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# Song recognition and heterospecific associations between 2 fairy-wren species (Maluridae)

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## Abstract

Although heterospecific associations beneficial to one or both species involved (e.g. commensalisms or mutualisms) are common, it is generally assumed that interactions between species are transient and not particular to individuals. However, long-term interactions between individuals of different species do occur. In such heterospecific social groups, discrimination between heterospecific individuals may be beneficial, allowing individuals to direct beneficial or aggressive behaviors towards appropriate targets. Here, we describe heterospecific groups composed of splendid and variegated fairy-wrens (*Malurus splendens* and *M. lamberti*) and provide the first experimental evidence that recognition of heterospecific group members occurs across species. In these species, family groups live on overlapping territories and co-defend shared territories against both heterospecific and conspecific intruders. Individuals on shared territories were frequently observed traveling and foraging together. Socially dominant males of both species responded more aggressively to

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songs of neighboring and foreign heterospecific fairy-wrens than they did to those of their co-resident heterospecifics. Although splendid fairy-wrens did not change their behavior when associating with heterospecifics, variegated fairy-wrens spent more time foraging, were less vigilant, had greater first-nest fledging success, and fewer extra-group young. These findings suggest heterospecific associations between these 2 species benefit the variegated fairy-wren. Our findings are novel and show that recognition and discrimination among individuals, often considered a prerequisite for conspecific cooperation, can occur across species.

**Keywords:** fairy-wrens, heterospecific interactions, mixed-species flock, recognition, sociality

## Introduction

Sociality exists as a continuum, from brief interactions to the highly complex associations of cooperative species (Alexander 1974; Emlen and Oring 1977). Although sociality is most often associated with interactions between individuals of the same species (i.e. conspecific interactions), associations between species (i.e. heterospecific interactions) are widespread and influence the behavior and ecology of the interacting species (Monkkonen and Forsman 2002; Parejo et al. 2005; Bshary et al. 2006; Seppanen et al. 2007; Valone 2007; Goodale et al. 2010; Zeigler et al. 2011). Cooperation, attraction, and information transfer between species is common; and though most examples of such associations are typically assumed to be transient (Monkkonen et al. 1997; Stensland et al. 2003; Seppanen et al. 2005; Schmidt et al. 2008; Seiler et al. 2013; Wheatcroft and Price 2013), lasting interactions between specific individuals have been observed in many systems (Munn and Terborgh 1979; Powell 1985; Grutter and Bshary 2003; Harrison and Whitehouse 2011; Vail et al. 2014). For example, some avian species place their nests preferentially near nests of larger, more aggressive species to deter nest predators, associations that last the duration of a breeding season (Quinn and Ueta 2008). Some mixed-species foraging flocks in the tropics maintain jointly defended territories that can last years (Munn and Terborgh 1979; Powell 1985; Harrison and Whitehouse 2011). However, how extended heterospecific associations are maintained has received little attention.

Interactions between species often rely on either intentional or inadvertent communication across species, be this eavesdropping on signals produced for conspecific interactions, recognition of species

identity, or transmission of widely recognized or learned alarm calls (Seppanen et al. 2007). Vocal cues in particular are widely recognized as important in heterospecific interactions. Avian mobbing or alarm calls not only influence the behavior of conspecific receivers, but heterospecific behavior as well, attracting other species to aid in group mobbing, inducing vigilance, or prompting predator-avoidance behaviors (Griffin et al. 2005; Magrath et al. 2015a). Within birds, alarm calls may be conserved across species or converge on similar components that facilitate widespread use (Marler 1957; Johnson et al. 2003; Randler 2012). Individuals have also been shown to learn alarm calls of sympatric species when heterospecific alarm calls are distinct from conspecific calls (Magrath et al. 2009; Haff and Magrath 2012; Wheatcroft and Price 2013; Magrath et al. 2015b), attesting to the importance of such heterospecific communication.

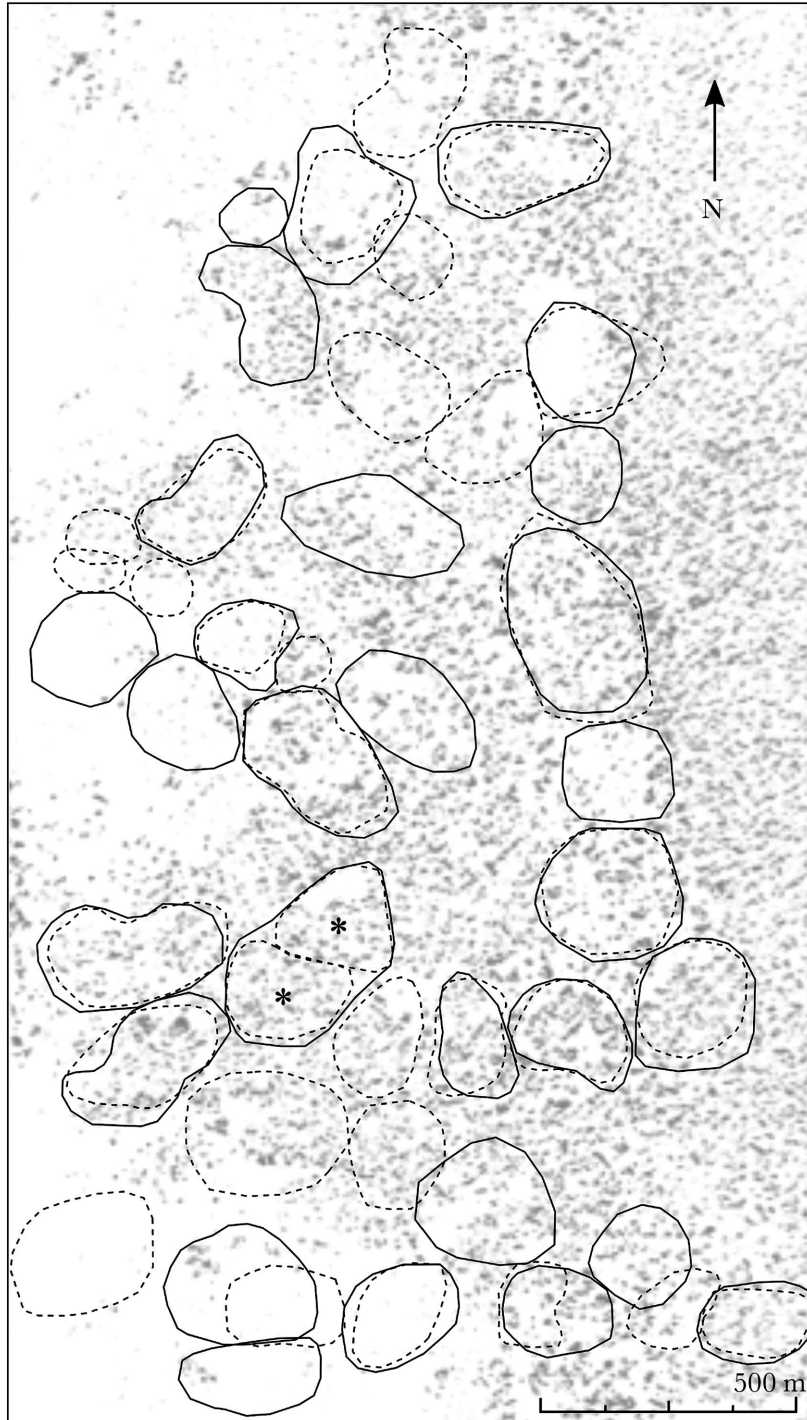
Within species, recognition and discrimination between individuals or classes of individuals often facilitates information sharing (Beecher et al. 1986; Stoddard et al. 1991; Clark et al. 2006; Masco 2013). In fact, most theoretical models and hypotheses for the evolution or maintenance of conspecific social behavior assume or require some degree of recognition (Hamilton 1964; Trivers 1971; Axelrod and Hamilton 1981; Wilkinson 1984; Crowley et al. 1996; Dugatkin 2002; Tibbetts and Dale 2007). Mate or group member recognition facilitates cooperative social behaviors by ensuring that costly behaviors are directed to appropriate individuals (Nowicki 1983; Boughman and Wilkinson 1998; Bull et al. 2000). Discrimination between neighbors and strangers allows individuals to adjust their aggressive responses based on the potential threat posed by familiar and unfamiliar rivals (Temeles 1994).

When heterospecific interactions are long-term or specific to individuals, recognition of and discrimination between heterospecific individuals or classes of individuals may facilitate associations, maintain group cohesion, and ensure that behaviors are directed to the appropriate individuals. For example, recognition of individual humans has been found in horses (*Equus caballus*), dogs (*Canis familiaris*), non-human primates, crows (*Corvus brachyrhynchos*), jackdaws (*Corvus monedula*), and giant Pacific octopuses (*Enteroctopus dofleini*; Adachi and Fujita 2007; Adachi et al. 2007; Proops and McComb 2012; Anderson et al. 2010; Marzluff et al. 2010; Sliwa et al. 2011).

