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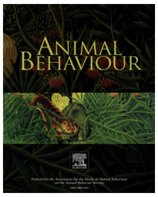

Interspecific vocal discrimination in Neotropical wrens: responses to congeneric signals in sympatry and allopatry

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When animals defend resources using territorial signals, they must distinguish between competitors and noncompetitors. Conspecific animals routinely compete for resources and regularly engage in aggressive signalling exchanges. Heterospecific animals may also compete for resources, and therefore animals may direct their aggression towards heterospecific as well as conspecific rivals. In both cases, animals should benefit by discriminating between nonthreatening individuals versus threatening conspecific and heterospecific competitors. Experience may play an important role in competitor discrimination; animals living in sympatry with heterospecific competitors may gain experience with heterospecific rivals, but animals living in allopatry will not. We investigated whether experience influences species discrimination between two congeneric Neotropical wrens (rufous-and-white wrens, *Thryophilus rufalbus*, and banded wrens, *Thryophilus pleurostictus*) that live in sympatry in some parts of their range and in allopatry in other parts of their range. We simulated the presence of male conspecific, congeneric and control intruders in the territories of rufous-and-white wrens at sites where they are sympatric or allopatric with banded wrens. If species discrimination is influenced by experience, we predicted that wrens would always respond strongly to conspecific songs, but that in sympatry, they would respond more strongly to the congeneric competitor than to the control songs. Conversely, we predicted that, in allopatry, wrens would show similarly low responses to congener and control songs. In contrast to our predictions, we found that rufous-and-white wrens discriminated between conspecific and heterospecific animals, but that this response did not differ in sympatry or allopatry, suggesting that experience with heterospecific competitors does not influence interspecific discrimination in this species. By contrasting the responses of sympatric and allopatric populations, we can better understand the effect of experience on interspecific discrimination and gain insight into the evolution of species discrimination signals.

Species discrimination is the identification and differentiation of conspecific animals from heterospecific animals (Bradbury & Vehrencamp, 2011). Misidentifying the species of a potential rival or a potential mate can have significant fitness consequences (Grether, 2011), and given the high cost of territorial displays, selection should promote species discrimination (Grether, Losin, Anderson, & Okamoto, 2009). Species discrimination may be innate, or shaped by experience (i.e. previous interactions with heterospecific rivals) or shaped by both genetics and experience. Experience with heterospecifics may allow animals to recognize competitors that they would not be able to identify in areas where heterospecifics are absent. In spite of the large body of research on species discrimination (Grether, 2011), there is no consensus on the importance of experience for interspecific discrimination between closely related competitor species.

Animals are understood to construct species-specific templates, whether they are learned or innate, which they use to distinguish conspecifics from heterospecifics (Bradbury & Vehrencamp, 2011; Hauber & Sherman, 2001). Many studies suggest that animals have an innate species template, which they expand or modify through learning (Hauber, Russo, & Sherman, 2001; Sandoval, Méndez, & Mennill, 2013). Other studies have suggested that there is a learned component to species discrimination, with animals learning the characteristics of conspecifics through experience with parents or other individuals (Catchpole, 1978; Grant & Grant, 1997; Irwin & Price, 1999; Lynch & Baker, 1990; Matyjasiak, 2004). Species discrimination may involve phenotype

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matching, where an individual learns the phenotype of parents or kin and then uses this template to discriminate between conspecifics and heterospecifics (Bradbury & Vehrencamp, 2011; Hauber & Sherman, 2001). This mechanism requires learning early in life but does not require prior experience with heterospecifics, since animals may respond appropriately to any species whose phenotype is different from their own (Kappeler, 2010). While phenotype matching is a potential mechanism for distinguishing conspecifics from heterospecifics, it does not allow for the differentiation of heterospecific competitors from heterospecific noncompetitors.

Most animals respond more intensely to the signals of conspecifics versus heterospecifics (e.g. frogs: Ryan & Rand, 1993; salamanders: Nishikawa, 1987; insects: Anderson & Grether, 2010; fish: Johnson & Peeke, 1972; birds: Baker, 1991). Conspecifics are expected to pose a greater threat because they compete for both resources and mates, whereas congeneric animals compete only for resources (Jankowski, Robinson, Levey, & Levey, 2010; Ord & Stamps, 2009). Although interspecific discrimination plays an important role in communication with conspecifics, it can also facilitate communication with heterospecifics, particularly when two or more species compete for access to similar resources such as foraging sites or nesting areas (Kodric-Brown & Brown, 1978; Ord & Stamps, 2009). Species that compete for resources on a regular basis should recognize each other as a potential threat. Red-cheeked salamanders, *Plethodon jordani*, for example, show similarly aggressive responses towards both conspecific and congeneric rivals (northern slimy salamanders, *Plethodon glutinosus*) in areas of high interspecific competition, but more aggressive responses towards conspecific than congeneric intruders in areas of low interspecific competition (Nishikawa, 1987). Likewise, mountain chickadees, *Poecile gambeli*, respond strongly to the songs of both conspecific and heterospecific rivals (black-capped chickadees, *Poecile atricapillus*), suggesting that both species' songs are equally threatening signals, whereas the socially dominant black-capped chickadees respond more strongly to conspecific songs (Grava, Grava, Didier, et al., 2012; Grava, Grava, & Otter, 2012). Species that never come into contact may not be able to discriminate between each other, as it may not be adaptive for species that have evolved in isolation to recognize one another (Grether et al., 2009).

