A comparative study of song form and duetting in neotropical *Thryothorus* wrens

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Summary

The traditionally-defined wren genus *Thryothorus* is notable for its diversity of singing styles
with some species producing highly coordinated duets or choruses in various formats while,
at the other extreme, songs are performed almost exclusively by males. In this comparative
study, we document the singing styles of almost all of the 27 or so species in this group,
relating these to a molecular phylogeny in an effort to identify the conditions that have led
to the evolution of duetting and chorus singing. In a previous study, we used molecular data
to demonstrate that *Thryothorus* is actually paraphyletic, leading us to propose its splitting
into three genera (one newly described) in addition to *Thryothorus*. Here we show that most
species within each of these four genera usually sing with the same style, and that these
styles tend to differ between the genera. We also show that a few species have songs that
differ markedly from those most typical of their genus. We argue that these exceptional cases
will provide important insights into the origins of duetting behavior, and tentatively suggest
factors that may have played a role in determining the extent to which male and female birds
combine their vocalizations together.

Keywords: *Thryothorus*, wren, duet, chorus, song evolution, comparative study.

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Introduction

Most bird song studies have been carried out in temperate regions, where song is largely used by males to expel rivals from their territories and to attract mates (Catchpole & Slater, 2008). In the tropics, however, female birds also often sing (Langmore, 1998), and there are many species in which both members of a pair combine their vocalizations to perform duets. These vary from being only a duet in loose terms (singing by the male and female of a pair at around the same time), to remarkably complex, coordinated performances. The phenomenon probably reaches a peak in chorus singing, in species where more than two individuals in a social group contribute in a coordinated fashion to produce a communal song (Kroodsma et al., 1996).

Broadly defined, duetting is found in at least 220 bird species in at least 44 different families (Farabaugh, 1982). Duets appear to fulfil several functions and this is probably so even within a species (see review by Hall, 2004). The reasons why they are present in some species, but may be absent in close relatives, remain enigmatic. Identifying the conditions that have led to the evolution of duetting requires a comparative approach, which we apply here to *Thryothorus* wrens, a group renowned for exhibiting a wide variety of singing styles.

The genus *Thryothorus*, as traditionally defined, consists of around 27 wren species, with one or two sub-species that are sometimes given specific status (Brewer, 2001). These species are largely confined to Central and South America, though the Carolina wren (*ludovicianus*) occurs through much of eastern North America. The range of the most southerly species, the long-billed wren (*longirostris*), extends into southern Brazil (Brewer, 2001). In common with many predominantly tropical birds, members of this group are territorial throughout the year and most, as far as is known, form monogamous pair bonds that typically persist for over a year and can last for several years. This has been shown recently, for example, for the buff-breasted wren, *leucotis* (Gill & Stutchbury, 2006). In contrast, Levin (1996) found that partnerships were not always long-term in bay wrens (*nigricapillus*), since 38% of pairs broke up at around the beginning of the breeding season; however, she did not report how long the remaining pairs stayed together. To date, group-living has been found in two species, the plain-tailed wren, *euophrys* (Mann et al., 2006b) and the Inca wren, *eisenmanni* (Mennill et al., data not shown), and helping-at-the-nest has been observed on at least one occasion in the buff-breasted wren (Gill, 2004).

The genus is notable for its diversity of 'singing styles', a term we use to encompass both the general characteristics of an individual bird's song phrase (e.g., note morphology, frequency characteristics, phrase length, presence or absence of repeated notes, etc.), and also the temporal relationship (if any) between the song phrases of the two sexes. Most members of this group produce coordinated duets in various formats (e.g., bay wren, Levin, 1996; plain wren, *modestus*, Mann et al., 2003; black-bellied wren, *fasciatoventris*, Logue & Gammon, 2004). In other cases, female songs are tied much more loosely to those of males, and their song rates are very much lower (e.g., rufous-and-white wren, *rufalbus*, Mennill & Vehrencamp, 2005; banded wren, *pleurostictus*, Molles & Vehrencamp, 1999), or they may sing hardly at all (Carolina wren, Brewer, 2001). Finally, it has recently been discovered that group-living plain-tailed wrens produce choruses (Mann et al., 2006b).

Two previous studies have addressed the variation in song forms within *Thryothorus* (Brown & Lemon, 1979 and Farabaugh, 1983, working in Mexico and Panama, respectively). However, both studies considered data from just a small subgroup of sympatric species (each compared six species, but in both cases detailed data were only collected on two of these); furthermore, neither study had access to a well-resolved phylogeny for the genus. For our study we focused particular attention on 21 species. For each of these, we made extensive field observations and recordings, as described below, at sites in Mexico, Costa Rica, Panama and Ecuador. We also collected similar data from several sub-species and acquired smaller samples of songs from five of the remaining species, using sound archive libraries, some personal recordings and other donated sound clips. We lack data for only one member of the genus, the grey wren, *griseus*, from western Brazil.

In addition to collecting the song data, we took blood samples from each individual that was caught. This was partly for sex determination, as the majority of species are more or less monomorphic, but also to prepare a molecular phylogeny so that we could identify places within the lineage where song had changed. The results of this molecular phylogeny are presented elsewhere (Mann et al., 2006b) and confirm the earlier suggestion that the genus is paraphyletic (Barker, 2004). Combining data from both of these studies prompted us to propose that the species previously all grouped in the genus *Thryothorus* should be placed in four separate genera. Figure 1 summarises the relationship of these four genera to each other and to other wrens.
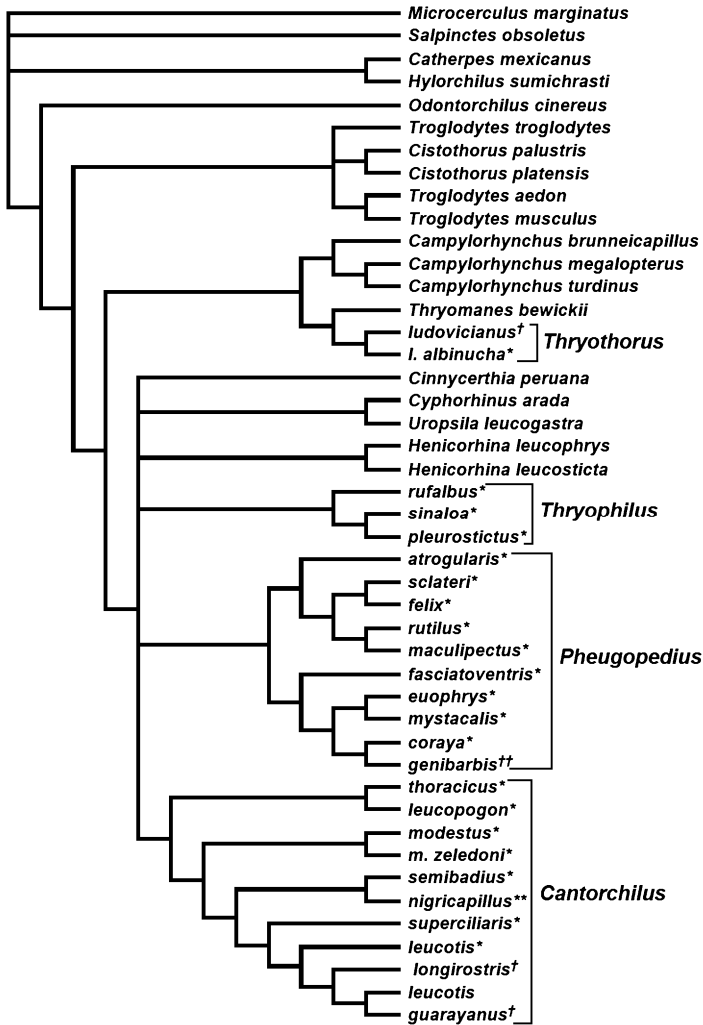
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Microcerculus marginatus
Salpinctes obsoletus
Catherpes mexicanus
Hylorchilus sumichrasti
Odontorchilus cinereus
Troglodytes troglodytes
Cistothorus palustris
Cistothorus platensis
Troglodytes aedon
Troglodytes musculus
Campylorhynchus brunneicapillus
Campylorhynchus megalopterus
Campylorhynchus turdinus
Thryomanes bewickii
ludovicianus†
l. albinucha*   **Thryothorus**
Cinnycerthia peruana
Cyphorhinus arada
Uropsila leucogastra
Henicorhina leucophrys
Henicorhina leucosticta
rufalbus*
sinaloa*   **Thryophilus**
pleurostictus*
atrogularis*
sclateri*
felix*
rutilus*
maculipectus*   **Pheugopedius**
fasciatoventris*
euophrys*
mystacalis*
coraya*
genibarbis††
thoracicus*
leucopogon*
modestus*
m. zeledoni*
semibadius*   **Cantorchilus**
nigricapillus**
superciliaris*
leucotis*
longirostris†
leucotis
guarayanus†

Figure 1. Phylogenetic framework (*sensu* Lanyon, 1993) of relationships among '*Thryothorus*' wrens and allies. Represented nodes were recovered with ⩾50% bootstrap support in individual parsimony or likelihood analyses, and/or with ⩾0.95 estimated Bayesian posterior probabilities (Barker, 2004; Mann et al., 2006a). The tree is shown unrooted because of uncertainty regarding the root's placement (Barker, 2004). Species groups highlighted by brackets were all formerly members of the genus *Thryothorus*. The framework does not include four other species from this genus *spadix*, *eisenmanni*, *nicefori*, or *griseus*. Species behaviorally sampled in this study are marked with an asterisk, and those analyzed with supplementary recordings provided by others by daggers (two symbols indicate sampling from more than one population).

