



# Acoustic Monitoring Reveals Congruent Patterns of Territorial Singing Behaviour in Male and Female Tropical Wrens

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## Abstract

Many animals defend territories against conspecific individuals using acoustic signals. In birds, male vocalizations are known to play a critical role in territory defence. Territorial acoustic signals in females have been poorly studied, perhaps because female song is uncommon in north-temperate ecosystems. In this study, we compare male vs. female territorial singing behaviour in Neotropical rufous-and-white wrens *Thryothorus rufalbus*, a species where both sexes produce solo songs and often coordinate their songs in vocal duets. We recorded free-living birds in Costa Rica using an eight-microphone Acoustic Location System capable of passively triangulating the position of animals based on their vocalizations. We recorded 17 pairs of birds for 2–4 consecutive mornings and calculated the territory of each individual as a 95% fixed kernel estimate around their song posts. We compared territories calculated around male vs. female song posts, including separate analyses of solo vs. duet song posts. These spatial analyses of singing behaviour reveal that males and females use similarly sized territories with more than 60% overlap between breeding partners. Territories calculated based on solo vs. duet song posts were of similar size and similar degrees of overlap. Solos and duets were performed at similar distances from the nest for both sexes. Overall, male and female rufous-and-white wrens exhibit very similar spatial territorial singing behaviour, demonstrating congruent patterns of male and female territoriality.

## Introduction

Territoriality in animals has historically been viewed as a male behaviour. White (1789) described territoriality occurring during the 'amorous season' as 'a jealousy [that] prevails among the male birds that they can hardly bear to be together in the same hedge'. Later, Ernst Mayr defined territory as 'an area occupied by one male of a species which it defends against intrusions of other males of the same species' (Mayr 1935; cited in Nice 1941). Today, territoriality is defined broadly as the defence of a space to the exclusion of conspecific individuals (Maher & Lott 1995) and often involves acoustic, visual or olfactory signals.

Although male territoriality has been studied in many different taxa, including mammals (e.g. Wronski & Plath 2006), fish (e.g. Market & Arnegard 2007), insects (e.g. Alcock & Kemp 2006) and birds (e.g. Krebs et al. 1978), there are many animals where females also demonstrate territorial behaviour. Female mice and voles defend their nest site from other females who may commit infanticide to take over a prime burrow (Wolff 1993). Female klipspringers *O. oreotragus* use scent marks to maintain their resource-based territories with or without male assistance (Roberts & Dunbar 2000). Female hummingbirds (e.g. *Panterpe insignis*) aggressively defend nectar-based territories from rival males and females (Wolf 1969, 1975). Very few

studies have compared male and female territoriality within a species, despite the potential for such a comparison to broaden our understanding of conflict and cooperation between the sexes. Some studies have focused on tropical birds where females engage in territorial behaviour in combination with their breeding partners, often involving both physical confrontations with rivals as well as territorial song (e.g. white-bellied antbirds *Myrmiciza longipes*, Fedy & Stutchbury 2005; black-bellied wrens *Thryothorus fasciatoventris*, Logue & Gammon 2004), demonstrating that tropical birds provide an opportunity for exploring male vs. female territoriality.

In this study, we compare the territory size of male and female rufous-and-white wrens *Thryothorus rufalbus*, a socially monogamous songbird where both sexes sing complex solo songs and combine their songs to produce duets (Mennill & Vehrencamp 2005). We used an Acoustic Location System – a multi-channel sound recording technique that triangulates the positions of animals based on sound recordings (Mennill et al. 2006) – to compare the territory sizes of males and females. As both sexes are known to engage in territorial behaviour (Mennill 2006), we predicted that the territories of males and females would be congruent and that size and overlap would be directly comparable between the sexes. We also analysed the importance of vocal duets for territory defence. Because both solos and duets play an important role in territory defence, as demonstrated in previous playback studies (Mennill 2006; Mennill & Vehrencamp 2008), we predicted that territories calculated using the location of duet songs would be congruent with territories calculated using the location of solo songs.

## Methods

### Study Species and Study Site

We monitored a population of rufous-and-white wrens in Sector Santa Rosa of the Area de Conservacion Guanacaste, Costa Rica (10°40'N, 85°30'W). Rufous-and-white wrens inhabit mature humid forest and late successional re-growth forest at this site. We captured birds with mist nets and banded them with unique combinations. We determined sex based on morphological measurements, observations of singing behaviour and behavioural observations of activities at the nest (see Mennill & Vehrencamp 2008; Topp & Mennill 2008). Colour-banded birds were monitored to assess their general areas of activ-

ity and nest locations, to inform the placement of our recording devices.