Several studies have shown that birds have the ability to recognize closely related species as competitors, and this capacity appears to vary with experience. For example, blue-winged warblers, *Vermivora cyanoptera*, living in sympatry with golden-winged warblers, *Vermivora chrysoptera*, respond aggressively to both conspecific and congeneric songs, showing more aggression towards conspecific songs (Gill & Murray, 1972). In allopatry, however, blue-winged warblers only respond aggressively to conspecific songs (Gill & Murray, 1972). This result is consistent with the idea that animals learn to distinguish threatening from nonthreatening rivals when they live in sympatry. Conversely, white-eared ground-sparrows, *Melozone leucotis*, show stronger aggressive responses to conspecific songs versus congeneric Prevost's ground-sparrow, *Melozone biarcuatum*, songs regardless of whether they live in sympatry or in allopatry (Sandoval et al., 2013). This latter result is more consistent with the idea that conspecific discrimination does not require learning. By contrasting the behaviour of more animals in sympatry versus allopatry, we can gain insight into the importance of experience in species discrimination.

In this study, we investigated species discrimination in Neotropical wrens that live in zones of sympatry and allopatry in different parts of their ranges. Rufous-and-white wrens, *Thryophilus rufalbus*, and banded wrens, *Thryophilus pleurostictus*, are sister species (Mann et al., 2006) that nest primarily in bullhorn acacias, *Vachellia collinsii* (Joyce, 1993; Molles & Vehrencamp, 1999), and occupy similar foraging niches (Ahumada, 2001; Molles & Vehrencamp, 1999). In zones of sympatry, banded and rufous-and-white wren territories do not overlap but may be abutting, with rufous-and-white wrens inhabiting mature evergreen forests and banded wrens favouring dry scrub forest. The two species are thought to engage in aggressive interactions where their territories meet (Battiston, Wilson, Graham, Kovach, & Mennill, 2015). We expect that rufous-and-white wrens living in sympatry with banded wrens have experience interacting with banded wrens, whereas the ones living in allopatry do not.

We tested the hypothesis that species discrimination in rufous-and-white wrens is influenced by experience by presenting conspecific and heterospecific songs to rufous-and-white wrens in an area of sympatry and allopatry with banded wrens. If species discrimination is influenced by experience, we predicted that rufous-and-white wrens living in allopatry with banded wrens would show a low response to both the congeneric and control songs, since neither represents a competitive threat, and that they would show a high response to conspecific songs. Conversely, we predicted that rufous-and-white wrens living in sympatry with banded wrens would show a stronger response to the congeneric songs than to the control songs, because they do represent a competitive threat, and that they would show the highest response to conspecific songs. Alternatively, if species discrimination does not require experience to distinguish competitive from noncompetitive heterospecific individuals, we predicted that wrens' responses would not differ between sympatry and allopatry.

METHODS

General Field Methods

We conducted a playback experiment at two sites within the Guanacaste Conservation Area in northwestern Costa Rica: Sector Santa Rosa (10°40′N, 85°30′W) and Sector Rincón de la Vieja (10°40′N, 85°30′W). Santa Rosa is a lowland dry-forest habitat where rufous-and-white wrens and banded wrens live in sympatry (hereafter, the ‘sympatric population’), with the former species occupying the mature evergreen habitats (Mennill & Vehrencamp, 2005), and the latter species occupying adjacent, less mature habitats (Molles & Vehrencamp, 1999). Rincón de la Vieja is a mid-elevation rainforest habitat where the two species live in allopatry (hereafter, the ‘allopatric population’). We have never encountered banded wrens at this second site. These two locations are approximately 45 km apart and separated by unsuitable habitat, and we therefore do not expect dispersal to occur between them; analysis of 13 years of banding returns from our laboratory suggests that rufous-and-white wrens disperse short distances from their natal territories. In the sympatric population, we studied only rufous-and-white wren pairs whose territory was within 200 m of a banded wren territory to increase the chance that they would have had previous competitive interactions with the congeneric species. For all of these territories, we could hear banded wrens singing nearby, and we assume that the resident rufous-and-white wrens could hear the congeners as well.

We conducted playback experiments from early April to early June 2013, during the end of the dry season and the beginning of the rainy season. This time of year coincides with the end of the nonbreeding season, when birds defend territories, and the early part of the breeding season, when birds build nests and lay their first clutches of the year (Topp & Mennill, 2008). Birds in both the sympatric and allopatric populations were in similar breeding stages of defending territories and building nests when the playback experiment was conducted. At this time of year, both rufous-and-white wrens and banded wrens are responsive to playback (e.g. Mennill, 2006; Molles & Vehrencamp, 2001). All playback experiments occurred between 0630 and 1030 hours, a time of day when countersinging interactions are common for rufous-and-white wrens (Mennill & Vehrencamp, 2005).

We captured birds in mist nets and uniquely colour-banded each captured animal to facilitate identification in the field ($N = 63$ of our 92 subjects were banded). For birds that we were not able to band ($N = 29$; 24 from Rincón de la Vieja and 5 from Santa Rosa), we distinguished between birds based on their ongoing occupation of the same area (as in Battiston et al., 2015; Kovach, Hall, Vehrencamp, & Mennill, 2014; Mennill, 2006), and we discriminated between males and females based on their vocalizations (Mennill & Vehrencamp, 2005). We conducted playback experiments to 46 rufous-and-white wren pairs (92 birds): 24 pairs (48 birds) in the sympatric population and 22 pairs (44 birds) in the allopatric population.

