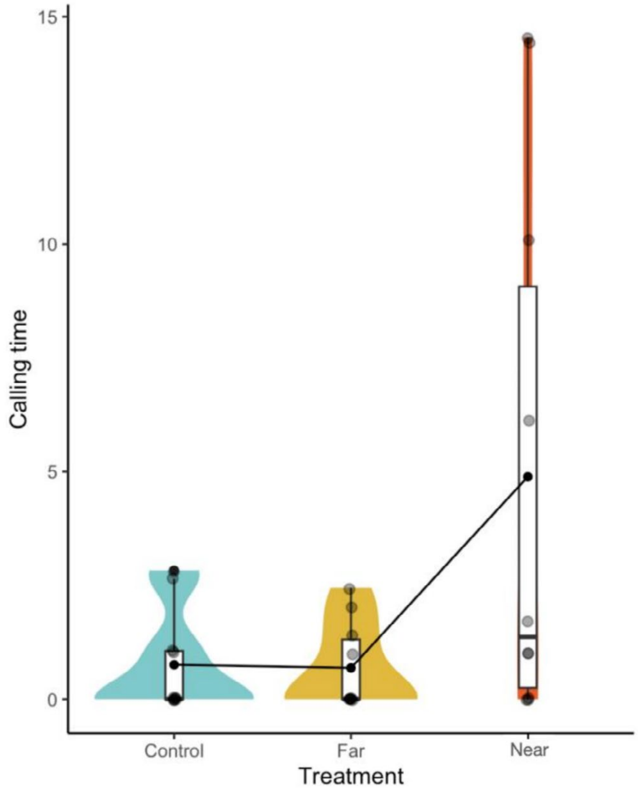

FIGURE 4 | The calling time of rufous-and-white wrens (number of seconds of calling per minute, square root transformed) to multi-modal simulations of a predator, the ferruginous pygmy owl (*Glaucidium brasilianum*), at two distances from the nest, far (20 m) and near (5 m), and a non-predator, the chestnut-capped warblers (*Basileuterus delattrii*). Violin plots show the data distribution. Box plots show means (black dots connected by lines), and 25th, 50th, and 75th percentiles, with whiskers showing the full extent of the data.

We found that wrens approached the model at very close distances during near-nest predator simulations (CLMM Wald-test $p = 0.01$), with a range of distances of closest approach of 1–2 m in the near-nest predator trials. We observed the wrens moving towards the predator model, perching on branches above or below the predator model, while calling regularly. During control and far-from-nest predator treatments, most wrens did not approach within 10 m of the model, and they often remained > 20 m beyond this distance (in six of ten trials for both the control and far-from-nest predator). Therefore, wrens were more likely to approach the model in near-nest predator treatment (Figure 3; CLMM likelihood ratio test: $\chi^2 = 11.42$, df = 2, $p = 0.003$).

Male and female wrens often performed "chatter" calls in response to the simulations. The combined call output of responding males and females was higher during near-nest predator compared to both far-from-nest predator and control treatments (Wald LMM $X^2 = 10.89$, df = 2, $p = 0.004$, Figure 4). In some cases, calls were performed by the female while the male was singing. We could not always attribute the calling to the resident male or female because of the thick vegetation at the study site, and because, unlike their songs, we have not detected any sex-based variation in the chatter calls of males versus females for this species.

In 25% of trials, including 3 near-nest trials and 2 far-from-nest treatments, the "chatter" calling behavior of the playback subjects elicited approach responses from heterospecific birds. We observed responses from black-striped sparrow (*Arremonops conirostris*), rufous-backed wren (*Campylorhynchus capistratus*), cabanis's wren (*Cantorchilus modestus*), chestnut-capped warbler (*Basileuterus delattrii*), dusky-capped flycatcher (*Myiarchus tuberculifer*), tropical royal flycatcher (*Onychorhynchus coronatus*), bright-rumped attila (*Attila spadiceus*), northern barred woodcreeper (*Dendrocolaptes sanctithomae*), clay-colored thrush (*Turdus grayi*), and white-throated magpie-jay (*Calocitta formosa*).

Song rate was similar for both male and female wrens (Wald LMM $X^2 = 0.95$, df = 2, $p = 0.62$, Figure 5B) across all three treatments. Song rate was higher for males compared to females (Wald LMM $X^2 = 33.03$, df = 1, $p < 0.001$, Figure 5).