We have studied the songs of most of the species in these four genera and our intention here is to summarise their singing styles and to recognise how these have diverged among close relatives so that we can identify positions in the phylogeny where the evolution of song demands closer scrutiny. Our discussion will centre on comparing the overall style of singing between species. Given that the taxonomic proposals based on our new molecular phylogeny have not yet been widely adopted, we will refer to species by their specific names but omit the generic part of the binomial. When discussing data from the four different groupings that Mann et al. (2006a) proposed, we will label them by their proposed generic names (*Thryothorus*, *Thryophilus*, *Pheugopedius* and *Cantorchilus*). To avoid confusion with the first of these, the group of species as a whole will henceforth be labeled as '*Thryothorus*'.

Methods

Table 1 lists the species that we targeted for detailed data collection as well as when and where they were studied. Table 2 lists the other seven '*Thryothorus*' species for which we have data, and includes the sources of the recordings. The necessary fieldwork averaged around 14 days for each taxon, but was longer where more than two species were studied simultaneously at a single site. Our intention was to carry out observations outside the peak of the breeding season for all species, to standardise the data and achieve a common baseline for comparison. This was largely achieved but, given the paucity of prior knowledge about the timing of reproduction for many of the taxa, and the relative lack of reproductive synchrony across pairs through an often extended breeding season, some variation in this regard was inevitable.

The same procedure was adopted for all species. We aimed to collect an extensive sample of songs from at least five territories, and this was achieved in most cases. The exceptions were *rufalbus*, *leucotis* and *ludovicianus albinucha*, for which we could only find four suitable territories at the study sites involved. The sooty-headed wren (*spadix*) proved to be particularly problematic and the data set we have available for this species, even with supplementation from sound archive libraries, is very poor. For *leucopogon*, we collected data from two sites because, despite the presence of many territories at the first, no female songs were heard. We decided to work on this species at the second site, in case the first data set was anomalous (e.g., we may have encountered an unexpected seasonal effect).

Table 1. The wren species recorded in the present study, together with the locations and dates of fieldwork.

Species/subspecies	English name	Location	Fieldwork dates
Thryothorus			
T. ludovicianus albinucha	White-browed wren	El Eden, Mexico	May 2003
Pheugopedius			
P. atrogularis	Black-throated wren	La Suerte, Costa Rica	Oct. 2001
P. sclateri paucimaculatus	Speckle-breasted wren	Cerro Blanco, Ecuador	Dec. 2002
P. felix felix	Happy wren	Chamela, Mexico	April-May 2003
P. rutilis hyperythrus	Rufous-breasted wren	Carara, Costa Rica	Dec. 2001
P. maculipectus maculipectus	Spot-breasted wren	El Eden, Mexico	April-May 2003
P. fasciatoventris melanogaster	Black-bellied wren	Manuel Antonio, Costa Rica	Nov. 2001, Jan. 2002
P. euophrys euophrys	Plain-tailed wren	Pasochoa, Ecuador	Oct. 2002
P. mystacalis mystacalis	Whiskered wren	Rio Palenque, Ecuador	Oct. 2002
P. coraya griseipectus	Coraya wren	Tiputini, Ecuador	Nov. 2002
Thryophilus			
T. rufalbus castanonotus	Rufous-and-white wren	Carara, Costa Rica	Jan.-Feb. 2001
T. sinaloa sinaloa	Sinaloa wren	Chamela, Mexico	April-May 2003
T. pleurostictus nisorius	Banded wren	Quilamula, Mexico	April 2003
Cantorchilus			
C. thoracicus	Stripe-breasted wren	La Suerte, Costa Rica	Jan. 2001
C. leucopogon leucopogon	Stripe-throated wren	Cana, Panama, Playa de Oro, Ecuador	Feb. 2002, Dec. 2002
C. modestus modestus	Plain wren	El Rodeo, Costa Rica	Dec. 2001
C. modestus zeledoni	Canebrake wren	La Suerte, Costa Rica	Oct.-Nov. 2001
C. semibadius	Riverside wren	Manuel Antonio, Costa Rica	Nov. 2001
C. nigricapillus costaricensis	Bay wren	La Suerte, Costa Rica	Oct. 2001
C. n. nigricapillus	Bay wren	Rio Palenque, Ecuador	Oct. 2002
C. n. connectens	Bay wren	Playa de Oro, Ecuador	Dec. 2002
C. n. schotti	Bay wren	Cana, Panama	Feb.-March 2002
C. superciliaris superciliaris	Superciliated wren	Cerro Blanco, Ecuador	Dec. 2002
C. leucotis galbraithii	Buff-breasted wren	Summit Gardens, Panama	March 2002

Table 2. Sources of supplementary wren recordings used as part of the analysis for the present study.

Species	English name	Location	Source
Thryothorus			
T. ludovicianus	Carolina wren	Florida, USA	DK
Pheugopedius			
P. eisenmanni	Inca wren	Machu Pichu & Cuzco, Peru	BSL, MSL
P. genibarbis	Moustached wren	Madre Selva, Peru	CH
P. genibarbis	Moustached wren	Mato Grosso, Brazil, Pando, Bolivia, Madre de Dios, Peru	MSL
P. genibarbis	Moustached wren	Madidi, Bolivia	PR
P. spadix	Sooty-headed wren	Caldas, Colombia	BSL
P. spadix	Sooty-headed wren	Darien, Panama	PR
Thryophilus			
T. nicefori	Nicefor's wren	Santander, NE Colombia	MSL
Cantorchilus			
C. guarayanus	Fawn-breasted wren	Santa Cruz, Bolivia, Mato Grosso, Brazil	BSL, MSL
C. guarayanus	Fawn-breasted wren	Beni, Bolivia	PR
C. longirostris	Long-billed wren	Various sites in Brazil	BSL, MSL

MSL = The Macaulay Library at the Cornell Lab of Ornithology, BSL = British Sound Library, PR = personal recordings, CH = donated by Cindy Hogan, DK = donated by Donald Kroodsma.

Our baseline data set for the bay wren (*nigricapillus*) was collected from the Caribbean slope of Costa Rica, but as different sub-species were present at three of our other study sites, we also took the opportunity to gather recordings of these. A detailed comparison of the songs of these sub-species will not be presented here. Comparisons will, however, be included for the two sub-species of plain wren that we worked on (*modestus modestus* and *m. zeledoni*), as these taxa have sometimes been given full species status (Brewer, 2001).

When a pair was selected for study one or both individuals were caught and marked with a unique combination of colour bands. A sample of approx. 50 μl blood was also taken by puncturing the brachial vein. Samples were stored in 100 mM Tris, 100 mM EDTA, 2% SDS buffer to prevent DNA degradation in the field. Upon return to St Andrews, the DNA was extracted using standard techniques and sex determined according to the method of

Griffiths et al. (1996). The blood was also used to obtain a sequence of 1000 base pairs from the cytochrome *b* gene to prepare the molecular phylogeny (see Mann et al., 2006a).

For song analysis, four separate 90-min recordings were made on different days from each marked pair, in most cases before 10:00 a.m. Supplemental recordings were made in some cases in late afternoon, or on further morning sessions, if the number of songs recorded from a territory was particularly low. We balanced the time of day of recordings as much as possible between pairs and across species. All recordings were made with Marantz CP430 cassette recorders linked to Sennheiser ME66 directional microphones. The microphone was mounted on a tripod so that it could be aimed at the pair being recorded, leaving the observer free to watch the birds through binoculars in order to determine which bird was singing and what its contribution was. This information was dictated onto the tape.

To stimulate the birds to sing, and encourage them to reveal a greater extent of their repertoire, two playbacks, each of a sequence of 10 songs, were carried out during the 90-min recording session, one after 15 min, the other after 60 min. A different playback stimulus was used for each of the four 90 min sessions. Further playbacks were used in a few cases to encourage singing when pairs otherwise sang very little. The types of vocalizations produced were catalogued according to their relationship to the timing of playbacks, as we found that different species respond to playbacks in different ways. These findings will be reported elsewhere. If the species was a duetter, the songs played back were of duets recorded from another local, conspecific pair. If we could obtain no recordings of duets, because of their rarity, we used only male solos for playbacks (*pleurostictus*, *sinaloa*, *ludovicianus albinucha* and *leucopogon*). In the case of two species (*leucopogon* and *thoracicus*), males use two quite distinct song forms, and so a playback of each type was used during every recording session.

The recorded vocalizations were digitised, and then sound spectrograms (prepared using Avisoft SASLab Pro, R. Specht, Berlin, Germany) were used to identify and catalogue the songs produced by each individual, pair or group. We defined a single 'song' as separated temporally from all others by $\geqslant 2$ s, either in the form of a solo or a duet (or chorus), to which two (or more) birds contribute. A phrase is composed of a stereotyped sequence of notes (defined as continuous traces on a spectrogram) produced by a single individual. A song can, thus, be a solo performance comprising one or more phrases from a single bird, or a duet or chorus with phrases from multiple birds.

Additional data were collected on the structure of the song, including the number and arrangement of the phrase types present, which bird started the song, which bird terminated it, how many full cycles it involved (in the case of cyclical duets) and whether the contributions of the two birds overlapped with one another. In many duetting species, across a wide range of taxa, pair members combine specific song phrases from their repertoires to form non-random associations (see Logue, 2006, for a list of references). We determined whether such associations were present following the methodology of Mann et al. (2003), using a *G*-test to compare the observed frequency of specific associations with the random expectation assuming a Poisson distribution. Logue (2006) points out that non-random phrase associations can arise in various ways, and uses the term 'duet code' for the case where one sex specifically selects a song phrase from its own repertoire in response to hearing a particular phrase from its mate. It was beyond the scope of this study to determine the mechanism leading to non-random phrase associations. We, therefore, use the term 'duet type' as a short-hand for the presence of such associations, without making any assumption as to how they might have arisen.