Natural Competitive Interactions

We scanned field notes taken by our research team at Sector Santa Rosa over a 13-year period (2003–2015) to identify naturally occurring competitive interactions between rufous-and-white wrens and two heterospecifics: banded wrens and long-tailed manakins, *Chiroxiphia linearis* (a control species in our playback experiment). Although we did not specifically target data collection on these interactions, an anecdotal tally of these interactions provides context for interspecific aggression. Our notes yielded reports of aggressive interactions between rufous-and-white wrens and banded wrens on 11 occasions. Eight occasions were naturally occurring aggressive interactions when we observed rufous-and-white wrens and banded wrens producing aggressive calls (including the harsh chattering calls produced by both species, as well as the low-pitched ‘hoot’ notes produced by rufous-and-white wrens; see Mennill & Vehrencamp, 2005), aggressive chases and supplanting behaviour. Three occasions occurred in the course of separate playback experiments and these instances included aggressive calls, aggressive chases and physical contact between rufous-and-white wrens and banded wrens. We found zero observations of aggressive interaction between rufous-and-white wrens and long-tailed manakins.

Playback Technique

We used playback experiments to simulate the presence of three species of birds intruding into the territories of rufous-and-white wrens: (1) a male rufous-and-white wren (conspecific treatment); (2) a male banded wren (congeneric treatment) and (3) an unrelated songbird (control treatment). We chose long-tailed manakins as a control because they are sympatric with rufous-and-white wrens in both study locations (Garrigues & Dean, 2007), and because these frugivorous manakins are not ecological competitors with insectivorous wrens.

Each playback treatment consisted of 5 min of stimulus followed by a 5 min silent period. We did not begin the playback until the subject pair was silent for at least 1 min. A previous study of neighbour–stranger discrimination found that rufous-and-white wrens do not respond differently to conspecific versus heterospecific playback at the edge of their large territories (Battiston et al., 2015). Therefore we conducted all playback trials from a position near the centre of the subjects' territories. We observed the behaviour of the resident birds (both the male and the female) during the 5 min stimulus period and the 5 min silent period. To minimize carryover effects, each treatment was presented on separate, consecutive days, always from the same loudspeaker location and at the same time of day for each subject. To minimize order effects, we assigned the order of the three treatments according to a factorial design.

The playback apparatus was a camouflaged wireless speaker (Scorpion TX200, FOXPRO Inc.) hung in vegetation 1 m above the ground. All treatments were played back at 85 dB SPL as measured with an analogue sound level meter (RadioShack 33-4050; C-weighting, fast response) positioned 1 m in front of the speaker. Banded wrens produce louder songs than rufous-and-white wrens, and the 85 dB SPL amplitude we used for playbacks reflects the average amplitude between the values used in previous playbacks to the two species (80 dB SPL for rufous-and-white wrens and 90 dB SPL for banded wrens: Kovach et al., 2014; Mennill, 2006; Molles & Vehrencamp, 2001), thereby ensuring that amplitude was not a confounding factor.

An observer (K.G.H.) sat concealed in vegetation 15–20 m from the speaker and recorded all treatments using a shotgun microphone (Audiotechnica AT8015) and a solid-state digital recorder (Marantz PMD660). Flagging tape was placed 2 m on either side of the playback speaker to aid in estimating the distance between the responding birds and the simulated intruder (i.e. the loudspeaker). The observer quietly dictated the identity and the behaviour of both the resident male and female, including their location in relation to the speaker. Trials where neighbouring pairs responded to the playback were aborted and repeated at least 1 week later ($N = 2$ trials were repeated at a later date).

Playback Stimuli

We generated playback stimuli by isolating songs from recordings we collected in the Sector Santa Rosa study site over the preceding 11 years. We used recordings of male solo songs that we collected at locations ≥ 2 km away from the subjects' territories to ensure that all stimuli were unfamiliar to the subjects. Although rufous-and-white wrens are well known for their male–female vocal duets, we chose to focus on male solo songs in this experiment because male rufous-and-white wrens have higher song output than females (Mennill & Vehrencamp, 2005; Topp & Mennill, 2008) and respond more intensely to playback (Mennill, 2006; Mennill & Vehrencamp, 2008). The stimuli were prepared using Audition software (v.3.0; Adobe, San Jose, CA, U.S.A.). We selected one song from each source recording, choosing a song with a high signal-to-noise ratio (assessed visually based on the spectrograms). We filtered out background noise with an 800 Hz high-pass filter (800 Hz is less than the minimum frequency of all songs used as stimuli). We standardized song amplitude to -1 dB, so that all stimuli were broadcast at the same amplitude. The prepared song was repeated at a rate of one song every 10 s for a total of 5 min. This song rate falls in the natural range of singing behaviour for males of both study species (Mennill & Vehrencamp, 2005; Molles & Vehrencamp, 1999). All birds in each population received different wren and control playback stimuli to avoid pseudoreplication.

Measuring Subjects' Responses

In the laboratory, we used Syrinx-PC (J. Burt, Seattle, WA, U.S.A.) to visualize the audio recordings made during the playback trials, and we annotated all songs and duets of the focal pair as well as their behaviours as dictated by the observer. This process created a time-stamped record of all acoustic and behavioural measures. We then extracted the following response measures for each male and female subject: (1) distance of closest approach, (2) latency to approach within 5 m of the speaker, (3) number of songs initiated (the number of solo songs plus the number of duets where the subject sang the first contribution) and (4) number of duets created (the number of duets where the subject sang in response to its partner's song). Birds that did not approach within 5 m of the speaker were given a latency score of 800 s (i.e. the length of the trial plus 200 s). Birds that did not approach the playback area were given a distance of closest approach score of 25 m since it was unlikely that the bird could have been within that distance without the observer noticing. Excluding these trials from the analysis did not change the significance of the results. These response variables are commonly used to assess aggression and species discrimination in bird species (e.g. De Kort, Eldermire, Cramer, & Vehrencamp, 2009; Grava, Grava, & Otter, 2012; Kovach et al., 2014; Sprau, Roth, Amrhein, & Naguib, 2014).

