

ASYMMETRIC RESPONSE TO HETEROSPECIFIC SONGS IN TWO SYMPATRIC WRENS (TROGLODYTIDAE) IN ARGENTINA: HOUSE WREN (*TROGLODYTES AEDON*) AND MOUNTAIN WREN (*T. SOLSTITIALIS*)

Paul R. Martin¹ & Robert C. Dobbs²

¹Department of Biology, Queen's University, Kingston, ON K7L3N6, Canada.

²Louisiana Department of Wildlife and Fisheries, Coastal and Nongame Resources Division, 102 Magnate Drive, Suite 201, Lafayette, LA 70508 USA. *E-mail*: pm45@queensu.ca

Resumen. – Respuesta asimétrica a cantos heterospecíficos en dos especies simpátricas de ratona (Troglodytidae) en Argentina: Ratona Común (*Troglodytes aedon*) y Ratona Ceja Blanca (*T. solstitialis*). – Las interacciones comportamentales entre especies estrechamente emparentadas suelen ser asimétricas, siendo una especie dominante sobre la otra. Aquí estudiamos las interacciones comportamentales asociadas al canto entre dos especies del género *Troglodytes* que coexisten en bosques montanos húmedos del noroeste de la Argentina: Ratona Común (*T. aedon*) y Ratona Ceja Blanca (*T. solstitialis*). Llevamos a cabo experimentos de playback recíprocos, con machos territoriales de ambas especies durante la época reproductiva, para evaluar su respuesta al canto de la especie opuesta. *Troglodytes aedon* vocalizó más y se acercó más a la fuente de playback en respuesta a cantos de *T. solstitialis* que al playback control. *Troglodytes aedon* también vocalizó más en respuesta a playback de *T. solstitialis* que en respuesta al playback de conspecificos, mientras que la mínima distancia de acercamiento no difirió de manera significativa. En contraste, *T. solstitialis* vocalizó menos y se alejó de la fuente de playback durante playbacks de cantos de *T. aedon* y control, comparado con el período pre-playback. Estas respuestas difieren de las observadas luego del playback de cantos de conspecificos, durante los cuales *T. solstitialis* vocalizó más y se acercó más a la fuente de playback comparado con control. Nuestros experimentos sugieren que *T. aedon* es agresiva y dominante sobre *T. solstitialis*, ocupando áreas abiertas grandes a lo largo de gradientes de disturbio de hábitat. Al contrario, *T. solstitialis* ocupa pequeños claros de bosque y bordes y aparenta evitar interactuar con *T. aedon*. Nuestros resultados constituyen un ejemplo de interacciones comportamentales asimétricas entre especies emparentadas que segregan a lo largo de gradientes de hábitats tropicales.

Abstract. – Behavioral interactions among closely-related species are often asymmetric, with one species socially dominant over the other. Here we test for response to congeneric songs between two sympatric species of *Troglodytes* wrens, House Wren, *T. aedon*, and Mountain Wren, *T. solstitialis*, which coexist in humid montane Andean forest in northwestern Argentina. We used reciprocal song playback experiments presented to territorial males of each species during the breeding season to assess their response to the opposite species. *Troglodytes aedon* sang more and approached the playback speaker closer in response to our broadcast of *T. solstitialis* songs than in response to control songs. *Troglodytes aedon* also sang more in response to *T. solstitialis* playback than in response to conspecific playback, while the minimum distance of approach did not differ significantly. In contrast, *T. solstitialis* sang less and were further from the speaker during both *T. aedon* and control periods relative to the minute preceding our experiments. These responses differed from responses to conspecific playback, where *T. solstitialis* sang more and approached the speaker closer in relation to controls. Our experiments suggest that *T. aedon* is aggressive to and dominant over *T. solstitialis*, occupying larger open areas along a gradient

of habitat disturbance. In contrast, *T. solstitialis* occupies small forest gaps and edges, and appears to avoid interactions with *T. aedon*. Our results provide an example of asymmetric, behavioral interactions among closely-related species that segregate along a habitat gradient in the tropics. *Accepted 21 November 2014.*

Key words: House Wren, *Troglodytes aedon*, Mountain Wren, *Troglodytes solstitialis*, aggressive interactions, asymmetric interactions, interference competition, interspecific interactions, Troglodytidae.