The singing behaviour of rufous-and-white wrens is well characterized. Both males and females have discrete repertoires of song types which they sing as solos or coordinate with their partner's songs in duets (Mennill & Vehrencamp 2005). Although song types are shared between neighbours, each bird's repertoire can be distinguished by subtle differences in frequency and fine-structural details. Both males and females sing solos and duets throughout the pre-breeding and breeding seasons (Topp & Mennill 2008; Hennin et al. 2009), and both solos and duets are common during territorial encounters with conspecific individuals (Mennill 2006; Mennill & Vehrencamp 2008). Males and females sing both solos and duets while separated by variable distances, ranging from 0.4 to 144.3 m; a prior investigation demonstrated that birds often approach each other following duets (Mennill & Vehrencamp 2008).

### Acoustic Location System

An Acoustic Location System offers an innovative approach for studying territoriality and movement in wild animals (Mennill 2011). This passive technique uses an array of microphones to estimate the positions of animals based on multichannel recordings of their vocalizations. Our Acoustic Location System is described in detail in Mennill et al. (2006). In brief, eight omnidirectional microphones were positioned around a resident pair's territory (inter-microphone distance of  $75.2 \pm 2.6$  m; mean  $\pm$  SE; rufous-and-white wren territories are large and separated from adjacent territories by distances of approx. 100 m; Mennill & Vehrencamp 2008). The eight microphones were connected by 1200 m of cable to a central computer, where sounds were recorded as eight-channel digital sound files using a multichannel data acquisition card (model: National Instruments DAQ-6260). The exact location of each microphone was determined using a survey-grade Global Positioning System (model: Ashtek ProMark2).

We analysed Acoustic Location System recordings of 17 pairs of rufous-and-white wrens collected over a 2-yr period. Each pair was recorded for the first 4–5 h of the morning (from approximately 5:00 am to between 10:00 and 11:00 am) on two to four consecutive mornings (May to June, 2003; April to May, 2004), providing a total recording time of  $9.65 \pm 3.20$  h per pair (mean  $\pm$  SE). Although this recording period is somewhat brief, anecdotal observations collected over years of studying birds in this

population suggest that birds move around their territories following a similar daily pattern, moving around most of their territory in the first hours of each morning, and suggest that these territories remain consistent throughout the year, providing partnerships do not change. Within the multimicrophone recordings collected over multiple days, our results show that both males and females demonstrated similar activity spaces across the 2–4 d of sampling. Consequently, we feel that our sampling period provides an adequate estimation of male and female territorial behaviour. Recordings were collected during the early stages of the breeding season, when both solo and duet output are high (Topp & Mennill 2008). The recordings used in this study were the same set of recordings used in a previous investigation of the distance between duetting pair members (Mennill & Vehrencamp 2008); recordings from mornings where birds received experimental playback in the previous investigation are not included in the current study, and two pairs from the previous investigation were excluded from the current analyses because of relatively low song rates.

### Multichannel Sound Analyses

In the laboratory, we used Syrinx-PC sound analysis software (J. Burt, Seattle, Washington) to annotate eight-channel sound spectrograms, surrounding each individual's song with the time and frequency cursors of Syrinx PC to create a database of all songs in our recordings. Each rufous-and-white wren has a repertoire of 4–14 song types that are individually distinctive, allowing us to assign all recorded songs to the resident male or female. Duets were distinguished as songs given by breeding partners that overlapped or occurred within 1.0 s of each other (following Mennill & Vehrencamp 2005).

We determined the position of singing birds using software written in MatLab (Mathworks Inc., Natick, MA, USA; details in Mennill et al. 2006 and Mennill & Vehrencamp 2008). This allowed us to calculate the position of each male and female with an accuracy of  $2.12 \pm 0.42$  m every time the bird sang a solo or duet (mean  $\pm$  SE; Mennill et al. 2006). We refer to these positions as 'song posts'. We did not include song posts where we could not obtain a repeatable, high-quality position estimate (i.e. recordings where songs were heavily overlapped by heterospecific sounds or ambient noise).

