Sexually antithetical song structure in a duet singing wren

David M. Logue1,2,3, Erika E. Droessler1, David W. Roscoe1, John R. Vokey4, Drew Rendall5 & Robyn M. Kunimoto1,5

(1 Department of Biological Sciences, University of Lethbridge, Alberta, Canada; 3 Smithsonian Tropical Research Institute, Balboa, Republic of Panama; 4 Department of Psychology, University of Lethbridge, Alberta, Canada)

(Accepted: 8 February 2007)

Summary
Black-bellied wrens (Thryothorus fasciatoventris) use loud songs to communicate sex over long distances. We compared male and female songs recorded from a central Panamanian population of black-bellied wrens. All nine measured features differed significantly between the sexes. Males sang lower fundamental frequencies than females, but this difference cannot be explained by simple body size-frequency scaling. A discriminant function analysis correctly discriminated the singer’s sex for all songs in the analysis. When viewed as sonograms, the terminal syllables of male and female songs exhibited opposite structure – all male songs ended in V-shaped syllables, and all female songs ended in arc-shaped syllables. The degree and character of dimorphism lead us to describe song structure in this population as ‘sexually antithetical’. Variation in song dimorphism throughout this species’ range provides an excellent opportunity to test the hypothesis that signal degradation during transmission selects for divergent signal structure.

Keywords: Darwin’s Principle of Antithesis, bird song, female song, acoustic adaptation hypothesis, sex differences, animal communication, signal evolution, Pheugopedius fasciatoventris.
Introduction

Two animals are said to communicate when one (the ‘sender’) emits a signal that affects the behavior of the other (the ‘receiver’, Bradbury & Vehrencamp, 1998, pp. 2-3). A signal’s effectiveness is determined largely by its structure (Marler, 1955). Selection tends to optimize signal structure, up to the point that further optimization is constrained. For a signal to function optimally, it must be recognized by a receiver. In nature, the probability of correct recognition is diminished by processes beyond the sender’s control: signals degrade during transmission (Morton, 1975) and both senders and receivers make mistakes (Wiley, 1994). For a signal to be evolutionarily stable, it must elicit beneficial behavior on average from receivers in spite of normal levels of random variation during signal production, transmission, and reception – otherwise non-signaling mutants will enjoy a selection advantage over signalers. In cases where a single receiver must attend to two classes of signals and signalers benefit from different responses to the two classes, optimization will select for signals that remain sufficiently distinct after transmission that receivers consistently distinguish one from the other. The degree of distinctiveness is expected to correlate positively with both (a) the degree of random variation during signal production, transmission and reception, and (b) the relative payoff to the sender for correct versus incorrect discrimination.

Signal distinctiveness can be achieved by structural divergence along one or more axes of variation. Darwin’s (1872) Principle of Antithesis describes the theoretical limit of signal divergence, in which two signals are structural opposites. His most famous example of the Principle involves visual signaling in the domestic dog (Canis lupus familiaris). Darwin explained that a hostile dog “walks upright and very stiffly; his head is slightly raised, or not much lowered; the tail is held erect and quite rigid... the pricked ears are directed forwards and the eyes have a fixed stare” (p. 50). He contrasts this posture with that of a submissive dog, in which “the body sinks downwards or even crouches, and is thrown into flexuous movements; his tail, instead of being held stiff and upright, is lowered and wagged from side to side... his ears are depressed and drawn backwards, but not closely to the head; and his lips hang loosely” (p. 51).

Research since Darwin suggests that the Principle of Antithesis describes a special case of a broader evolutionary pattern. Namely, that two signals selected to elicit different responses from a given class of receivers will evolve
Sexually antithetical bird song

Sexually antithetical bird song toward opposite ends of one or more axes of variation (Morton, 1977; Hurd et al., 1995; Collias, 2000). Strictly speaking, for two signals to be antithetical (that is, opposites) they must occupy opposing sides of a threshold (as in ‘upward’ and ‘downward’) or opposing extremes of a continuum (as in ‘black’ and ‘white’). According to these criteria, the signal pair ‘tail erect’ versus ‘tail lowered’ is antithetical because these signals occupy opposing sides of the threshold ‘tail level’, whereas the signal pair ‘short call’ and ‘long call’ are not antithetical (example from Collias, 2000), because no duration threshold exists and calls could evolve to be longer or shorter than they actually are. Nevertheless, selection favoring signals that would not be misinterpreted by receivers may have driven the evolution of both forms of signal distinctiveness.