INTRODUCTION

Closely-related species that coexist in nature often interact aggressively with each other (Peiman & Robinson 2010). These interactions are commonly asymmetric, with one species behaviorally dominant to the other and able to exclude, supplant, or displace the subordinate from preferred resources (Morse 1974, Robinson & Terborgh 1995; Martin & Martin 2001a, 2001b; Freshwater *et al.* 2014, Martin & Ghalambor 2014). Asymmetric interactions among species may be an important proximate cause of habitat and resource partitioning among closely-related species (Rosenzweig 1981, Orians 2000, Peiman & Robinson 2010), in particular in diverse tropical environments (Wolf *et al.* 1976, Feinsinger & Colwell 1978, Gill & Wolf 1978, Robertson & Gaines 1986, Robinson & Terborgh 1995, Jankowski *et al.* 2010). For example, studies of birds suggest that many of the closely-related species that occupy different habitats within a community in Amazonian Peru interact aggressively and asymmetrically (Robinson & Terborgh 1995). Additionally, a recent study of species segregation along a tropical elevational gradient suggested that closely-related thrushes (*Catharus*) and wrens (*Henicorbina*) interact aggressively (both genera) and asymmetrically (at least in *Catharus*), and that these interactions may influence how habitats are partitioned along the gradient (Jankowski *et al.* 2010). Collectively, these studies suggest that aggressive and competitive interactions among ecologically-similar species may have a greater and more widespread influence on the

distributions of species than is presently recognized.

Here we examine interspecific interactions between two closely-related species of wrens in the genus *Troglodytes* (Troglodytidae: *T. solstitialis* and *T. aedon*, the latter sometimes treated as *T. musculus*; Martínez Gómez *et al.* 2005) that coexist in montane Andean forest in northwestern Argentina. The Mountain Wren (*Troglodytes solstitialis*) is a small (11.8 g) wren that breeds from 1700–3500 m a.s.l. along the Andes mountains, from western Venezuela south to northwestern Argentina, where it descends to 700 m (Ridgely & Tudor 1989, Fjeldså & Krabbe 1990, Brewer 2001, Hilty 2003, del Hoyo *et al.* 2005). On our study sites in northwestern Argentina, this species nests in natural cavities in the canopy and subcanopy of humid montane forests (nest height: mean \pm SE = 12.1 \pm 1.6 m; range 2.0–20.0 m; N = 15 nests; Auer *et al.* 2007) and defends territories around tree fall and other small gaps and edges in mature forest (authors, pers. observ.). Mountain Wrens forage primarily in mid-levels to the sub-canopy (foraging height: mean \pm SD = 15.2 \pm 3.01 m; range 12–22 m; N = 10 individuals; authors, pers. observ.) by creeping along trunks and limbs and searching vine tangles, epiphytes, and bark surfaces, presumably for invertebrates (Ridgely & Tudor 1989, Brewer 2001, Hilty 2003, authors, pers. observ.). The House Wren (*Troglodytes aedon*) is widespread throughout the Americas, breeding from southern Canada to Tierra del Fuego in southern South America, from sea level to a maximum of 4500 m elevation (Ridgely &

Tudor 1989, Fjelds  & Krabbe 1990, Johnson 1998, Brewer 2001). South and Central American populations are small (12 g) and feed perhaps exclusively on invertebrates (Brewer 2001, del Hoyo *et al.* 2005). On our study sites in northwestern Argentina, *T. aedon* occupies larger forest gaps and more open habitats than *T. solstitialis* (fewer trees, more open canopy), nesting in natural and man-made cavities lower to the ground (nest height: mean \pm SE = 4.3 ± 1.0 m; range 1.0–17.0 m; N = 18 nests; Auer *et al.* 2007). House Wrens on our study sites typically forage at lower levels of forest edge and disturbed areas (foraging height: mean \pm SD = 4.45 ± 2.67 m; range 2–10 m; N = 10 individuals) by searching foliage and bark surfaces (authors pers. observ.). While *T. solstitialis* and *T. aedon* segregate their distributions along a gradient of habitat disturbance, both species coexist and overlap breeding territories in some areas of our study sites. The two species also overlap their breeding seasons, nesting from early October through to mid-late December (Auer *et al.* 2007, authors pers. observ.). In addition, we have previously observed heterospecific counter-singing between these two species on overlapping territories, suggesting that the two species may interact. The two species sing distinct songs (Figs 1A, B); *T. aedon* songs are lower in frequency and sound similar to bubbling, gurgling and chattering in comparison to *T. solstitialis* songs, which are higher pitched, thin and tinkling (Hilty 2003; Fig. 1).