4 | Discussion

Tropical songbirds, rufous-and-white wrens, showed shorter latencies of response, longer calling periods, and closer distances of closest approach to predatory ferruginous pygmy-owls simulated near their nests compared to far from their nests. Both female and male wrens sang during all simulations, showing similar song output across all treatments. Nest defense against a predator poses a trade-off between two key components of fitness—survival and reproduction—a topic that has not been explored in this species previously. We found that rufous-and-white wren males and females responded faster to predators simulated near their nests, suggesting that both sexes prioritize

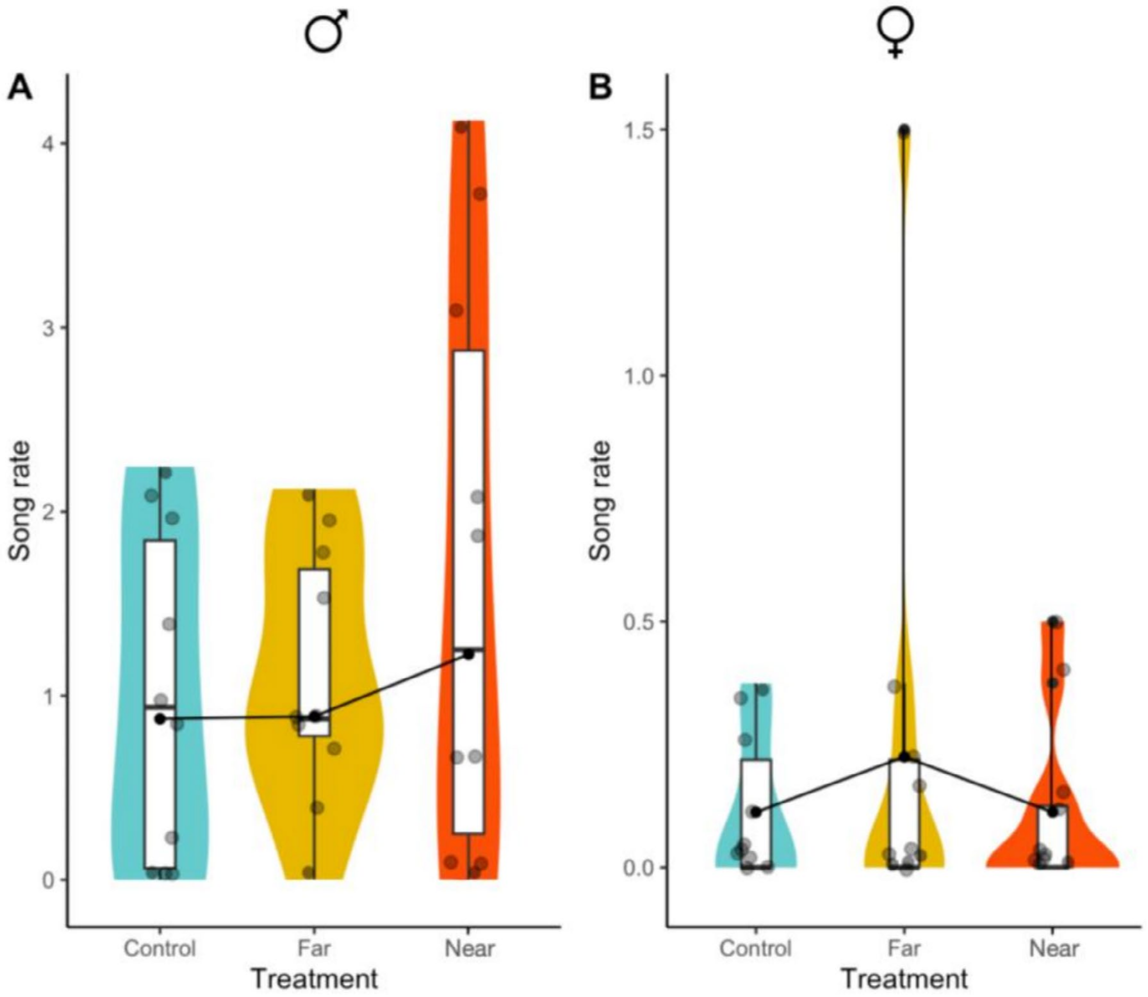

FIGURE 5 | The song rate (number of independent songs per minute) to multi-modal simulations of a predator, the ferruginous pygmy owl (*Glaucidium brasilianum*), at two distances from the nest, far (20 m) and near (5 m), and a non-predator, the chestnut-capped warblers (*Basileuterus delattrii*). Data are shown for males (A) and females (B). Violin plots show the data distribution. Box plots show means (black dots connected by lines), and 25th, 50th, and 75th percentiles, with whiskers showing the full extent of the data.

nest defense over survival when facing a high risk predator closer to their nest. Males responded faster than females during near-nest risk simulations. Calling time was consistent with the hypothesis that the predation risk near the nest is perceived as a stronger threat (Fernández and Carro 2022), where calling by both members of the pair might deter the potential predator and attract other bird species to join in mobbing behavior. We conclude that rufous-and-white wren responses vary with perceived predation risk, responding more strongly to predators near their nest site.

