

Sexual differentiation and seasonal variation in response to conspecific and heterospecific acoustic signals

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Abstract

Interspecific territoriality is frequently reported between closely related species; however, few studies have demonstrated interspecific territoriality between distantly related species living in sympatry. We conducted playback experiments to investigate territorial behaviour in male and female White-bellied Wrens (*Uropsila leucogastra*) in response to simulated conspecific and heterospecific intruders during the breeding and non-breeding seasons. We explored whether heterospecific songs of the Happy Wren (*Pheugopedius felix*), a distantly related species and ecological competitor, elicited antagonistic responses from focal White-bellied Wrens, and whether such responses differed between the sexes. We also examined whether male and female responses to conspecific and heterospecific rivals varied with season. We found that male White-bellied Wrens always responded to conspecific song, and responded significantly more to heterospecific song compared to a control stimulus (Tropical Parula, *Setophaga pitiayumi*). In contrast, although female White-bellied Wrens responded strongly to conspecific song, their response to heterospecific song did not differ significantly from the control stimulus. The proportion of males that responded to heterospecific songs and the proportion of females that responded to conspecific songs varied seasonally, showing significantly lower responses during the breeding season. The intense responses of male White-bellied Wrens to playback of heterospecific songs suggest that they recognise ecological competitors based on their vocal signals. Furthermore, the decrease in agonistic interactions during the breeding season is in line with the hypothesis that aggressive behaviour may be detrimental to reproductive and parental activity, and the hypothesis that heterospecific animals pose less of a threat during the breeding season.

KEYWORDS

interaction, interspecific, playback, season, song, territoriality

1 | INTRODUCTION

Competitive interspecific interactions between species have been reported in a variety of animals including insects (Lawton & Hassell, 1981), fish (Bay, Jones, & McCormick, 2001), amphibians (Cunningham, Rissler, & Apodaca, 2009), reptiles (Langkilde & Shine, 2004; Pacala & Roughgarden, 1982), mammals (Brown, 1971; Simeonovska-Mikolova, 2007) and birds (Catchpole, 1978; Robinson & Terborgh, 1995; Terborgh, 1971). Such interactions may reflect competition for

limited dispersal opportunities, niche space and breeding territories (Jankowski et al., 2012). For example, interspecific territoriality to secure breeding territories against members of a different species may result from competition between closely related species occurring in sympatry (Catchpole, 1978; Jankowski, Robinson, & Levey, 2010; Orians & Willson, 1964).

In birds, interspecific territoriality appears to be commonplace, influencing habitat selection (Martin & Martin, 2001), spatial partitioning of closely related species along successional gradients

(Robinson & Terborgh, 1995), settlement patterns of migratory birds arriving to their breeding grounds (Fletcher, 2007), and range expansion or compression in response to competitors (Jankowski et al., 2010). Consequently, interspecific interactions could potentially influence range distributions and patterns of diversity and abundance in tropical avifauna (Jankowski et al., 2012). Most studies, however, have focused on competition between closely related species, often belonging to the same genus (Hick, Doucet, & Mennill, 2016; Martin & Martin, 2001; Robinson & Terborgh, 1995). Nevertheless, competition also occurs between distantly related species. The Least Flycatcher (*Empidonax minimus*) and the American Redstart (*Setophaga ruticilla*) overlap in their use of food resources and breeding grounds (Martin, Fotheringham, Ratcliffe, & Robertson, 1996), but American Redstarts avoid habitats where they detect heterospecific vocal cues, although Least Flycatchers are attracted to habitats where they detect both conspecific and heterospecific vocal cues (Fletcher, 2007). By documenting competitive interspecific interactions we can develop a better understanding of competition within communities (Jankowski et al., 2010).

White-bellied Wrens (*Urosila leucogastra*) are small songbirds that inhabit lowland areas of Mexico, Guatemala, and Belize. Part of the Pacific population of this species occurs in sympatry with Happy Wrens (*Pheugopedius felix*), which are slightly larger songbirds, restricted to the Mexican lowlands and highlands from Sonora to southern Oaxaca (Brewer, 2001; Howell & Webb, 1995). White-bellied Wrens and Happy Wrens share several ecological and behavioural characteristics: both belong to the family Troglodytidae; both are insectivores sharing similar foraging behaviours in low to mid-levels of the forest; and both nest in bushes or thickets, usually on acacia trees (Brewer, 2001; Howell & Webb, 1995). These similarities in feeding and nesting behaviour suggest that, although they belong to different genera, these songbird species may compete with one another, but little is known of their interspecific interactions.