The quantitative details of duet structure were averaged over all recordings from each territory and then a mean and standard deviation across territories was calculated. It is known that some characteristics (e.g., the relative frequency of duet initiation by a particular sex, the frequency of replies to partner songs and the types and organisation of songs used from a repertoire) can vary depending on the time of day (Molles & Vehrencamp, 1999; Gill et al., 2005; Trillo & Vehrencamp, 2005) and whether they are in response to playback or not (pers. obs.). However, the purpose of the current paper is to categorise broad differences in singing styles, and such fine detail will not be considered.

Results

During the course of this study we recorded, digitised and analysed over thirty thousand songs from 32 taxa (species and sub-species). For the following song descriptions, the species are subdivided into the four genera that we proposed, based on our recent molecular phylogeny (Mann et al., 2006a). Table 3 summarises some of the song characteristics found within each group,

Table 3. Summary of a selection of song characteristics of '*Thryothorus*' wrens.

Species	No. of pairs	Duet phrases	% duets with M phrase at start (mean, range)	% duets with M phrase at end (mean, range)	% of phrases overlapped by partner (mean)	Presence of trill in duet cycle phrases	Sex with most note-types per phrase	Sex with highest max. note frequency
Thryophilus								
rufalbus	4	A, B	68.4 (61.7–79.7)	38.5 (28.2–48.6)	♂: 39.6, ♀: 51.6	♂ and ♀	NS (†♂*)	♀*
sinaloa	7	A, B	X	X	X	♂ (♀?)	NS?	NS?
pleurostictus	5	A, B	X	X	X	♂ and ♀	♂ (*c)	X
Pheugopedius								
atrogularis	6	A, B	74.7 (63.9–89.2)	74.1 (51.0–97.3)	♂: 79.2, ♀: 75.7	♂ and ♀	♂**	NS
sclateri	5	A, B	66.0 (47.4–87.0)	86.4 (79.6–93.1)	♂: 38.2, ♀: 75.8	♂ only[b]	♀* (†♂*)	NS
felix	6	A, B	70.1 (28.6–89.7)	68.6 (63.9–77.9)	♂: 58.0, ♀: 52.1	♂ only	♂**	♀**
rutilis	6	A, B	74.0 (68.3–79.7)	80.8 (71.1–88.3)	♂: 55.1, ♀: 60.3	No	♂**	NS
maculipectus	7	A, B	83.5 (72.6–92.7)	80.1 (70.5–89.3)	♂: 61.3, ♀: 85.1	No	♂**	NS
fasciatoventris	5	A, B[a]	77.6 (42.2–97.8)	53.9 (24.7–77.7)	♂: 83.3, ♀: 56.6	No	♂**	♀**
euophrys	5	A, B, C, D	22.3 (14.1–34.6)	23.3 (10.2–44.0)	♂: 8.6, ♀: 3.7	No	Neither (+)	Neither (++)
mystacalis	5	A, B[a]	74.4 (52.8–86.4)	82.5 (75.3–93.4)	♂: 38.2, ♀: 73.0	No	♂**	♀*
coraya	6	A, B	69.6 (37.0–90.4)	71.1 (46.6–87.1)	♂: 76.9, ♀: 29.6	♂ only	♀** (†♂**)	♀*
genibarbis	DR	I, A, B	X	X	Overlaps common	♂ and ♀[b]	♂**	NS?

Table 3. (Continued.)

Species	No. of pairs	Duet phrases	% duets with M phrase at start (mean, range)	% duets with M phrase at end (mean, range)	% of phrases overlapped by partner (mean)	Presence of trill in duet cycle phrases	Sex with most note-types per phrase	Sex with highest max. note frequency
Cantorchilus								
thoracicus	5	A, B + D	81.9 (77.6–86.2)	88.3 (79.1–100)	♂: 14.4, ♀: 39.3	No	NS	♀**
modestus	5	I, A, B	93.6 (82.5–99.5)	72.1 (44.7–81.7)	♂: 0.8, ♀: 1.0	No	NS	♀**
m. zeledoni	5	I, A, B	96.1 (88.4–100)	60.8 (34.1–86.5)	♂: 1.3, ♀: 0.0	No	♀**	♀**
semibadius	6	I, A, B	66.6 (22.7–90.8)	85.5 (76.5–94.4)	♂: 8.1, ♀: 2.1	No	♀*	NS
nigricapillus	12	I, A, B	57.8 (25.0–72.7)	51.8 (34.9–68.3)	♂: 4.9, ♀: 1.5	♂ only	NS (†♂**)	♀**
superciliaris	5	I, A, B	71.6 (63.2–80.1)	69.9 (49.7–90.6)	♂: 20.5, ♀: 77.4	♂ only	NS?	♀*
leucotis	4	I, A, B	67.9 (20.7–91.9)	84.8 (82.6–88.9)	♂: 0.2, ♀: 0.0	No	♀**	♀*

The following species are omitted from the table because we had insufficient data on the songs of one or both sexes: *ludovicianus, l. albinucha, longirostris, guarayanus, leucopogon, eisenmanni, spadix* and *nicefori*. To calculate the mean values presented in the table, we first obtained mean values for individual pairs and then calculated the mean of these. Key: DR = donated/sound archive recordings. A, C = female song categories; B, D = male song categories; I = introductory phrase from male. X = a reliable estimate is not available, generally because female song was very rare or absent. Significance levels for the last two columns indicated by *($p < 0.05$) and **($p < 0.01$), using Mann–Whitney tests; NS = no significant difference. † indicates that a different result for this measure was obtained, shown in parentheses, when all notes were totalled even when they occurred as repeats. + indicates that the A-phrase of the male contained significantly fewer note-types on average than both female phrases, whereas the male C-phrase contained significantly more note-types. ++ indicates that the average maximum frequency for the female B-phrase was higher than that for both male phrases, whereas the average maximum frequency for the female D-phrase was lower.

[a] A repertoire of additional male phrases/calls was also present which may be equivalent to the introductory phrases of *genibarbis*; however, these did not appear to be linked to the duet.

[b] A single repeat of one note was usually present within the phrase.

[c] From Molles & Vehrencamp (1999).

Table 4. Definitions of singing styles found within the '*Thryothorus*' wrens.

Code for singing style	Definition
1	Only the male sings, or female occasionally adds a rattling call. Each male song consists of a rapid series of short, repeated phrases.
2	Females sing much less than males, and songs only loosely associated. Song phrases of males are relatively long and varied, usually beginning with tonal notes and containing a loud trill. Female phrases are similar, but simpler.
3	Female sings more frequently but still less than male, songs often closely associated into clear duets, but arrangement is inconsistent with variable overlaps. Song structure essentially similar to 2, but male and female phrases are more alike.
4	Duets common, with the phrases of the two sexes alternating and usually overlapping. Phrases usually contain more four or more syllables, often including tonal notes and sometimes a trill.
5	As for 4, an alternation of overlapping phrases from each sex, but an additional repertoire of male phrases is present. The latter are not obviously associated with the duet.
6	An additional repertoire of male phrases is again present, but this time these phrases typically immediately precede the duet. Duet phrases usually overlap.
7	An introductory call or phrase is present, but the following duet cycle consists of precisely-timed, non-overlapping phrases. The antiphonal phrases usually consist of fewer syllables (four or fewer) than in the previous singing styles, and tonal notes are usually absent. Trills are usually absent: if present, they are brief.
8	Again, precisely-timed, non-overlapping phrases, but the cycle consists of two separate contributions from each sex. There is no introductory phrase.
9	Somewhat anomalous singing style, with two distinctly different categories of male song, both of which occur in a series of repeated phrases increasing in amplitude through the course of the song. One consists of single tonal notes, the other of more complex phrases. Duets are formed by females singing with the complex phrases; contributions may overlap slightly or are precisely antiphonal.

Table 4 provides a description of the different singing styles present and Table 5 indicates how these singing styles are distributed across '*Thryothorus*' wrens. Details of individual phrase structure, not directly related to how the two sexes combine their phrases within a song, are given in the Appendix. The phrase repertoire sizes across the four genera have also been placed in

Table 5. Classification of singing styles of *Thryothorus* wrens.

Species	No. of pairs	Code for singing style	Species	No. of pairs	Code for singing style
Thryothorus			*Cantorchilus*		
ludovicianus	DR	1	*thoracicus*	5	9
l. albinucha	4	1	*leucopogon*	6	9?[b]
			modestus	5	7
Pheugopedius			*m. zeledoni*	5	7
atrogularis	6	4	*semibadius*	6	7
spadix	(2) DR	?	*nigricapillus*	12	7
sclateri	5	4	*superciliaris*	5	4, 6, 7
felix	6	4	*leucotis*	4	7
rutilis	6	4	*guarayanus*	DR	6, 7
maculipectus	7	4	*longirostris*	DR	?
fasciatoventris	5	5			
euophrys	5	8	*Thryophilus*		
eisenmanni	DR	8?[a]	*rufalbus*	4	3
mystacalis	5	5	*nicefori*	DR	3?
coraya	6	4	*sinaloa*	7	2
genibarbis	DR	6	*pleurostictus*	5	2

DR, donated/sound archive recordings.

[a] Tentative classification, based on gross song similarity with *euophrys*.