We calculated multiple estimates of birds' territories based on their song posts. First, we calculated territory size based on all song posts for each of the

34 birds (17 pairs). In this species, however, male song output is much higher than female song output, solo song output is much higher than duet song output, and individuals vary in their propensity to perform solos and duets (Mennill & Vehrencamp 2005; Topp & Mennill 2008). To account for these sources of variation in vocal output, we also subsampled our data to conduct comparisons of males vs. females with an equivalent number of song posts, balancing the number of song posts available for analysis against an attempt to maintain as large a sample size as possible for each comparison. Our dataset included 10 pairs with  $\geq 35$  female song posts (including both solo and duet songs), so we calculated territories based on 35 randomly selected song posts for these birds. Our dataset included 10 pairs with  $\geq 25$  female duet song posts, so we calculated territories based on 25 randomly selected duet song posts for these birds. Female solo songs were quite rare in our recordings, with only four pairs recorded producing  $\geq 25$  female solo song posts; we calculated fixed territories based on 25 randomly selected solo song posts for these pairs. Altogether we calculated six different types of territories based on estimates calculated around the following song posts: (1) all song posts for 34 birds (17 pairs); (2) all solo song posts for 34 birds (17 pairs); (3) all duet song posts for 34 birds (17 pairs); (4) 35 randomly selected song posts for 20 birds (10 pairs); (5) 25 randomly selected solo song posts for eight birds (four pairs); (6) 25 randomly selected duet song posts for 20 birds (10 pairs).

Male and female territories overlapped substantially for each pair, yet they usually had small regions that did not overlap (see Results). To evaluate the portion of the territory that was overlapping between pair members, we calculated the shared territory using the 'tabulate areas' function in ArcView. We calculated unshared area by subtracting shared area from the each bird's overall territory size, producing a measurement of the size of area that each pair member possessed beyond the part of their territory that overlapped with their partner.

The areas occupied by both males and females may be influenced by the position of their nests. We evaluated whether solo or duet song posts were given at different distances from the nest for both sexes. We calculated the average distance between each pair's nest and (1) male solo song posts, (2) female solo song posts, (3) male duet song posts and (4) female duet song posts. We conducted pairwise comparisons between the sexes and between solo vs. duet songs.

### Spatial Analysis

We used the kernel density estimator approach to calculate territory sizes based on song posts. Ninety-five per cent fixed kernel estimates are increasingly common in studies of home range and territory size (e.g. Thogmartin 2000; Mack et al. 2003; Franzreb 2006; Anich et al. 2009) and provide a robust technique for estimating territory size and shape (Seaman & Powell 1996). We used ArcView Geographic Information Systems software version 3.2 (Esri, Redlands, CA, USA) to calculate territories based on the birds' song posts. We calculated 95% fixed kernel estimates using the Animal Movement ArcView extension (Hooge & Eichenlaub 2000). We used least-squares cross-validation calculated within this extension to determine the appropriate smoothing parameter. As in Anich et al. (2009), we considered the areas inside the kernels to be an estimate of each bird's territory, based on the assumption that bird song is used as a territorial defence signal, an assumption that holds true in birds generally (Catchpole & Slater 2008) and is supported by playback studies of rufous-and-white wrens in particular (Mennill 2006; Mennill & Vehrencamp 2008). Past experience has taught us that the areas occupied by breeding pairs are largely exclusive for this species, except for very rare incursions by birds from neighbouring territories or floater males. Given that the birds' songs are individually distinctive, we can rule out the possibility that birds other than the focal pair are included in our territory estimates.

Although many previous studies have used minimum convex polygons to measure home range and territory size, the kernel estimation technique is considered to be superior (e.g. Seaman & Powell 1996; Seaman et al. 1999; Anich et al. 2009; Mennill 2011). Minimum convex polygon estimates of territory sizes are influenced heavily by outliers and sample size (Worton 1987). Kernels, on the other hand, require few points to calculate accurate areas of territory size (Seaman et al. 1999; Borger et al. 2006; Anich et al. 2009), and instead of using points on the periphery of the animal's home range, the kernel estimation approach uses densities of points to determine areas where animals are most likely to be located over time (Franzreb 2006).

Many researchers have argued that accurate home range and territory estimates require independence of observations (see de Solla et al. 1999). Recent studies, however, suggest that this is not always fea-