Statistical Analysis

We analysed our data using generalized linear mixed models (GLMMs), which allowed us to account for non-normal data and include a random effect (Bolker et al., 2008). Our models included four main factors: (1) playback treatment (three levels: conspecific, heterospecific or control); (2) population (two levels: sympatric or allopatric); (3) sex of the focal bird (two levels: male or female); and (4) order in which the treatments were presented (three levels: first, second or third). Pair identity was included as a random factor since each pair received all three playback treatments. We used a Poisson error distribution with a log link function for the acoustic variables (songs initiated, duets created) and a Gamma distribution with a log link function for the behavioural variables (latency to approach within 5 m, distance of closest approach). GLMMs with a Poisson error distribution have been used in previous studies analysing social aggression with skewed count data, and Gamma distributions have been used for noncount data skewed to higher values (e.g. Hasegawa, Ligon, Giraudeau, Watanabe, & McGraw, 2014; Santos, Maia, & Macedo, 2009). We included all first-order interaction terms in our analyses. We ran post hoc pairwise comparisons for all the main effects and first-order interactions using a sequential Bonferroni correction, which increases P values (rather than decreasing the alpha value), to adjust for multiple comparisons; we report corrected P values for post hoc pairwise comparisons. Post hoc comparisons for the main effects are reported in the text and post hoc comparisons across the six groups are shown in Figs. 1 and 2 (see Results). All analyses were conducted using SPSS software (v.21; IBM, Chicago, IL, U.S.A.).

RESULTS

Overall, rufous-and-white wrens showed stronger responses to conspecific stimuli compared to congeneric stimuli and control stimuli, initiating more songs, performing more duets and approaching the loudspeakers more closely. Responses did not differ, however, between the sympatric and allopatric populations. Males consistently showed significantly stronger responses to stimuli than females. Below, we present results for each of our four response measures, providing results for the effects of treatment, population, sex and playback order in that sequence for all four response variables.

Distance of Closest Approach

Distance of closest approach differed significantly across experimental treatments (Table 1), with wrens approaching the speaker more closely for the conspecific treatment compared to the congeneric and control treatments (post hoc pairwise comparisons: conspecific versus congeneric: $t_{256} = 6.14$; conspecific versus control: $t_{256} = 7.77$, $P < 0.001$ for both), but approaching the congeneric playback more closely than the control playback ($t_{256} = 2.15$, $P = 0.032$; excludes the effect of population, with data pooled across the two populations). Importantly, the distance of closest approach for each treatment did not differ between the populations (Table 1, Fig. 1a).

The distance of closest approach varied between the sexes (Table 1), with males approaching more closely than females ($t_{256} = 8.54$, $P < 0.001$). The distance of closest approach varied across the treatments for males versus females (Table 1), with males approaching more closely than females for all three treatments (conspecific male versus female: $t_{256} = 6.31$; congeneric male versus female: $t_{256} = 5.04$; control male versus female: $t_{256} = 3.33$, $P < 0.01$ for all). The sex∗population interaction showed an overall effect (Table 1), with males in the allopatric population approaching more closely than males in the sympatric population ($t_{256} = 2.21$, $P = 0.03$). There was no difference between the females from each population ($t_{256} = 0.92$, $P = 0.36$).

Distance of closest approach did not vary with playback order (Table 1). The effect of playback order on distance of closest approach showed an overall effect of population (Table 1); however, the post hoc comparisons did not show any significant effects within the populations (overall tests: sympatric population: $F_{2,256} = 1.98$, $P = 0.14$; allopatric population: $F_{2,256} = 2.77$, $P = 0.06$).

Latency to Approach within 5 m

Latency to approach within 5 m of the playback speaker differed significantly across treatments (Table 1), with wrens approaching within 5 m sooner for the conspecific treatment versus the heterospecific treatments (post hoc pairwise comparisons: conspecific versus congeneric: $t_{256} = 7.45$; conspecific versus control: $t_{256} = 8.76$, $P < 0.001$ for both). There was no difference in the latency to approach within 5 m for the congeneric versus control treatments ($t_{256} = 1.42$, $P = 0.16$). The latency to approach within 5 m for each treatment differed between the populations (Table 1, Fig. 1b), with wrens in the sympatric population approaching within 5 m sooner than wrens in the allopatric population for the conspecific treatment (sympatric versus allopatric population: $t_{256} = 3.07$, $P = 0.002$). There was no difference between the populations in their responses to congeneric and control treatments (congeneric sympatric versus allopatric: $t_{256} = 1.00$, $P = 0.32$; control sympatric versus allopatric: $t_{256} = 0.02$, $P = 0.98$).

Males showed shorter latencies to approach within 5 m than did females ($t_{256} = 4.82$, $P < 0.001$; Table 1). There was also an effect of sex∗treatment (Table 1); for the conspecific treatment, males approached to within 5 m sooner than females ($t_{256} = 6.16$, $P < 0.001$), but there was no difference between the sexes in their responses to the heterospecific treatments (congeneric male versus female: $t_{256} = 1.75$, $P = 0.08$; control male versus female: $t_{256} = 0.19$, $P = 0.85$). The latency to approach within 5 m did not differ between the populations for either sex (Table 1).

