The Condor 109:686–692

THE DUETTING BEHAVIOR OF PACIFIC COAST PLAIN WRENS

JESSICA L. CUTHBERT[1] AND DANIEL J. MENNILL
Department of Biological Sciences, University of Windsor, 401 Sunset Ave., Windsor, Ontario, N9B3P4, Canada

Abstract. We provide the first detailed analysis of the vocal behavior of Pacific coast Plain Wrens (*Thryothorus modestus modestus*). Male Plain Wrens sing two categories of song phrase; one phrase is given as a solo song or duet introduction (I-phrases), while the other is sung primarily during duets (M-phrases). Females sing only one category of song phrase, usually during duets (F-phrases). Both sexes have repertoires of their respective song categories. Plain Wren duets show extreme temporal coordination: duets typically begin with male I-phrases, which are followed by the rapid alternation of female F-phrases and male M-phrases. These patterns are congruent with the solo and duet singing behavior of a sister taxon to the Plain Wren, the Canebrake Wren (*Thryothorus modestus zeledoni*). Our analyses of Plain Wren songs and duets reveal pronounced differences between males and females and contribute to our understanding of the complex duetting behavior of *Thryothorus* wrens.

Key words: Canebrake Wren, duet, Plain Wren, song, Thryothorus modestus.

Comportamiento de Canto en Dueto en *Thryothorus modestus modestus*

Resumen. Presentamos el primer análisis completo del comportamiento vocal de *Thryothorus modestus modestus*. Los machos emiten dos categorías de frases de canto; una frase es presentada como un canto solitario o una introducción al dueto (frases I), mientras que la otra sólo es emitida durante los duetos (frases M). Las hembras sólo emiten una de las categorías de canto, generalmente durante los duetos (frases F). Ambos sexos tienen repertorios propios de sus respectivas categorías de canto. Los duetos de *T. m. modestus* mostraron un alto grado de coordinación: los duetos generalmente empiezan con las frases I del macho, las cuales son seguidas por una rápida alternancia de las frases F de las hembras y las frases M de los machos. Estos patrones concuerdan con el comportamiento de canto solitario y en dueto de *T. m. zeledoni*. Nuestro análisis de los cantos y duetos de *T. m. modestus* revela diferencias pronunciadas entre machos y hembras y contribuye al entendimiento del complejo comportamiento de canto en dueto de las aves del género *Thryothorus*.

Vocal duets are joint vocalizations usually given by the male and female of a mated pair. Duets are sung in widely varying forms by more than 220 bird species worldwide (Hall 2004). Many species of *Thryothorus* wren sing highly complex duets, including the Black-bellied Wren (*T. fasciatoventris*; Logue and Gammon 2004), Rufous-and-white Wren (*T. rufalbus*; Mennill and Vehrencamp 2005), Bay Wren (*T. nigricapillus*; Levin 1996a), Buff-breasted Wren (*T. leucotis*; Gill et al. 2005), and Plain Wren (*T. modestus*; Mann et al. 2003). Plain Wrens are divided into two groups based on body size, plumage coloration, and geographic distribution. Canebrake Wrens (*Thryothorus modestus zeledoni*) are larger, grayer, and occur along the Caribbean coast of Central America, while Pacific coast Plain Wrens (*Thryothorus modestus modestus*) are smaller, browner, and occur along the Pacific coast of Mexico and Central America (Brewer 2001). Whether these groups represent different species or subspecies is controversial (Ridgeley and Gwynne 1989, Stiles and Skutch 1989, Brewer 2001). However, recent analyses show that substantial genetic differentiation exists between Canebrake and Plain Wrens (Mann et al. 2006).

Mann et al. (2003) described remarkably complex patterns of coordinated singing in Canebrake Wrens. Male Canebrake Wrens begin duets with a high-frequency introductory phrase (termed the ''I-phrase''), which is answered by a female ''F-phrase'' (Marshall-Ball et al. 2006; previously referred to as female ''A-phrase'' by Mann et al. [2003]). The male then sings a low-frequency ''M-phrase'' (male ''B-phrase'' of Mann et al. [2003]) and the duet that follows is composed of rapidly alternating female F-phrases and male M-phrases, represented by the expression $I(FM)_n$ (Mann et al. 2003, Marshall-Ball et al. 2006). Whether Plain Wrens share a similar pattern of coordination in their duet songs has not been rigorously evaluated.