sible in biological systems (de Solla et al. 1999). A common method to test whether sampled points are independent is to determine Schoener's ratio, which is defined as the quotient of the mean squared distance between successive observations ( $t^2$ ) and the mean squared distance between each observation and the geometric centre of the territory ( $r^2$ ); a ratio of 2 indicates that points are independent (de Solla et al. 1999; Barg et al. 2005). We calculated Schoener's ratio for all of our points ( $0.80 \pm 0.07$ ; range 0.11–1.98) and for the randomly selected 35 points ( $1.05 \pm 0.07$ ; range 0.11–1.98; means  $\pm$  SE). Randomly selected points showed a higher Schoener's ratio indicating approach to independence, but neither measure met the criterion of a Schoener's ratio of 2. The value of using Schoener's ratio has been questioned, however, because animal movements are often non-random and thus autocorrelated observations are to be expected (de Solla et al. 1999). Subsampling as a method to reduce autocorrelation has been used in several studies; however, this technique reduces the sample size and may underestimate home range or territory size (de Solla et al. 1999). Studies that have attempted to control for independence often fail, even when subsampling (Barg et al. 2005; Franzreb 2006). de Solla et al. (1999) argue that eliminating autocorrelation in biological studies reduces their accuracy by removing animal's typical movement patterns. We argue that as our points are taken over a relatively lengthy sampling period ( $9:65 \pm 3:20$  h over 2–4 d of recordings, mean  $\pm$  SE, including many independent song bouts), they give a robust representation of rufous-and-white wren territorial behaviour.

### Statistical Analysis

Statistical analyses were performed with JMP 8.0 (SAS, Cary, NC, USA). Most of our data were normally distributed, except territory sizes based on duets which were log-transformed to achieve normality. We used paired tests to compare male vs. female territorial behaviour within each pair. All tests are two-tailed, and all values are shown as mean  $\pm$  SE. To explore the power of our non-significant results, we follow the advice of Nakagawa & Cuthill (2007) and report mean effect size (unstandardized effect size, expressed as differences in paired tests in units of m, m<sup>2</sup>, or percent) and 95% confidence intervals (CI<sub>0.95</sub>) around the unstandardized effect size.



## Results

### Territory Size and Number of Song Posts

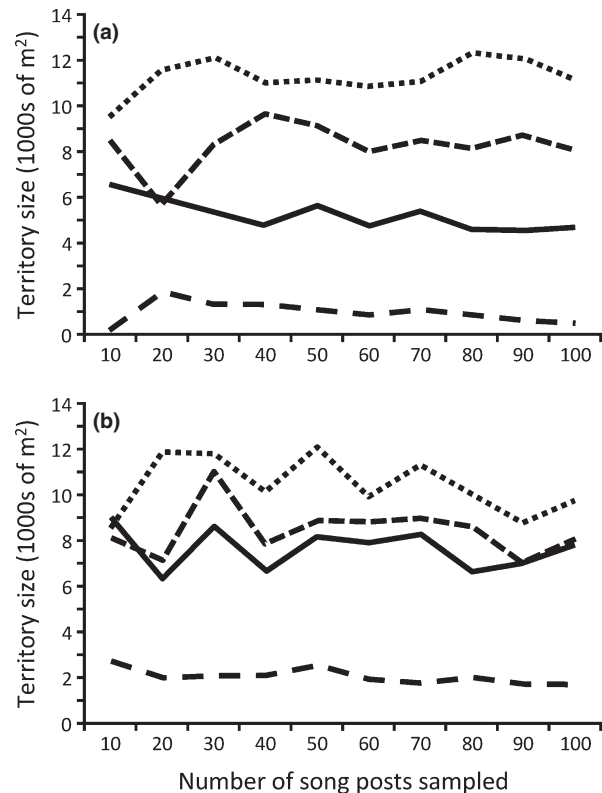
To evaluate whether our sampling of song posts allowed us to produce reliable estimates of territory size, we calculated territories based on randomly selected subsets of songs for each individual and evaluated how these territory sizes compared to the total estimated territory size based on all of their song posts. We found that the size of territories calculated using even very few song posts produced territory estimates that provide a reliable estimate of territory size (Fig. 1), as has been shown in previous studies that use kernelling methods (Seaman et al. 1999; Borger et al. 2006). For example, territories calculated using 100 randomly selected song posts produced measures of territory size that were not statistically different from measures calculated using 25 randomly selected song posts (paired *t*-test for *n* = 17 males: *t* = 1.2, *p* = 0.23; effect size: 428 m<sup>2</sup>, CI<sub>0.95</sub> = -299 to 1154 m<sup>2</sup>) or 35 randomly selected song posts (paired *t*-test for *n* = 17 males: *t* = 0.9, *p* = 0.39; effect size: 283 m<sup>2</sup>, CI<sub>0.95</sub> = -399 to 966 m<sup>2</sup>).