[b] Tentative classification, based on male song only (female song not recorded).

the Appendix. Sound files corresponding to all of the sound spectrograms can be accessed at http://media.brill.nl/behaviour/146/1/

Thryothorus

The genus *Thryothorus* now includes only one species, the Carolina wren, *ludovicianus*, although *l. albinucha*, one of the taxa we studied, is sometimes given full specific status (e.g., by Brewer, 2001). This sub-species is referred to as the white-browed wren and ranges from Mexico to Nicaragua. The songs of male *albinucha* from our study population in the Yucatan peninsula, Mexico, were very similar to those of male *ludovicianus* (Figure 2A–C). Female *ludovicianus* do not sing in the strict sense, but may add an alarm-call-like rattle, or chatter, to their mate's song to form a simple duet (Figure 2D). This combined performance lacks precision and occurs relatively rarely (e.g., Shuler, 1965; Kroodsma, 2005). In our work with *albinucha*, we
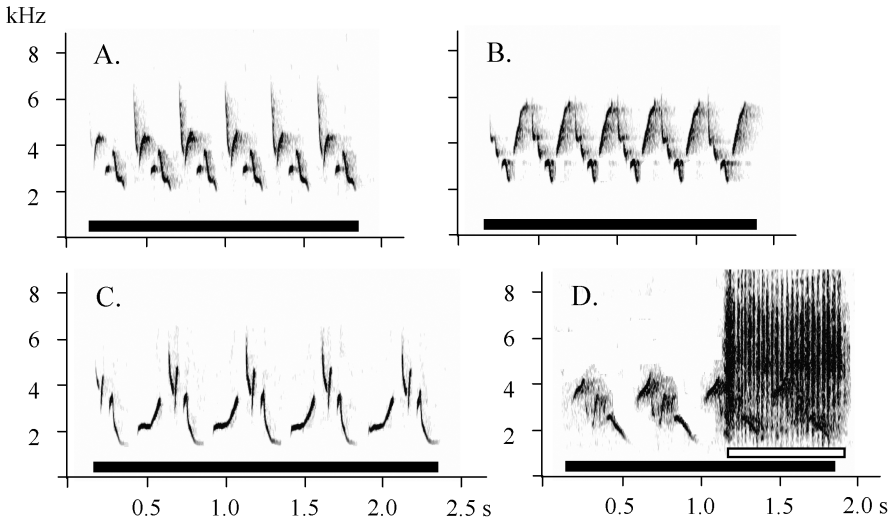
Figure 2. Sound spectrograms of songs from wrens which we propose should remain in the genus *Thryothorus*. A–B: male white-browed wren (*ludovicianus*) *albinucha*. C: male Carolina wren *ludovicianus*. D: female call associated with male song in the Carolina wren. For this and all subsequent figures, male vocalizations are indicated by a solid black line, female vocalizations by an open line. Time intervals for *x*-axis subdivisions are the same for all spectrograms (the Carolina wren spectrograms were made from recordings donated by D.E. Kroodsma). Full-size spectrograms plus soundfiles can be found at
http://media.brill.nl/behaviour/146/1

did not encounter any songs (or *ludovicianus*-like calls) from females. See Appendix for further details of song structure for this genus.

Thryophilus

Our molecular analysis placed the rufous-and-white (*rufalbus*), banded (*pleurostictus*) and Sinaloa (*sinaloa*) wrens in this genus, and we collected field data from all three. The endangered Niceforo's wren (*nicefori*), endemic to small area of Colombia, no doubt also belongs to this genus, as it is sometimes regarded as a sub-species of the morphologically very similar *rufalbus* (Brewer, 2001). We have no molecular data for this taxon, and did not study this species in the field.

Each of our three focal species in the *Thryophilus* group has also been the subject of earlier song work (*sinaloa*, e.g., Brown & Lemon, 1979; *pleurostictus*, e.g., Molles & Vehrencamp, 1999; *rufalbus*, e.g., Mennill & Vehrencamp, 2005). More detailed descriptions of their vocalizations can

be found in these sources. Examples of the songs of *Thryophilus* wrens are shown in Figure 3 and the phrase structure for each species is described in the Appendix. Females sing in all three of our focal species, but their songs are relatively rare, and the precisely timed and coordinated duetting that will be described later for other wren species does not occur. We were not able to make conclusive recordings of female song in our relatively brief sessions with *pleurostictus* in Mexico (see Discussion and Appendix for description of female song in Costa Rican *pleurostictus* by Vehrencamp and co-workers), and we only occasionally encountered *sinaloa* females singing (Figure 3C), usually in association with male songs. On one such occasion, a sequence of numerous female songs was associated with an escalated vocal encounter between her mate and a neighbouring male. Female song for this species and for the other members of the genus can be distinguished from male song, although both share essentially similar structural characteristics (see Appendix).

Compared to the other two species, female song in *rufalbus* is considerably more common, with approx. 25% of songs recorded in our study being from this sex. The songs of the two sexes often overlap with one another (see Figure 3F and G and Table 3), although this association is rather loose. That they sing at much the same time as each other certainly justifies the label 'duet', especially as, within a song bout in which both members of a pair are singing, they choose to utilize particular songs from their respective repertoires, to form duet types (also described in this species by Mennill & Vehrencamp, 2005). The majority of the duets of this species occur when the female replies to a male song (a per pair average of 68.4% of songs followed this pattern in our study) and they do not form the long sequences of alternation (termed duet 'trains' by Brown & Lemon, 1979) found in some other wrens. Typically, they comprise a single response of one bird to the song of the other or, less commonly, to a duet 'sandwich' (Mennill & Vehrencamp, 2005), where the phrase of one sex occurs between two phrases of its partner.

It was clear from the sound archive recordings we had access to that the songs of *nicefori* are remarkably similar to those of *rufalbus* (see Figure 3H and I; also, see Discussion for an account of differences that do exist, based on a recent study by Valderrama et al., 2007).

Pheugopedius

Based on our molecular analysis, this genus includes at least 10, and almost certainly 12, species. The two species that were not part of our molecular
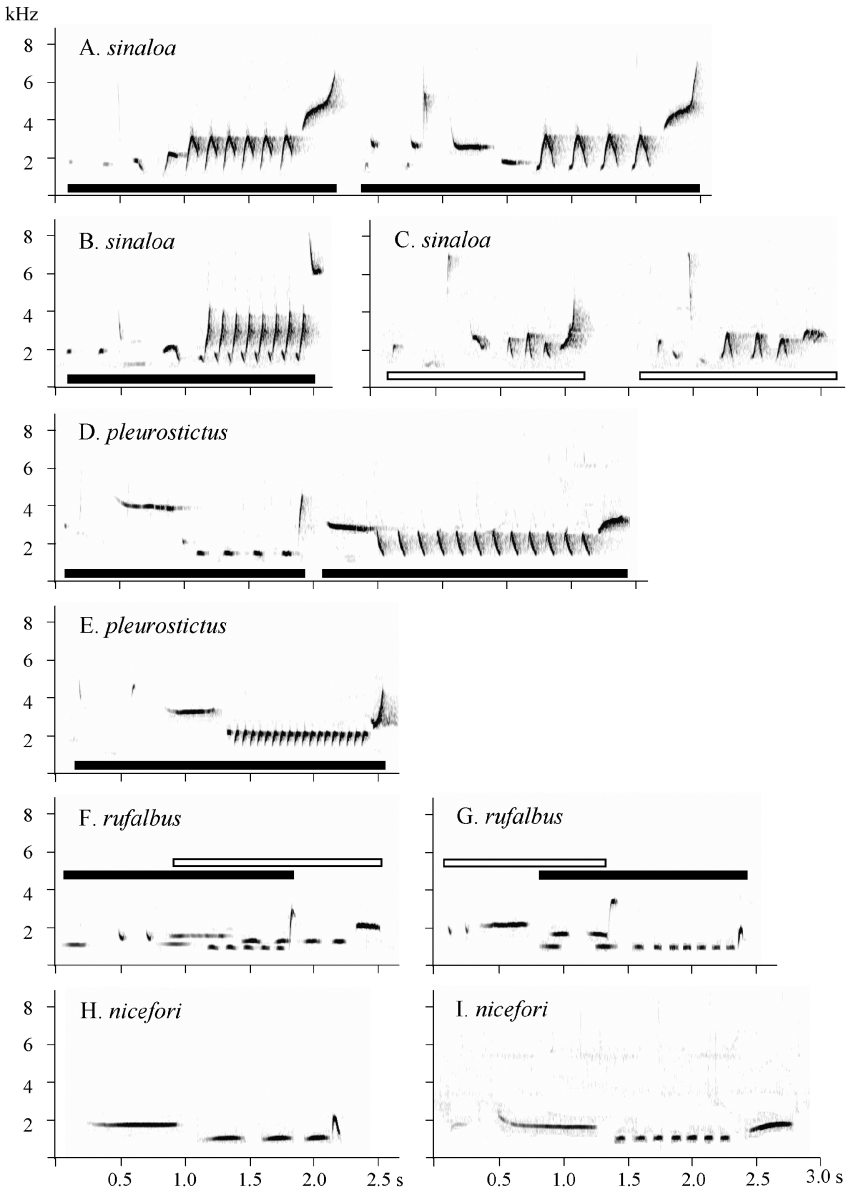
Figure 3.   Sound spectrograms of songs from wrens in the proposed genus *Thryophilus*. A–B: male Sinaloa wren, *sinaloa* (first is a compound song). C: two phrases from female Sinaloa wren. D–E: male banded wren, *pleurostictus* (first is a compound song). F–G: rufous-and-white wren, *rufalbus*, duets. H–I: Niceforo's wren, *nicefori*, solo songs. Sex not identified. Spectrograms of *nicefori* made from Macaulay Sound Library recordings. Time intervals for *x*-axis subdivisions are the same for all spectrograms. Full-size spectrograms plus sound-files can be found at http://media.brill.nl/behaviour/146/1/

analysis, but that we expect would fall into this group are the Inca wren *eisenmanni* (which closely resembles the plain-tailed wren, *euophrys* in appearance, behaviour and habitat) and the sooty-headed wren, *spadix* (Brewer, 2001, notes that this species is sometimes considered conspecific with the black-throated wren, *atrogularis*). For the present study we recorded large samples of recordings from nine of these 12 species. We have also obtained smaller song samples for the remaining 3 species, *spadix*, *eisenmanni* and *genibarbis*.