In this study, we investigate the vocal and physical responses of White-bellied Wrens to conspecific and heterospecific acoustic signals during both the breeding and non-breeding seasons. We ask whether White-bellied Wrens respond to songs of a heterospecific bird species that shares similar behaviour and habitat, whether these responses differ between males vs. females, and whether these responses differ between the breeding vs. non-breeding season. We used playback to simulate conspecific and heterospecific intruders within the territories of White-bellied Wren pairs. We predicted that the most intense responses should be directed towards simulated conspecific intruders (i.e., White-bellied Wrens), as conspecific animals threaten an animal's paternity and territory possession; that intermediate intensity responses would be directed towards simulated heterospecific intruders (i.e., Happy Wrens) that only threaten territory possession; and that the lowest intensity responses would be directed towards playback of a control stimulus (i.e., songs of Tropical Parula, *Setophaga pitiayumi*), which does not threaten either paternity or territory possession. We then examined whether male

and female responses to conspecifics and heterospecifics varied with season. Levels of testosterone, which stimulates aggression during the reproductive season (Hau, Stoddard, & Soma, 2004; Wingfield, Hegner, Dufty, & Ball, 1990), are known to be high early in the breeding season while individuals establish territories (Gill, Alfson, & Hau, 2007). Aggression due to high testosterone levels has a detrimental effect on reproductive and parental behaviours of birds (Rutkowska, Cichoń, Puerta, & Gil, 2005; Searcy, 1988). Thus, we predicted that the strongest response would occur during the pre-breeding season when the likelihood of losing a territory is higher, and that responsiveness should decrease in the breeding season when individuals are involved in parental activities.

2 | METHODS

2.1 | Study site and species

We conducted this study at the Estación de Biología Chamela, of the Instituto de Biología, Universidad Nacional Autónoma de México, on the coast of Jalisco, Mexico (19°30'N, 105°03'W). The study site consists of lowland tropical dry forest, which is characterised by a marked seasonality in rainfall and plant phenology, with a prolonged dry season from Nov. to Jun. (Bullock, 1986). This site receives an average annual rainfall of 748 mm, 85% of which occurs during the rainy season months of Jun.–Oct. (Bullock, 1986).

Our focal species, the White-bellied Wren, is a small insectivorous songbird that forages from ground level to mid-story, and is a sedentary species distributed from northeastern Mexico to northern Guatemala (Brewer, 2001). In our experiments, we used vocalisations of the Happy Wren as a heterospecific competitor stimulus, and the Tropical Parula as an heterospecific control stimulus (Figure 1). The Happy Wren is a sedentary Mexican endemic songbird species that has similar foraging behaviour to that of White-bellied Wrens, being a small understory-to-midstory insectivore (Brewer, 2001). The Tropical Parula is also a small, insectivorous, sedentary species, distributed from northwestern Mexico and southern Texas to northern Argentina (Howell & Webb, 1995). Unlike White-bellied Wrens and Happy Wrens, Tropical Parulas forage in the midstory-to-upperstory levels (J. R. Sosa-López, personal observation, February 2014; Howell & Webb, 1995). All three species are common at our study site, and their territories often overlap. Tropical Parulas and White-bellied Wrens have similar body size, while Happy Wrens are slightly larger (Howell & Webb, 1995). Preliminary playback trials suggested that although White-bellied Wrens live in sympatry with Tropical Parulas, they do not respond aggressively to their vocalisations (J. R. Sosa-López, personal observation, March 2014) making them a compelling choice for a control stimulus in this experiment.