In this study, we used playback experiments of the songs of *T. aedon*, *T. solstitialis*, and *Thraupis sayaca* (Sayaca Tanager, Thraupidae; negative control) to address two questions: (1) Do *T. aedon* and *T. solstitialis* respond to the opposite species' songs on breeding territories in northwest Argentina? (2) If these species respond to each other's songs, do their responses to the opposite species' songs differ from their response to conspecific songs? We selected *Thraupis sayaca* as a negative control

because this species is distantly related to Troglodytidae, commonly breeds on our study plots, regularly overlaps territories with both focal species of *Troglodytes*, and we have not observed any interactions between *Thraupis* and *Troglodytes*. *Thraupis sayaca* is a mid-sized tanager (32 g) that builds an open-cup nest in thick foliage and usually forages in the upper foliage of trees, eating primarily fruit, but also other plant materials and invertebrates (Isler & Isler 1987). *Thraupis sayaca* songs are a series of high pitched, squeaky notes that include ascending and descending slurs (Fig. 1C), distinct from *T. aedon* songs, but with some similar qualities (frequency and some syllables) to *T. solstitialis* songs (Fig. 1).

METHODS

Study site. We conducted playback experiments in humid montane "Yungas" forest on the east slope of the Andes in Parque Nacional El Rey in Salta Province, Argentina (24°42'S, 64°38'W). For a more detailed description of the study site, habitat, and climate, see Auer *et al.* (2007). We conducted our experiments on study plots between 1000 and 1700 m a.s.l..

Focal males. We presented song playback experiments to 12 focal male *T. aedon* and 12 focal male *T. solstitialis*. We distinguished focal males from females prior to experiments by their singing behavior, and then followed these focal males for the entire playback experiment. We were unable to simultaneously follow females, and thus we have no detailed information on female response to our stimuli. In addition, many pairs had active nests, and some females were incubating eggs or brooding nestlings during our playback experiments.

Our experiments were conducted during the breeding season of most bird species on our study plots, including *Troglodytes* (Auer *et al.* 2007). All focal males were paired, but we

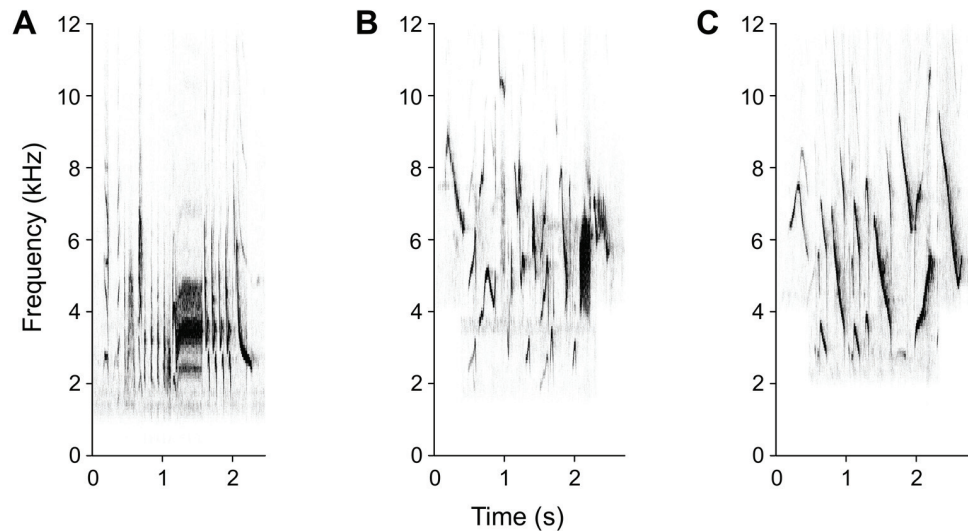


FIG. 1. Songs of male (A) House Wren (*Troglodytes aedon*), (B) Mountain Wren (*T. solstitialis*), and (C) Sayaca Tanager (*Thraupis sayaca*, negative control), all recorded from our field site in Parque Nacional El Rey, Salta Province, Argentina.

did not know their breeding stage. Some experiments occurred in the vicinity of heterospecific *Troglodytes*, and thus our focal males likely included males that had previous experience with heterospecific wrens. We did not map territories and thus do not know the degree of territory overlap between the two *Troglodytes* species, nor do we have precise values for the proportion of birds that overlapped or abutted territories with the other species. We note that focal birds may also have interacted with heterospecific wrens as birds dispersed in search of territories, even if their territory was not close to heterospecific wrens at the time of playback experiments. While we are certain that some of our focal birds had experience with the opposite *Troglodytes* species, most or even all of our birds may have had experience as well.