Figure 4 shows examples of the songs of each species within this group. Eight of them (*atrogularis*, *felix*, *sclateri*, *maculipectus*, *rutilus*, *coraya*, *mystacalis* and *fasciatoventris*; Figure 4A–I and 4N) sing in a very similar fashion, each producing an alternating cyclical duet, with the contributions of the two sexes generally overlapping in time. In this group, both sexes have a repertoire of phrase types that can be used during this interchange, with each generally repeating the same phrase type within one duet train. In all eight species, pairs arrange their duet contributions into a series of duet types as described for *rufalbus* in the *Thryophilus* group.

Duet trains in this subset of the *Pheugopedius* wrens usually started with a male phrase (see Table 3) although, in some species, one of our sample of pairs behaved atypically (*sclateri*, *felix*, *fasciatoventris* and *coraya*), with the female leading most songs. Males also usually produced the final vocalization in a duet in these species (Table 3). For only two pairs, one a *fasciatoventris*, the other a *coraya*, did we have song samples in which female-ended songs were the most common. The modal song format for all eight species was a three phrase song with a single female phrase sandwiched between two male phrases. However, longer songs were also common, with exceptionally long strings of up to 40 alternated phrases occurring especially following playback.

In this group of *Pheugopedius* wrens both sexes had a high proportion of their phrases overlapped by those of their partner (Table 3). It is difficult to make species-level generalisations concerning the frequency with which this overlapping occurs because in our study we found considerable pair-specific variability. For example, in one pair of *atrogularis*, the female overlapped 87.5% of her partner's phrases ($N = 192$ transitions), while the male overlapped only 44% of her phrases ($N = 153$): in contrast, in another pair, the female overlapped 70.7% of her partner's phrases ($N = 294$), while her
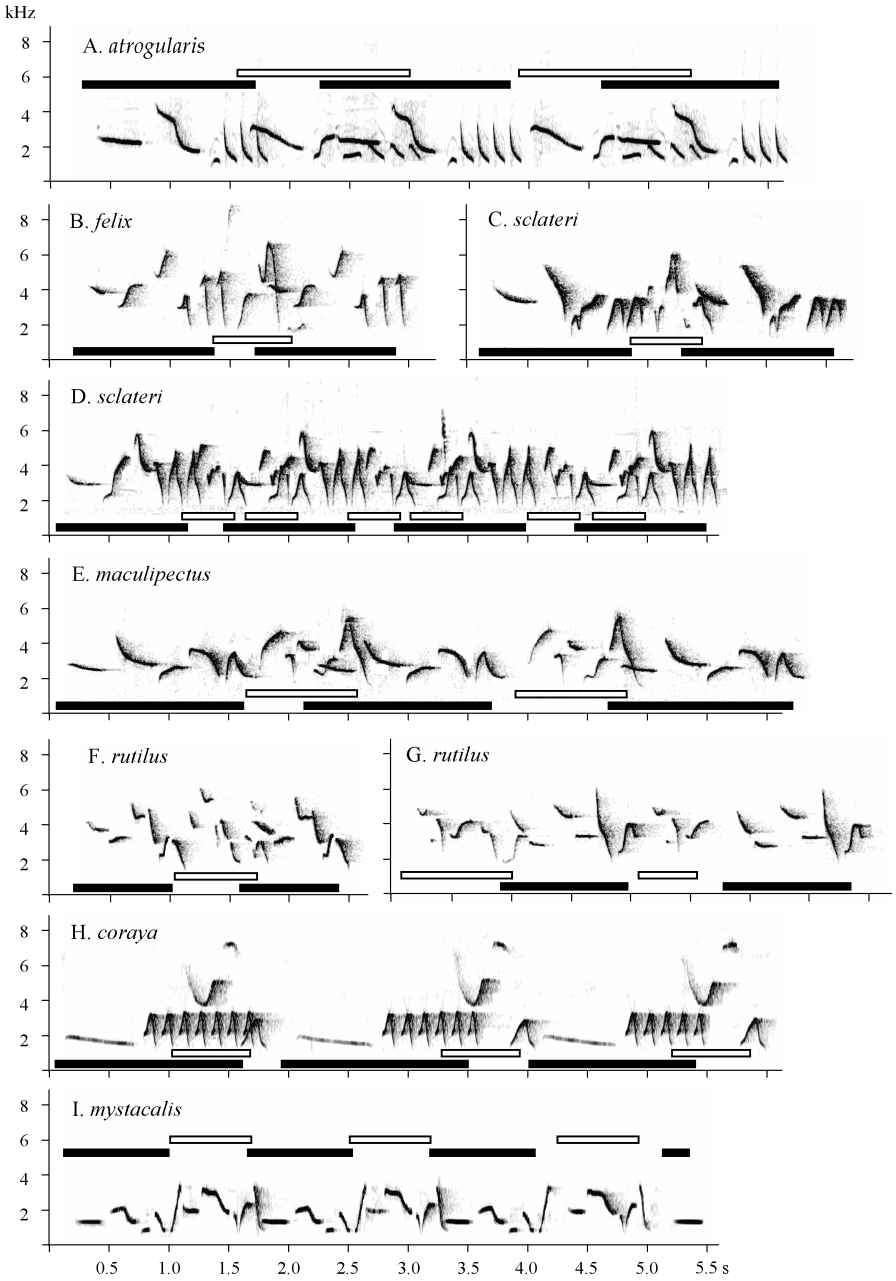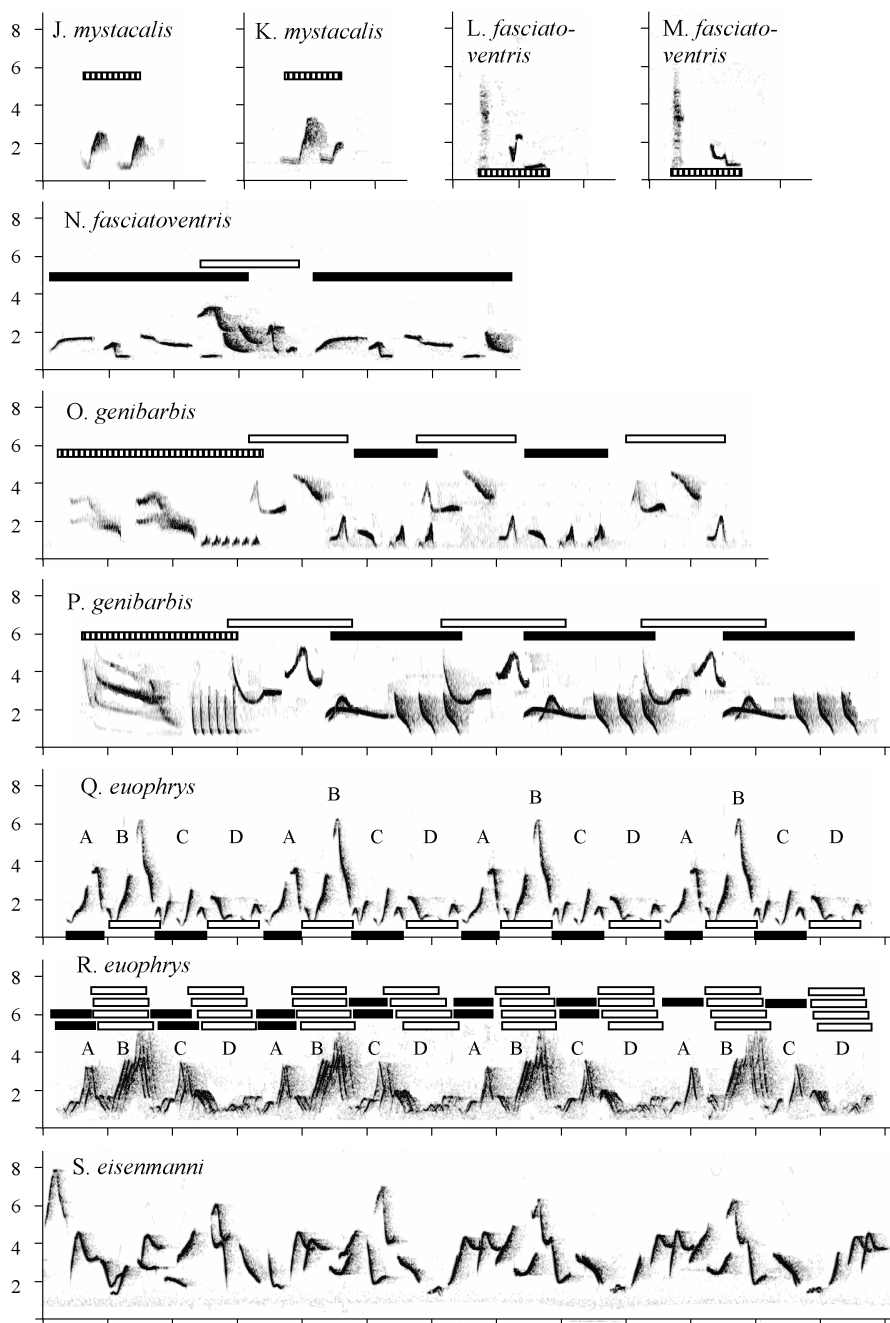
Figure 4.

Figure 4. (Continued.)

phrases were overlapped 94.0% of the time ($N = 319$). In this species, and in *felix* and *rutilus*, there was no clear pattern concerning which sex was most likely to have its phrases overlapped. In three species, *maculipectus*, *sclateri* and *mystacalis*, female phrases were overlapped by those of the male more often than *vice versa* for each of the 5–7 pairs sampled. Conversely, in *fasciatoventris* and *coraya*, pairs tended to show more overlapping of the male phrases. For specific details of individual phrase structure for this group of eight species, see Appendix.