There was no overall order effect for latency to approach within 5 m (Table 1), but there was a significant effect of population∗playback order (Table 1). Wrens in the sympatric population showed the shortest latency to approach within 5 m for the second playback versus the first and third (second versus first: $t_{256} = 2.29$, $P = 0.04$; second versus third: $t_{256} = 2.64$, $P = 0.03$). There was no significant difference for the latency to approach within 5 m between the first and third playback trials ($t_{256} = 0.36$, $P = 0.72$).

Number of Songs Initiated

The number of songs initiated (solo songs plus the first song in a duet) differed significantly across treatments (Table 1), with more songs being initiated during the conspecific treatment than during the heterospecific treatments (post hoc pairwise comparisons:

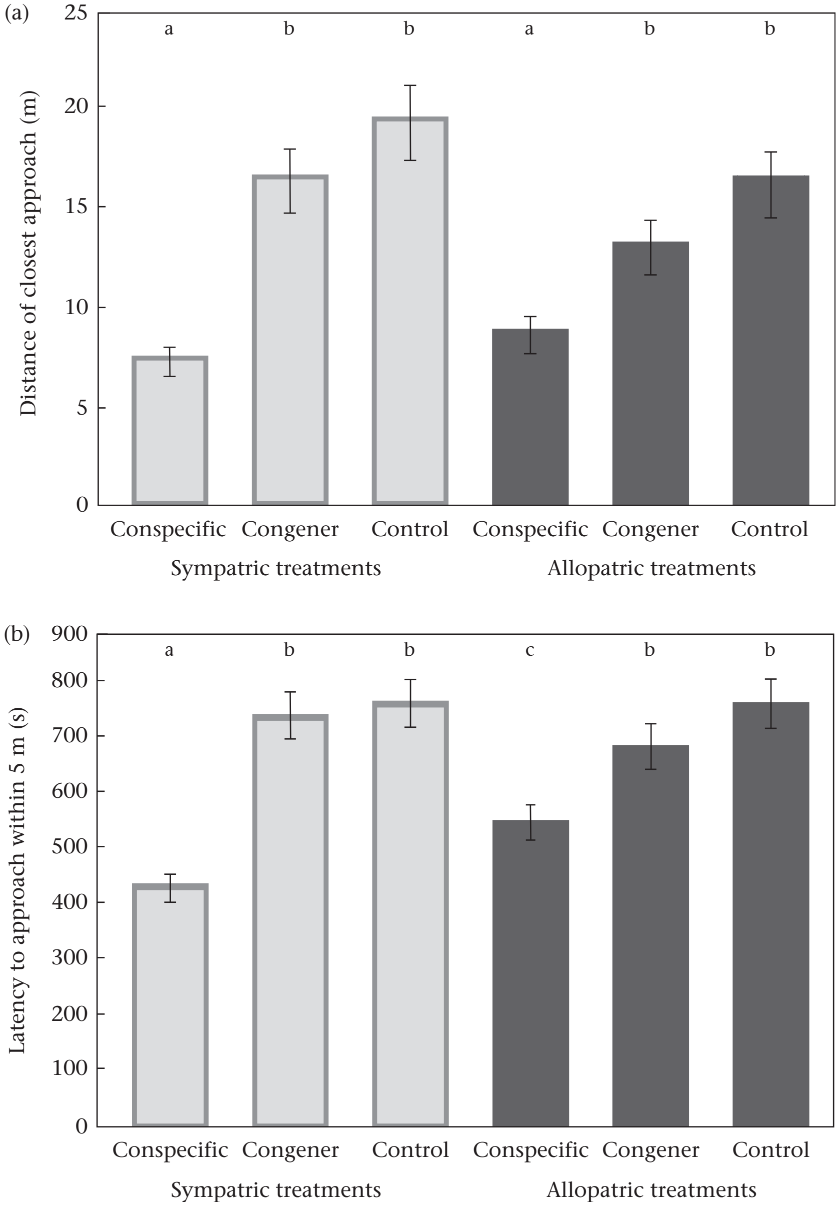

Figure 1. Behavioural response of rufous-and-white wrens to playback of male conspecific, congeneric and control songs in an area of sympatry and allopatry with banded wrens. (a) Distance of closest approach to the playback speaker. (b) Latency to approach within 5 m of the playback speaker. Different letters above bars indicate statistical significance. Graphs show means ± SE from treatment∗population post hoc pairwise comparison.

conspecific versus congeneric: $t_{256} = 10.81$, $P < 0.001$; conspecific versus control: $t_{256} = 10.8$, $P < 0.001$) and no difference in the number of songs initiated during the congeneric versus control treatments ($t_{256} = 0.23$, $P = 0.82$). There was a significant population∗treatment interaction (Table 1, Fig. 2a), whereby wrens in the sympatric population initiated significantly more songs in response to the conspecific treatment than wrens in the allopatric population ($t_{256} = 3.58$, $P < 0.001$). There was no difference between the populations in their response to the congeneric ($t_{256} = 0.75$, $P = 0.45$) and control ($t_{256} = 1.44$, $P = 0.15$) treatments.

Males initiated significantly more songs than females (Table 1) in response to all three playback treatments (conspecific male versus female: $t_{256} = 14.16$; congeneric male versus female: $t_{256} = 12.43$; control male versus female: $t_{256} = 11.57$, $P < 0.001$ for all). There was a significant sex∗population interaction, with females in the sympatric population initiating more songs than females in the allopatric population ($t_{256} = 3.55$, $P < 0.001$). Conversely, males in the allopatric population initiated more songs than males in the sympatric population ($t_{256} = 3.8$, $P = 0.002$).