We studied the vocalizations of a population of Plain Wrens inhabiting tropical dry forests on the northern Pacific coast of Costa Rica. We sought to describe the songs and duets of these Pacific coast Plain Wrens, and to compare the acoustic characteristics of Plain Wren vocalizations with those of their sister taxon, the Canebrake Wren (Mann et al. 2003).

Manuscript received 31 August 2006; accepted 25 April 2007.

[1] E-mail: cuthbe2@uwindsor.ca

METHODS

FIELD TECHNIQUES

We studied Plain Wrens living in Santa Rosa National Park in the Area de Conservación Guanacaste, Costa Rica (10°40′N, 85°30′W), at an altitude of 300 m above sea level. The Neotropical dry forest habitat in Santa Rosa is composed of a mosaic of mature humid forest and late-successional regenerating forest.

We recorded Plain Wren songs over a period of 44 days between May 2003 and June 2004. As part of a larger study of *Thryothorus* wrens in Costa Rica, we positioned eight stationary microphones around each of 11 nonoverlapping sites, recording at each site for four consecutive mornings between 05:00 and 09:00. This produced over 160 hr of eight-channel recordings. Ten of the 11 recording sites were occupied by a territorial pair of Plain Wrens, and the remaining site was occupied by a lone male. At many recording sites, a neighboring pair of wrens could often also be detected. We color-banded four males and three females, and all color-banded birds were consistently observed in the same small area of the study site. Consequently, we are confident that each recording site represented a different Plain Wren territory.

DEFINITION OF VOCALIZATIONS

Plain Wren vocalizations are loud and have unique frequency characteristics. Male and female songs are composed of phrases, and each phrase is made up of a number of distinct syllables (terminology follows Mann et al. [2003]). Plain Wrens can produce songs as solos or duets. Solos may be composed of a single phrase or a phrase repeated many times in tandem, which we distinguish as ''tandem solos.''

ANALYSES OF SOLO SONGS AND DUETS

To quantify the fine structure of each Plain Wren phrase type, we randomly chose four or five well-recorded phrases from each male and female to be measured (n = 11 males, 10 females). In total, we analyzed 55 male I-phrases, 46 male M-phrases, and 46 female F-phrases. Due to the large vocal repertoires of both sexes (see below) and extensive variation in phrase types among individuals, we were unable to classify phrases by ''phrase type,'' and the four or five phrase types measured differed for each individual. We measured maximum frequency, minimum frequency, phrase bandwidth, song length, and number of distinct syllables for each song using SYRINX-PC (J. Burt, Seattle, Washington). We distinguished male from female songs by analysis of subtle patterns of song overlap during duets, comparison to patterns of singing in Canebrake Wrens (Mann et al. 2003), and direct observation of color-banded birds. We used discriminant function analysis to quantitatively evaluate differences among the three phrase types; factors with eigenvalues greater than one were considered to contribute substantially to differentiation. For detailed analysis of male tandem solos, we chose ten well-recorded tandem solos from each of the ten paired males. For detailed analysis of duets, including the number of phrases in duets, duet precision, and the order of contribution of male and female phrases, we chose five duets from each wren territory when possible. To calculate male singing rate we counted all solos sung in one hour from each morning, and to calculate duetting rate we counted all duets sung in two hours from each morning. To ensure that we measured song rates that were independent of interactions with conspecifics, we selected periods when our recordings contained no songs from neighboring birds. All values are presented as mean ± SE.