Variegated and splendid fairy-wrens are small passerines endemic to Australia (Rowley and Russell 1997). Both species exhibit cooperative breeding, in which older offspring or unrelated group members contribute to rearing of young (Cockburn 1998). These species co-occur over part of their distribution and, when sympatric, may occur on partially or fully overlapping territories (referred to as “shared”; see **Figure 1**), forming heterospecific social groups (Tibbetts and Pruett-Jones 1999). Individuals on shared territories frequently travel and forage together, appearing to behave aggressively toward heterospecific co-residents only when they are close to nests. However, both species exhibit territorial behavior towards non-co-resident heterospecific fairy-wrens (Johnson 2016). We hypothesized that these associations were beneficial to one or both species and that recognition of group members facilitated group maintenance and territoriality.

Using a combination of song playbacks and behavioral observations, we investigated whether splendid and variegated fairy-wrens recognize heterospecific individuals and whether this association affects their behavior and reproductive success. Heterospecific playback experiments were designed to test not only whether birds discriminated between co-resident and non-co-resident fairy-wren songs, but also whether they discriminated between neighbor and stranger non-co-residents. The dear-enemy effect, in which individuals display lower aggression to neighboring individuals than to unfamiliar individuals (Fisher 1954; Temeles 1994), is widespread in territorial species (Stoddard et al. 1991; Mackin 2005; Breifer et al. 2008). This discrimination is hypothesized to help individuals direct antagonistic interactions towards either heterospecific neighbors or strangers, according to the differing threats that they pose to resources (Heinze et al. 1996; Langen et al. 2000; Tanner and Adler 2009).

We hypothesized that fairy-wrens may similarly distinguish between known and unknown heterospecific rivals. Heterospecific neighbor-stranger discrimination has been investigated in at least one avian species pair (the rufous-and-white and the banded wren, *Thryophilus rufalbus* and *T. pleurostictus*, respectively), but no such discrimination was observed (Battiston et al. 2015). Because conspecific neighbor-stranger discrimination has not been addressed for either splendid or variegated fairy-wrens, we also performed conspecific playback experiments within each species (see Cooney and Cockburn 1995; Colombelli-Negrel et al. 2011 for related studies in the Maluridae).



**Figure 1** Territories of splendid (dashed lines) and variegated fairy-wrens (solid lines) from a portion of BCP during 2014. The 2 splendid fairy-wren territories denoted with an asterisk were a single territory in the previous year, and in 2014 the son of the dominant male (an auxiliary group member in 2013) budded off a portion of the territory. The variegated group continued to interact with both splendid fairy-wren groups.

## Methods

### *Study site and population*

Between October and December of 2013–2015, we followed color-banded splendid and variegated fairy-wren family groups on both shared and non-shared territories at Brookfield Conservation Park (BCP) in South Australia (S 34°21', E 139°29'). We monitored 53 splendid fairy-wren and 34 variegated fairy-wren groups in 2013, 59 splendid fairy-wren and 61 variegated fairy-wren groups in 2014, and 48 splendid fairy-wren and 54 variegated fairy-wren group in 2015 for which territory status (shared or solitary) and nesting behavior were known. An additional 23 variegated fairy-wren groups monitored in 2012, for which we knew territory status and had blood samples for all group members and offspring, were included in analyses of extra-pair paternity. Otherwise, data from 2012 were not included in any other analyses as monitoring of nesting success was less rigorous that year.

Birds were caught on their territories with mist nets. Upon capture, birds were banded with a unique combination of 3 color bands as well as a numbered metal band issued by the Australian Bird and Bat Banding Scheme. Each bird was then measured, and a blood sample was taken from the brachial vein. Birds were followed daily to determine group composition, territory boundaries, and nest location. Blood samples of nestlings were taken at 5 to 6 days of age, at which time they were also banded with a metal band. Juveniles who survived and remained in the study population to 1 year of age were re-captured and given color bands. Locational data were recorded in the field with hand-held GPS units (Garmin eTrek units, Garmin Ltd., Schaffhausen, Switzerland) and later plotted on study area maps and examined with Google Earth Pro (Google, Menlo Park, CA). Territory boundaries were identified through patterns of space use and observation of aggressive interactions of neighboring groups.

Both species exhibit cooperative breeding at BCP, but variegated fairy-wrens live in larger groups than splendid fairy-wrens. Mean group size for variegated fairy-wrens across all 3 years averaged 3.17 (SD = 1.21, range = 2–9). A total of 97 variegated fairy-wren groups (65.10%) had at least one auxiliary individual, and 40.94 % of groups had auxiliary females. In contrast, splendid fairy-wren group sizes

ranged from 2 to 5, with a mean group size of 2.22 (SD = 0.47). A total of 31 splendid fairy-wren groups (19.38%) had auxiliaries, and just 7.50% of groups had one or more auxiliary females.

Both male and female auxiliaries have been observed to help in this population of variegated fairy-wrens, contributing to nest provisioning. However, some auxiliary females do not help at all, and those that do help contribute less to nest provisioning than male helpers (Johnson 2016). Variegated fairy-wren groups with auxiliary females exhibited plural breeding (in which the dominant female and one or more helper females nested during the breeding season) at a low rate of approximately 5% (Johnson 2016). In this population of splendid fairy-wrens, only male auxiliaries have been observed contributing to nestling provisioning (personal observation), and plural breeding by females is extremely rare (Van Bael and Pruett-Jones 2000, but see Rowley et al. 1989 for studies in another subspecies). For simplicity, we refer to all group members who are not the dominant breeding pair as auxiliary group members throughout.

### ***Territory overlap***

Variegated and splendid fairy-wren social groups live on exclusive territories that are actively defended from other conspecific groups. Males and females of both species participate in the defense of their individual territory and, as we report, when the territories of the 2 species overlap the individuals of both species defend it from heterospecific intruders.

We categorized territories as either solitary or shared. Territories were considered shared if the following 3, non-mutually exclusive, criteria were met: 1) each species' territory contained the nest of the other species, 2) the species overlapped in space use, and 3) the species were regularly seen traveling and foraging together.

### ***Behavioral interactions***

To examine whether the behavior of each species changed in the presence of their heterospecific co-resident, we performed focal observations of males in 11 splendid and 12 variegated fairy-wren groups on shared territories (heterospecific groups) in 2014. Of the total



number of territories monitored, 5 shared territories (5 variegated and 5 splendid fairy-wren groups that shared the same territory) were monitored for the behavior of each species. For these pairs, each species was monitored on separate days to avoid over counting behaviors observed when the species were associating. All splendid fairy-wren groups followed consisted of a single pair while the variegated fairy-wren groups included both single pairs and groups with one or more helpers (average group size of  $3.1 \pm 0.31$ , standard error [SE]). For each species, we recorded the behavior of the dominant male of the focal group at 1-min intervals during 100–120 min observation periods (mean =  $113.5 \pm 15.78$  min, standard deviation [SD]) between 0700 h and 1100 h. Behaviors were categorized as “foraging,” “traveling,” “singing,” “contact calling,” and “mobbing” (see Supplementary Table 1 for descriptions of these behaviors). For analysis, observations were split into the time when the male was in association with the hetero-specific co-resident and that time when the male was alone. The category contact calling was square-root transformed prior to analysis; all other categories were non-transformed. Mobbing data could not be normalized and was analyzed using a non-parametric Friedman test, while the other behavior categories were analyzed using paired samples *t*-test. *P* values were then combined using *Z*-transform to test for overall changes in behavior (Whitlock 2005).

Reduced vigilance behavior is one possible benefit of increased effective group size within species (Pulliam 1973). To assess if this was true for heterospecific associations, we quantified vigilance behavior in the focal group during each min of the focal follow. We recorded the proportion of 1-min sampling intervals during which any group member was vigilant. We recorded an individual as being vigilant if it was perched in an exposed area and scanning their surroundings (See Supplementary Table 1 for a more explicit definition of vigilance behavior). Because vigilance occurred in concert with other behaviors and was measured for the whole group, we analyzed it separately using a general linear mixed model (GLMM). The model included the percent of time spent vigilant as the dependent variable, with species, association status (with co-resident or alone), and group size as fixed effects, and group identity as a random effect. We selected models based on a stepwise backward elimination of non-significant terms in order of their *P* value. Only fixed parameters with a *P* value of  $< 0.1$  or the last

parameter with the lowest  $P$  value were retained in the final model. The models were evaluated using likelihood ratio tests.