The number of songs initiated differed with playback order (Table 1); birds initiated more songs for the first and third treatments compared to the second treatment (first versus second: $t_{256} = 4.01$, $P < 0.001$; third versus second: $t_{256} = 2.96$, $P = 0.007$). There was a significant playback order∗treatment interaction (Table 1), with wrens initiating more songs if the congener treatment was presented first or third versus second (first versus second: $t_{256} = 5.31$, $P < 0.001$; third versus second: $t_{256} = 3.08$, $P = 0.002$).

Number of Duets Created

The number of duets created (the number of songs a bird sang in response to its partner's songs) differed significantly across treatments (Table 1), with birds creating significantly more duets during

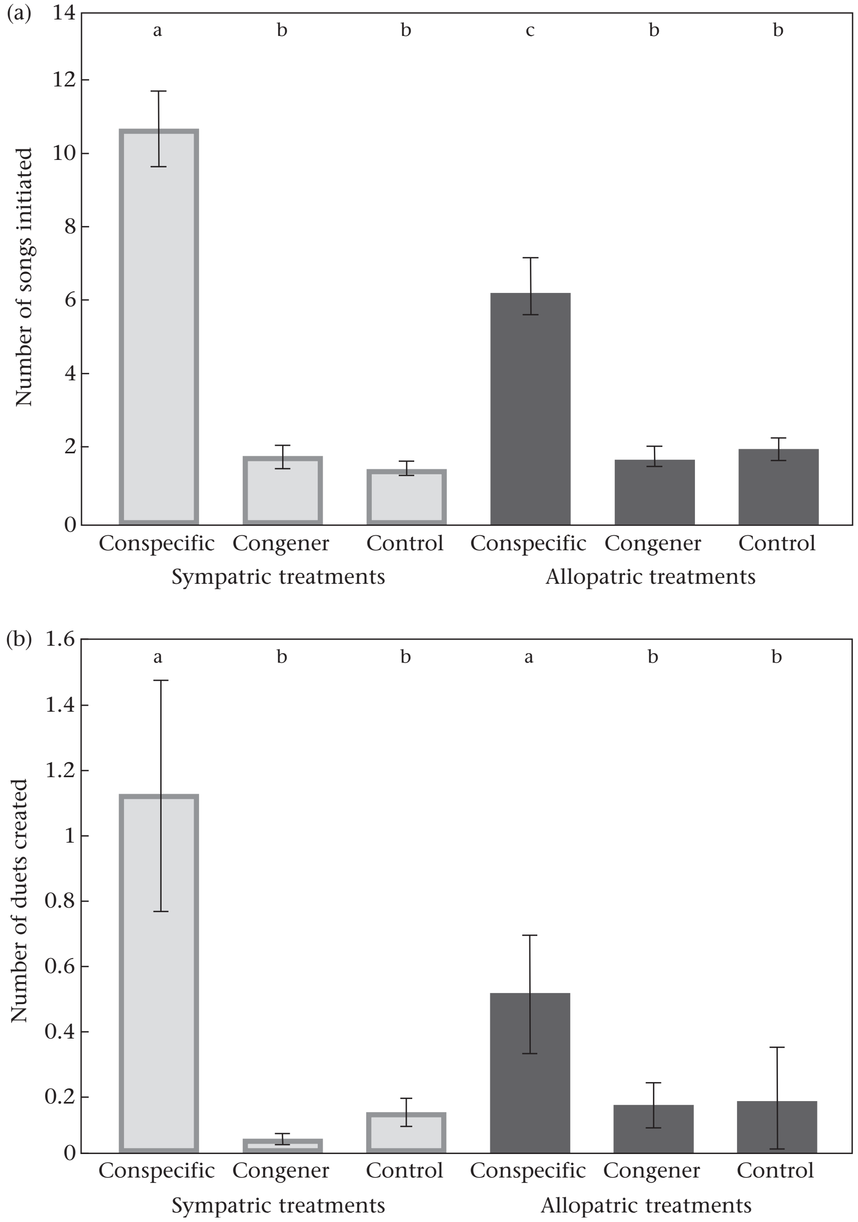

Figure 2. Acoustic response of rufous-and-white wrens to playback of male conspecific, congeneric and control songs in an area of sympatry and allopatry with banded wren. (a) Number of songs initiated (number of solos songs plus first song in a duet). (b) Number of duets created (song sung in response to a solo song). Different letters above bars indicate statistical significance. Graphs show means ± SE from treatment∗population post hoc pairwise comparison.

Table 1
Generalized linear mixed model results of the response of rufous-and-white wrens to playback simulating conspecific, congeneric and control intruders, with significant values shown in bold

	Distance of closest approach			Latency to approach within 5 m			Number of songs initiated			Number of duets created		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Treatment	42.7	2, 256	**<0.001**	48.6	2, 256	**<0.001**	138.9	2, 256	**<0.001**	37.7	2, 256	**<0.001**
Population	0.7	1, 256	0.4	1.0	1, 256	0.31	0.8	1, 256	0.37	0.5	1, 256	0.5
Sex	93.3	1, 256	**<0.001**	23.8	1, 256	**<0.001**	543.4	1, 256	**<0.001**	18.1	1, 256	**<0.001**
Order	0.7	2, 256	0.49	0.3	2, 256	0.71	9.0	2, 256	**<0.001**	5.1	2, 256	**0.007**
Population∗treatment	2.8	2, 256	0.065	5.9	2, 256	**<0.001**	24.6	2, 256	**<0.001**	6.4	2, 256	**0.002**
Sex∗treatment	4.3	2, 256	**0.015**	608.1	2, 256	**0.003**	11.2	2, 256	**<0.001**	1.3	2, 256	0.27
Treatment∗order	1.5	4, 256	0.21	0.8	4, 256	0.54	13.5	4, 256	**<0.001**	1.5	4, 256	0.22
Sex∗population	6.4	1, 256	**0.012**	1.2	1, 256	0.27	55.8	1, 256	**<0.001**	0.9	1, 256	0.35
Population∗order	4.3	2, 256	**0.015**	11.0	2, 256	**<0.001**	0.8	2, 256	0.44	5.6	2, 256	**0.004**
Sex∗order	1.3	2, 256	0.27	0.5	2, 256	0.59	4.4	2, 256	**0.013**	1.5	2, 256	0.22