RESULTS

PLAIN WREN SONG PHRASES

We identified three distinct categories of Plain Wren song phrases. The first was sung exclusively by males and made up the majority of Plain Wren vocalizations. We termed these male songs I-phrases (after Mann et al. 2003) because they typically ''introduced'' duets, although they were frequently sung as solos. Each male possessed a repertoire of I-phrases, and we detected more than 40 different types of I-phrase in this population. We conservatively estimate that each male possessed a repertoire of at least 20 I-phrases, although our repertoire sampling was not exhaustive, with only 16 hr of recording per male. Male I-phrases were typically high-frequency whistled phrases, although they were highly variable in the number of syllables and syllable structure (Fig. 1). I-phrases consisted of 2–8 syllables (average: 4.8 ± 0.2 syllables per phrase; n = 55) and covered a broad frequency range of 2.0–9.1 kHz (average minimum frequency: 4.2 ± 0.1 kHz; average maximum frequency: 7.5 ± 0.2 kHz), with an average bandwidth of 3.3 ± 0.1 kHz (n = 55). The average length of an I-phrase was 0.68 ± 0.03 sec (n = 55). Males sang solo I-phrases at a rate of one song every 23.5 ± 4.5 sec (6.4 ± 0.4 sec when silent intervals greater than 30 sec were excluded). Males sang with eventual variety, singing one type of I-phrase many times before switching to another type.

We identified two subcategories of I-phrase, distinguished by frequency characteristics and syllable structure. Some I-phrases were tonal, mid-to-high-frequency songs that typically ended with a high-frequency syllable (e.g., leftmost four I-phrases shown in Fig. 1). These I-phrases showed the greatest variation in number of syllables and frequency characteristics. Other I-phrases were mechanical, atonal songs, with three or four short introductory syllables and three or four loud, broadband syllables (e.g., rightmost two I-phrases shown in Fig. 1). These atonal I-phrases exhibited lower frequency characteristics than the tonal I-phrases. It is unclear whether these structural differences in tonal and atonal I-phrases correspond to functional differences.

In addition to I-phrases, male Plain Wrens also sang M-phrases, typically composed of a quick, low-frequency syllable (Fig. 1). M-phrases covered a broad frequency range between 1.6 and 7.2 kHz (average minimum frequency: 2.0 ± 0.0 kHz; average maximum frequency: 5.4 ± 0.2 kHz), with an average bandwidth of 3.4 ± 0.2 kHz (n = 46). The average