### ***Territory overlap and reproductive success***

To determine if sharing a territory with a heterospecific group influenced breeding success, we monitored reproduction in 160 splendid fairy-wren family groups and 149 variegated fairy-wren family groups for whom territory overlap and reproductive behavior was known. Each group per year that initiated breeding (completed a nest) was monitored for nest success on both solitary and shared territories. When possible and when appropriate, we determined whether or not each group 1) fledged young from their first initiated nest ( $n = 158$  and 140 for splendid and variegated fairy-wren group-years respectively), 2) fledged young at any point during the field season ( $n = 148$  and 147 for splendid and variegated fairy-wren group-years respectively), and 3) initiated re-nesting behavior following first nest failure ( $n = 120$  and 99 for splendid and variegated fairy-wren group-years, respectively).

Although there are multiple ways to measure reproductive success (e.g. clutch size, brood size, nest success, lifetime reproductive success, etc.; Murray 2000), we considered only fledging success, defined as the production of any fledged young regardless of number. While this measure does not truly reflect the potential contribution of breeding individuals to the next generation, we chose this measure because we were not always able to determine the number of young surviving to fledging. Although group size positively correlated with fledging success in the variegated fairy-wren (Johnson 2016), group size did not significantly differ between shared and solitary territories (see Results) and thus was not included in analyses of nest success.

We used generalized linear mixed models (GzLMMs) with binomial distributions to determine if frequencies of fledging and re-nesting differed on solitary or shared territories for each species. Each model included heterospecific overlap as the fixed effect, as well as breeding female identity, breeding male identity, and year as random effects. Each model was compared to a null model with no fixed effects using a likelihood ratio test.

## ***Playback experiments***

### *Heterospecific recognition*

We conducted reciprocal playback experiments on shared territories to test whether individuals recognized and discriminated between the songs of co-resident and non-co-resident heterospecific fairy-wrens. Focal birds were presented with 3 test stimuli, consisting of songs of a dominant male heterospecific fairy-wren that either 1) occupied the same territory (co-resident treatment), 2) occupied an adjacent territory (neighbor treatment), or 3) occupied an area 5 or more territories away (foreign treatment). Each focal bird was also presented with 4) a control treatment consisting of songs of the red-capped robin (*Petroica goodenovii*), a common species at our study site which is frequently encountered by the fairy-wrens, but from whom they do not defend their territories. Treatments 1 and 4 were not intruders, one being a heterospecific group member and the other a heterospecific that is neither a competitor nor a cooperator. Treatment 2 served as a familiar intruder, and Treatment 3 as an unfamiliar intruder. This experimental protocol allowed us to test if splendid and variegated fairy-wrens discriminated between the songs of one another. It also allowed us to test whether they exhibit a generalized form of neighbor-stranger discrimination (discriminating between known and unknown individuals—co-resident and non-co-residents) or if they discriminate between multiple categories of males of the other species (co-resident vs. neighbor non-co-resident vs. foreign non-co-resident).

In 2013, we conducted playback trials in 15 variegated fairy-wren territories shared with splendid fairy-wrens. In 2014, we performed the reciprocal experiment, conducting trials in 15 splendid fairy-wren territories shared with variegated fairy-wrens, again with all 4 treatment types, but in this case the heterospecific fairy-wren songs were from variegated fairy-wrens. Because 2-bird groups with no auxiliaries was the most common social group structure in splendid fairy-wrens at BCP, playback experiments for this species were limited to 2-bird groups.

To create playback stimuli, we recorded songs of males of both fairy-wren species during the dawn chorus (0430–0700 h) when ambient noise was minimal. Songs of both species were recorded during

multiple years, but only songs recorded during the field season in which the experiment was conducted were used as stimuli. All recordings were made using Sennheiser ME66 and ME67 shotgun microphones (Sennheiser Electronic Corporation, Old Lyme, CT) and Marantz PMD-661 digital recorders (D&M Professional, Itasca, IL). Songs were recorded as uncompressed wav files at a sample rate of 44 100 Hz. Using Syrinx-PC (J. Burt, Seattle, WA, USA). We edited these recordings to produce stimuli, each consisting of 8 songs with 5 s of silence between each song (total duration of ~1 min).

Male fairy-wrens sing 3 song types, the Type I and Type I+II that function in territorial defense (Greig and Pruett-Jones 2008), and the Type II alone that is a predator-elicited vocalization sung exclusively by males. The Type II song is hypothesized to function as a sexual display to conspecific females (Greig and Pruett-Jones 2008, 2009; Greig et al. 2010). As our interest was in territoriality, only Type I and Type I+II were used in the playback stimuli. Stimuli produced from variegated fairy-wren songs used only Type I songs as males of this species almost exclusively sang this song type. Splendid fairy-wrens were observed to produce both song types commonly, and thus stimuli produced from splendid fairy-wren songs used both song types at a frequency that represented each individual's typical singing behavior.

Songs were only used in the playback stimuli if they contained relatively few background vocalizations from other species, a high signal to noise ratio, and low degradation. Although we tried to use 8 unique songs for each stimulus created, this was not always possible. Twenty-one splendid fairy-wren song stimuli were created for presentations to variegated fairy-wrens in 2013, with an average of 7.95 unique songs ( $\pm 0.22$  SD) across stimuli. Twenty-one variegated fairy-wren song stimuli were created for presentations to splendid fairy-wrens in 2014, with an average of 7.4 unique songs ( $\pm 1.14$  SD) across stimuli. Across stimuli, the maximum amplitude of each song was standardized to ensure that the playback volume remained constant within and across trials. Stimuli were presented to multiple focal birds if they could serve as more than one stimulus category (co-resident, neighbor, or foreign). Splendid fairy-wren song stimuli were presented to an average of 2.14 focal male variegated fairy-wrens ( $\pm 0.72$  SD). Variegated fairy-wren stimuli were presented to an average of 2.14 focal male splendid fairy-wrens ( $\pm 0.85$  SD).

One control stimulus of the red-capped robin was used across all trial groups. This playback was composed of 4 unique songs, each repeated once to create the 8-song playback, recorded from a red-capped robin male in 2013 from the study site but who was not on any fairy-wren focal territory.

Playback experiments were conducted in the morning (0700– 1100 h). The experiments were only performed if the focal birds were found on their territories to ensure that the birds heard the stimuli. Both species often intrude into other territories, so if they were not found, it was possible they were absent from the territory. As far as possible, we began experiments only when the heterospecific co-resident of the focal group was not visible to avoid interference with the response of the focal group. However, the co-resident would sometimes respond upon hearing a conspecific stimulus even when they were not initially present. For playbacks to variegated fairy-wrens, the splendid fairy-wren co-residents were present during one control presentation, 2 overlap presentations, and 2 neighbor presentations. For playbacks to splendid fairy-wrens, the variegated fairy-wren co-residents were initially absent but joined 2 control presentations, 9 overlap presentations, 6 neighbor presentations, and 10 foreign presentations. The presence of the co-resident did not appear to influence recorded behaviors of the focal species (see Results). Stimuli were played with an amplified field speaker (Saul Mineroff Electronics Inc., Elmont, NY) and an iPod Classic (Apple Inc., Cupertino, CA). The speaker was positioned on the ground approximately 30 m from the focal bird. Stimuli began within 10–15 min after the speaker was placed and the focal group resumed normal behavior. If the focal group did not resume normal behavior or began reacting to the presence of the observer, the experiment was not started and was attempted on a subsequent day. The stimulus was played 3 times with 5 min of silence in between, yielding a trial duration of 18 min. The field amplitude for all playback stimuli was approximately 87.0 dBC SPL 1 m from the speaker. Each focal group was presented with one treatment per morning for 4 mornings, and the order of the playbacks was randomized.

The response variables “latency to first response” and “duration of vigilance” were recorded, as well as the number of occurrences of “song,” “scold,” and “approach” (see Supplementary Table 2 for descriptions of each behavior). As these responses are measures of

**Table 1** Loadings derived from PCA of the 5 aggressive response variables for splendid and variegated fairy-wrens recorded during the heterospecific playback experiments

<i>Response variable</i>	<i>Splendid fairy-wren PC1</i>	<i>Splendid fairy-wren PC2</i>	<i>Variegated fairy-wren PC1</i>
Eigenvalue	2.32	1.04	2.69
Percent variation	46.44	20.71	53.69
Latency of response	-0.77		-0.76
Approach	0.87		0.69
Songs (Type I and Type I+II)	0.74		0.81
Duration of vigilance	0.38	0.87	0.69
Scolds	0.55	-0.47	0.71

Analysis was done on variegated and splendid fairy-wren responses separately to account for species-specific behavior. Only PC1 was used in analyses.

aggression (Greig and Pruett-Jones 2008) and intercorrelated ( $r > |0.3|$  for at least one pairwise correlation for each variable within species), we performed a principle component analysis (PCA) to derive a single composite score used in subsequent analyses (**Table 1**; McGregor and Avery 1986). For both species, response variables loaded heavily on principle component 1 (PC1), thus only PC1 was used in subsequent analyses. Of the 15 territories studied for each species, 4 were utilized for both species; however, group composition changed for one or both species between experimental years. Because the heterospecific playback experiments were performed on 2 different species in 2 different years, we analyzed the playback responses for each species independently of one another. All statistical analyses (unless otherwise stated) were performed in IMB SPSS Statistics for Windows v23.0 (IBM Corp 2015). We compared response strength to playback stimuli for each species using GLMM. All models had focal group identity and playback song identity as random effects. We compared response strength to each treatment types using pairwise contrasts generated by GLMM analysis in SPSS. All pairwise comparison  $P$  values are adjusted for multiple comparisons using least significant differences. One splendid fairy-wren focal group was unable to receive its last treatment, the co-resident; however, because GLMMs allow for unbalanced designs, we included this group in the final analysis.