2.2 | Identification of territorial pairs

We conducted field observations and playback experiments in three seasons: two pre-breeding seasons (from 15 to 26 Mar. 2014, and 28

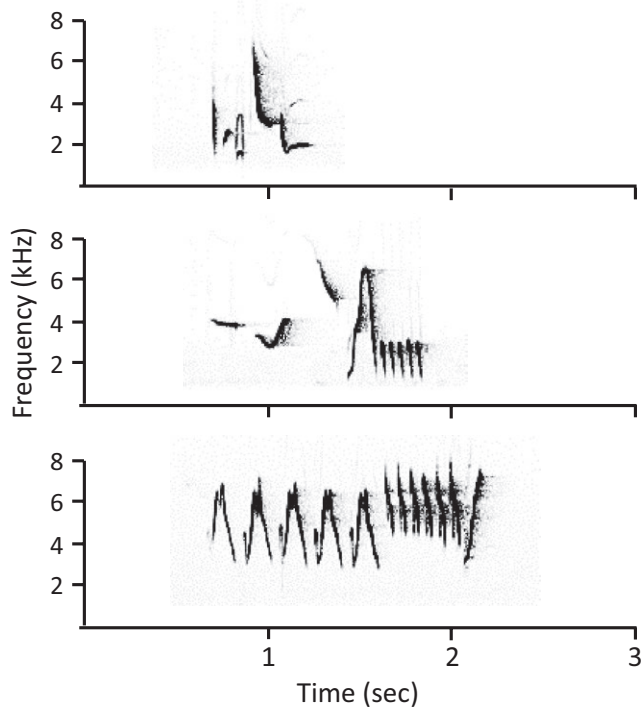


FIGURE 1 Sound spectrograms depicting songs of the three species simulated with playback. Top: song of the White-bellied Wren, *Uropsila leucogastra*. Middle: song of a heterospecific ecological competitor, the Happy Wren, *Pheugopedius felix*. Bottom: song of a heterospecific non-competitor, the Tropical Parula, *Setophaga pitaiyumi*, used as a control

Feb. to 8 Mar. 2015); and one breeding season (8–27 Jul. 2014). We located territories of 28 pairs of White-bellied Wrens, and were able to test 19 pairs across all three seasons. We used mist-nets to capture territorial pairs and gave birds a unique combination of coloured leg bands to facilitate identification. We colour-banded at least one individual in 14 of the 19 territories (in 10 territories we banded only the male; in two territories we banded only the female; in two territories we banded both birds). We identified the unbanded birds as unique individuals based on their territory position relative to known neighbours, and based on similarity in their vocal repertoires during their playback responses; between seasons, we confirmed the identity of the unbanded birds based on territory position and vocal repertoires. Our field observations suggested that all banded individuals held their territories throughout the year, based on our repeated observation of the same animals across at least two of the three observation periods (it was more difficult to confirm female identity during the breeding season due to their cryptic behaviour while nesting). We observed no reproductive behaviour in Mar. 2014 or in Feb.–Mar. 2015. During Jul. and Aug. 2014, we observed several reproductive behaviours: on 17 Jul. we observed two females incubating; on 18 Jul. we observed a male participating in nest construction; between 30 Jul. and 6 Aug., we mist-netted four females with a brood patch; and from 17 Jul. to 6 Aug., we observed one to two fledglings on repeated occasions in six different territories. These observations confirm that our estimates of breeding seasonality are correct.

2.3 | Playback treatments

We used playback to simulate three types of conspecific and heterospecific intruders: conspecific White-bellied Wren songs, heterospecific Happy Wren songs, and heterospecific control Tropical Parula songs. Each focal pair of White-bellied Wrens received all three treatments in each of three different time periods: the first set of treatments during the pre-breeding season (Mar. 2014), the second set of treatments during the following breeding season (Jul. 2014), and the third set of treatments during the next pre-breeding season (Feb.–Mar. 2015). Each treatment had a duration of 10 min, where the first 5 min was a pre-playback silent period (allowing us to confirm that birds were not already engaged in an aggressive interaction with a rival), followed by a 5 min experimental period. The experimental period consisted of a 2 min stimulus followed by 3 min silence. We assessed the response of subjects during the playback and in the 3-min silent period following the playback. Each subject pair received all three treatments on different, consecutive days at the same time of day (i.e., if the first treatment was performed at 0700 hr in a particular territory, the following treatment in that territory was given at the same time the next day). We followed a Latin square design for the presentation order of treatments within each of the three seasons (Ott & Longnecker, 2001).