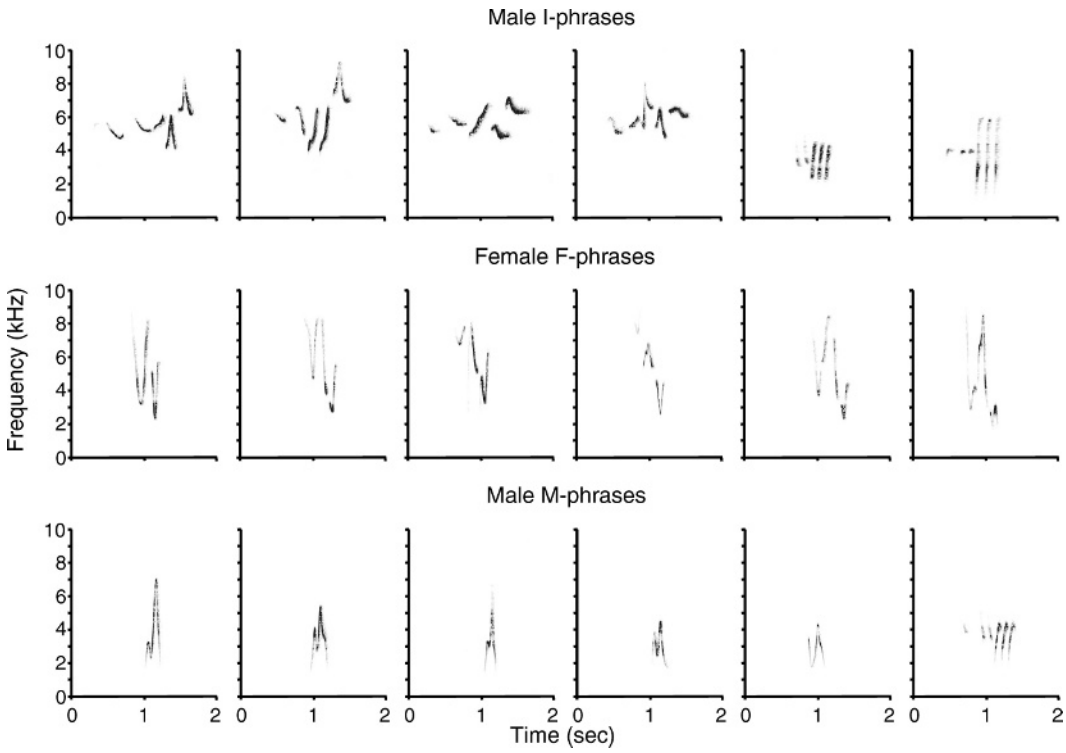

FIGURE 1. Sound spectrograms of Pacific coast Plain Wren songs, showing examples of male I-phrases (top row), female F-phrases (middle row), and male M-phrases (bottom row).

length of an M-phrase was 0.15 ± 0.01 sec (n = 46). Rarely, male M-phrases were composed of a series of seven syllables (e.g., rightmost M-phrase in Fig. 1), which closely resembled the atonal subcategory of I-phrase. Although similar in fine structure, these phrases were clearly distinguishable by context, with atonal I-phrases sung repeatedly as part of the male's solo songs, and the multisyllable M-phrase only being contributed to duets in conjunction with female song. M-phrases were most often sung during duets (see below).

Plain Wren males often sang tandem solos (Fig. 2) consisting of a series of phrases repeated in rapid succession, frequently at the beginning of a bout of song. One type of tandem solo was composed of multiple I-phrases, usually a single I-phrase sung repeatedly, but occasionally two types of I-phrase. These tandem solos contained an average of 6.4 ± 0.2 repeated I-phrases (range: 2–13; n = 100). A second type of tandem solo was composed of both I- and M-phrases, and was widely variable in structure. Most of these tandem solos were composed of rapidly alternating I- and M-phrases, while some were composed of repetitions of an IMM arrangement. Rarely, tandem solos were composed of a single I-phrase followed by many M-phrases.

Female Plain Wrens sang only one category of song phrase (Fig. 1), termed F-phrases. F-phrases consisted of 1–4 syllables (average: 2.6 ± 0.1; n = 46). F-phrases usually began with a high-frequency chevron-shaped syllable followed by a rapid downward frequency sweep. F-phrases covered a broad frequency range from 1.9 to 9.4 kHz (average minimum frequency: 2.8 ± 0.1; average maximum frequency: 8.0 ± 0.1 kHz), with an average bandwidth of 5.2 ± 0.1 kHz (n = 46). The average length of an F-phrase was 0.30 ± 0.01 sec. F-phrases were sung as solos and, very rarely, as F-phrase tandem solos (Fig. 2). Usually, these female tandem solos were closely followed by a male song. F-phrases were most commonly sung as part of duets; we encountered only 50 F-phrase solos, but several hundred duets containing F-phrases.

Discriminant function analysis clearly separated I-, M-, and F-phrases on the basis of fine structural features, assigning songs to the correct phrase type with 94% accuracy. Song length and minimum frequency contributed strongly to the differentiation of I-phrases (longer, higher minimum frequency) from M- and F-phrases (shorter, lower minimum frequencies); song length and maximum frequency contributed strongly to the differentiation of M-phrases (shorter, lower maximum frequencies) from F-phrases (longer, higher maximum frequencies).