Playback stimuli. We recorded the natural songs of *T. aedon*, *T. solstitialis*, and *Thraupis sayaca* from 6 different territorial males for each spe-

cies on our study sites in October and November 1997 (during the breeding season for all three species; Auer *et al.* 2007; authors pers. observ.) using a ME-66 short shotgun microphone, SME-BA3 pre-amplifier, and a Sony TCM-5000 high frequency tape recorder (all from Saul Mineroff Electronics, Elmont, New York, USA). All focal males that we recorded were paired, but we did not know their breeding stage. Examples of songs of each species are provided in Figure 1. To create playback stimuli, we repeated songs at equal intervals and adjusted sound levels for songs so that levels were equal across species and stimuli. Each playback stimulus contained one repeated song of one individual male of each species (*Troglodytes aedon*, *T. solstitialis*, and *Thraupis sayaca*). Playback stimuli reflected natural song rates from 1-min recordings of focal males during the breeding season. Natural song rates based on field observations at our study site (N = number of individual males): *T. aedon* = 6 songs/min (N = 5), *T. solstitialis* =

7 songs/min ($N = 5$), *Thraupis sayaca* = 5 songs/min ($N = 5$).

We note that our playback design represents a simplified presentation of songs to territorial males. Our focal species may alter their song types, rates, amplitude, or other behaviors in natural interactions with heterospecifics, and our song playback design would have captured none of this detail. Nonetheless, in the absence of detailed information on the singing behaviors of these two species in interactions with each other, we used a simplified song presentation in our experiments. We also note that we did not know the context for the songs presented in our playback experiments. For example, the songs that we recorded may have been directed at other males, females, heterospecifics, or any combination of possible receivers. Thus, we do not know if the songs that we used as stimuli represent songs that would normally be sung by a male intruding onto a territory. Nonetheless, the songs that we broadcast would simulate a male intruding onto a territory, but possibly singing songs not typically used in this context.

Playback design. Song playback design followed Martin *et al.* (1996). Each experiment lasted 11 minutes during which one observer (RCD) followed the focal male and dictated the position of the male relative to the speaker and verbally noted all songs sung by the male into a portable recorder. The first minute of the experiment was a pre-stimulus control that allowed us to control for the location and behavior of the focal males before the experiment began. The second minute consisted of one minute of songs of the first treatment (control, conspecific or heterospecific wren; the order was block-randomized). We followed the first treatment with one minute of post-stimulus during which all focal behaviors were recorded. We then allowed two minutes of break before the second stimulus was

broadcast to allow the bird to resume normal behaviors. Following the break, we broadcast the second treatment, followed again by one minute of post-stimulus recording and a two-minute break. We then completed the experiment with the final treatment followed by one minute of post-stimulus, for a total of 11 minutes for the experiment.

We block-randomized treatment order such that control, conspecific, and heterospecific wren songs were equally represented in the first, second and third treatment positions, and all possible orders were represented in equal frequency across experiments. Thus, any order effects would be represented equally across treatments and would not cause disproportionate bias in our results. In cases where the focal male could not be followed through the 11-minute experiment, we abandoned the experiment and moved to another focal male. We abandoned experiments in cases where the focal male was chased by another bird during the experiment. We did not identify any cases where our focal species chased each other; however, we could not identify both participants in many chases.

Field experiments. We conducted song playback experiments between the 07:00–13:00 h ART from 28 November to 7 December 1997. For experiments, we placed the playback speaker inside the territories of focal birds, as judged by their movements prior to our experiments. We did not map the territories of focal birds, and thus we do not have precise measures of where the speaker was placed relative to the center or edge of the territories. We used the same amplitude across all of our trials, and chose our playback amplitude to match the amplitude of singing wrens on our study sites.

Behavioral variables in the field. *Troglodytes* wrens typically respond to conspecific territorial intrusions by moving towards the intruder in an attack and by singing (e.g., Johnson 1998).

Thus, we measured both approach to the playback speaker and song rates of focal territorial males during our experiments. We estimated the horizontal distance of the focal male to the playback speaker by eye, using measured flags positioned at 5 m and 10 m distance from the speaker to assist our distance estimations.

Behavioral variables for analysis. For our statistical analyses, we calculated two variables for each treatment: (1) approach towards the playback speaker (meters), and (2) change in song rate (songs per minute). (1) Approach towards the playback speaker was calculated as: the minimum horizontal distance of the focal bird to the playback speaker during the minute of song playback and the minute following song playback (post-stimulus) - minimum horizontal distance of the focal bird to the playback speaker during the minute preceding the broadcast of any treatments (pre-stimulus). A value of zero indicates that the focal bird did not approach or move away from the playback speaker in response to our treatment. (2) Change in song rate (songs per minute) was calculated as the average song rate prior to the experiment, subtracted from the song rate during the minute of song stimulus and the minute following: [the number of songs sung during the minute of song playback + the number of songs sung during the minute following song playback (post-stimulus)]/2 - the number of songs sung during the minute preceding the broadcast of any treatments (pre-stimulus). A value of zero indicates that the focal bird did not change its song rate in response to our treatment.