Sexually Distinctive Behavior and Song Structure

In most north temperate breeding birds, only the males emit the long, loud vocalizations known as ‘songs’. Among tropical and southern hemisphere breeders, however, female song is quite common (Slater & Mann, 2004). In those (mostly tropical) species in which it has been studied, an individual’s response to song playback depends on the sex of the recorded bird, indicating that receivers recognize a conspecific’s sex based on song alone (reviewed in Logue, 2005). In at least some species, neighbors and non-territorial floaters are attracted to opposite sex solo-singing birds (Levin, 1996; D.M.L., unpubl. data). Honest and effective communication of sex will generally benefit singing birds, because a bird that is mistaken for the wrong sex risks attracting same-sex rivals and repelling potential mating partners. Strongly dimorphic song structures would be most effective at accurately conveying sex to extra-pair birds when random processes affect signal production, transmission, or reception. In species with sex-specific vocal traditions (Wickler & Seibt, 1988; Levin et al., 1996; Price, 1998), highly dimorphic song features may also facilitate offspring learning of sex-appropriate song types.

While studying duet singing in a central Panamanian population of black-bellied wrens (T. fasciatoventris, nominate Pheugopedius fasciatoventris, Mann et al., 2006), we noticed remarkably strong sexual dimorphism in the structure of the birds’ songs. We herein quantify this dimorphism and interpret our findings with respect to the Principle of Antithesis.
Methods

Species and study sites

Ranging from Costa Rica to Northern Colombia, Black-bellied Wrens are socially monogamous insectivores that hold territories year-round. Males are substantially larger than females (average ± SD: male weight 27.86 ± 2.4 g, female weight 22.16 ± 2.1 g), but otherwise the sexes appear identical to human observers. Adults of both sexes sing repertoires of discrete song types. Songs are loud, with the great majority of sound energy concentrated in the fundamental frequency (Figures 1, 2 and 6). Both sexes sing solo songs, and mated pairs sing in rapid alternation to form duets. Each individual shares about half of its song types with neighbors of the same sex (Logue, 2004). Several lines of evidence indicate that both sexes learn the structural details of their songs: (1) individual repertoires vary (Logue, 2004, 2006), (2) repertoires are partially shared (Logue, 2006), (3) levels of song sharing decrease with increasing geographical distance (D.M.L., unpubl. data), (4) wrens belong to the Suborder Passeres in which all members are believed to learn songs (Kroodsma, 2004) and (5) learning by both sexes has been demonstrated in the congeneric Bay Wren (T. nigricapillus, Levin et al., 1996). In addition to songs, black-bellied wrens emit brief (1-3 note), sex specific, tonal vocalizations, which have been termed male cream-o-wheat calls and female bell calls (Ridgely & Gwynne, 1989; Logue, 2004). These vocalizations appear in different contexts and elicit different responses than songs, so we did not consider them in the present study.

The study site is in and around the village of Gamboa (9°07′N, 79°41′W), near the geographic center of the Republic of Panama. We made an effort to sample broadly from within the study site by including pairs from three different forest patches. The pairs at the farthest extremes of the study site were separated by approximately 10 km. With the exception of one male who eluded several capture attempts, all birds in this study were trapped with mist nets and marked with unique combinations of colored leg bands. Birds were sexed by body size; the accuracy of this method of sexing has been verified with genetic techniques (Logue & Gammon, 2004).