DUET STRUCTURE AND DUET RATE

Plain Wren duets were highly coordinated antiphonal displays, integrating all three Plain Wren phrases

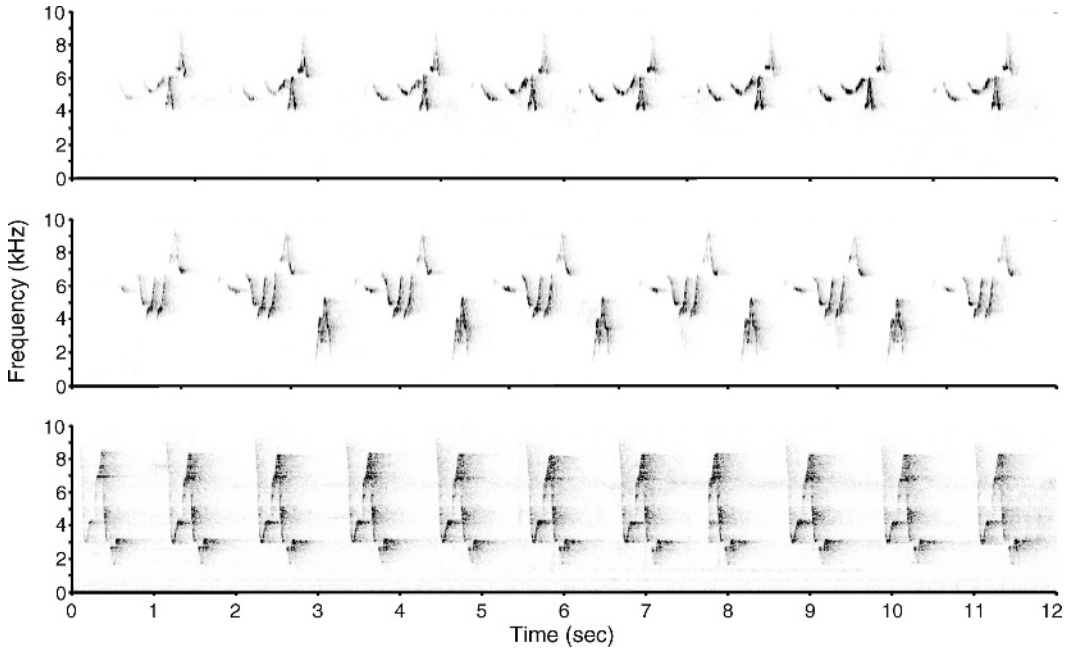

FIGURE 2. Sound spectrograms of Pacific coast Plain Wren tandem solos. The top spectrogram shows a male tandem solo composed solely of I-phrases and the middle spectrogram shows a male tandem solo composed of I- and M-phrases. The bottom spectrogram shows an example of a female F-phrase tandem solo. This song format is rare.

(Fig. 3). Most duets (88% ± 2%) began when a female contributed an F-phrase in response to a male I-phrase. The male then switched to an M-phrase and the ensuing duet was composed of repeating alternations of F- and M-phrases. Males terminated the majority of duets (79% ± 2%, $n = 396$) by singing a final M-phrase or by switching back to I-phrases when the female stopped contributing F-phrases. This was the most common type of duet we recorded, represented by the expression $I(FM)_n$. A minority of duets began with a female F-phrase followed by a male I-phrase or M-phrase, and duets occasionally began with a female tandem solo, in which the male inserted his I- or M-phrase between two female F-phrases (Fig. 3). Duets varied widely in the number of FM repeats (range: 1–16 repeats per duet, average: 5.4 ± 0.6 repeats, $n = 46$ duets). Many bouts of duetting contained multiple repetitions of the $I(FM)_n$ pattern, where the male switched back to sing an I-phrase following one of the female's F-phrases. Rarely, duets were composed of only male I-phrases and female F-phrases, i.e., $(IF)_n$, with the singing male never switching to an M-phrase. Duets were often immediately followed by one or more unanswered male I-phrases or by one or more cycles of male I- and M-phrases.

The duet rate was extremely variable among pairs. Some pairs performed over 30 duets in the 2 hr studied each morning, while others performed no duets during this time. The average duet rate was 3.5 ± 0.7 duets hr^{-1} ($n = 10$ pairs).