We created playback stimuli based on recordings we collected at the study site. Each stimulus was designed using stimuli of a single recorded exemplar of a given song type (approximately 0.6 s length), repeated every 5 s for 2 min, which is a normal rate of song presentation for White-bellied Wrens based on our preliminary observations. Every subject pair received stimuli that came from different individuals, and a different set of stimuli between trials (i.e., a given focal pair received three different conspecific, heterospecific and control stimuli). Song rates of the stimuli were held constant across all the treatments and trials, so that song rate could not confound different responses to the three treatments. We avoided the use of neighbouring males' songs as stimuli, and did not test adjacent males on the same day or on subsequent days. We normalised the amplitude of the playback stimuli to -1 dB in Audacity (version 2.0.0; Free Software Foundation, Inc., Boston, MA, USA), to standardise amplitude across treatments and trials. For all stimuli, we applied a 1 kHz high-pass filter in audacity to minimise low-frequency background noise.

2.4 | Playback experiments

Playback experiments in each of the three seasons were conducted between 0700 and 1200 hr. We placed a loudspeaker (model: Foxpro FX5) near the centre of the subject pair's territory, hanging the loudspeaker from a branch at a height of 1.8 m. The loudspeaker was placed in the same location within the subject's territory for all playback treatments across the three experimental seasons. All sounds were broadcast at an amplitude of -85 dB, measured at 1 m from the loudspeaker using a sound level metre (model: Radio Shack 33-2055; C-weighting; fast response). Although the normal amplitude of these species' songs has not been quantified in the field, the two wren

species produce sounds that are similar in amplitude, and similar to our playback amplitude, based on our auditory perception in the field. During experiments, we recorded responses of territorial pairs to playback using a digital recorder (model: Marantz PMD660; settings: WAV format, 44.1 kHz sampling frequency; 16 bit accuracy) with two shotgun microphones (model: Sennheiser MHK67), each connected to a different channel. The observer quietly dictated behavioural observations of the focal pair on one microphone, while the second microphone recorded vocal responses of the focal pair on the second channel. The observer sat at a position 18–25 m from the speaker.

We quantified responses to playback stimuli as categorical responses for the male and female of each pair of subjects. Male and female White-bellied Wrens responded to conspecific songs by vocalising (producing either songs or calls), moving towards the speaker, and remaining in the area near the speaker. Males sang multiple songs, sometimes in combination with calls, made frequent movements, and used exposed perches 2–6 m above the ground, often in close proximity to the speaker. Females showed more cryptic behaviour than males, producing only calls (not songs), making fewer movements, and remaining closer to the ground among dense vegetation. Birds often cocked their tails and flapped their wings rapidly near the speaker; these behaviours are consistent with the idea that birds were exhibiting aggressive territorial behaviour towards the loudspeakers (J. R. Sosa-López, personal observation, March 2014). We considered that a stimulus had elicited a response when focal subjects displayed both vocal behaviours (calls or songs) and physical behaviours (movement towards the speaker), regardless of the distance from the speaker, and if the focal individual stayed in the area for the duration of the experiment. White-bellied Wrens do not differ morphologically between sexes (Howell & Webb, 1995), but we could differentiate between males and females based on their band combinations, or in the case of unbanded birds, based on their behaviour during playback given that our field observations of banded individuals confirmed that males used songs when responding to conspecific playback, but females did not (J. R. Sosa-López, personal observation, March, 2014; although Brewer, 2001, suggest that both sexes do sing).

2.5 | Statistical analysis

We used a Cochran's Q test to test the null hypothesis of equal frequencies of response to treatments. We first tested for differences in responses to conspecific (i.e., White-bellied Wren) and heterospecific stimuli (i.e., Happy Wren) by comparing the proportion of subjects that responded to conspecific, heterospecific, and control playbacks in each season. We analysed males and females separately within each season conducting a total of six tests. Secondly, we tested whether responses of White-bellied Wrens to conspecific and heterospecific playbacks varied with reproductive stage by comparing the proportion of individuals that responded to each playback among the three seasons by sex. We performed post hoc pair-wise comparison tests using Bonferroni correction in all the analyses. Statistical analyses were performed in IBM SPSS Statistics (version 20.0; Chicago, IL, USA).