Recording and song classification

Songs were record from 2001-2004 during both spontaneous singing and song playback. In 2001, recordings were collected with a RadioShack® (Fort
Sexually antithetical bird song

Worth, TX, USA) condenser microphone (product No. 33-3014) in a 45 cm aluminum parabolic reflector and a Marantz® (Itasca, IL, USA) audiocassette recorder (PMD-222). In 2002, recordings were taken with a Sennheiser (Old Lyme, CT, USA) condenser microphone (ME62) mounted in a 60 cm Telinga (Tobo, Sweden) Pro Universal parabola and a Sony (New York, NY, USA) MiniDisc recorder (MZ-R700; Logue et al., 2005). In 2003 and 2004, recordings were collected with the same Sennheiser microphone mounted in a 45 cm aluminum parabolic reflector, and a Sony Minidisc recorder (MZ-N1). All recordings were played into the microphone input of a Compaq Presario 1693 (Hewlett-Packard, Palo Alto, CA, USA) with an ESS Technology Solo sound card (Fremont, CA, USA) and digitized at 44.1 kHz in Syrinx (John Burt, http:www.syrinxpc.com/index.html).

We compiled the known repertoires of ten mated pairs. We chose pairs for analysis based on their location (to produce a geographically broad sample within our study population) and on the number of songs recorded (well recorded birds were preferred). Our song collections, though extensive, are almost certainly subsets of the birds’ true repertoires. However, we see no reason why incomplete repertoire sampling would systematically bias our results. For the purpose of classifying song types, songs were visualized as sonograms (Hanning window, 1024 points per window) in Syrinx 2.3a (John Burt, http:www.syrinxpc.com/index.html). One observer (D.M.L.) compiled the highest quality recordings of each song type sung by each individual. Two observers (E.E.D. and R.M.K.), working independently, inspected these known repertoires from all twenty subjects. The observers compared each song to holotypes of song types defined for a previous study, and either assigned the song to an existing type or labeled the song as a new type (thereby defining a new holotype). If the two observers agreed on the assignment of a particular song, the song was accepted as belonging to that type. If the two observers did not agree, they met with a third observer (D.M.L.), and arrived at a consensus classification.

Measuring song features

The following song features were examined: (1) number of notes, (2) song duration, (3) note rate, (4) minimum fundamental frequency, (5) maximum fundamental frequency, (6) fundamental frequency range, (7) mean fundamental frequency, (8) degree of frequency modulation, and (9) shape of the
terminal syllable on a sonogram. One observer scored each feature in all songs.

We used sonograms generated in Syrinx to extract features one through six and feature nine. All measurements were made with the viewing window maximized, the time axis fixed at 2 ms per line, and with a visible frequency range 0-6.0 kHz. Sonograms used to measure features one through three were generated using a Hanning window shape with 512 points per window. Notes were defined as unbroken traces on a sonogram. We measured song durations to the nearest 0.1 s. Note rate was the number of notes divided by the song duration. Sonograms used to measure features four through seven were constructed with Hanning windows using 1024 points per window. This large window size allows good frequency resolution (9.0 Hz). Minimum and maximum frequencies were measured by placing the on-screen cursors in the vertical center of the lowest and highest frequency traces, respectively. The minimum frequency was subtracted from the maximum frequency to arrive at the frequency range.

The terminal syllable of each song was characterized as belonging to one of three categories: ‘V’, ‘arc’, or ‘other’. We use the term ‘syllable’ to mean stereotyped units comprising songs and including one or more notes. ‘V’ syllables appear on sonograms as traces that decreased, and then increased in frequency (Figure 1). ‘Arc’ syllables appeared as traces that increased, and then decreased in frequency (Figure 2). Both ‘V’ and ‘arc’ syllables sometimes included an amplitude break near the temporal center of the syllable. We defined any terminal syllable that was neither a ‘V’ nor an ‘arc’ as ‘other’.

We used the Explore and Score module of Sound Analysis Pro 1.04 (hereafter ‘SA+’, Tchernichovski et al., 2004) to extract features seven and eight. This module uses multi-taper spectral analysis to automatically measure a variety of acoustic features from recorded sounds. Prior to analysis with SA+, songs were band pass filtered (0.6-5.5 kHz) in Syrinx. Extraneous sounds from non-focal animals were removed using Syrinx’s cursor-delimited filter. Songs in which extraneous sounds could not be eliminated without damaging the signal were not analyzed with SA+. In SA+, we adjusted the Feature Calculation options so that the program attended to the frequency range 0.3-5.5 kHz. All other options were set to default. By adjusting amplitude and entropy thresholds for each song, one observer (D.W.R.) ensured that SA+ measured the song while ignoring as much of the background and reverberation as was possible. SA+ automatically measures many
Sexually antithetical bird song