We provide a second analysis using raw data in place of changes relative to pre-stimulus measures to address the possibility that our calculated measures obscure some of our results. For these second analyses, we calculated minimum distance from speaker (m) as the minimum horizontal distance of the focal

bird to the playback speaker during the minute of song playback and the minute following song playback (post-stimulus), and song rate as the number of songs sung during the minute of song playback + the number of songs sung during the minute following song playback (post-stimulus). We compared these results to our pre-stimulus measures of minimum distance from speaker [minimum horizontal distance of the focal bird to the playback speaker during the minute preceding the broadcast of any treatments (pre-stimulus)] and song rate [the number of songs sung during the minute preceding the broadcast of any treatments (pre-stimulus) \times 2 (to correspond to the 2 minute duration of the other stimulus periods)].

Statistical analyses. We ran our statistical analyses in R (R Core Team 2014) using the nlme library (Pinheiro *et al.* 2014), following Zuur *et al.* (2009: Chapter 5). We ran 4 different analyses: one analysis for each variable (minimum approach to speaker, change in song rates) for each of the two species (*T. aedon*, *T. solstitialis*). For each analysis, we ran two models: (1) a linear mixed effects (lme) model with approach to speaker or song rate as the response variable, treatment as the predictor variable, and individual as a random effect, and (2) a linear mixed effects model with the same variables, but incorporating both individual and 'tape' as random effects, with individual nested within 'tape.' The six different 'tapes' represented songs from different individuals that could have differentially influenced our results. We compared these two models using the Akaike Information Criterion (AIC) values for each model, and selected the best model as the model with the lowest AIC value (Zuur *et al.* 2009). We report only the results of models with individual as a random effect because the multiple data points that we collected from each male were not statistically independent.

Once the best model was selected and run, we verified that the model adequately fit our data following the methods described in Zuur *et al.* (2009). Specifically, to validate each final model, we examined residuals versus fitted values to verify homogeneity, used a Shapiro-Wilk test to verify normality of residuals, used a Bartlett's test to verify homogeneity of variance structures across treatments, and examined plots of residuals to identify any outlier data points that could have biased our results (Zuur *et al.* 2009). Our data did not require any transformations, but some variables required us to model heterogeneous variance structures.

For all analyses, the best models were the lme models with only individual as a random effect. For both *T. aedon* analyses, we found one outlier (a control point for minimum distance, and a conspecific point for change in song rate) that could have influenced our results. Specifying a heterogeneous variance structure across treatments did not improve our models, so we reran our analyses without the outlier points and found no major changes in our results (i.e., the treatment effects retained the same significance – $P < 0.05$ or $P > 0.05$ – when the outlier was dropped). In the case of *T. solstitialis* minimum distance, residual variance differed between treatments and thus we specified heterogeneous variance structure across treatments (see Zuur *et al.* 2009: Chapter 4) that improved our model. For our four final models, we compared the intercepts for both control and conspecific treatments to the heterospecific treatment only, because our questions centered on how wrens responded to the songs of the opposite species of wren.

For our second analysis of raw data, the best models for all analyses were the lme models with only individual as a random effect. For the *T. aedon* distance analysis, we found one outlier (a control point) that could have influenced our results. We reran our

analyses without the outlier point and found no major changes in our results (i.e., the treatment effects retained the same significance – $P < 0.05$ or $P > 0.05$ – when the outlier was dropped). For the *T. solstitialis* song analysis, residual variance differed between treatments and thus we specified heterogeneous variance structure across treatments (see Zuur *et al.* 2009: Chapter 4) that improved our model.

RESULTS

Troglodytes aedon approached the speaker when presented with *T. solstitialis* songs. Approach in response to *T. solstitialis* songs was significantly closer to the speaker than their response to control songs ($t = 3.4$, $P = 0.003$), but was not significantly different from approach to conspecific songs ($t = -0.9$, $P = 0.40$) (Fig. 2A). *Troglodytes aedon* also sang significantly more songs in response to our *T. solstitialis* treatment compared to control ($t = -3.6$, $P = 0.002$) and conspecific treatments ($t = -2.5$, $P = 0.02$) (Fig. 2B).