PRECISION OF DUET TIMING

Plain Wren duets were sung with extreme precision with regard to alternating male and female phrases. Gaps between duet components were very short (average gap between I- and F- phrases: 0.13 ± 0.02 sec; between F- and M- phrases: 0.05 ± 0.01 sec; and between M- and F- phrases: 0.18 ± 0.01 sec; $n = 46$ duets). During the rapidly alternating cycle of F- and M-phrases, the delay between female F-phrases and male M-phrases was significantly shorter than the delay between male M-phrases and female F-phrases (paired t-test: $t = 7.0$, $P < 0.001$). Overlapping male and female phrases were rare; of the 46 duets we analyzed in detail, eight showed overlapping I- and F-phrases, one showed overlapping F- and M-phrases, and one showed overlapping M- and F-phrases.

DISCUSSION

Plain Wrens in the tropical dry forest of northwestern Costa Rica demonstrate complex and coordinated singing behavior with pronounced intersexual differences. Males and females exhibit variation in both the fine structure of their phrases and the timing of their songs. Male Plain Wrens sing solos throughout the

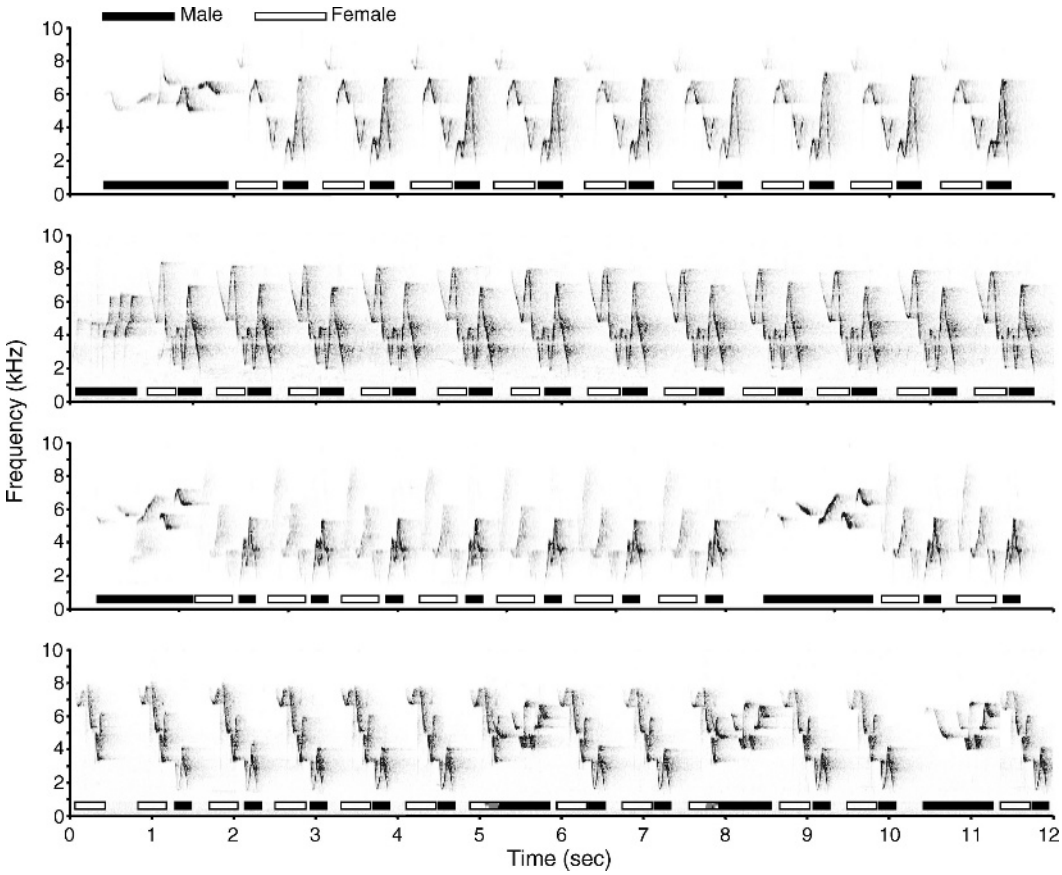

FIGURE 3. Sound spectrograms of the highly coordinated duets of Pacific coast Plain Wrens. White bars underscore female songs and black bars underscore male songs (overlapping male and female songs in the bottom spectrogram are shown in gray). The top two spectrograms depict the typical cyclic $I(FM)_n$ structure of duets. The third spectrogram depicts a male Plain Wren immediately commencing a new duet cycle with an I-phrase when the female fails to offer an F-phrase in response to his preceding M-phrase. The bottom spectrogram depicts a duet that begins with a female F-phrase.