Figure 1. Sonograms of three male black-bellied wren song types (rows), each sung by two males (columns). Note the variation in the structure of the V-shaped terminal syllables, including amplitude breaks in songs a, a′, c, and c′. Notice also the variation between song types (compare rows), between renditions of a song type (compare columns), and between the sexes (compare to Figure 2). Examples were chosen for sonograms on the basis of recording quality. Sonograms for this Figures 1, 2, and 5 were created in Syrinx (Hanning window, 1024 points) and then digitally airbrushed to reduce the appearance of reverberation, background noise, and vocalizations from other birds.

Figure 2. Sonograms of three female black-bellied wren song types (rows), each sung by two females (columns). The arc-shaped terminal syllables are clearly visible in all sonograms. Terminal syllables include amplitude breaks in songs c and c′.
acoustic features, but we determined a priori that we were interested in the features mean mean frequency (hereafter, ‘mean frequency’) and mean frequency modulation (hereafter, ‘FM’) because variation in these features should persist in spite of environmentally induced perturbations. Mean frequency measures the average fundamental frequency of the song. FM is the average absolute value of the slope of the frequency traces. FM is measured in degrees such that for a flat trace (no change in frequency over time) FM = 0°, and for a vertical trace (instant change in frequency) FM = 90° (Ofer Tchernichovski personal comment). A high FM value indicates that the fundamental frequency is intensely modulated.

Statistical analyses

Univariate tests for sex differences

When analyzing behavioral data, the individual subject is almost always defined as the independent unit of analysis. Researchers make this choice because they want to extrapolate their findings to the population of individuals from which the sample was drawn. Indeed, in most cases the individual is the appropriate unit for studying questions of selection, because selection acts most directly on individuals (as opposed to genes, groups, etc.). Our data, however, are extracted from learned song types that evolve by cultural transmission in a population of birds (Freeberg, 2000; Gammon et al., 2005), and may be subject to cultural selection. Because song types are sex specific, it is not possible to compare song characteristics between the sexes while fully and simultaneously accounting for variation in the random factors ‘song type’ and ‘individual’. We reasoned that of these two factors, the one with the greatest among-group variance should be defined as the independent unit of analysis. In both sexes, for all quantitative variables, the among-song type variance exceeded the among-individual variance (Table 1). We therefore analyzed the data at the level of the song type, while accounting for some of the variability attributable to individual differences within song-type. There are two important consequences of this choice: (1) Our findings should be extrapolated to the population of song types from which our recordings were drawn, rather than the population of individuals from which our subjects were drawn; and (2) Each individual’s influence on the data is dependent on the number of song-types recorded from that individual (more song-types are more influential) and the rarity of those song-types in our data set (rarer
Table 1. Variance of song feature values among individuals and among song types.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Male among individual variance</th>
<th>Male among song type variance</th>
<th>Female among individual variance</th>
<th>Female among song type variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Notes</td>
<td>0.075</td>
<td>0.87</td>
<td>0.057</td>
<td>0.73</td>
</tr>
<tr>
<td>Duration(s)</td>
<td>0.0045</td>
<td>0.037</td>
<td>0.0044</td>
<td>0.027</td>
</tr>
<tr>
<td>Note rate (s⁻¹)</td>
<td>0.21</td>
<td>0.88</td>
<td>0.095</td>
<td>1.1</td>
</tr>
<tr>
<td>Minimum frequency (kHz)</td>
<td>0.00079</td>
<td>0.0049</td>
<td>0.0041</td>
<td>0.041</td>
</tr>
<tr>
<td>Maximum frequency (kHz)</td>
<td>0.014</td>
<td>0.037</td>
<td>0.093</td>
<td>0.38</td>
</tr>
<tr>
<td>Frequency range (kHz)</td>
<td>0.014</td>
<td>0.092</td>
<td>0.088</td>
<td>0.45</td>
</tr>
<tr>
<td>Mean frequency (kHz)</td>
<td>0.0050</td>
<td>0.017</td>
<td>0.010</td>
<td>0.083</td>
</tr>
<tr>
<td>FM(degrees)</td>
<td>1.3</td>
<td>17</td>
<td>6.1</td>
<td>28</td>
</tr>
</tbody>
</table>

songs are more influential). In our analyses, no one individual’s influence exceeded 17%, and the median influences (males = 9.9%, females = 9.9%) corresponded closely to the mean influences (males = 10.0%, females = 10.0%) for both sexes. We conclude that the level of heterogeneity of influence is acceptable and that our data are representative of the songs from our study area.