### *Conspecific recognition*

Although we were primarily interested in the role of individual recognition in heterospecific association and territoriality, we also examined neighbor–stranger discrimination within each species, as no studies have addressed conspecific neighbor-stranger discrimination in either splendid or variegated fairy-wrens. In 2015, we conducted species-specific playback experiments in which 14 dominant males of each species were presented with songs of a dominant male conspecific from 1) a neighboring territory and 2) a foreign territory (5 or more territories away) as well as 3) a control song, the red-capped robin. Stimuli production and presentation time were the same as described above. Twenty-two splendid fairy-wren stimuli were created for playback. Splendid fairy-wren conspecific stimuli had an average of 3.23 unique songs ( $\pm 0.97$  SD) and were presented to an average of 1.27 focal groups ( $\pm 0.46$  SD). Twelve variegated fairy-wren stimuli were created for use as playbacks. Variegated fairy-wren conspecific stimuli had an average of 3.08 unique songs ( $\pm 1.24$  SD) and were presented to an average of 2.33 focal groups ( $\pm 0.98$  SD). Rather than being played within the territory as the heterospecific stimuli were, conspecific stimuli were played from the territory border appropriate for the neighbor stimulus and were used to indicate a threat of intrusion (Stoddard 1996).

The response variables for the conspecific playback included those recorded for the heterospecific playback (as above) as well as 3 variables only observed in the conspecific experiments (“look,” “mate-guarding,” and “bill-wipe”; see Supplementary Table 2 for descriptions of each behavior and the method of quantifying them). All response variables were correlated with at least one other variable ( $r > |0.3|$ ), except for scold, which did not vary across treatments and was thus removed from the analysis. We performed a PCA on the response data for each species separately to derive a composite response score (**Table 2**). Splendid fairy-wren response variables all loaded strongly onto PC1. Variegated responses all loaded heavily on PC1 and 3 responses loaded onto PC2, however, because all responses were present on PC1 this was used in all subsequent analyses. Conspecific playback responses were analyzed in the same manner as the heterospecific playback responses. The analysis of conspecific playback responses could not be combined with that of the heterospecific playback responses because each involved different numbers of treatments.

**Table 2** Loadings derived from PCA of the aggressive and mate-guarding response variables for splendid and variegated fairy-wrens recorded during the conspecific neighbor-stranger experiments

<i>Response variable</i>	<i>Splendid fairy-wren PC1</i>	<i>Variegated fairy-wren PC1</i>	<i>Variegated fairy-wren PC2</i>
Eigenvalue	3.33	2.88	1.25
Percent variation	47.49	41.23	17.92
Latency of response	-0.52	-0.66	
Approach	0.80	0.85	
Bill-wipe	0.70	0.49	0.62
Mate-guarding	0.63	0.57	-0.56
Look	0.66	0.30	0.68
Songs (Type I and Type I+II)	0.55	0.70	
Duration of vigilance	0.89	0.77	

Analysis was done on variegated and splendid fairy-wren responses separately to account for species-specific behavior. Only PC1 was used in analyses.

### ***Extra-group paternity in variegated fairy-wrens***

We quantified rates of extra-group paternity (young sired by males outside of their social group) for broods from 120 variegated fairy-wren groups studied from 2012 to 2015. Each year as many of the birds in the population as possible were genotyped using 6 highly variable microsatellite loci to accurately assess population wide allele frequency and to include the majority of males in paternity analyses (see Johnson and Pruett-Jones (2018) for methods of DNA extraction, loci optimization, and paternity analyses). Paternity analyses were carried out in Cervus 3.0 (Marshall et al. 1998; Kalinowski et al. 2007; see Johnson and Pruett-Jones 2018 for details and statistics). Only nests in which all group members were sampled and territory status was known (shared with a splendid fairy-wren or solitary) were included in subsequent analyses ( $n = 96$ , 38 solitary and 58 shared).

GzLMMs were used to assess how territory overlap (shared or solitary) affected the occurrence of extra-group young (EGY). We focused on EGY rather than extra-pair young, a more typical examination of paternity, because we were interested in whether heterospecific territorial defense assisted in excluding male intruders. Extra-pair males within the group would not be excluded by heterospecific co-residents, therefore offspring produced by auxiliary males and those sired by the dominant male were both considered within-group young. The full



model included the proportion of extra-group young as the dependent variable, territory status (shared or solitary) and number of conspecific male helpers (because number of male helpers is known to impact paternity; Johnson and Pruett-Jones 2018) as fixed effects, and breeding female identity, breeding male identity, and year as random effects. The model used a binomial distribution, weighted by brood size. As above, we selected models based on a stepwise backward elimination of non-significant terms in order of their  $P$  value. Only fixed parameters with a  $P$  value of  $<0.1$  or the last parameter with the lowest  $P$  value were retained in each final model, which were then compared to the null model (random effects only) using a likelihood ratio test. All models described were analyzed using R v3.3.2 (R Core Team 2016) and the package lme4 (Bates et al. 2015).

## Results

### *Territory overlap*

Across all 3 years, 99 out of 160 (61.88%) breeding splendid fairy-wren groups shared territories with variegated fairy-wrens, and a comparable 102 out of 149 (68.45%) breeding variegated fairy-wren territories were shared with splendid fairy-wrens. For those 99 splendid fairy-wren groups sharing a territory with variegated fairy-wrens, 98 (98.90%) associated with just one variegated fairy-wren group. Similarly, for those 102 variegated fairy-wren groups sharing a territory with splendid fairy-wrens, 98 (96.08%) associated with just one splendid fairy-wren group. Average group size of breeding variegated fairy-wrens did not significantly differ between shared and solitary territories ( $n = 149$ , Anova,  $F = 0.375$ ,  $P = 0.54$ ). Similarly, for breeding splendid fairy-wrens, average group size did not differ significantly between shared and solitary territories ( $n = 160$ , Anova,  $F = 1.34$ ,  $P = 0.25$ ). Nor were variegated or splendid fairy-wren social groups that had auxiliaries (presence of) more likely to form heterospecific social groups ( $\chi^2 = 1.31$ , 0.91;  $P = 0.25$ , 0.33 for variegated and splendid fairy-wrens, respectively).

To evaluate longevity of territory overlap, we examined group persistence as it related to overlap. Between 2013 and 2015, there

were 14 variegated fairy-wren social groups for which at least 1 breeding adult (male or female) survived for all 3 years, the group used the same territory, and the territory was shared with splendid fairy-wrens. Of these 14 groups, 11 (78.57%) shared the site with the same splendid fairy-wren social group for 2 or more years. In other words, if birds survived from one year to the next, they likely shared their territory with the same social group of the other species for multiple years.

### ***Time budgets on shared territories***

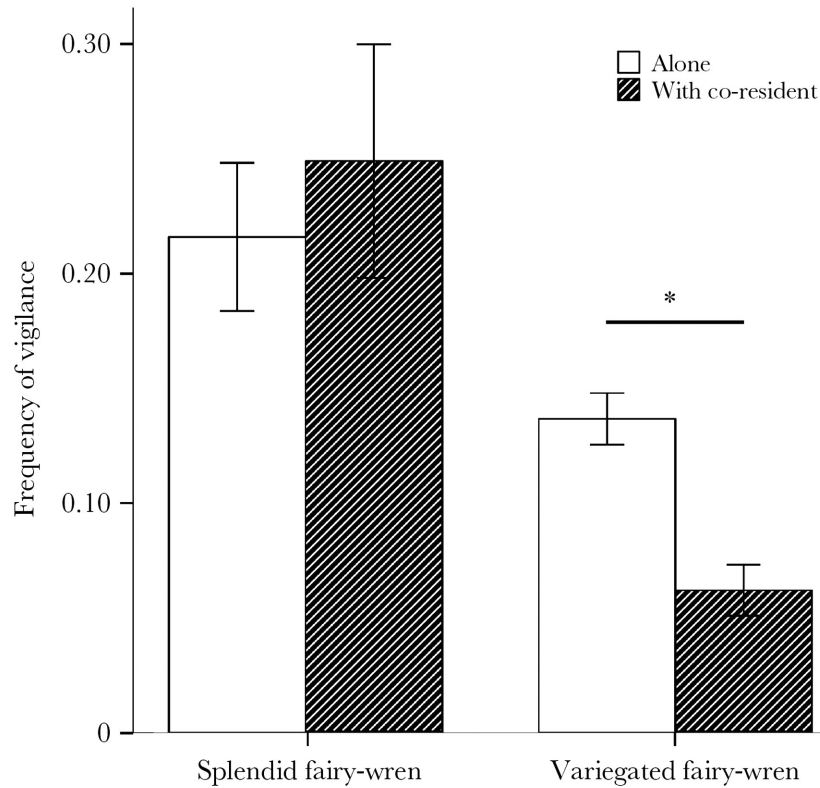
Variegated and splendid fairy-wrens spent on average 45% of their time within 20 m of their co-resident heterospecific group. The behavior of splendid fairy-wrens did not change when interacting with the other species ( $Z$ -transform test  $Z = -0.61$ ,  $P = 0.27$ : for independent test  $P$  values see **Table 3**; see Supplementary Table 1 for description of behaviors) but the behavior of variegated fairy-wrens did ( $Z$ -transform test  $Z = -3.25$ ,  $P \leq 0.001$ : for independent test  $P$  values see Table 3; see Supplementary Table 1 for description of behaviors). Variegated fairy-wrens spent more time foraging when in the presence of