When we analyzed raw behavioral data from our *T. aedon* experiments, we found similar results. *T. aedon* approach in response to *T. solstitialis* songs was significantly closer to the speaker than their response to control songs ($t = 3.9$, $P = 0.0005$) and their position during the minute prior to the experiment (pre-stimulus; $t = 3.5$, $P = 0.001$), but was not significantly different from approach to conspecific songs ($t = -1.0$, $P = 0.33$). *Troglodytes aedon* also sang significantly more songs in response to our *T. solstitialis* treatment compared to control ($t = -4.0$, $P = 0.0004$), pre-stimulus ($t = -4.4$, $P = 0.0001$), and conspecific treatments ($t = -2.8$, $P = 0.009$).

Troglodytes solstitialis did not approach the speaker when presented with *T. aedon* songs. The distance of *T. solstitialis* from the speaker during *T. aedon* songs was not significantly different from their distance during control songs ($t = -0.8$, $P = 0.44$), but was significantly

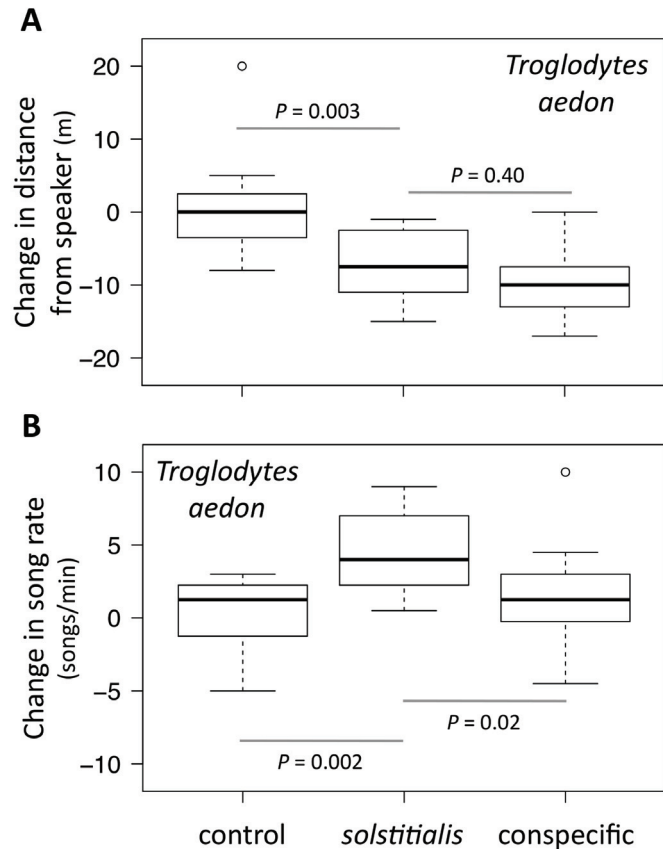


FIG. 2. Response of male House Wrens (*Troglodytes aedon*), to songs of Sayaca Tanager (*Thraupis sayaca*, negative control), Mountain Wren (*Troglodytes solstitialis*), and conspecific (positive control) in Parque Nacional El Rey, Salta Province, Argentina. (A) Change in distance of males from the playback speaker (meters) in response to control, *T. solstitialis*, and conspecific songs. Negative values indicate an approach towards the speaker. (B) Change in song rate (songs/minute) of males in response to control, *T. solstitialis*, and conspecific songs. Box plots show means (dark middle lines), 25th to 75th percentiles (boxes), 1.5 times the interquartile ranges (whiskers), and outliers (circles).

farther than their distance during conspecific songs ($t = -3.8$, $P = 0.001$) (Fig. 3A). *Troglodytes solstitialis* did not sing more frequently in response to *T. aedon* songs compared with control songs ($t = -0.3$, $P = 0.75$) but sang significantly more in response to conspecific songs ($t = 5.7$, $P < 0.0001$) (Fig. 3B).

When we analyzed raw behavioral data from our *T. solstitialis* experiments, we found

similar results, with additional evidence for a response to both *T. aedon* and control songs. The distance of *T. solstitialis* from the speaker during *T. aedon* songs was not significantly different from their distance during control songs ($t = -0.6$, $P = 0.53$), but was significantly farther than their distance during conspecific songs ($t = -5.1$, $P < 0.0001$) and during the minute prior to the experiment