We conducted randomization analyses (Manly, 1997) to assess each of the continuous variables (i.e., all measured variables except terminal note shape) at the level of song type, while accounting for some of the within-type variation among individuals. For each analysis, we randomized the observed data to generate a null distribution that assumes no sex difference in song structure. We then compared the observed difference between male and female songs to this null distribution to test the null hypothesis that chance alone can explain the observed magnitude of sex differences. We offer the following example using ‘duration’, but the procedure was identical for all of the continuous variables.

We programmed a routine in Poptools to randomly select one representative of each song type. The routine generated a column containing the duration of each of these songs. The values in that column were then randomly assigned to the groups ‘simulated male’ or ‘simulated female’. The number of songs assigned to each group matched the true number of song types recorded from male and female birds, respectively. The program determined the arithmetic means of the two groups, and stored the difference (simulated male mean – simulated female mean). This routine (select repre-
sentatives of each song type → randomly assign them to a sex → store the
mean sex difference) was iterated 10,000 times, generating the frequency dis-
tribution of simulated sex differences expected if ‘sex’ does not affect song
duration. We calculated the observed average durations of all song types,
from which we derived the male and female averages (the average song type
duration within each sex). We subtracted the observed female mean from the
observed male mean, to arrive at the observed sex difference. Poptools then
determined the proportion of the null distribution that was greater than the
observed sex difference. This proportion is the realized probability (p-value)
of obtaining the observed sex difference (or greater) from a population in
which male and female song types are of equal mean duration.

The influence of size on fundamental frequency
Male black-bellied wrens are larger than females (Logue & Gammon, 2004),
and as a general rule, large organisms are capable of producing lower fre-
quencies than small organisms (Morton, 1977; Fitch & Hauser, 1995). Since
we are interested in selection for dimorphic song rather than body size con-
straints on sound production, we wanted to know if body size dimorphism
alone could account for the observed use of lower frequencies by male black-
bellied wrens (see Results). We used principal component analysis to reduce
the tarsus length, flat wing length, and weight to a single variable indicative
of overall size. We then set up a general linear model (GLM) with ‘mean
frequency’ as the dependent variable, the principal component representing
‘size’ as a covariate, and ‘sex’ as a fixed factor. In this analysis, ‘mean fre-
quency’ is the average mean frequency of the individual’s repertoire, and the
individual is the independent unit of analysis. We wanted to know whether
sex explained a significant amount of variation in song frequency beyond the
variation explained by size, so we constructed a complete model as well as
a model without ‘sex’. The difference in $r^2$ between the models ($r^2_{\text{effect}}$) was
used to generate an $F$-ratio according to the following formula:

$$F(k, N - k - 1) = \frac{r^2_{\text{effect}}}{1 - r^2_{\text{complete}}} \times \frac{(N - k - 1)}{k},$$

where $N$ is the number of subjects and $k$ is the treatment degrees of freedom
(Vokey, 2003). This $F$-ratio was used to test the null hypothesis that sex per
se, had no effect on mean frequency when accounting for variation in body
size. We repeated the analysis with ‘minimum frequency’ as the dependent
variable.
Multivariate test for sex differences
In addition to the univariate analyses described above, we entered the eight continuous variables from all songs (i.e., all types recorded from all individuals) into a discriminant function analysis (DFA). Including all songs allows us to examine the full range of variation present in the sample, but also introduces bias because common song types are more influential than rare song types (this bias turns out to be irrelevant, see Results). Variables were entered together, and songs with missing measures were excluded from the analysis. The variable ‘frequency range’ and ‘note rate’ did not contribute to the DFA because they were completely redundant with other variables.

Test for sex differences in terminal note shape
The shape of the terminal syllable was consistent within song type, simplifying the analysis of that variable. We used Fisher’s exact test to test the hypothesis that sex is associated with terminal syllable type among all sampled song types.