Diverse birds respond to predator presentations by increasing their calling rate. Blue tits (*Cyanistes caeruleus*) respond with a higher calling rate in a multimodal simulation of a sparrowhawk (*Accipiter nisus*), across diverse types of simulations, including a moving predator, a calling predator, and a predator holding a dead conspecific (Carlson et al. 2017). In Carolina wrens (*Thryothorus ludovicianus*), females perform specific calls associated with alert predator detections, whereas males show lower calling rates, suggesting that Carolina wren females engage in higher risk behavior, possibly because they cannot maintain a territory without a male (Morton and Shalter 1977). In superb fairy-wrens (*Malurus cyaneus*), some males sing songs and other males remain silent during predator simulations (Langmore and Mulder 1992); song may be used to communicate with the predator that the male is in good condition and able to escape predation, or song may be a signal to females to evaluate male quality during dangerous situations (Langmore and Mulder 1992). In our experiment, in the presence of a predator, both males and females increased their calling rate, consistent with previous studies, and showed aggressive responses approaching closer distances to the predator in the near-nest simulations. In a quarter of trials, the calling behavior of the playback subjects elicited approach responses from heterospecific birds from diverse species of songbirds.

An unexpected response observed during our experiment was the singing behavior of wrens. Males and females sang during the low risk and the high-risk simulation, and males often continued to sing when females started calling. Singing in the presence of a predator is not a common response among birds (Klumpg and Shalterm 1984). Rufous-and-white wrens perform duets, mainly for territorial defense and to maintain acoustic contact with the partner (Mennill 2006), and the most common duet form is when the female joins in to sing in response to a male song (Mennill and Vehrencamp 2005). In the context of predation risk, it is possible that the male sings to maintain acoustic contact with the female when the simulated predator was present. Acoustic contact between pair members may provide an advantage, allowing pair members to respond jointly to the threat (Lima 2009), or possibly making the predator's presence evident to other bird species to facilitate mobbing. Song could also contain alarm information to conspecific animals (Langmore and Mulder 1992), and certain aspects of the use of syllables or vocal modulations could be predation-risk dependent (Lima 2009; as in one study of song used to deter predators: Cresswell 1994). Future research exploring the use of song in the context of nest predators would allow further exploration of these ideas.

Previous studies have examined birds' responses to diverse predators and, more recently, to varying behaviors exhibited by a single predator. Here, we consider a scenario in which prey face a tradeoff, balancing parental self-preservation with risky behaviors that protect offspring from detection by a predator (Fontaine and Martin 2006; Lima 2009). Although our sample size of ten pairs could be at the lower end of experimental studies testing multilevel behavioral responses in birds, we aimed for a paired design that strengthens the within sub-contrast of risk perception by breeding territorial pairs. In the context of the STRANGE framework (Webster and Rutz 2020), our investigation does not suffer from problems associated with sampling bias given that the birds were selected arbitrarily from a larger population, or representativeness given that there is no reason to expect that the animals we sampled were not representative individuals of the study species. In terms of generalizability, the challenges of field work meant that we had a limited time window for the experiment, and we sampled birds in only one population; our results should be interpreted in light of this limitation.

Our approach revealed that rufous-and-white wren males and females responded both vocally and behaviourally in higher-risk situations when the predator was near to the nest. In the tropical dry forest, where mortality is high and predation risk is high, reproductive success plays an important role in determining individual fitness. The flexibility we observed in rufous-and-white wrens reacting differently in different predation scenarios may be important in unpredictable conditions, particularly in the biodiverse and predator-rich Tropics. More broadly, predation risk appears to shape the evolution of vocal communication by influencing how animals signal and adjust their behavior in the presence of threats.

Author Contributions

Natalie V. Sánchez: conceptualization, data curation, formal analysis, investigation, methodology, writing – original draft, writing – review and editing. **Daniel J. Mennill:** conceptualization, investigation, writing – review and editing, supervision, resources, funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available as Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** eth70052-sup-0001-AppendixS1.docx.