### Male vs. Female Territory Size

Male and female rufous-and-white wren territories varied dramatically in size between pairs, from territories smaller than 1000 m<sup>2</sup> to territories larger than 13 000 m<sup>2</sup> (Figs 2 and 3). Within pairs, male and female territories were similar in size when we compared kernel estimates using all song posts (males: 5678 ± 548 m<sup>2</sup>; females: 5240 ± 548 m<sup>2</sup>; paired *t*-test: *t* = 22.5, *p* = 0.31, *n* = 17 pairs with 97 ± 12 song posts per bird; effect size: 438 m<sup>2</sup>, CI<sub>0.95</sub> = -724 to 1600 m<sup>2</sup>). However, male song output is much higher than female song output in rufous-and-white wrens (Mennill & Vehrencamp 2005; Topp & Mennill 2008). When we controlled for sex differences in song output by using 35 randomly selected song posts for each sex, the same relationship held true; male and female territory size remained similar in pairwise comparisons (Fig. 2a; *t* = 0.24, *p* = 0.82, *n* = 10 pairs; effect size: 179 m<sup>2</sup>, CI<sub>0.95</sub> = -1506 to 1864 m<sup>2</sup>).

### Male and Female Solo vs. Duet Territory Size

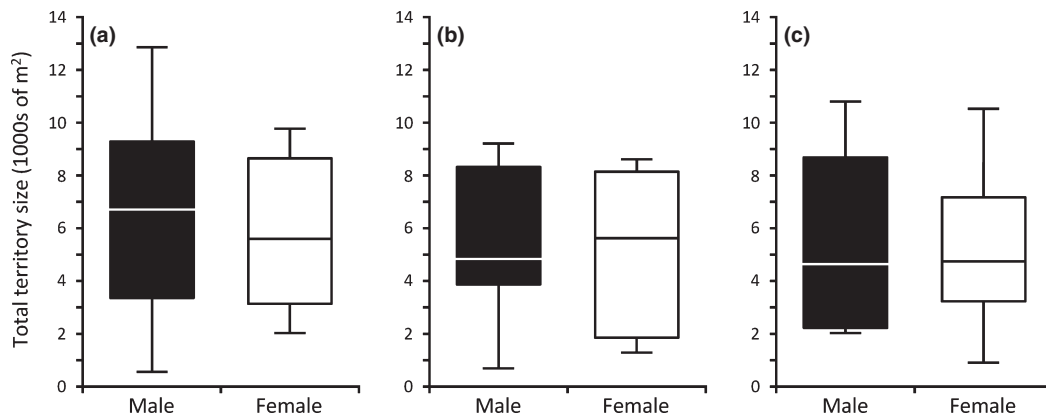
Males had similar territory sizes calculated on the basis of solos vs. duets whether all songs were considered (duets: 6676 ± 1005 m<sup>2</sup>; solos: 4991 ± 1005 m<sup>2</sup>;



**Fig. 1:** Territory sizes based on fixed kernel estimates around song posts of rufous-and-white wrens recorded with an eight-channel Acoustic Location System. Territory sizes are shown as a function of the number of song posts sampled for the four most extensively sampled males (a) and females (b). Territory size estimates vary dramatically across individuals, but are consistent within individuals as the number of song posts sampled increases.

*t* = 1.7, *p* = 0.11, *n* = 17 males with 127 ± 13 song posts per male; effect size: 1684 m<sup>2</sup>, CI<sub>0.95</sub> = -446 to 3815 m<sup>2</sup>) or whether 25 randomly selected song posts were considered (duets: 5363 ± 664 m<sup>2</sup>; solos: 4694 ± 664 m<sup>2</sup>; *t* = 1.0, *p* = 0.34, *n* = 10 males; effect size: 669 m<sup>2</sup>, CI<sub>0.95</sub> = -834 to 2171 m<sup>2</sup>). Females showed significantly larger territories calculated on the basis of their duet song posts compared to solo song posts (duets: 6023 ± 522 m<sup>2</sup>; solos: 4357 ± 522 m<sup>2</sup>; *t* = 3.2, *p* = 0.007, *n* = 15 females with 71 ± 18 song posts per female). We conducted the same comparison using only 25 randomly selected song posts on four birds (duets: 6916 ± 1102 m<sup>2</sup>; solos: 5209 ± 1102 m<sup>2</sup>) and found that female solo and duet territory sizes were similar, although the small sample size precluded statistical analysis.