The GLM and DFA were conducted in SPSS 11.0.1 (2001). Results are summarized as means ± standard deviations.

Songs from other locations
We reviewed additional recordings of black-bellied wren songs from the northern (Carara and Manuel Antonio, Costa Rica), central (Summit Gardens, Republic of Panama) and southern (Cana, Republic of Panama) portions of the species range. A detailed analysis of song structure from these sites is beyond the scope of this report, but we offer a qualitative comparison between these recordings and the Central Panamanian recordings that constitute our primary data set.

Results
The two independent observers agreed on song type assignments for 79.2% of songs, leaving 20.8% of songs to be assigned by consensus with a third observer. Male’s known repertoires averaged 21.60 ± 8.26 song types (N = 10 males). Consistent with previous studies (Logue, 2004, 2006, 2007) we recorded fewer song types from females. The average female known repertoire included 12.20 ± 2.97 song types (N = 10 females). Within pairs, we always recorded more songs from males than females.
Univariate tests for sex differences

The results of our randomization analyses indicate that female song types differed from male song types in all eight continuous variables (Figure 3). Sex differences were both statistically significant and large in magnitude (sample sizes are indicated by $N =$ male song types, female song types). In comparison to male song types, female song types contained fewer notes ($N = 107, 58$; male $= 5.59 \pm 0.93$ notes; female $= 2.98 \pm 0.85$ notes, $p < 0.0001$), were of a shorter duration ($N = 107, 58$; male $= 0.98 \pm 0.19$ s; female $= 0.65 \pm 0.16$ s, $p < 0.0001$), and included fewer notes per second ($N = 107, 58$; male $= 5.86 \pm 0.94$ s$^{-1}$; female $= 4.70 \pm 1.06$ s$^{-1}$, $p < 0.0001$). Female song types were further characterized by higher minimum frequencies ($N = 106, 57$; male $= 0.83 \pm 0.07$ kHz; female $= 1.27 \pm 0.20$ kHz, $p < 0.0001$), higher maximum frequencies ($N = 106, 57$;
Sexually antithetical bird song

male = 2.25 ± 0.29 kHz; female = 3.85 ± 0.62 kHz, p < 0.0001), broader frequency ranges (N = 106, 57; male = 1.42 ± 0.30 kHz; female = 2.58 ± 0.67 kHz, p < 0.0001), higher mean frequencies (N = 104, 56; male = 1.35 ± 0.13 kHz; female = 2.38 ± 0.29 kHz, p < 0.0001), and greater FM (N = 104, 56; male = 18.29 ± 4.06°; female = 23.59 ± 4.88°, p < 0.0001).

The influence of size on fundamental frequency

In the principal component analysis of body size, the first component accounted for 77% of the variance in body size measures, making it a useful indicator of size. Sex accounted for substantial variation in mean frequency and minimum frequency beyond the variation attributable to body size (effect of adding ‘sex’ to GLM: mean frequency, $F_{1,17} = 170, p < 0.001$; minimum frequency, $F_{1,17} = 106, p < 0.001$, Figure 4).

Figure 4. Scatter plots of two measures of song fundamental frequency versus body size for male (filled circles) and female (open circles) black-bellied wrens. The arrow points in the direction of increasing body size. The x-axis is a composite variable generated by principal component analysis of three morphological measurements (wing length, tarsus length, and weight). If simple size-frequency scaling were sufficient to explain frequency dimorphism, all points would fall on a single line in each plot. See text for statistics.
Figure 5. Histogram showing complete discrimination between male songs (filled bars) and female songs (open bars) on the basis of song structure. The x-axis is a composite variable derived from six song measures (mean frequency, minimum frequency, maximum frequency, number of notes, duration, and frequency modulation) using discriminant function analysis.

Multivariate test for sex differences

After excluding songs with missing data, the DFA analyzed 199 male songs and 113 female songs. The most heavily loaded variable in the discriminant function was ‘mean frequency’, followed by (in descending order), ‘minimum frequency’, ‘maximum frequency’, ‘number of notes’, ‘duration’ and ‘FM’. Using cross-validation, the first discriminant function successfully classified all songs by the sex of the singer, allowing us to depict multivariate group differences along a single dimension, and rendering irrelevant the bias discussed in the Methods section (Figure 5).