**Table 3** The behavior of splendid and variegated fairy-wrens when they are or are not associating with their heterospecific co-residents

<i>Species</i>	<i>Behavior</i>	<i>Mean associating</i> $\pm SE$	<i>Mean solitary</i> $\pm SE$	<i>Test</i> <i>statistic</i>	<i>P</i>
Splendid fairy-wren ( $n = 11$ )	Foraging	0.64 $\pm$ 0.04	0.56 $\pm$ 0.05	1.41	0.19
	Singing	0.25 $\pm$ 0.04	0.25 $\pm$ 0.04	0.03	0.98
	Traveling	0.07 $\pm$ 0.06	0.09 $\pm$ 0.02	-1.11	0.29
	Contact calling	0.13 $\pm$ 0.04	0.21 $\pm$ 0.06	-1.97	0.08
	Mobbing	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	3.00	0.23
	Vigilance	0.24 $\pm$ 0.05	0.22 $\pm$ 0.03		
Variegated fairy-wren ( $n = 12$ )	Foraging	0.76 $\pm$ 0.03	0.66 $\pm$ 0.04	2.31	0.04*
	Singing	0.14 $\pm$ 0.02	0.19 $\pm$ 0.02	-1.52	0.16
	Traveling	0.03 $\pm$ 0.01	0.06 $\pm$ 0.02	-3.01	0.01*
	Contact calling	0.19 $\pm$ 0.04	0.24 $\pm$ 0.05	-0.74	0.49
	Mobbing	0.01 $\pm$ 0.00	0.00 $\pm$ 0.00	4.00	0.59
	Vigilance	0.06 $\pm$ 0.01	0.14 $\pm$ 0.01		

Categories were analyzed with a paired-samples  $t$ -test except mobbing (Friedman test) and vigilance (GLMM; see text for test statistics for vigilance).

\*  $P \leq 0.05$ . Due to multiple comparisons,  $P$  values from  $t$ -tests were combined using  $Z$ -transform test for overall comparison of behavioral changes (see text).



**Figure 2** Frequency of vigilance behavior in splendid and variegated fairy-wrens in shared territories in the absence (alone, clear bars) or presence (with co-resident, hashed bars) of their heterospecific co-resident, grouped by species. Error bars indicate  $\pm 1$  SE. \*factor significance of  $P < 0.05$  in the best fit GLMM of vigilance behavior.

splendid fairy-wrens than when solitary ( $t = 2.31$ ,  $P = 0.04$ ) and less time traveling in the presence of splendid fairy-wrens than when solitary ( $t = 3.01$ ,  $P = 0.01$ ; Table 3).

Across all sampling times, variegated fairy-wren groups were marginally less vigilant than splendid fairy-wren groups (10% and 22% of the total observed time on average, respectively, GLMM: estimate =  $-7.92 \pm 4.23$ ,  $t_{35.53} = -1.87$ ,  $P = 0.07$ ). However, variegated fairy-wrens were significantly less vigilant when they were associating with their splendid fairy-wren co-resident (GLMM: species \* association: estimate =  $-10.77 \pm 4.53$ ,  $t_{21} = -2.38$ ,  $P = 0.03$ ; association: estimate =  $3.31 \pm 3.27$ ,  $t_{21} = 1.01$ ,  $P = 0.32$ ; likelihood ratio test comparison with null model:  $\chi^2_3 = 18.01$ ,  $P \leq 0.01$ ; **Figure 2**; see Table 3 for descriptive statistics). Group size was non-significant and dropped from the final

model. Although the fit of the simplified model was improved over the model containing group size, it was not a significantly better fit than the model that included group size (AICc = 333.19 and 333.48, respectively; likelihood ratio test:  $\chi^2_1 < 0.01$ ,  $P = 0.98$ ; see Supplemental Table 3 for full model description).

### ***Reproductive success***

There was no difference in the proportion of groups that successfully fledged young during the breeding season on shared versus solitary territories for either splendid or variegated fairy-wrens (GzLMM, binomial distribution: estimate =  $0.61 \pm 0.37$ ,  $0.17 \pm 0.48$ ;  $Z_{143, 142} = 1.61$ ,  $0.35$ ;  $P = 0.11$ ,  $0.73$ ; likelihood ratio test:  $\chi^2_{1,1} = 2.68$ ,  $0.12$ ,  $P = 0.11$ ,  $0.72$ ; 37.36% and 38.00 % of groups fledging young on shared and 24.56% and 38.30% of groups fledging young on solitary territories across years for splendid and variegated fairy-wrens, respectively). There was marginally increased fledging success of the first nest in splendid fairy-wren groups on shared territories relative to solitary territories (GzLMM, binomial distribution: estimate =  $0.83 \pm 0.47$ ,  $Z_{153} = 1.76$ ,  $P = 0.08$ ; likelihood ratio test:  $\chi^2_1 = 3.49$ ,  $P = 0.06$ ; 27.55% of groups fledging their first nest on shared and 15.00% of groups fledging their first nest on solitary territories across years) and no difference in whether or not re-nesting occurred following initial nest failure (GzLMM, binomial distribution: estimate =  $0.18 \pm 0.37$ ,  $Z_{115} = 0.49$ ,  $P = 0.63$ ; likelihood ratio test:  $\chi^2_1 = 0.24$ ,  $P = 0.62$ ; 53.52% of groups re-nesting on shared and 48.98% of groups re-nesting on solitary territories across years). However, more variegated fairy-wren groups occupying shared territories fledged young from their first nest (GzLMM, binomial distribution: estimate =  $11.61 \pm 2.87$ ,  $Z_{135} = 4.04$ ,  $P \leq 0.01$ ; likelihood ratio test:  $\chi^2_1 = 31.38$ ,  $P \leq 0.01$ ; 31.31% groups fledging their first nest on shared and 14.63% groups fledging their first nest on solitary territories across years). Also, more variegated fairy-wren groups attempted to re-nest following initial nest failure if they were on a shared territory (GzLMM, binomial distribution: estimate =  $1.02 \pm 0.50$ ,  $Z_{94} = 2.04$ ,  $P = 0.04$ ; likelihood ratio test:  $\chi^2_1 = 4.53$ ,  $P = 0.03$ ; 46.27% of groups re-nesting on shared and 25.00% of groups re-nesting on solitary territories across years). See Supplementary Table 4 for all full model descriptions and Supplementary Table 5 for sample sizes for each subcategory.

Variiegated fairy-wren nests on shared territories had lower proportions of extra-group young than those on non-shared territories, and, as expected, nests of territories with male auxiliaries had lower proportions of extra-group young than those without ( $n = 58$  shared territories, mean =  $0.30 \pm 0.40$  SD EGY;  $n = 38$  solitary territories, mean =  $0.45 \pm 0.41$  SD EGY; GzLMM, binomial distribution, territory shared: territory status estimate =  $-1.29 \pm 0.61$ ,  $z_{90} = -2.11$ ,  $P = 0.04$ ; number of auxiliary males estimate =  $-0.54 \pm 0.28$ ,  $z_{90} = -1.93$ ,  $P = 0.05$ ; likelihood ratio test  $\chi^2_2 = 9.35$ ,  $P \leq 0.01$ ; see Supplementary Table 4 for full model description). As both fixed effects had  $P$  values of less than 0.1, both were retained as the final model.