Males and females shared similar territory sizes when considering all solo song posts (males: 5129 ± 905 m<sup>2</sup>; females: 4357 ± 905 m<sup>2</sup>; *t* = 0.9,



**Fig. 2:** Neotropical rufous-and-white wren territory size estimates for males (black) and females (white). The sexes are compared for fixed kernel estimates around 35 randomly selected song posts (a), 25 randomly selected solo song posts (b) and 25 randomly selected duet song posts (c). Box plots show the full range of data, with whiskers showing maximum and minimum values, boxes showing 25th to 75th quartiles, and the central line showing the median.

$p = 0.41$ ,  $n = 15$  pairs with  $54 \pm 8$  song posts per bird; effect size:  $772 \text{ m}^2$ ,  $CI_{0.95} = -1169$  to  $2712 \text{ m}^2$ ) or 25 randomly selected solo song posts, although a statistical test could not be performed with the low sample size (Fig. 2b). For duet song posts, males and females also shared similar territory sizes on the basis of all duet song posts (males:  $6676 \pm 679 \text{ m}^2$ ; females:  $5642 \pm 679 \text{ m}^2$ ;  $t = 1.5$ ,  $p = 0.15$ ,  $n = 17$  pairs with  $43 \pm 8$  song posts per bird; effect size:  $1033 \text{ m}^2$ ,  $CI_{0.95} = -405$  to  $2473 \text{ m}^2$ ) or 25 randomly selected duet song posts (Fig. 2c;  $t = 0.9$ ,  $p = 0.42$ ,  $n = 8$  pairs; effect size:  $632 \text{ m}^2$ ,  $CI_{0.95} = -1118$  to  $2383 \text{ m}^2$ ).

#### Male vs. Female Shared and Unshared Territory Spaces

When all song posts were used to calculate the size of shared area between males and females, we found males and females shared a similar percentage of their territory in common with their breeding partner (males:  $61.7 \pm 8.0\%$ , females:  $65.8 \pm 8.0\%$ ;  $t = 0.5$ ,  $p = 0.40$ ,  $n = 17$  pairs; effect size:  $4.1\%$ ,  $CI_{0.95} = -13.0$  to  $21\%$ ). Similar results were found for males and females using 35 song posts (males:  $65.5 \pm 8.0\%$ ; females:  $63.0 \pm 8.0\%$ ;  $t = 0.3$ ,  $p = 0.78$ ,  $n = 10$  pairs; effect size:  $2.5\%$ ,  $CI_{0.95} = -16.7$  to  $21.7\%$ ). When all song posts were used to calculate the size of their unshared territory spaces (i.e. spaces occupied by only one pair member extending beyond the shared territory area; Fig. 3), males had similar-sized unshared territory spaces to females (males:  $2097 \pm 548 \text{ m}^2$ ; females:  $1659 \pm 548 \text{ m}^2$ ;  $t = 0.8$ ,  $p = 0.44$ ,  $n = 17$  pairs; effect size:  $438 \text{ m}^2$ ,

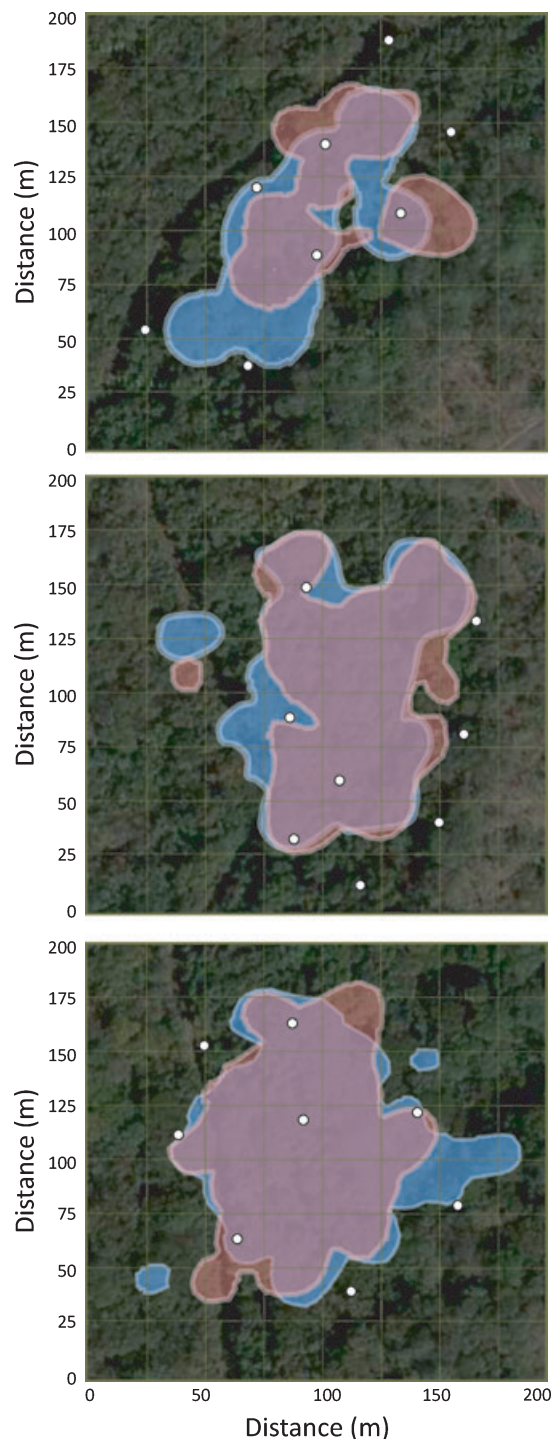
$CI_{0.95} = -725$ – $1600 \text{ m}^2$ ). When unshared territory size was calculated using 35 randomly generated points for each sex, again the sexes shared similar unshared territory spaces (males:  $2062 \pm 744 \text{ m}^2$ ; females:  $1883 \pm 744 \text{ m}^2$ ;  $t = 2.5$ ,  $p = 0.05$ ,  $n = 10$  pairs; effect size:  $179 \text{ m}^2$ ,  $CI_{0.95} = -1506$  to  $1864 \text{ m}^2$ ).