Test for sex differences in terminal note shape

The shape of the terminal syllable was perfectly correlated with the sex of the singer in our sample. All male song types ended with a V-shaped syllable, and all female song types ended in an arc-shaped syllable ($N = 107, 58$; Fisher’s exact test: $p < 0.001$).

Songs from other locations

Of the recordings from the other study sites, only those from Summit Gardens (a site adjacent to our primary study area) exhibited consistently V-shaped and arc-shaped terminal syllables in male and female songs, respectively. Frequency and duration dimorphism, however, are apparent throughout the species range with males consistently singing lower frequency, longer songs than females (Figure 6).
Figure 6. Sonograms of male (a-d) and female (a’-d’) black-bellied wren songs from four locations. The northern extent of the range is represented by birds from Carara (a and a’) and Manuel Antonio (b and b’), Costa Rica. Birds from Summit Gardens (c and c’) are near the primary study site in central Panama; note the characteristic shapes of the terminal syllables. Birds recorded in Cana (d and d’), Panama, are near the southern reaches of the species range. Sonograms are printed by permission of the recordist, Nigel Mann.

Discussion

We found strong differences between male and female song structure in black-bellied wrens. All nine song features we measured differed significantly between the sexes, demonstrating sexual dimorphism in the time domain (notes, duration, and note rate), the frequency domain (minimum frequency, maximum frequency, frequency range, and mean frequency), and changes in frequency over time (FM, terminal note shape). A discriminant function based on six of the song measures was able to discriminate the singer’s sex for every song in the data set. Simple frequency-body size relationships are insufficient to explain intersexual variation in song frequency. In fact, size variation within sex had no apparent effect on song frequency, as shown by the flat distribution of points within sex in Figure 4. Most striking is the finding that the pattern of frequency modulation in the terminal syllable of male songs is antithetical to the pattern of frequency modulation in the terminal syllable of female songs across all songs in our primary
Logue, Droessler, Roscoe, Vokey, Rendall & Kunimoto study area. Although terminal syllable shape is the only feature meeting the strict definition of ‘antithetical’ put forward in the Introduction, the strong sex differences in all measured song features suggest selection for sexual distinctiveness generally.

There are several documented cases of sex differences in bird song. For example, there is sexual dimorphism in the innate (i.e., not learned) songs of Eastern screech-owls (Otus asio, Klatt & Ritchison, 1993) and spotted antbirds (Hylophylax naevoides, Bard et al., 2002). There are also many species in which males sing learned songs but females emit innate, atonal ‘calls’. For example, in the Carolina wren (Thryothorus ludovicianus, Shuler, 1965), Nava’s wren (Hylochilus navai), and Sumichrast’s wren (H. sumichrasti, de Silva et al., 2004), females use rattling calls to accompany the song of their pair mates forming simple ‘duets’ (de Silva et al., 2004). There is also evidence of relatively subtle song dimorphism in species in which both sexes learn songs. For example, northern cardinals (Cardinalis cardinalis, Yamaguchi, 1998), rufous-and-white wrens (T. rufalbus, Mennill & Vehrencamp, 2005) and Australian magpie-larks (Grallina cyanoleuca, Hall, 2006) share song types between sexes, but birds of all three species respond differently to playbacks of male versus female song, indicating that song dimorphism is relevant to their communication systems (Yamaguchi, 1998; Mennill, 2006; Hall, 2000; Mulder et al., 2003). Less subtle are the sex differences in the duet contributions of eastern whipbirds (Psophodes olivaceus), although males of that species occasionally sing female-typical duet contributions and female solo songs are similar in structure to male songs (Rogers, 2005). The sexual dimorphism in black-bellied wren song is noteworthy because both sexes learn songs, because sex differences are consistent along all measured axes of variation, and because of the antithetical structure of the terminal note.