3 | RESULTS

3.1 | Responses to heterospecific signals

The proportion of male White-bellied Wrens that responded to playback differed significantly among the three treatments of conspecific, heterospecific, and control stimuli in each of the three seasons (Figure 2; year 1, pre-breeding season: Cochran's Q: $\chi^2 = 28.7$, $p < .005$, $n = 19$; year 1, breeding season: Cochran's Q: $\chi^2 = 32.9$, $p < .005$, $n = 19$; year 2, pre-breeding season: Cochran's Q: $\chi^2 = 28.7$, $p < .005$, $n = 19$). Post hoc pair-wise comparisons demonstrated that in the pre-breeding seasons of 2014 and 2015, responses of male White-bellied Wrens differed significantly for each of the three stimuli (conspecific, heterospecific, and control), showing a higher proportion of responses to conspecific stimuli, an intermediate proportion of responses to heterospecific stimuli, and no responses to control stimuli. In the breeding season, however, responses of male White-bellied Wrens to heterospecific stimuli did not differ from control stimuli, although responses to conspecific stimuli differed significantly from both heterospecific and control stimuli. In all seasons, all males responded to playback of conspecific stimuli and no males responded to playback of control stimuli (Figure 2a,c,e). Most males also responded to heterospecific stimuli during the pre-breeding season (Figure 2a,e), but only a few males responded to heterospecific stimuli during the breeding season (Figure 2c).

Female White-bellied Wrens also demonstrated significantly different responses to conspecific, heterospecific, and control stimuli (i.e., a significant effect of treatment), a pattern that held true across all three seasons (Figure 2; year 1, pre-breeding season: Cochran's Q: $\chi^2 = 22.6$, $p < .005$, $n = 19$; year 1, breeding season: Cochran's Q: $\chi^2 = 8.4$, $p = .015$, $n = 19$; year 2, pre-breeding season: Cochran's Q: $\chi^2 = 26.3$, $p < .005$, $n = 19$). Post hoc pair-wise comparisons demonstrated that in all three seasons a significantly greater proportion of females responded to playback of conspecific stimuli compared to heterospecific and control stimuli, but female responses to playback of heterospecific stimuli did not differ significantly from playback of control stimuli in any season (Figure 2b,d,f).

3.2 | Seasonal variation in response to playback

Male White-bellied Wrens consistently responded to playback of conspecific stimuli during both the non-breeding seasons and breeding season, and never responded to the control stimuli (Figure 2a,c,e). In contrast, males showed variation in response to heterospecific stimuli. We found that responses of male White-bellied Wrens to heterospecific stimuli varied significantly across seasons (Cochran's Q: $\chi^2 = 7.0$, $p = .03$, $n = 19$; i.e., middle bars in Figure 2a,c,e). Post hoc pair-wise comparison revealed that males were more responsive to heterospecific stimuli in the two pre-breeding seasons compared to the breeding season.

Female White-bellied Wrens showed consistently low levels of response to playback of heterospecific stimuli across the seasons, and never responded to the control stimuli (Figure 2b,d,f). Females