morning, whereas females sing very few songs outside of duets. Plain Wren duets follow a cyclic pattern of phrase alternation. Males typically begin duets and, after females reply, pairs alternate F- and M- phrases in rapid succession one to 16 times.

The three phrase types sung by Plain Wrens are sexually distinctive and easily distinguished by discriminant function analysis based on basic temporal and frequency measurements. Our analyses revealed a novel similarity in fine structure between atonal I-phrases and an alternative type of M-phrase. Neither the atonal I-phrases nor the alternative M-phrases have been found in previous studies of song in this species (Mann et al. 2003, Marshall-Ball et al. 2006). In a recent study of singing behavior of the related Banded Wren (*Thryothorus pleurostictus*), Trillo and Vehrencamp (2005) showed that particular song types were used preferentially in different contexts. Future studies should examine novel Plain Wren phrase types and investigate the contexts in which these phrase types are produced, to determine whether these acoustic differences parallel functional differences.

Many hypotheses explain the function of duetting in birds (reviewed by Hall 2004). Our descriptive account of differences in song performance between male and female Plain Wrens offers some insight into duet function. The overwhelming majority of Plain Wren duets (88%) are created by females singing an F-phrase in response to their partner's I-phrase, demonstrating that females control the realized production of duets. Independent female songs are rare; when females do begin singing independently, males usually respond with their own song, creating a duet. As Mann et al. (2003) suggest, the highly temporally coordinated nature of Plain Wren duets

seems to indicate a cooperative function of duets, and our observations of intensive counterduetting at territory boundaries indicate that Plain Wren duets do play a role in territory defense (JLC and DJM, pers. obs.). However, the intersexual differences in Plain Wren singing strategies—including an apparent reluctance for males to permit female song to occur without being followed by a male phrase, as well as a significantly shorter delay of male responses to female phrases during duets—suggest that Plain Wren duets may also represent a form of mate guarding. If female solos are attractive to rival males, then a territorial male may attempt to acoustically guard his partner by combining his song with hers to create a duet and advertise her status as a mated female. The mate-guarding hypothesis was rejected in a study of Buff-breasted Wrens (Gill et al. 2005), but supported in studies of Bay Wrens (Levin 1996b) and Canebrake Wrens (Marshall-Ball et al. 2006), suggesting that duet function varies for even closely related species. For Plain Wrens, future studies should include experimental playback techniques, such as those used by Marshall-Ball et al. (2006), to test whether duets play a role in acoustic mate guarding.

The structure of Plain Wren songs closely matches the structure of Canebrake Wren songs described by Mann et al. (2003), although there are some fine-scale differences. For example, males of both taxa sing multisyllable I-phrases with frequencies in the 4–9 kHz range, but the I-phrases of male Plain Wrens extend into lower frequencies (2.0 kHz) than those of the Canebrake Wren. Plain Wren I-phrases may contain up to eight syllables, and those of Canebrake Wrens only six. The duets of both taxa follow the $I(FM)_n$ pattern, however Mann et al. (2003) found that 96% ± 2% of all Canebrake Wren duets began with male I-phrases, whereas we found that 88% ± 2% of all Plain Wren duets began with this phrase. Mann et al. (2003) did not find a clear pattern in the sex of the bird that terminates duets, whereas we found that more than three-quarters of Plain Wren duets were terminated by males. In addition, we found significantly shorter latencies from female F-phrases to male M-phrases relative to the latencies from male M-phrases to female F-phrases, whereas Mann et al. (2003) found no such differences in Canebrake Wrens.