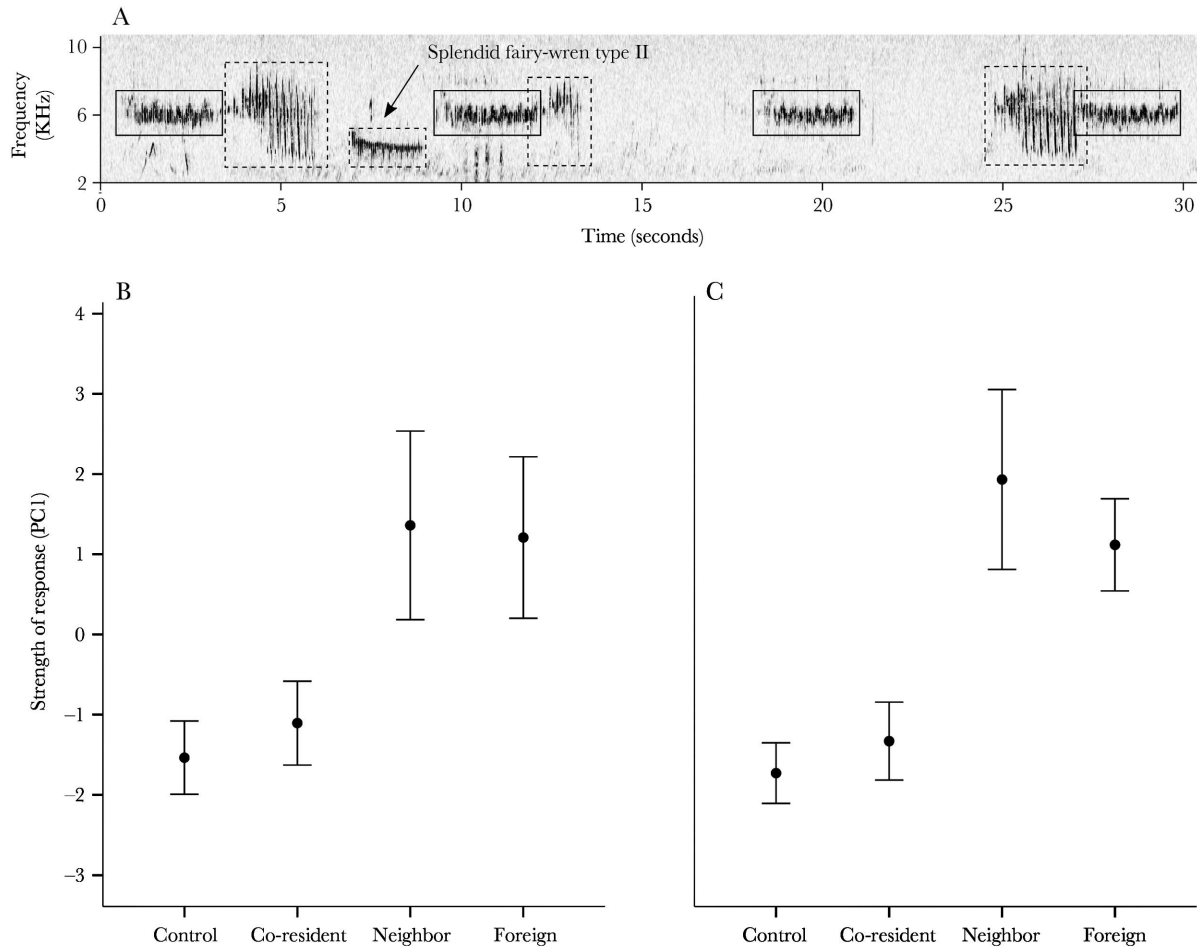
### ***Discrimination among heterospecific songs***

Both variegated and splendid fairy-wrens responded more aggressively to the songs of neighboring and foreign heterospecific fairy-wrens than to either their co-resident's songs or control songs (see **Figure 3A** for an example response to stimuli; variegated fairy-wren heterospecific response GLMM:  $F_{3,56} = 28.282$ ,  $P < 0.001$ ; splendid fairy-wren heterospecific response GLMM:  $F_{3,55} = 12.826$ ,  $P < 0.001$ ; see **Table 4** for pairwise  $P$  values, Figure 3B and C; see Supplementary Table 2 for response variables and Supplementary Table 6 for descriptive statistics). Although we attempted to present stimuli to focal males when their co-resident was not present, this was not always possible. In 2 cases where the splendid fairy-wren was present for the playing of their own song to focal variegated fairy-wrens, the variegated fairy-wrens did not approach the speaker, but rather their splendid fairy-wren co-resident

**Table 4** Pairwise comparisons from GLMMs of responses (principle component scores) of males of each species to heterospecific playbacks

<i>Species</i>	<i>Treatment</i>	<i>Co-resident</i>	<i>Neighbor</i>	<i>Foreign</i>
Splendid fairy-wren	Control	0.32	$\leq 0.01^*$	$\leq 0.01^*$
	Co-resident		$\leq 0.01^*$	$\leq 0.01^*$
	Neighbor			0.79
Variiegated fairy-wren	Control	0.44	$\leq 0.01^*$	$\leq 0.01^*$
	Co-resident		$\leq 0.01^*$	$\leq 0.01^*$
	Neighbor			0.18

\*  $P \leq 0.01$ ,  $P$  values are adjusted using least significant differences to account for multiple comparisons.



**Figure 3** (A) Spectrogram illustrating a splendid fairy-wren's vocal response to a variegated fairy-wren intruder treatment. Solid boxes indicate variegated fairy-wren song stimuli and dashed boxes indicate splendid fairy-wren responses. All responses are Type I songs except for indicated exception. (B) The principle component score measure of male splendid and (C) variegated fairy-wren responses to heterospecific song stimuli. Pairwise comparisons between control-neighbor, control-foreign, co-resident neighbor, and co-resident foreign are significant ( $P < 0.05$ ) for both species based on GLMMs. Error bars indicate 95% confidence intervals.

### ***Conspecific neighbor-stranger discrimination***

Splendid fairy-wrens responded more strongly to neighboring and foreign conspecific songs than to control songs but showed no difference in their response to neighboring and foreign conspecific songs (splendid fairy-wren conspecific response GLMM:  $F_{2,39} = 20.80$ ,  $P < 0.001$ ; see **Table 5** for pairwise  $P$  values; Supplementary Figure1A;

**Table 5** Pairwise comparisons from GLMMs of responses (principle component scores) of males of each species to conspecific playbacks

<i>Species</i>	<i>Treatment</i>	<i>Neighbor</i>	<i>Foreign</i>
Splendid fairy-wren	Control	$\leq 0.01^*$	$\leq 0.01^*$
	Neighbor		0.87
Variegated fairy-wren	Control	0.61	$\leq 0.01^*$
	Neighbor		0.03

\*  $P \leq 0.01$ ,  $P$  values are adjusted using least squares differences to account for multiple comparisons.

see Supplementary Table 2 for response variables, and Supplementary Table 7 for descriptive statistics). Variegated fairy-wrens responded more strongly to foreign conspecific songs than to control or neighbor songs and showed no significantly different response to control or neighbor songs (variegated fairy-wren conspecific response GLMM:  $F_{2,38} = 6.59$ ,  $P = 0.003$ ; see Table 5 for pairwise  $P$  values; Supplementary Figure 1B; see Supplementary Table 1 for response variables, and Supplementary Table 7 for descriptive statistics).

## Discussion

Like many species, fairy-wrens have been shown to use vocalizations to recognize conspecific group members (Payne et al. 1988; Payne et al. 1991; Colombelli-Negrel et al. 2011). Such recognition assists in coordination of group behaviors, allowing altruism or aggression to be directed toward appropriate individuals (Nowicki 1983; Boughman 1998; Hopp et al. 2001). We have shown here that song recognition can also occur across species. Male splendid and variegated fairy-wrens distinguish between the songs of heterospecific co-residents (group members) and non-co-residents (non-group members). Responses of both species to non-co-resident playbacks were rapid, with birds approaching the playback speaker, singing and scolding almost immediately after the presentation began. Both species responded more aggressively to non-co-residents than to co-residents, treating co-residents the same as a non-competitive heterospecific control. Such behavior may help the groups maintain joint territories, with individuals excluding non-co-resident heterospecifics while avoiding expending costly aggressive behaviors on known individuals.

Associations between heterospecifics can benefit individuals in many ways, and perhaps the most widely recognized method is through information sharing. For example, eavesdropping on alarm signals is known in other avian systems, but also in many mammalian systems and even in reptiles (Sullivan 1984; Randler 2006; Vitousek et al. 2007; Aschmeier and Maher 2011). Birds that are followers in mixed-species foraging flocks are able to increase foraging rates and decrease vigilance rates, perhaps relying on the information provided by flock leaders (Sridhar et al. 2009). However, such benefits in mixed-species assemblages do not necessarily rely on associations between particular individuals, but rather through broadcast information.