the conspecific treatment versus the heterospecific treatments (post hoc pairwise comparisons: conspecific versus congeneric: $t_{256} = 3.83$, $P < 0.001$; conspecific versus control: $t_{256} = 3.7$, $P = 0.001$), but creating a similar number of duets in response to congeneric versus control treatments ($t_{256} = 1.69$, $P = 0.09$). These results showed a significant population∗treatment interaction (Table 1), but this was likely driven by the strong treatment effect within a population because the post hoc comparison showed no significant patterns, with wrens in both populations creating a similar number of duets in response to all treatments (Fig. 2b).

The number of duets created by playback subjects varied between the sexes (Table 1), with females creating significantly more duets than males ($t_{256} = 3.07$, $P = 0.002$). In addition, females created significantly more duets than males for the conspecific ($t_{256} = 2.68$, $P = 0.008$) and congeneric ($t_{256} = 2.18$, $P = 0.03$) treatments. Males and females created a similarly low number of duets for the control treatment ($t_{256} = 1.76$, $P = 0.08$).

The number of duets created varied with playback order (Table 1), with birds creating more duets in response to the first playback compared to the second ($t_{256} = 2.51$, $P = 0.01$), with the third playback eliciting an intermediate response. In addition, the results showed a significant population∗order interaction (Table 1); in the allopatric population, birds created the greatest number of duets for the first playback versus the second ($t_{256} = 2.56$, $P < 0.03$), with the third playback eliciting an intermediate response.

DISCUSSION

We quantified the responses of rufous-and-white wrens to conspecific and congeneric playback in two populations, one living in sympatry with banded wrens and one living in allopatry, to study the influence of experience on species discrimination. Our results demonstrate that rufous-and-white wrens discriminate between the songs of conspecific and heterospecific rivals, but that this response does not differ between areas of sympatry versus allopatry. Rufous-and-white wrens in both populations showed intense responses towards conspecific playback and much weaker responses to both the congeneric and control playbacks. For the distance of closest approach, rufous-and-white wrens showed an intermediate response to the congeneric playback versus the conspecific and control, demonstrating that rufous-and-white wrens distinguish between congeneric rivals versus control stimuli. However, since this is the only instance of a significant difference in response to congeneric and control stimuli, it should be interpreted cautiously. Nevertheless, we found no differences in responses to congeneric rivals between the sympatric versus allopatric populations, and these results therefore provide no evidence that experience with sympatric congeners influences interspecific discrimination in rufous-and-white wrens.

Consistent with many previous studies, rufous-and-white wrens displayed more intense responses to conspecific songs than heterospecific songs (e.g. Baker, 1991; Catchpole, 1978; Grava, Grava, & Otter, 2012; Martin & Martin, 2001; Seddon & Tobias, 2010). This result held true for both sexes, indicating that males and females both use song to distinguish conspecific animals. In contrast to our predictions, however, wrens displayed very little aggression in response to playback of a congeneric ecological competitor (banded wrens) in both the sympatric and allopatric populations. We expected wrens in our allopatric population to show weak responses to the congeneric treatment because they do not interact with banded wrens and thus should not perceive them as rivals for shared resources. However, we predicted a stronger response to the congeneric treatment in the sympatric population where the two species interact and compete for nest sites. We did find that rufous-and-white wrens approached the banded wren stimulus more closely than the control stimulus, suggesting that they distinguished between congeners and noncompetitors, but this pattern did not differ between the sympatric and allopatric populations.

Studies investigating species discrimination in warblers (Brambilla, Janni, Guidali, & Sorace, 2008) and ground-sparrows (Sandoval et al., 2013) found that prior experience was not necessary for animals to discriminate between competitors. Males of two subspecies of Moltoni's warblers, *Sylvia cantillans*, for example, showed a strong response to playbacks of their own subspecies and a weak response to playbacks of the other subspecies in both sympatry and allopatry (Brambilla et al., 2008). These studies are consistent with our findings, where experience did not seem to influence species discrimination in rufous-and-white wrens. By contrast, other studies have found differing responses in areas of sympatry and allopatry. For example, indigo buntings, *Passerina cyanea*, and lazuli buntings, *Passerina amoena*, responded similarly to conspecific songs in sympatry and allopatry but more strongly to heterospecific songs in the sympatric population than in the allopatric population (Baker, 1991).

Our results suggest that familiarity arising from previous experience with the congener is not necessary for species discrimination. Rufous-and-white wrens are still able to discriminate conspecifics from heterospecifics without previous experience with the other species in our allopatric population. This suggests that the discrimination ability is either innate or guided by phenotype matching. Phenotype matching is a mechanism of species discrimination that does not require prior experience with the heterospecific animals; instead an individual uses the learned template of their parents or kin to discriminate between conspecifics and heterospecifics (Hauber & Sherman, 2001; Irwin & Price, 1999). Our results are consistent with this idea. If rufous-and-white wrens learn to distinguish conspecific songs from all other songs, we would expect them to respond similarly to songs of congeners and other heterospecifics, whether or not they live in sympatry or allopatry. Rufous-and-white wrens recognize conspecific animals as competitors and respond aggressively, but they show little aggression in response to the songs of species that appear different from their own.