Canebrake Wrens and Plain Wrens occupy markedly different habitats. Canebrake Wrens on the Caribbean slope of Costa Rica inhabit lowland moist forest, swamp, scrub, and cattle pasture (Mann et al. 2003). Plain Wrens in our study population on the Pacific coast occupy mature humid forest and late-successional regenerating forests. We speculate that the lower frequency of some Plain Wren I-phrases may be adapted to maximize transmission through a more densely vegetated forest habitat, while the more open vegetation that the Canebrake Wren inhabits may favor the transmission of higher-frequency vocalizations (Brown and Handford 2000), but only one population of each sister taxon has been studied. Although recent molecular evidence indicates significant genetic differences between these sister taxa (Mann et al. 2006), our analyses reveal a high level of similarity between Plain Wren and Canebrake Wren song and duet structure.

Neotropical *Thryothorus* wrens are renowned as singers of some of the most complex duet songs in the animal kingdom (Mann et al. 2003), yet their duets vary tremendously in structure across species. Duet structure varies from loosely coordinated, overlapping male and female songs, as in Rufous-and-white Wrens (Mennill and Vehrencamp 2005), to coordinated, alternating male and female songs, as in Black-bellied Wrens (Logue and Gammon 2004), to tightly coordinated, interposing male and female songs, as in Bay Wrens (Levin 1996a), Buff-breasted Wrens (Gill et al. 2005), and Canebrake Wrens (Mann et al. 2003). Our analysis of songs from the Pacific coast of northwest Costa Rica demonstrates that Plain Wrens sing among the most complex duets in this genus.

Support for this study was provided by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the University of Windsor. We thank N. Mann, L. Marshall-Ball, and P. Slater, whose research on Canebrake Wrens inspired this investigation. We thank two anonymous referees for their helpful comments.

LITERATURE CITED

BREWER, D. 2001. Wrens, dippers and thrashers. Christopher Helm, London.

BROWN, T. J., AND P. HANDFORD. 2000. Sound design for vocalizations: quality in the woods, consistency in the fields. Condor 102:81–92.

GILL, S. A., M. J. VONHOF, B. J. M. STUTCHBURY, AND E. S. MORTON. 2005. No evidence for acoustic mate-guarding in duetting Buff-breasted Wrens (*Thryothorus leucotis*). Behavioral Ecology and Sociobiology 57:557–565.

HALL, M. L. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology 55:415–430.

LEVIN, R. 1996a. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. Animal Behaviour 52:1093–1106.

LEVIN, R. 1996b. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. Animal Behaviour 52:1107–1117.

LOGUE, D. M., AND D. E. GAMMON. 2004. Duet song and sex roles during territory defence in a tropical bird, the Black-bellied Wren, *Thryothorus fasciatoventris*. Animal Behaviour 68:721–731.

MANN, N. I., F. K. BARKER, J. A. GRAVES, K. A. DINGESS-MANN, AND P. J. B. SLATER. 2006. Molecular data delineate four genera of "*Thryothorus*" wrens. Molecular Phylogenetics and Evolution 40:750–759.

MANN, N. I., L. MARSHALL-BALL, AND P. J. B. SLATER. 2003. The complex song duet of the Plain Wren. Condor 105:672–682.

MARSHALL-BALL, L., N. MANN, AND P. J. B. SLATER. 2006. Multiple functions to duet

singing: hidden conflicts and apparent cooperation. Animal Behaviour 71:823–831.

MENNILL, D. J., AND S. L. VEHRENCAMP. 2005. Sex differences in singing and duetting behavior of Neotropical Rufous-and-white Wrens (*Thryothorus rufalbus*). Auk 122:175–186.

RIDGELY, R. S., AND J. A. GWYNNE. 1989. A guide to the birds of Panama with Costa Rica, Nicaragua and Honduras. Princeton University Press, Princeton, NJ.

STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.

TRILLO, P. A., AND S. L. VEHRENCAMP. 2005. Song types and their structural features are associated with specific contexts in the Banded Wren. Animal Behaviour 70:921–935.