We suggest that in fairy-wrens, the heterospecific song discrimination may arise for at least 3 possible reasons. First, established heterospecific relationships may be more beneficial than new relationships. In established relationships, information sharing may be more efficient, information may be more reliable, or the joint group would be better able to coordinate behaviors such as territory defense, joint foraging, or predator detection. Alternatively, the heterospecific groups on shared territories may actually be cooperating with each other. Birds may have to exclude heterospecifics outside of a shared territory in a form of reciprocal cooperation to gain the benefits of heterospecific sociality (e.g., “pay-to-stay” hypothesis; Gaston 1978; Kokko et al. 2002). For example, a splendid fairy-wren may only tolerate a variegated fairy-wren that it shares a territory with if that individual helps exclude other splendid fairy-wrens. Our data do not allow us to test for cooperation, but we consider it a likely possibility. Further experiments examining each species’ response to heterospecific neighbors, strangers, and intruders when on a shared territory compared to a non-shared territory will be necessary to answer this question. A third possibility is that certain territories are of higher quality, and that although both species would prefer to exclude all heterospecific fairy-wrens, the costs of excluding other groups may exceed the benefits. Instead, individuals may permit the presence of one group and cooperate to exclude others. In this study, we were unable to address habitat quality of shared and solitary territories. However, because variegated fairy-wrens spend more time foraging and reduce their vigilance when associating with splendid fairy-wrens within a territory,



we hypothesize that the presence of the heterospecific is likely beneficial, regardless of territory quality. Additional studies of habitat use, territory quality, and costs and benefits of these heterospecific groups are required to begin to untangle these possible explanations.

Variiegated fairy-wrens were found to exhibit conspecific neighbor-stranger discrimination, whereas splendid fairy-wrens did not. This difference may reflect an insufficient sample size, but it is also possible that it is a result of differing levels of sperm competition in these 2 species (Webster et al. 2004; Rowe and Pruett-Jones 2011; Johnson and Pruett-Jones 2018). Other species are known to alter their response to competitors based on threat level. For example, song sparrows adjust their aggressive responses to neighbors based on the fertility of their social mate, exhibiting the dear-enemy effect only when their mate was not fertile (Moser-Purdy et al. 2017). Most fairy-wren species exhibit extreme reproductive promiscuity, including splendid and variegated fairy-wrens (Webster et al. 2004; Cockburn et al. 2013; Johnson and Pruett-Jones 2018), and neighbors should represent a reproductive threat to conspecific males. However, the presence of conspecific auxiliaries (Johnson and Pruett-Jones 2018) and territory sharing mitigates high levels of extra-pair paternity in the variegated fairy-wren while the presence of conspecific auxiliaries is associated with an increase in extra-pair paternity in the splendid fairy-wren (Webster et al. 2004). Thus, for splendid fairy-wrens, neighbors may represent a higher threat to paternity than they would to variegated fairy-wrens. In fairy-wrens, heterospecific group members either do not distinguish between neighbors and strangers or are responding to individuals that represent threats to their co-residents, regardless of their familiarity.

Significant changes in behavior when heterospecific group members were associating were only observed in variegated fairy-wrens. Many avian species have been observed to associate with more aggressive species that help deter nest predators (Bogliani et al. 1999; Quinn and Ueta 2008; Polak 2013). As splendid fairy-wrens are slightly more vigilant than variegated fairy-wrens, associating with splendid fairy-wrens may improve the ability of the group to detect and deter nest predators.

Both splendid and variegated fairy-wrens are cooperative breeders and helpers at the nest may improve nestling survival through

increased total provisioning rates (Clutton-Brock et al. 2001). However, variegated fairy-wrens have larger group sizes than splendid fairy-wrens, and the presence of auxiliary group members positively affects fledging success (Johnson 2016). Because of the importance of group size for reproductive success in variegated fairy-wrens, this species may show a greater benefit to heterospecific association, including the increased first nest fledging success, increased likelihood to re-nest following nest failure, and decreased extra-group paternity observed as a part of this study. We hypothesize that associations with splendid fairy-wrens allow variegated fairy-wrens to increase their effective group size without incurring the potential reproductive or resource competition costs represented by additional conspecific helpers (Seppanen et al. 2007; Sridhar et al. 2009). Although splendid fairy-wrens did not exhibit significant behavioral changes on shared territories, they did show a slight increase in foraging rates when associating with their co-resident. Splendid fairy-wrens also exhibited a marginally greater first nest fledging success on shared territories suggesting that they may benefit from the association. If splendid fairy-wrens do benefit from this association, their benefits may be less significant than variegated fairy-wrens or they may receive benefits that were not addressed by the methods of this study.

Because variegated and splendid fairy-wrens are non-migratory, their heterospecific associations can persist across years; and if these associations are mutually beneficial, they could have long-term consequences to survival and reproduction. This is a hypothesis that will require further testing and experimentation. Nevertheless, our demonstration of heterospecific song discrimination suggests one mechanism by which long-term associations can occur. Cooperative associations between individuals of different species are common in many other systems as well (Isack and Reyer 1989; Grutter and Bshary 2003; Goodale et al. 2010; Vail 2014; Dinets and Eligulashvili 2016), and these associations or responses to heterospecific information could be maintained by recognition and discrimination between known and unknown individuals as we have shown here. Such long-term associations have unique consequences for the behavior and ecology of the species involved, and further study into this system and others like it are merited to elucidate the role of recognition in heterospecific social group maintenance and behavior.

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**Data accessibility** Analyses reported in this article can be reproduced using the data provided by Johnson et al. (2018).

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## Supplementary Tables

**Table 1**

**Ethogram of behaviors recorded during focal follows of splendid and variegated fairy-wrens**

Behavior	Description
Foraging	Capturing and consuming insects or capturing and giving insects to other social group members.
Traveling	Flying short or long distances between vegetation that results in a change in location.
Singing	Producing Type I or Type I + II songs while not engaging in any of the behaviors foraging, traveling, or mobbing. Singing may occur during bouts of vigilance behavior. See Greig and Pruett-Jones (2008) for detailed descriptions of song types.
Contact calling	Producing contact calls while not engaging in any of the behaviors foraging, traveling, or mobbing. Contact calling may occur during bouts of vigilance behavior.
Mobbing	Approaching a potential threat (predator or intruder) while scolding, alarm calling (“seet” call), or clacking bill.
Vigilance	Perching high on a bush or exposed tree branch, head moving from side to side while not engaging in any of the behaviors foraging, traveling or mobbing. Contact calling or singing may occur during bouts of vigilance behavior.

**Table 2****Ethogram of response variables recorded during heterospecific and conspecific playback experiments**

Response	Description
Latency to first response	Length of time before the focal bird responded to the playback stimulus. First response could be any of the recorded behaviors (vigilance, song, scold, or approach).
Duration of vigilance	Amount of time the focal bird was vigilant. Vigilance consisted of perching high on a bush or exposed tree branch, head moving from side to side or looking toward the speaker.
Song	Number of Type I or Type I + II songs produced. See Greig and Pruett-Jones (2008) for detailed descriptions of song types. Type II songs were not included as an aggressive response as these songs are display songs aimed primarily at females and produced in duet form with predator calls (Greig and Pruett-Jones 2008).
Scold	Number of short calls produced in response to threat (predator or intruder), see Greig and Pruett-Jones (2008) for further description.
Approach	Number of times the focal bird moves towards the speaker location (flying or ground hopping), looking toward the speaker. Movement towards the speaker that was part of foraging behavior was not considered an approach.
Look*	Number of times the focal bird turned head toward the speaker.
Mate-guarding*	Number of mate guarding behaviors performed, which included display behaviors directed at the female, as well as chasing, or finding the female.
Bill-wipe*	Number of times the focal bird moves bill back and forth across perch.

Responses with \* were only recorded for conspecific experiments.