Another possible explanation for the low level of aggressive response by rufous-and-white wrens towards banded wren songs is that that they may not perceive the congeneric species as a threat. Note, however, that response intensity might vary with each individual's experience with the congeneric species. A rufous-and-white wren that has had numerous competitive interactions with banded wrens may respond more aggressively to the congeneric playback than one that has rarely interacted aggressively with banded wrens. Although we have observed aggressive interactions between rufous-and-white and banded wrens, these may be rare occurrences, and perhaps these congeners are not threatening territorial rivals. Furthermore, the two species may differ in their aggressiveness towards one another, causing their response to congeneric signals to vary. Asymmetry in aggressive responses to conspecifics and congenerics has been found in previous studies (see Jankowski et al., 2010; Martin & Martin, 2001; Robinson & Terborgh, 1995). For example, two species of chickadees show just such a relationship: black-capped chickadees showed stronger responses to conspecific stimuli and little response to heterospecific stimuli, whereas mountain chickadees responded strongly to both stimulus types (Grava, Grava, & Otter, 2012), suggesting that they are equally threatening to this species. These two species use similar resources, and the authors suggested that they are competitors, but that black-capped chickadees are the socially dominant species (Grava, Grava, Didier, et al., 2012). The reciprocal playbacks to banded wrens would aid in understanding the competitive relationship between the two wren species we studied here. If these two species have a dominant/subordinate relationship with rufous-and-white wrens being the dominant species (rufous-and-white wrens are larger than banded wrens; Brewer, 2001), we would expect banded wrens to respond more similarly to conspecific and congeneric stimuli. Investigating this type of relationship is important to our understanding of how competitive species of birds may adapt if their distributions are altered due to changing environments, which may force the birds currently living in allopatry into sympatry (see Jankowski et al., 2010; Toms, 2013).

Although we were unable to detect differences in how rufous-and-white wrens responded to congeneric banded wrens in zones of sympatry and allopatry, we did find differences in response to playback between the two populations. In particular, in response to the conspecific treatment, wrens in the sympatric population initiated more songs and approached within 5 m of the speaker more quickly than wrens in the allopatric population. Playback stimuli for both populations were composed of songs from the sympatric population (i.e. Sector Santa Rosa). We chose to present only stimuli made from recordings of the sympatric population because the congeneric banded wren songs could only be recorded at the sympatric site, and thus we ensured that birds in both populations received the same playback stimuli. These two populations are 45 km apart, and therefore birds from these two locations may exhibit different dialects; ongoing studies from our research group are quantifying these differences. The existence of local dialects could be responsible for the stronger vocal and behavioural responses to conspecific treatments in the sympatric population. In other songbirds, territorial males respond more strongly to songs from a conspecific local dialect than to a conspecific foreign dialect (e.g. Nicholls, 2007; Reichard, 2014; Searcy, Nowicki, & Hughes, 1997).

Interestingly, we found a sex difference in how birds responded to conspecific stimuli in our two populations. Males in the allopatric population initiated more songs and approached the speaker more closely than males in the sympatric population. Females in the sympatric population, however, initiated more songs than females in the allopatric population. The response of males is similar to a widespread pattern that males respond more strongly to unfamiliar stimuli versus familiar stimuli, most commonly found in neighbour–stranger discrimination studies (Temeles, 1994). Our results do however contradict the studies previously mentioned where males respond more strongly to local versus foreign dialects. The response of females is consistent with the stronger response to local dialects seen in other male songbirds (Nicholls, 2007; Reichard, 2014; Searcy et al., 1997). In a pattern that parallels our study, captive oestradiol-injected female song sparrows, *Melospiza melodia* (Searcy, Nowicki, Hughes, & Peters, 2002), great tits, *Parus major* (Baker, McGregor, & Krebs, 1987), and rufous-collared sparrows, *Zonotrichia capensis* (Danner et al., 2011), showed more copulation solicitation displays to local male songs than to foreign male songs. However, this is the first study to find female differences in response to male local and foreign songs in the wild without injection of oestradiol. Note, however, that the studies mentioned above were testing female preferences for male song, whereas our study aimed to test how females respond to a male intruder. Another possible explanation is that in order to defend their territory, females in the sympatric population increased their song output to compensate for their mates' low singing rate. Further work is required to understand this response, including reciprocal playback of songs from our allopatric population to females in our sympatric population.

Rufous-and-white wrens and banded wrens use similar foraging sites and nest sites in bullhorn acacia trees, whose resident ants offer protection from predators (Haemig, 2001). Nest sites are crucial for birds to breed successfully, and therefore they should be aggressively defended. To minimize interference with nesting and reproductive behaviour, we conducted playback experiments at least 15 m away from a tree containing a nest or that had been previously used as a nesting site. Conducting playback near nesting trees might have elicited stronger responses to congeneric stimuli in our experiment. The use of visual signals might also increase the strength of the response by providing a close-range signal for the presence of a competitor in the territory. Future studies should consider the addition of a visual model to elicit a stronger response to playbacks while also testing the importance of visual and acoustic signals for species discrimination (e.g. Uy, Moyle, & Filardi, 2009; Uy & Safran, 2013). Future studies should also investigate the importance of the types of signals birds use for species discrimination by coupling playback experiments with visual models. Likewise, reciprocal playback experiments directed at the competitor species, banded wrens, would provide more insight into the relationship between these two species and how they compete for resources. Investigating ecological interactions between competitor species and how they coexist is important for understanding how they will react to changing environmental conditions and how species discrimination signals have evolved.

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