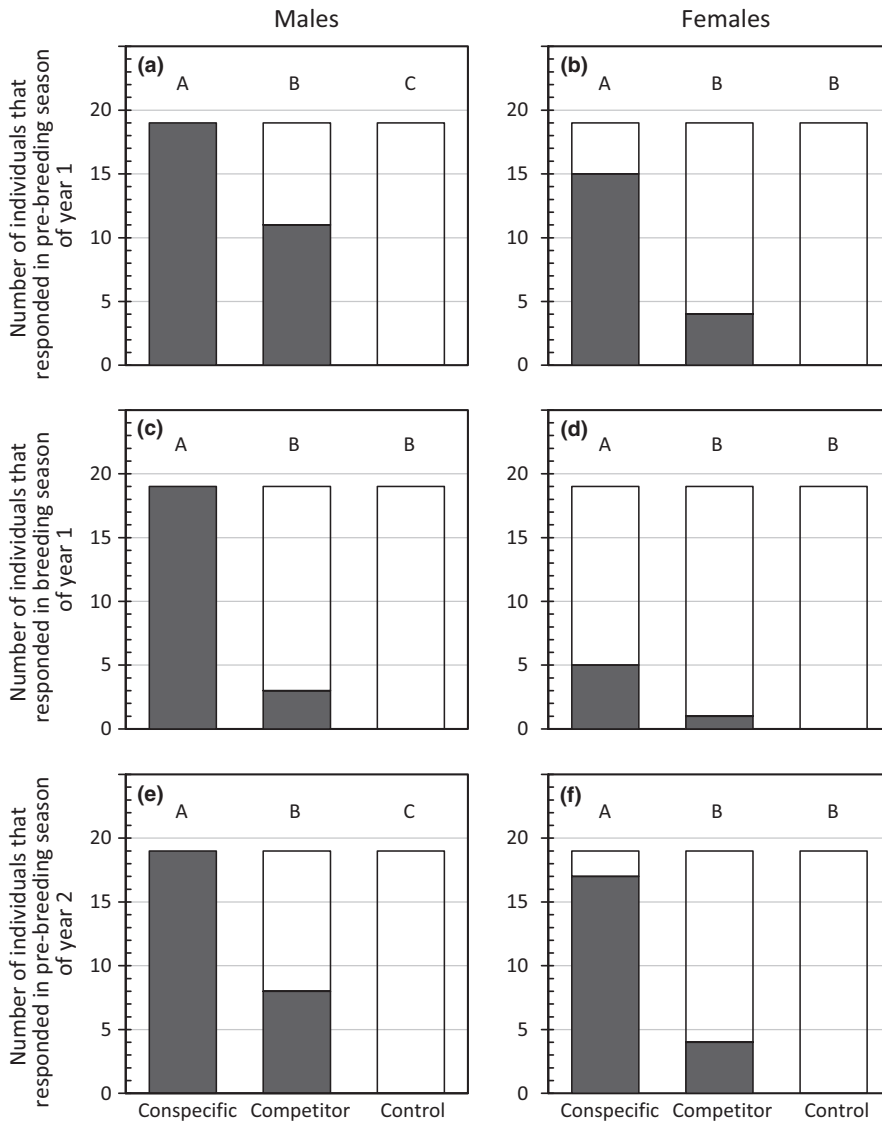


FIGURE 2 Relative proportion of males (left) and females (right) that responded to simulated intruders in each of the three seasons: pre-breeding season of 2014 (top), breeding season of 2014 (middle) and pre-breeding season of 2015 (bottom). Black bars show the proportion of individuals that responded to stimuli, while white represents individuals that did not respond to stimuli. Different letters indicate significant variation between treatments in the post hoc pair-wise comparisons analysis

however showed variation in response to conspecific stimuli, which differed significantly across seasons (Cochran's $Q: \chi^2 = 13.8, p = .001, n = 19$; i.e., left-most bars in Figure 2b,d,f). Post hoc pair-wise comparison revealed that females were more responsive to conspecific stimuli in the two pre-breeding seasons compared to the breeding season.

4 | DISCUSSION

White-bellied Wrens exhibited territorial behaviour in response to playback of both conspecific songs and heterospecific Happy Wren songs, although males responded more to heterospecific songs than did females. Territorial responses to playback varied with the breeding season. Males showed consistently high responses to conspecific songs across seasons, but higher responses to heterospecific competitor songs in the pre-breeding season; females showed higher responses to conspecific songs in the pre-breeding season, and consistently low responses to heterospecific songs across seasons. Based on these patterns, we conclude that male White-bellied Wrens

recognise Happy Wren songs as potential competitors. Further, the lower proportion of responses in the breeding season support the idea that aggressive behaviour may be detrimental to reproductive and parental activity, or that territory intrusions are more threatening during the pre-breeding season than the breeding season when territories are already established.

The difference in response to playback of heterospecific compared to control songs by male White-bellied Wrens suggests that males discriminated between stimuli. Such discrimination has been reported in other wrens, including Grey-breasted Wood-Wrens (*Henicorhina leucopryis*), White-breasted Wood-Wrens (*Henicorhina leucosticta*), Rufous-and-white Wrens (*Thryophilus rufalbus*) and Banded Wrens (*Thryophilus pleurostictus*) (Hick, Doucet, & Mennill, 2015; Jankowski et al., 2010), as well as other bird groups (Catchpole, 1978; Fletcher, 2007; Jankowski et al., 2010). A common explanation for this behaviour is that males treat heterospecific songs as coming from potential competitors (Hick et al., 2015). Our behavioural study suggests that this may be the case for male White-bellied Wrens. Alternatively, the responses to heterospecific songs could be the result of a mistaken identity (Murray,

1971). Closely related species often share similar vocal traits and these similarities may foster responses to sister species, as is known to occur in *Troglodytes* wrens (Sosa-López, Martínez Gómez, & Mennill, 2016). However, White-bellied Wrens and Happy Wrens have divergent songs with very different spectro-temporal features. We argue that the explanation of mistaken identity is unlikely, and that the responses we observed during the experiments are likely the result of a learned component, as has been documented in other bird species, including wrens (Fletcher, 2007; Hick et al., 2015; Robinson & Terborgh, 1995). Further studies could experimentally describe the territorial behaviour of male White-bellied Wrens in areas where the Happy Wren is absent to corroborate this hypothesis (Catchpole, 1978; Hick et al., 2015; Jankowski et al., 2010).