#### Distance of Solos and Duets from Nest Site

Males sang solos and duets at similar distances from the nest (solos:  $38.4 \pm 3.8 \text{ m}$ , duets:  $40.9 \pm 3.8 \text{ m}$ ;  $t = 0.7$ ,  $p = 0.51$ ,  $n = 17$  males; effect size:  $2.5 \text{ m}$ ,  $CI_{0.95} = -5.5$  to  $10.6 \text{ m}$ ). Females also sang solos and duets at similar distances from the nest (solos:  $36.1 \pm 3.4 \text{ m}$ , duets:  $41.9 \pm 3.4 \text{ m}$ ,  $t = 1.7$ ,  $p = 0.11$ ,  $n = 15$  females; effect size:  $5.8 \text{ m}$ ,  $CI_{0.95} = -1.4$  to  $13.0 \text{ m}$ ). Comparing between the sexes, males and females sang solos at similar distances from the nest (males:  $38.2 \pm 4.2 \text{ m}$ , females:  $36.1 \pm 4.2 \text{ m}$ ,  $t = 0.5$ ,  $p = 0.72$ ,  $n = 15$  pairs; effect size:  $2.0 \text{ m}$ ,  $CI_{0.95} = -6.9$  to  $11.0 \text{ m}$ ), and they sang duets at similar distances from the nest (males:  $42.0 \pm 2.5 \text{ m}$ , females:  $41.8 \pm 2.5 \text{ m}$ ,  $t = 0.1$ ,  $p = 0.93$ ,  $n = 16$  pairs; effect size:  $0.2 \text{ m}$ ,  $CI_{0.95} = -5.0$  to  $5.5 \text{ m}$ ).

#### Discussion

Tropical animals often exhibit different behaviours and life-history traits from their better-studied north-temperate counterparts. For example, many tropical birds defend territories throughout the year, experience high nest predation and may experience low levels of extra-pair matings (Stutchbury &



**Fig. 3:** Maps showing fixed kernel estimates of the territories of male and female rufous-and-white wrens calculated using the song posts for birds recorded with an Acoustic Location System. Male territories are shown in blue, female territories in red, and areas of overlap are shown in purple. Three example pairs of territories in Santa Rosa National Park, Costa Rica, are shown. White dots show the positions of the eight microphones of the Acoustic Location System used to triangulate the positions of the birds.

Morton 2001; Macedo et al. 2008; Tori et al. 2008). These features may contribute to similar sex roles for some behaviours in tropical birds, including the shared use of song in territory defence (Slater & Mann 2004). Our spatial analyses of rufous-and-white wren singing behaviour reveal similarities in territorial behaviour between the sexes; based on the spatial position of their song posts, males and females show congruent patterns of territoriality. In addition, territories calculated on the basis of solo and duet song posts are congruent both within and between the sexes.