Three of the four *Pheugopedius* species not yet discussed in detail, *genibarbis*, *euophrys* and *eisenmanni*, have songs that stand out from the rest. Although we have a relatively limited sample of *genibarbis* songs available for analysis (those donated by C. Hogan plus a small sample of recordings made by the authors), it is clear that the major part of the duet of this species is typical for *Pheugopedius*, and in fact closely resembles that of *coraya* (compare Figure 4H with Figure 4O and P). In common with that species, overlapping between male and female components occurred regularly, and the individual phrase structure is similar. The duet of *genibarbis* is very unusual for the group, however, in that the antiphonal interchange of phrases between the sexes was regularly preceded by an additional song component produced by the male (Figure 4O and P). We term this component the introductory phrase and, interestingly, it is a distinctive characteristic of the next group to be discussed, *Cantorchilus*. Just as in most *Cantorchilus* wrens, the

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Figure 4. (Continued.) Sound spectrograms of songs from wrens in the proposed genus *Pheugopedius*. A: black-throated wren, *atrogularis*, duet. B: happy wren, *felix*, duet. C–D: speckle-breasted wren, *sclateri*, duets. Second duet includes double phrases by female. E: spot-breasted wren, *maculipectus*, duet. F–G: rufous-breasted wren, *rutilus*, duets. H: coraya wren, *coraya*, duet. I: whiskered wren, *mystacalis*, duet. J–K: 'introductory-type' calls from male whiskered wren. L–M: 'introductory-type' calls from male black-bellied wren *fasciatoventris*. N: black-bellied wren, duet. O–P: moustached wren, *genibarbis*, duets, each preceded by a male introductory phrase. Sources: O from Cindy Hogan, P from Macaulay Sound Library. Q: plain-tailed wren, *euophrys*, duet. Males produce both the A and C phrases, while females sing B and D. R: plain-tailed wren chorus from group of two males and four females. The number of birds singing each phrase is indicated by the number of lines drawn above. S: Inca wren, *eisenmanni*, chorus (probably three birds singing). Male and female contributions not identified. This spectrogram was made from a Macaulay Sound Library recording. T: Solo song phrases from sooty-headed wren, *spadix*. Dotted lines present on some spectrograms indicate examples from an extra category of male vocalisation (explained in the text). Time intervals for x-axis subdivisions are the same for all spectrograms. Full-size spectrograms plus soundfiles can be found at http://media.brill.nl/behaviour/146/1/

genibarbis introductory phrases occurred in a repertoire of forms, but the data were too few to determine whether the selection of subsequent phrases within a song was influenced by which particular introductory phrase was used at the start. Some differences in *genibarbis* songs between a Peruvian and a Bolivian population will be described by Maccormick et al. (in prep.).

As with the antiphonal part of the song, these introductory phrases were produced with eventual variety (for a description of their structure, see Appendix). They are perhaps the most common vocalization of *genibarbis*, and often occur as long strings of solo songs. Equivalent vocalizations appear to be completely lacking in the other wrens discussed so far in this group, with the exception of *mystacalis* and *fasciatoventris*. Both of these species also used a repertoire of repeated phrases that did not form part of the alternating interchange of the duet song (for examples see Figure 4J–M; also see Appendix for description). As with *genibarbis*, these *mystacalis* and *fasciatoventris* vocalizations were only observed to be produced by males; however, unlike that species, there was no evidence of a close link between these phrases and the duet song (very rarely was such a phrase followed immediately by a female response).

The plain-tailed wren, *euophrys*, has a singing style that is even more distinct from all the others in the *Pheugopedius* group. This species lives communally and has a group song that may involve several birds singing together. The song contains four components, ABCD, with males singing A and C, females B and D. The details of the song are described elsewhere (Mann et al., 2006a), but the key features (see Figure 4Q and R) are: (i) the song contributions are usually non-overlapping (Table 3) yet the replies are rapid and are timed with great precision; (ii) the performance is most often initiated by a female (Table 3); (iii) all four song components occur in a repertoire of forms, with each phrase consisting of 1–3 (usually 2) notes; (iv) as with other species a limited number of combinations of these components are present, although in this case there is an association of specific phrases from the repertoires of all four components; (v) when more than one bird of the same sex is singing, they match each other's timing and also phrase-type selection (Figure 4R); (vi) songs may be very long, occasionally comprising over 40 ABCD cycles.

The social system and song characteristics of *euophrys* may well be shared by another Andean species, the Inca wren, *eisenmanni*. Sound archive recordings similarly reveal long sequences of notes that are morphologically

similar to those of *euophrys*, and there is evidence of multiple birds simultaneously singing identical phrases (Figure 4S), suggesting the presence of song choruses. A description of the song of this species will be provided in a future publication (data not shown).

The singing style of the final species in the *Pheugopedius* group, the sooty-headed wren, *spadix*, remains somewhat enigmatic. The few recordings we made of this species, or that we obtained from sound libraries, were not of duets, and were presumably of male solo songs (see Figure 4T for example and Appendix for description). We, therefore, cannot comment on how duets may be formed in this species, or on the characteristics of female song.

Cantorchilus

The remaining seven focal species in this study belong to this newly-proposed genus, as do *guarayanus* and *longirostris*, two species for which we have molecular data but access only to limited song recordings.

The molecular data placed two species rather separately from the others: the stripe-breasted wren, *thoracicus*, and the stripe-throated wren, *leucopogon*. These also sang very differently from the rest, since males had two quite distinct song types. In *thoracicus*, one song type was a repeated sequence of 2–4 note phrases, which usually started quietly, increasing gradually up to maximum amplitude (Figure 5B). The second song type (Figure 5A) differed in that the components were single, low frequency, generally pure-tone 'hoots'. The latter songs tended to be longer, with up to 28 notes in a sequence, each separated from the next by approx. 0.5 s. We call this second song form the 'hoot song' and the first form the 'complex song'. Both paired and unpaired males may repeatedly sing both types of song as solos and a repertoire of both forms of song was present.

Duets were usually formed in this species when females interjected their own phrases between the complex phrases of their partners (Figure 5B) and specific male and female phrases were associated within each pair to form a series of duet types. On average, males led over 80% of all duets recorded and produced the last vocalization in nearly 90% (Table 3). Very few duets (<1%) combined female phrases with male hoot songs, and female solo songs were equally rare. Slight overlapping of phrases by both sexes occurred quite regularly in duets, but was less frequent than in most *Pheugopedius* (Table 3).
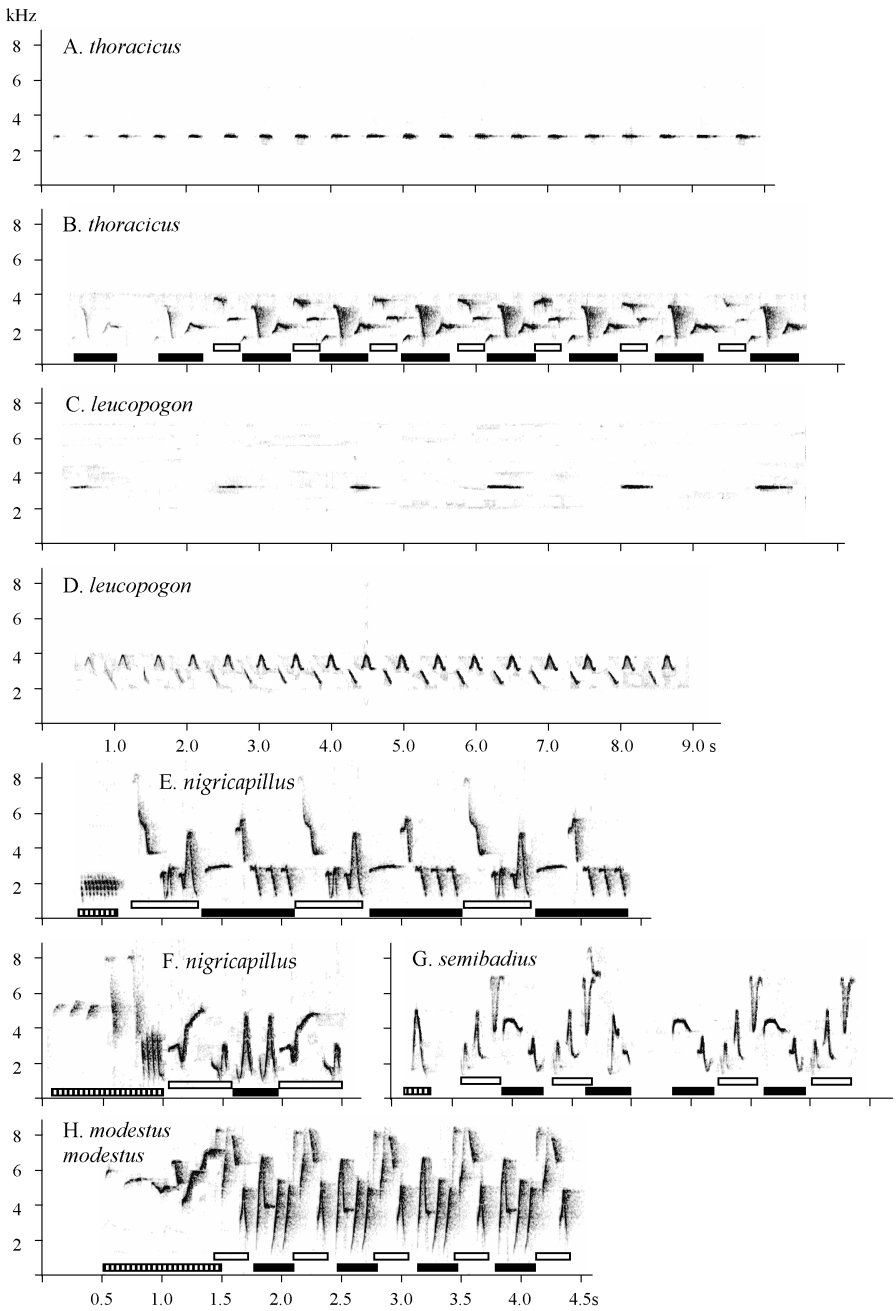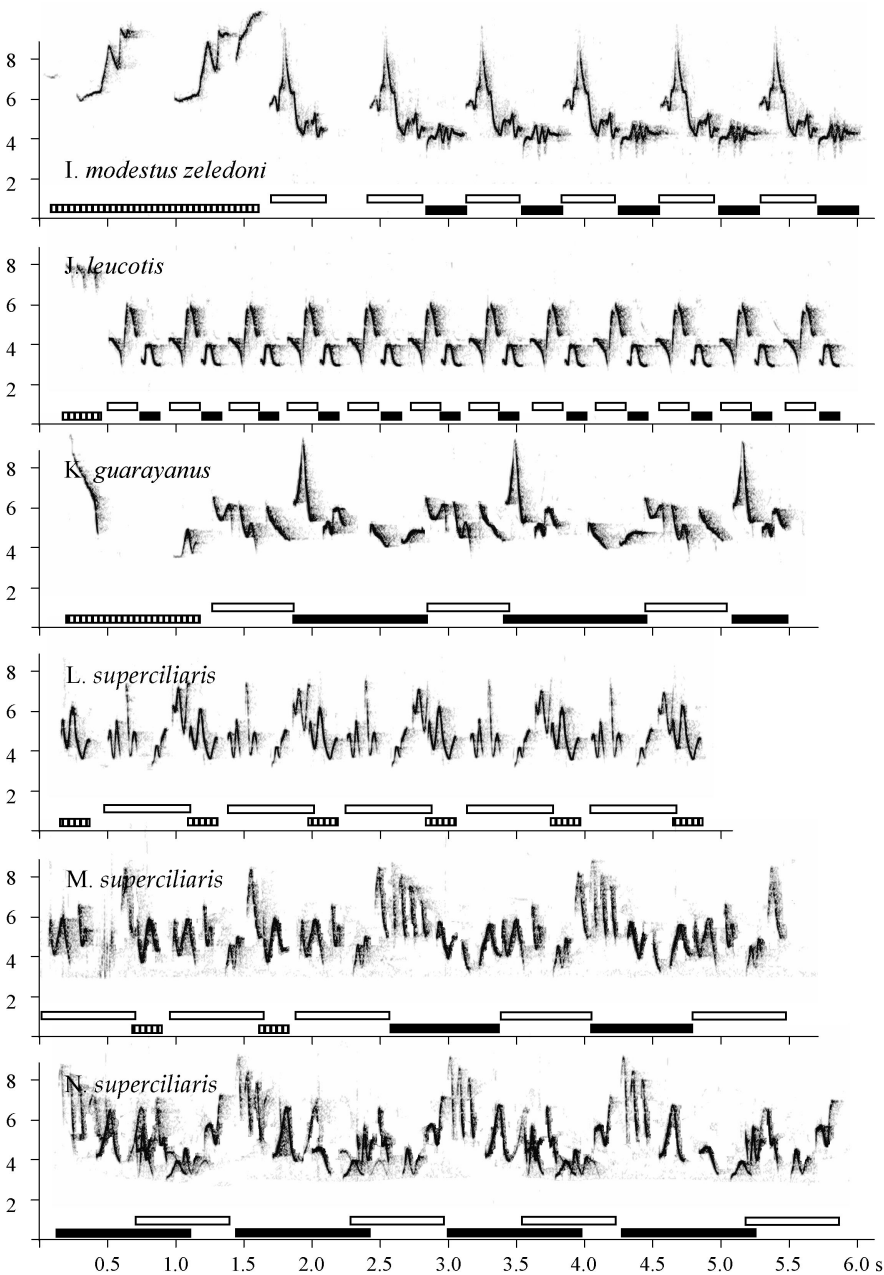
Figure 5.