Why are black-bellied wren songs profoundly dimorphic, when many other species communicate sex with subtler song dimorphism? Before considering the adaptive argument described in the Introduction, we will address the alternative hypothesis: that dimorphism arose as a by-product of different selection regimes on male and female signals. This hypothesis predicts that males and females should (1) use song in different contexts and respond to song playback differently, (2) communicate over different spatial scales, or (3) be subject to different morphological constraints on song production, and that (4) male and female songs should differ in only those features salient to
Sexually antithetical bird song

the difference in selection regimes. Contrary to the first prediction, males and females sing at elevated rates in similar contexts, such as during dawn chorusing, territory disputes, intrusions, and prior to nesting, and pair mates often sing together (i.e., duet; Logue, 2004). Further, both sexes respond aggressively to same-sex and duet playback, and both answer songs recorded from their mates, although males respond more strongly to opposite sex playback (Logue & Gammon, 2004; Logue, 2007). Our data fail to support the second prediction; the songs of both sexes comprise loud, slowly modulated whistles with energy concentrated at the fundamental frequency, suggesting they function as long distance signals. Indeed, songs of both sexes can be distinguished by humans over distances greater than one territory away, and wild birds often respond to neighbor’s songs at such distances (D.M.L., pers. obs.).

We propose two reasons why sexually dimorphic constraints on the evolution of the singing apparatus are unlikely to be the driving force behind the profound dimorphism in this species. First, there exists some overlap of male and female feature distributions on most of the features we measured (Figure 3), so males and females are capable of producing songs with similar feature values. Second, several congeners of the black-bellied wren produce approximately monomorphic songs (e.g., Molles & Vehrencamp, 1999; Mennill & Vehrencamp, 2005). Finally, and most importantly, the ‘dimorphism as biproduct’ hypothesis predicts that only one or a few salient features should differ between male and female songs, yet we found strong differences in all of the features we measured. Although we cannot exclude the possibility that sex differences in song structure are by-products of selection acting differently to shape male and female songs, we fail to find support for the predictions generated by this hypothesis.

We propose that selection favored sexually antithetical song structure in the black-bellied wren because senders benefit from the accurate communication of sex over long distances in an acoustically complex environment. Radio telemetry has revealed that the long axis of a territory can exceed 160 m (D.M.L., unpubl. data). Black-bellied wrens live in lowland tropical forests, near natural or anthropogenic forest edges (Ridgely & Gwynne, 1989). They sing while foraging, typically in dense tangles of hanging vines or just under the forest canopy. As songs propagate through this dense vegetation, they are subjected to high levels of global attenuation, frequency dependent attenuation, and reverberation. Noise levels are also high in this
habitat, although black-bellied wren songs occur in a relatively quiet noise window, above the low frequency wind noise, yet below the high frequency insect noise (Morton, 1975).

Of the recordings taken outside of our primary study site, only the Summit Gardens recordings (taken very near to our primary study site) contained antithetically structured terminal syllables. Thus, the exact form of sexual dimorphism in our study area is not characteristic of this species over its entire range. A qualitative assessment of song frequency and duration, however, suggests that dimorphism is strong throughout the species range. Thus, sexually distinctive song structure appears to be widespread in black-bellied wrens, but the degree and type of distinctiveness is variable and may be determined in part by geographic variation in the forest types and hence in the song degradation challenges faced by birds in different locations. This hypothesis warrants more systematic testing with detailed comparisons of male and female song structure within and among populations.

Acknowledgements

We thank Billi Veber for assistance in the field, Dave Gammon for help recording, and Nigel Mann for providing black-bellied wren recordings from outside of our study area. We also appreciate the constructive suggestions from the two anonymous referees. D.M.L. was supported by the Smithsonian Tropical Research Institute, the American Museum of Natural History, the Cooper Ornithological Society, an Abbott grant to E.S. Morton administered via the Smithsonian Office of Fellowships and Grants, and a postdoctoral fellowship based partially on a grant to William Cade from the National Sciences and Engineering Research Council of Canada. Permission to conduct fieldwork was granted by Autoridad del Canal de Panamá, Autoridad Nacional del Ambiente (permits SE/A 034-02, SE/A 093-02, and SE/A-61-04), and the Animal Care and Use Committee of Colorado State University (Protocols 01-105A-01 and 01-105A-03). The Poptools statistical package can be downloaded from http://www.cse.csiro.au/poptools/.

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Sexually antithetical bird song


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