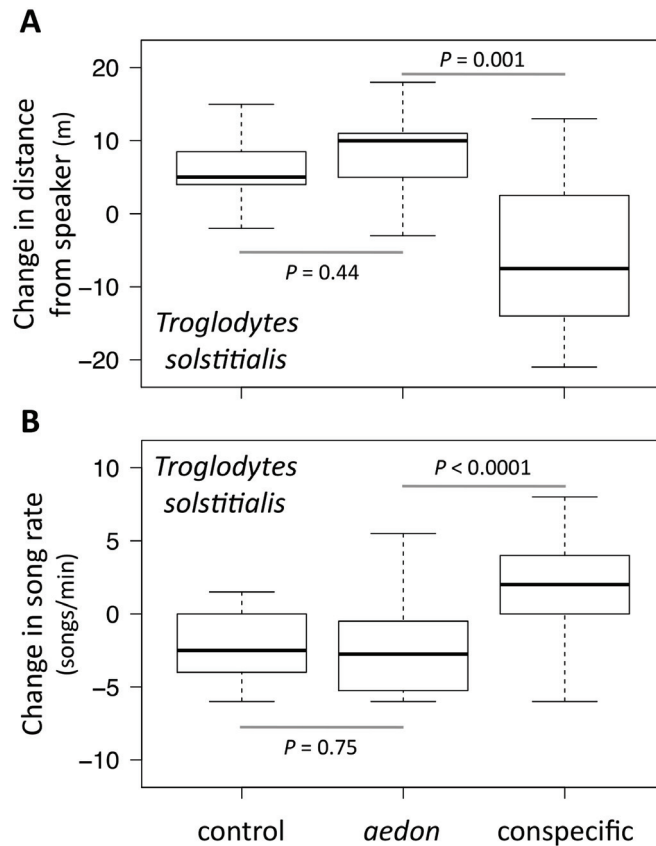


FIG. 3. Response of male Mountain Wrens (*Troglodytes solstitialis*), to songs of Sayaca Tanager (*Thraupis sayaca*, negative control), House Wren (*Troglodytes aedon*), and conspecific (positive control) in Parque Nacional El Rey, Salta Province, Argentina. (A) Change in distance of males from the playback speaker (meters) in response to control, *T. aedon*, and conspecific songs. Negative values indicate an approach towards the speaker. (B) Change in song rate (songs/minute) of males in response to control, *T. aedon*, and conspecific songs. Box plots show means (dark middle lines), 25th to 75th percentiles (boxes), 1.5 times the interquartile ranges (whiskers), and outliers (circles).

(pre-stimulus; $t = -2.9$, $P = 0.006$). The approach of *T. solstitialis* to conspecific songs was closer than the distance during the pre-stimulus ($t = -2.2$, $P = 0.038$), suggesting that *T. solstitialis* approached the speaker in response to conspecific songs, but avoided the speaker in response to both control (versus pre-stimulus; $t = 2.3$, $P = 0.029$) and *T. aedon* songs. *T. solstitialis* did not sing more frequently in response to *T. aedon* songs com-

pared with control songs ($t = 0.5$, $P = 0.65$) and sang significantly more in response to conspecific songs ($t = 5.2$, $P < 0.0001$) and during the pre-stimulus period ($t = 2.8$, $P = 0.009$). Song rates were higher in response to conspecific songs compared with the pre-stimulus period ($t = 2.0$, $P = 0.058$), suggesting that *T. solstitialis* increased song rates in response to conspecific songs, but reduced song rates during both control (versus pre-

stimulus; $t = -2.7$, $P = 0.01$) and *T. aedon* song periods.

DISCUSSION

Song playback experiments revealed asymmetric responses between the two *Troglodytes* wrens with respect to approach and song: *T. aedon* responded aggressively to the songs of the opposite species, while *T. solstitialis* did not. *Troglodytes aedon* responded to *T. solstitialis* songs by approaching the playback speaker and by increasing song rates (Fig. 2). Both of these behaviors characterize an aggressive response in *T. aedon* (Johnson 1998), consistent with *T. aedon* being behaviorally dominant over *T. solstitialis* in aggressive interactions. The behavior of *T. solstitialis* during our experiments is also consistent with this species being subordinate to *T. aedon*. Focal male *T. solstitialis* showed no difference in behaviors in response to control versus *T. aedon* songs, despite responding aggressively to conspecific songs by approaching the speaker and increasing song rates (Fig. 3).

While *T. aedon* did not approach or move away from the playback speaker during control songs (Fig. 2A), *Troglodytes solstitialis* avoided the playback speaker and sang less during both control and *T. aedon* treatments (Fig. 3). This result suggests that *T. solstitialis* may avoid, and reduce singing in the presence of, *T. aedon*. We are not sure why *T. solstitialis* would reduce song rates and avoid the playback speaker in response to our control, the Sayaca Tanager, but the results suggests that the tanager was not a suitable control for *T. solstitialis*. We cannot rule out aggression by *Thraupis sayaca* towards *Troglodytes solstitialis* on our study sites - the two species' songs have similar components (Fig. 1) and they may overlap in diet or other resources at times on our study sites. We do not think that *T. solstitialis* avoiding the human observer during our experiments would cause avoidance of the

playback speaker because the observer followed the focal wren and was not stationed at the speaker. Additionally, we did not observe focal wrens moving away from the playback speaker or reducing their song rates during the first minute preceding the playback experiment, when the observer was similarly following the bird.