Figure 5. (Continued.)

In line with their close genetic relationship, the singing style of male *leucopogon* was found to be very similar to that of male *thoracicus*, with the presence of separate repertoires of both complex songs (Figure 5D) and hoot songs (Figure 5C). For an account of the subtle differences between these species in phrase structure, see Appendix. We cannot comment on the song form of the female or the structure of duets in *leucopogon* as, despite working with the species at two sites in different countries, we only recorded songs from males.

Most other wrens in this group (*nigricapillus*, *semibadius*, *modestus* and *leucotis*) had a very similar singing style (Figure 5E–J), as previously described for *m. zeledoni* (Mann et al., 2003). These all had a cyclical duet in which, unlike most *Pheugopedius*, the male and female contributions usually did not overlap (Table 3) or only did so fractionally (this occurred particularly when the pair members were widely separated). The lack of overlaps was all the more notable since the latency between responses was generally 0.06–0.1 s and was regularly as little as 0.02 s. The mean number of phrases per duet ranged from 7–12 across four of these taxa, with *leucotis* standing out with a higher mean of 19.7 ± 2.70 SD. All species occasionally produced much longer songs, with species maxima of 28–37 interchanged phrases. Such songs would be more likely following a playback or an escalated encounter with neighbours. Solos of either of these male or female vocalizations did occur in all four species, but only very rarely.

The cyclical part of the duet among these species was almost always initiated by the female (means per species above 90%). However, the cycle itself was frequently preceded by a separate call or phrase by the male (Figure 5E–J), so males usually produce the first phrase in a duet (Table 3). We regard the introductory component plus the female–male cycle as being the

Figure 5. Sound spectrograms of songs from wrens in the proposed genus *Cantorchilus*. A: stripe-breasted wren, *thoracicus*, male 'hoot' solo song. B: stripe-breasted wren duet. C: stripe-throated wren, *leucopogon*, male 'hoot' solo song. D: stripe-throated wren, male 'complex' solo song. E–F: bay wren, *nigricapillus*, duets. G: riverside wren, *semibadius*, duet. H: plain wren, *modestus modestus*, duet. I: canebrake wren, *modestus zeledoni*, duet. J: buff-breasted wren, *leucotis*, duet. K: fawn-breasted wren, *guarayanus*, duet. L–N: superciliated wren, *superciliaris*, duets. Dotted lines present on some spectrograms indicate male introductory phrases. Time axis subdivisions are each of 1 s for spectrograms A–D, but are of 0.5 s for spectrograms E–N. Full-size spectrograms plus soundfiles can be found at http://media.brill.nl/behaviour/146/1/

complete song, even though the former was often unanswered, occurring in series on its own, and even though the cycle did sometimes begin without it. Two factors argue for the inclusion of the introductory phrase as part of the duet performance:

(i) All three components (the introductory phrase and the subsequent male and female phrases) occurred in a repertoire of forms that were organized within each pair into a set of duet types; i.e., a switch in the introductory phrase type was usually followed by a switch in the other phrases.

(ii) A high proportion of all duet cycles closely followed (latency < 2 s) the introductory phrase, although there was considerable variation in this at the species and pair level (Table 3). In both sub-species of *modestus* 80–100% of duets across all 10 pairs were initiated by an introductory phrase. Some pairs of *semibadius* and *leucotis* also had a similarly high proportion of duets started by the introductory phrase, although in these species other pairs began duets in this way much less often (approx. 20% of the time in two cases). In *nigricapillus*, the percentage of leads by male introductory phrases was 25–73% for the five pairs studied in detail.

The standard duet structure for this group of species is, therefore, $I(AB)_n$, where I is the introductory phrase and A and B are, respectively, the female and male contributions to the cyclic part of the duet. The number of cycles in the latter is represented by n. There was considerable variation regarding which sex produced the last phrase in a duet (Table 3). In almost all *semibadius* and *leucotis* pairs, the males produced the final phrase on over 80% of occasions. In the two races of *modestus* the tendency for males to finish the song in this way was still present but reduced, while in *nigricapillus*, both sexes were equally likely to end the duet (males produced the final phrase on 34.1–68.3% of occasions, $N = 5$). Most female-ended songs in this group were of the form $I-A$. Males were much more likely to end the song once at least one AB exchange had occurred. The *leucotis* songs were somewhat unusual, in that approx. 25% of all duets were ended by an extra introductory phrase (this happened 51.9% of the time for one pair). Such an ending to the song was very rare in the other species. Details about the individual phrase structure for all three duet components present in this group of *Cantorchilus* wrens are provided in the Appendix.

Three species of *Cantorchilus* wrens remain to be covered. The few sound archive recordings we had access to for *longirostris* were insufficient for interpreting song structure, although the impression was that the species

has the fast, alternating (but rarely overlapping) interchanges typical of the genus. It was not clear whether an introductory phrase is present. The song of *guarayanus* is currently being studied, and will be described elsewhere (Maccormick et al., data not shown). A preliminary analysis based on sound archive recordings, and on a small sample of recordings made by NIM in Bolivia, has shown that an introductory phrase of 1–3 notes is present (Figure 5K). The *A* and *B* phrases have a form typical for the genus, although overlapping may be more common than in the other species covered so far.

The final species is *superciliaris*. Although the molecular data suggest that it is nested in among the other species of *Cantorchilus*, its singing style is unusual for the group. While other close relatives alternated the so-called *A* and *B* phrases in their antiphonal singing, with the *I*-phrase being limited to introducing the duet or to solo singing, male *superciliaris* often mixed repeated single-note, or double-note, calls with the female *A*-phrases (Figure 5L). These calls, which we believe to be the equivalent of the *I*-phrase, occurred in a repertoire of forms and appeared to be distinct from a repertoire of more complex phrases that we consider to be the equivalent of male *B*-phrases.

Approx. 51% of all *superciliaris* duets consisted of a combination of female phrases alternating loosely with male introductory 'calls' (Figure 5L), 25% comprised female phrases and only male *B*-phrases (Figure 5N) and 24% were 'typical' *I*–(*AB*) songs comprised female phrases, and both male calls and male *B*-phrases. In each case where males used both types of vocalization in a duet, they began with the calls and switched to complex phrases (Figure 5M), consistent with them representing the introductory calls and male song phrases proper found in their relatives. Interestingly, females also have identical, or near identical, call notes to those of the male, and these call notes can be exchanged in call-duets. On a single occasion we recorded a female singing the call-note phrase along with a male's complex song phrase.