**Table 3**

**Model parameters for general linear mixed models examining vigilance behavior for splendid and variegated fairy-wrens when associating with their heterospecific co-resident and when alone.**

Model	Parameter	Estimate $\pm$ SE (Variance $\pm$ SD)	<i>t</i> value	<i>P</i>
Vigilance				
Final model	Intercept	21.59 $\pm$ 3.06	7.06	$\leq$ 0.01*
	Species	-7.92 $\pm$ 4.23	-1.87	0.07
	Species*association status	-10.77 $\pm$ 4.53	-2.38	0.03*
	Association status	3.31 $\pm$ 3.27	1.01	0.32
Random terms	Conspecific group ID	(43.90 $\pm$ 6.63)		
Rejected terms	Conspecific group size	-0.05 $\pm$ 1.89	-0.03	0.98

\* indicates significance at  $P \leq 0.05$

**Table 4**

**Model parameters for binomial, generalized linear mixed models examining reproductive success of splendid and variegated fairy-wrens and for proportion of extra-group young in variegated fairy-wren nests.**

Model	Parameter	Estimate $\pm$ SE or (Variance $\pm$ SD)	<i>z</i> value	<i>P</i>
Splendid fairy-wren any nest fledged				
Fixed effects	Intercept	-1.12 $\pm$ 0.31	-3.65	$\leq 0.01^*$
	Territory status	0.61 $\pm$ 0.38	1.61	0.11
Random effects	Social mother ID	(0.00 $\pm$ 0.00)		
	Social father ID	(0.00 $\pm$ 0.00)		
	Year			
Splendid fairy-wren first nest fledged				
Fixed effects	Intercept	-1.89 $\pm$ 0.50	-3.77	$\leq 0.01^*$
	Territory status	0.83 $\pm$ 0.47	1.76	0.08
Random effects	Social mother ID	(0.46 $\pm$ 0.68)		
	Social father ID	(2.32 $\times 10^{-8}$ $\pm$ 1.52 $\times 10^{-4}$ )		
	Year	(1.43 $\times 10^{-8}$ $\pm$ 1.19 $\times 10^{-4}$ )		
Splendid fairy-wren reneest				
Fixed effects	Intercept	-0.04 $\pm$ 0.29	-0.14	0.89
	Territory status	0.18 $\pm$ 0.37	0.49	0.63
Random effects	Social mother ID	(3.88 $\times 10^{-12}$ $\pm$ 1.97 $\times 10^{-6}$ )		
	Social father ID	(0.00 $\pm$ 0.00)		
	Year	(0.00 $\pm$ 0.00)		
Variegated fairy-wren any nest fledged				
Fixed effects	Intercept	-0.76 $\pm$ 0.47	-1.61	0.11
	Territory status	0.17 $\pm$ 0.48	0.35	0.73
Random effects	Social mother ID	(1.71 $\times 10^{-10}$ $\pm$ 1.31 $\times 10^{-5}$ )		
	Social father ID	(1.32 $\pm$ 1.15)		
	Year	(0.13 $\pm$ 0.36)		
Variegated fairy-wren first nest fledged				
Fixed effects	Intercept	-21.86 $\pm$ 3.82	-5.73	$\leq 0.01^*$
	Territory status	11.61 $\pm$ 2.87	4.04	$\leq 0.01^*$
Random effects	Social mother ID	(127.1 $\pm$ 11.27)		
	Social father ID	(922.3 $\pm$ 30.37)		
	Year	(0.00 $\pm$ 0.00)		
Variegated fairy-wren reneest				
Fixed effects	Intercept	-1.14 $\pm$ 0.45	-2.55	0.01*
	Territory status	1.02 $\pm$ 0.50	2.04	0.04*
Random effects	Social mother ID	(6.98 $\times 10^{-10}$ $\pm$ 2.64 $\times 10^{-5}$ )		
	Social father ID	(2.23 $\times 10^{-10}$ $\pm$ 1.49 $\times 10^{-5}$ )		
	Year	(6.28 $\times 10^{-2}$ $\pm$ 0.25)		
Proportion of extra-group young				
Final model	Intercept	0.12 $\pm$ 0.49	0.25	0.81
	Territory status	-1.29 $\pm$ 0.61	-2.11	0.04*
	# Conspecific male auxiliaries	-0.53 $\pm$ 0.28	-1.93	0.05
Random terms	Social mother ID	(3.99 $\pm$ 2.00)		
	Social father ID	(0.66 $\pm$ 0.81)		
	Year	(0.00 $\pm$ 0.00)		

\* indicates significance at  $P \leq 0.05$

**Table 5**

**Sample sizes for nesting categories of splendid and variegated fairy-wrens on shared and solitary territories**

		Solitary territory	Shared territory	
Splendid fairy-wren	Fledged first nest	10	26	
	Did not fledge first nest	26	72	
	Fledged (any nest)	15	42	
	Did not fledge (any nest)	42	58	
	Re-nested	24	38	
	Did not re-nest	24	34	
	Variegated fairy-wren	Fledged first nest	7	29
		Did not fledge first nest	38	66
Fledged (any nest)		20	34	
Did not fledge (any nest)		32	61	
Re-nested		9	30	
Did not re-nest		26	35	

**Table 6****Descriptive statistics of splendid and variegated fairy-wren responses to heterospecific playback stimuli**

Species	Behavior		Control	Co-resident	Neighbor	Foreign
Splendid fairy-wren	Latency to response (sec)	Mean	720.07	513.36	175.07	84.53
		Median	1080.00	295.50	29.00	27.00
		Std. Error	128.84	124.38	83.30	32.06
	Approach	Mean	0.07	0	1.71	1.47
		Median	0	0	2.00	1.00
		Std. Error	0.07	0.00	0.29	0.42
	Songs	Mean	0.73	1.64	5.07	5.00
		Median	0	0.50	4.00	3.00
		Std. Error	0.56	0.98	1.13	1.41
	Duration of vigilance (sec)	Mean	0	6.29	7.92	7.47
		Median	0	0	10.00	0
		Std. Error	0	4.01	13.84	5.58
	Scold	Mean	0.20	0.14	12.21	7.33
		Median	0	0	4.00	3.00
		Std. Error	0.14	0.14	7.13	2.51
Variegated fairy-wren	Latency to response (sec)	Mean	564.73	452.80	14.07	22.97
		Median	457.00	380.00	12.00	18.00
		Std. Error	118.06	104.27	2.65	5.55
	Approach	Mean	0	0.33	1.47	1.26
		Median	0	0	1.00	1.00
		Std. Error	0	0.16	0.29	0.21
	Songs	Mean	0.60	2.00	6.87	5.20
		Median	0	1.00	3.00	5.00
		Std. Error	0.34	0.82	1.59	1.22
	Duration of vigilance (sec)	Mean	0	0	38.20	16.60
		Median	0	0	0	0
		Std. Error	0	0	12.58	9.09
	Scold	Mean	1.27	0.27	14.80	11.27
		Median	0	0	11.00	7.00
		Std. Error	1.02	0.18	3.71	3.87

The response “songs” contains both Type I and Type I+II songs, but excludes Type II songs that are sung in response to predators and function as a signal to females (Greig & Pruett-Jones 2010).

**Table 7****Descriptive statistics of splendid and variegated fairy-wren responses to conspecific****playback stimuli**

Species	Behavior		Control	Neighbor	Foreign	
Splendid fairy-wren	Latency to response (sec)	Mean	460.90	77.18	21.36	
		Median	390.72	30.73	20.91	
		Std. Error	96.83	31.80	5.07	
	Approach	Mean	0.07	3.21	2.64	
		Median	0	2.00	2.50	
		Std. Error	0.07	0.64	0.60	
	Bill-wipe	Mean	0	0.21	0.14	
		Median	0	0	0	
		Std. Error	0	0.11	0.10	
	Mate-guarding	Mean	0.21	0.93	1.86	
		Median	0	0	1.00	
		Std. Error	0.11	0.40	0.66	
	Look	Mean	0	1.00	0.50	
		Median	0	0	0	
		Std. Error	0	0.42	0.23	
	Songs	Mean	2.79	6.36	10.43	
		Median	0.50	2.50	9.50	
		Std. Error	1.11	1.99	1.89	
	Duration of vigilance (sec)	Mean	37.51	219.12	225.93	
		Median	22.82	125.06	133.96	
		Std. Error	11.75	48.70	64.79	
	Variegated fairy-wren	Latency to response (sec)	Mean	381.40	132.74	58.45
			Median	223.31	31.06	16.41
			Std. Error	98.67	55.79	20.21
Approach		Mean	0	2.54	3.57	
		Median	0	2.00	4.00	
		Std. Error	0	0.53	0.49	
Bill-wipe		Mean	0	0.23	0.14	
		Median	0	0	0	
		Std. Error	0	0.12	0.10	
Mate-guarding		Mean	0	0.54	0.86	
		Median	0	0	0	
		Std. Error	0	0.24	0.34	
Look		Mean	0	0.46	0.50	
		Median	0	0	0	
		Std. Error	0	0.24	0.31	
Songs		Mean	2.50	4.69	7.64	
		Median	1.00	5.00	8.00	

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	Std. Error	1.32	0.84	1.22
Duration of vigilance (sec)	Mean	1.46	79.78	171.49
	Median	0	46.35	187.14
	Std. Error	1.03	35.94	35.61

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## Supplementary Figures

**Figure 1** The component score measures of male A) splendid and B) variegated fairy-wrens to conspecific neighbor and stranger songs as derived from the seven conspecific aggressive and mate-guarding variables. Treatment categories are songs of a 1) control, the red-capped robin, 2) neighboring conspecific male and 3) foreign conspecific male. Pairwise comparisons between control-neighbor and control-foreign are significant ( $P < 0.05$ ) for splendid fairy-wrens based on pairwise comparisons from generalized linear mixed models. Pairwise comparisons between control-foreign and neighbor-foreign are significant ( $P < 0.05$ ) for variegated fairy-wrens based on pairwise comparisons from generalized linear mixed models. Error bars indicate 95% confidence intervals.