The response of male White-bellied Wrens to simulated heterospecific intruders varied significantly with season. In line with our expectations, a greater proportion of males responded antagonistically to heterospecifics during the pre-breeding season, whereas fewer individuals responded during the breeding season. This would agree with the findings of Gill et al. (2007), where Buff-breasted Wrens (*Cantorchilus leucotis*) present higher testosterone levels during the pre-breeding season when territory owners are more likely to be challenged by other individuals, promoting increased aggression to maintain territories. Such levels of aggression—and levels of testosterone—diminish during the breeding season, when individuals are involved in parental activities (Gill et al., 2007). In our study, we would also expect decreased response of male White-bellied Wrens to conspecifics during the breeding season, but this did not occur. It is possible that conspecifics pose an additional threat to male White-bellied Wrens, such as the risk of extra-pair paternity, and thereby represent a greater threat compared to heterospecifics. We, however, did not assess the intensity of the responses, and there is a possibility that intensity of responses could vary with season, providing further support to the hypothesis of low aggression during parental activities. Further studies should aim at understanding the association between seasonality in testosterone levels, threat degree, and responses to better understand territorial behaviour of male White-bellied Wrens.

By comparison, our data suggest that female White-bellied Wrens do not discriminate heterospecific competitor signals in the same way that males do, but the response of female White-bellied Wrens to conspecifics varied with season. We determined a significantly higher territorial response of female White-bellied Wrens to conspecifics during the pre-breeding season, which could be influenced by the aggressive behaviour of their male partner at this stage of the breeding cycle. Such associations have been documented in Buff-breasted Wrens, Rufous-and-white Wrens and Banded Wrens, indicating an association between female and male responses, and not necessarily a link between female responses and the stimulus (Gill et al., 2007; Hall, Rittenbach, & Vehrencamp, 2015; Mennill & Vehrencamp, 2008). However, if that were the case we would expect females also to demonstrate high responsiveness to heterospecific songs, mirroring male responses. Males also maintained high territorial responsiveness to conspecific songs during the breeding seasons, whereas females did not. This suggests

that male behaviour did not influence female responses, at least during the breeding season. Our results are in line with the hypotheses that aggression has a detrimental effect on reproductive and parental behaviours (Rutkowska et al., 2005; Searcy, 1988), and that intrusion is more threatening early in the breeding season (when individuals are first establishing territories) than during the breeding season (when territories are already established; Gill et al., 2007).

Why do male White-bellied Wrens respond to simulated Happy Wren intruders? Although both species are insectivores and feed in low to mid-levels of the forest (Brewer, 2001; Howell & Webb, 1995), the size and shape of their beaks are highly different: male White-bellied Wrens weigh 9.6 g, while Happy Wrens are 14.4 g (Dunning, 2008). Thus, intensity of competition for food is probably low between the two species. In contrast, both species select bushes or thickets to build their nests (Brewer, 2001; Howell & Webb, 1995). Assuming that the number of suitable sites (bushes or thickets) to build a nest is limited, and the number of individuals is high in the study area (J. R. Sosa-López, personal observation, March 2014 to March 2015), then competition to secure breeding territories against members of another species may be high. Future research could explore resource competition between White-bellied Wrens and Happy Wrens.

Our study shows that male White-bellied Wrens discriminate between both conspecifics and an heterospecific species. We argue that such interactions could be due to competition for resources. We also determined sexual differentiation in response to White-bellied Wrens, and that male and female responses varied with season, supporting the hypotheses that aggression is a detrimental factor on reproductive and parental behaviours in birds and that intrusion is more threatening early in the breeding season (Gill et al., 2007; Rutkowska et al., 2005; Searcy, 1988). This study adds to our knowledge of interactions between distantly related species, providing new insights for the understanding of behavioural mechanisms structuring bird communities in the tropics (Jankowski et al., 2010).

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