Very few studies have compared male and female territoriality in birds, and the three north-temperate zone studies that have made such a comparison did not statistically evaluate differences between males and females (Howell & Chapman 1997; Elchuk & Wiebe 2003; Walker et al. 2005). These studies revealed different patterns: male red-shouldered hawks *Buteo lineatus* tended to have larger territories than females (Howell & Chapman 1997), the opposite was true for northern flickers *Colaptes auratus* (Elchuk & Wiebe 2003), whereas both sexes of golden eagle *Aquila chrysaetos* had similar-sized territories (Walker et al. 2005). Several studies on mammals have found that males tend to have larger home ranges than females (Madison 1980; Lambin & Krebs 1991; Schülke & Kappeler 2003). Mammals, however, exhibit different mating systems and behaviours than birds, and consequently they are difficult to compare. Our own study of tropical birds shows that both males and females have very similar patterns of territory use, with similar degrees of overlap between territories calculated on the basis of song posts. Depending on the analysis, we found that 60–66% of a bird's territory overlaps with their partner's territory. Whether this is a small or large amount of overlap is hard to determine because so few studies have looked at territory overlap in males and females. Female red-shouldered hawks had 100% overlap with their partners territories, while 75% of the males home range overlapped with their partner's (Howell & Chapman 1997). Future studies need to be completed on both tropical and temperate species to determine whether similarities in male and female territorial behaviour are widespread or rare, and whether temperate and tropical animals differ.

Comparisons of duet and solo singing behaviour may help to illuminate the functions of duet and solo songs in duetting birds. To date, very few studies have compared duets and solos in duetting species (Hall 2009; but see Hennin et al. 2009). Our

analyses show that rufous-and-white wrens have similar-sized solo and duet territories, and that birds perform solo and duet songs at similar distances from the nest. This suggests that solo and duet songs share similar functions. If solos and duets are used for territory defence (Wiley & Wiley 1977) – as has been shown through playback experiments with rufous-and-white wrens (Mennill 2006) and other duetting birds (reviewed in Douglas & Mennill 2010) – then we would expect birds to perform both solos and duets at similar locations, and for their occurrence to be common during interactions with rivals. Although the recordings we analysed here did not include interactions with rival birds, our study shows that duets and solos are performed over similar areas, which is consistent with the idea that duets and solos function similarly in territory defence.

Many duetting animals live in environments with dense vegetation where maintaining visual contact with a breeding partner may be challenging. Previous studies have offered empirical support for the acoustic contact hypothesis for duets, where duetting is understood to allow breeding partners to locate each other in thick vegetation (Thorpe 1963), a hypothesis that is not mutually exclusive with the territory defence hypothesis. The congruent patterns we found for male and female wren territories are compatible with the acoustic contact hypothesis. If duets are used by mated pairs to maintain acoustic contact in dense vegetation (Thorpe 1963) – as has been shown in a previous spatial investigation in this species (Mennill & Vehrencamp 2008) and possibly other species (Mays et al. 2006; Logue 2007) – then the sexes should have similar-sized territories, and they should be expected to perform both solos and duets within a similar area.

Territories calculated on the basis of song posts showed substantial overlap between pair members, but also revealed peripheral unshared territory spaces. Whether calculated using all song posts or a randomly selected subset of 35 song posts, males and females had similarly sized unshared territory spaces. This phenomenon may be a sampling artefact; song posts sampled near the periphery of a bird's territory may contribute to protrusions in the kernel estimate beyond the bird's core territory area. Sampling for longer periods than in the current study might result in even greater congruence between male and female territories as birds' positions at less-frequently visited edges of their territories become better sampled. Alternatively, males and females might exhibit differences in behaviour near territory edges. For example, male and female

rufous-and-white wrens may vary subtly in their foraging strategies, which could contribute to these unshared territory areas. Different foraging strategies have been found in male and female sea birds, where females tend to travel further out to sea than males (Weimerskirch et al. 1997; Lewis et al. 2002), although our observations of foraging rufous-and-white wrens, together with other researchers' observations (Ahumada 2001), have revealed no such sex differences in this species. The excess territory spaces we measured do not appear to represent extraterritorial forays; such forays generally occur in silence (Naguib et al. 2001; Fedy & Stutchbury 2005; Anich et al. 2009), and the presence of singing indicates that rufous-and-white wrens were not making these movements covertly.

In summary, our recordings of male and female song posts using an Acoustic Location System reveal congruent patterns of male and female territoriality in rufous-and-white wrens; pair members occupy territories of similar size and with a high degree of spatial overlap. In addition, territories calculated on the basis of solo vs. duet songs are directly similar for both sexes. Like many aspects of the behaviour of tropical animals, female territorial behaviour is largely unexplored. Our results show convergent territorial behaviour in male and female rufous-and-white wrens, which parallels sex similarities in singing behaviour.

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