In natural interactions, the most aggressive *Troglodytes* wrens usually fly immediately and directly towards the song source and engage in a fight, rather than increasing their song rates (authors, pers. observ.; compare with Johnson 1998 who describes different behaviors). Given this, we interpret our *T. aedon* results as *aedon* responding more aggressively to conspecific songs than to *T. solstitialis* songs, although we cannot rule out the alternatives of equal aggression or greater aggression towards *solstitialis*. *T. aedon* approached the playback speaker closer in response to conspecific songs than *T. solstitialis* songs (Fig. 2A), consistent with greater conspecific aggression, but the difference was not significant. We suspect the lack of significance simply reflects the small sample size for our experiments. The increase in song rates by *T. aedon* in response to *T. solstitialis* songs, but not conspecific songs, may indicate that singing is often an adequate response by *T. aedon* to displace *T. solstitialis* from their territories, or may signify an alternative response that corresponds to a lower level of threat from a heterospecific versus conspecific intruder.

The distribution of *Troglodytes aedon* has expanded with the cutting of forest (Johnson 1998, Brewer 2001, del Hoyo *et al.* 2005), allowing *aedon* to access montane forest that may have been previously occupied exclusively by *T. solstitialis*. Such an expansion of *T. aedon* into regions occupied by *T. solstitialis* could explain, in part, the strong aggressive response of *T. aedon* towards *solstitialis* that we observed. While we lack historical data on the distributions of these two species at our study

site, *T. aedon* commonly breeds in human-caused clearings and in the vicinity of park buildings, sometimes nesting within cavities in the buildings themselves (authors pers. observ.). In view of the increased loss and degradation of montane forest, we might expect an additional cost to *T. solstitialis* of intensified interspecific aggression by colonizing *T. aedon* (e.g., Kennedy & White 1997). Such added costs of habitat degradation for subordinate species may be more common than currently recognized.

We suspect that the behavioral responses that we observed between wren species reflects underlying interspecific competition, in line with interpretations of interspecific responses to song in other tropical birds (Robinson & Terborgh 1995, Tobias & Seddon 2009, Jankowski *et al.* 2010). We also suspect that *T. aedon* aggression towards *T. solstitialis* may reduce potential costs of overlapping territories with *T. solstitialis*, for example, by (1) reducing the amount of territory overlap, (2) delaying breeding in *T. solstitialis* to reduce temporal overlap in breeding schedules with *T. aedon* (e.g., Martin & Martin 2001b), or (3) increasing the likelihood that only inexperienced or poor quality *T. solstitialis* will settle on overlapping territories (e.g., Sherry & Holmes 1988), assuming that inexperienced or poor quality *T. solstitialis* would inflict lower costs on coexisting *T. aedon*. Our experiments, however, did not test the fitness costs of coexistence for *T. aedon* and *T. solstitialis*, whether *T. aedon* restricts the distribution of *T. solstitialis* along a habitat gradient, or potential fitness benefits of aggression, and thus we cannot be certain that the interactions we describe here reflect competition. Nonetheless, our results suggest that *T. aedon* is behaviorally dominant to *T. solstitialis* and that these two species use songs in their interactions with each other.

Closely-related species often segregate along environmental gradients, and frequently

show asymmetric, aggressive interactions (Morse 1974, Peiman & Robinson 2010, Martin & Ghalambor 2014). The pervasiveness of these patterns across taxonomic groups (Morse 1974, Martin & Martin 2001a, Peiman & Robinson 2010, Freshwater *et al.* 2014, Martin 2014), and in diverse tropical environments (Wolf *et al.* 1976, Feinsinger & Colwell 1978, Gill & Wolf 1978, Robertson & Gaines 1986, Robinson & Terborgh 1995, Jankowski *et al.* 2010, our study), suggests that asymmetric interactions may proximately influence the distributions of many species in nature (see also Rosenzweig 1981, Orians 2000). If true, then predicting the effects of human perturbations such as climate change or habitat degradation on the distributions of species may require the consideration of asymmetric interactions among ecologically-similar species, in addition to the direct effects of changes in climate and habitat.

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