Apart from a more extensive use of the introductory phrase equivalent within duet strings, the other notable (and related) feature of *superciliaris* song, is that it was much more common for the duet contributions to overlap. Over 80% (and up to 97%) of duets across the pairs studied included some overlapping of phrases. Female phrases were overlapped by those of the males much more often than vice versa (Table 3), largely the consequence of the relatively long, complex phrases of females being regularly partnered

with the short, more rapidly produced, *I*-phrases of the males. Nevertheless, even when both sexes were alternating longer phrases (the *A* and *B*-phrases) it was still more likely that female phrases would be overlapped, although in this case overlaps were often only marginal.

The complex *B*-phrases of male *superciliaris* were associated non-randomly with the female *A*-phrases to form duet types. It was not clear from our analysis whether specific *I*-phrases were similarly linked to the *A*- and *B*-phrases. The *I*-phrase calls were frequently produced in solo strings containing up to 15 repetitions. Solos of the more complex male phrases (*B*-phrases) and of female phrases were relatively rare.

Discussion

Two general points emerge from this study. First, the majority of species sing with the same style within each of the four genera into which we consider that '*Thryothorus*' should now be split. These styles differ between the genera (Table 5). Since certain song features are shared within the proposed genera but differ between them, it is likely that song form evolved shortly after the genera split, or even perhaps during the process of diversification, with relatively slow subsequent rates of song evolution. Thus, ecological or other factors associated with these phylogenetic splits might also have impacted on song evolution. The second general point arising from the study is that, despite the predominant uniformity of song features within clades, in several instances species differ markedly in song form from that most typical of their closest relatives. These exceptions to the rule provide important 'natural experiments' that may yield critical insights into the origins of duetting behaviour.

Genus-level song characteristics

Thryothorus (*sensu stricto*) includes only one (*ludovicianus*) or two species (if *ludovicianus albinucha* is given full-species status) and in these only males sing using the loud, clear phrases typical of wrens throughout the original genus '*Thryothorus*' (singing style 1, Table 4). Female *ludovicianus* from North America do occasionally vocalize with their partners, using fairly simple rattle vocalizations which sound quite like alarm calls. These often overlap male songs, but not in a consistent, well-coordinated fashion (Shuler,

1965; Kroodsma, 2005). Although we did not detect female song at all from our population of *albinucha*, it is possible that females do also occasionally vocalize with their mates.

Interestingly, females of tropical forms of the house wren (e.g., *Troglodytes aedon musculus*, sometimes considered to be a full species) also associate a rattle call with male songs (pers. obs. in Costa Rica). The involvement of female calls may represent a route towards more complex duetting behavior, at least in those species in which male-only song was the ancestral state (Harcus, 1977, argued for an alarm call origin of duet contributions in a variety of African bird species). However, as the current wren distribution pattern suggests a neotropical origin for the group, duetting may well have been the ancestral condition, subsequently lost in species ('*Thryothorus*' or otherwise) which expanded their range into temperate latitudes. If so a call-note origin to female duet contributions would be less likely. A transitional 'male song plus female call' stage might also seem somewhat unlikely since it would demand an additional level of developmental complexity: 'song' vocalizations in oscine passerines must be learnt, whereas this is not true for typical 'call' notes (e.g., Catchpole & Slater, 2008).

In *Thryophilus*, both sexes sing but they do not perform well-coordinated duets (singing styles 2 and 3, Table 4). The songs are complex, containing a mixture of trills, 'clicks' and drawn-out whistles (see Appendix). The temporal connection between female and male songs is not tight or consistent for either *sinaloa* or for *pleurostictus* (Molles & Vehrencamp, 1999), although the female songs do tend to occur at times when the male is also singing. In *rufalbus*, female singing is much more frequent, although male solo song is still much the most common song form: 93% of songs were produced by males in an extensive study on the species by Mennill & Vehrencamp (2005). We obtained a higher proportion of female songs than this, no doubt the result of the periodic use of playbacks, which stimulate an increase in the frequency of duets (pers. obs.). Also, this species is known to show seasonal variation in the absolute and relative amount of singing by the two sexes (Topp & Mennill, 2008). It was clear from our analysis of sound archive recordings that songs produced by *nicefori*, the fourth member of *Thyrophilus*, are very similar to those of *rufalbus*, but a more detailed study has recently shown that the songs nevertheless show species-level differences (Valderrama et al., 2007; see also Appendix). Given the similarity

of their songs, it is likely that the same male–female differences that exist in *rufalbus* are also likely to be present in *nicefori*.

In most *Pheugopedius* the sexes sing alternating, overlapping songs with the duet train usually initiated by the male (singing style 4, Table 4). It should be noted that because these songs tend to start with a male vocalization, it is the females that actually instigate the duet by choosing to respond to their male partners. *Pheugopedius* phrases have a shorter duration than those of *Thryophilus*, but tonal whistles (that is, notes with an even frequency) are again common, especially at the start of male phrases, and trills are present in the males in some species, and also in the female in one. In most *Cantorchilus* there is also an alternating duet, but this is sung more rapidly with shorter phrases, usually lacking tonal notes, and is generally non-overlapping with the female contribution coming first. Significantly, the performance tends to be preceded by a male phrase or call in advance of the alternating duet (singing style 7, Table 4) so that male initiation is the norm in this genus too. In previous work on the bay wren *nigricapillus*, Levin (1996) reported that females led almost all duets, and used this observation as part of her argument for duetting being driven by mate-guarding by males in this species. However, this argument is weakened by the frequent occurrence of male introductory calls before the duet proper, meaning that there is no bias towards the female leading.

Male and female phrase-type associations

In all of the duetting (or chorusing) species we studied, both sexes contribute to the duet by selecting from a sex-specific repertoire of phrases (which we term phrase-types). Information about phrase-type repertoire size across the four genera is given in the Appendix. For all species where we were able to collect a large song sample from both sexes, phrases within duets were associated non-randomly to form a series of duet types, suggesting that this feature may have been present in the common ancestor to *Thryophilus*, *Pheugopedius* and *Cantorchilus*. Determining its presence or absence in other wren genera would be illuminating in this regard. The presence of duet types almost certainly reflects the existence of a duet code between the members of each pair, as shown for *fasciatoventris* (Logue, 2006), whereby one or both members of a pair select a particular phrase type depending on their partner's choice of phrase type. Such singing codes may function in helping to identify an individual to its partner, or in identifying a pair to others that may be

listening (Logue, 2006); alternatively, or in addition, they may play a role in improving duet coordination.

The introductory phrases present in several *Cantorchilus* species and in *Pheugopedius genibarbis* were also linked non-randomly with the alternating female and male phrases that followed. This initial duet component, thus, appears to act as a cue to the format for the rest of the song, perhaps helping to further improve the coordination of the performance (Mann et al., 2003). Precise duet coordination without overlapping phrases is achieved by answering a partner's phrase neither too soon nor too late, and is a prominent feature of *Cantorchilus* songs, but not of those of *Pheugopedius* and *Thryophilus*. Recent studies of the magpie lark, *Grallina cyanoleuca* (Hall & Magrath, 2007) and *Pheugopedius fasciatoventris* (Logue et al., 2008) have indicated the value of such coordination to a pair's territorial defense.

Atypical species

In *rufalbus*, females sing more, and their songs are more closely associated temporally with those of males (singing style 3, Table 4), than is the case for others in the genus *Thryophilus* (also see Mennill & Vehrencamp, 2005). Demographic or ecological characteristics distinguishing this species from other members of the genus may provide insight into the origins of complex duetting.

Perhaps the most exceptional song is produced by the group-living *euophrys*, of the genus *Pheugopedius.* In this species, unlike any of the others we studied closely, there is a four-part song, with two parts contributed by each sex; the parts do not also generally overlap with each other (singing style 8, Table 4). All group members contribute to the song so that it is a chorus rather than a duet (Mann et al., 2006b). Its precise form is exceptional among bird species (Mann et al., 2006b), with the closest parallel perhaps being in white-browed sparrow weavers *Ploceplasser mahali* (Voigt et al., 2006). Although we are not aware of any other wrens having the same singing arrangement as *euophrys* (with the possible exception of *eisenmanni*), with its remarkable combination of precise synchrony and antiphony, chorus singing, with overlapping contributions by group members, is nevertheless a prominent feature of other cooperatively-breeding species in the family (e.g., in the genera *Cinnycerthia* and *Campylorhynchus*).

A tentative suggestion at this stage is that learning to contribute appropriately to these songs imposes a considerable challenge to prospective group

members: they have to remember which specific songs from their two sets of song types are to be associated with each song of the two sets sung by members of the opposite sex. The difficulty of this task may represent the imposing of a substantial investment of time and energy, allowing core members to assess the likely helping ability of others, thus influencing whether such individuals are tolerated within the group. In addition to this possibility, it is likely that coordinated nature of the chorus song communicates the motivation of group members to cooperatively defend their territory, just as a coordinated duet song may convey equivalent information about a mated pair in other species (Hall & Magrath, 2007; Brumm & Slater, 2007).

A complex song system is probably also present in *eisenmanni*, which is clearly a very close relative of *euophrys*, living in a similar habitat on high Andean slopes. This species also appears likely to live in extended social groups (Mennill et al., data not shown). A bioacoustic and ecological comparison between these wrens and group-living species in the related genera *Campylorhynchus* and *Cinnycerthia* may shed light on the selection pressures leading to complex song chorusing.

Although we did not focus on *genibarbis* during our field studies, this species (singing style 6, Table 4) is another outlier within the *Pheugopedius* group. This and its sister species, *coraya*, have a similar phrase structure and a similar pattern of alternating (but overlapping) song phrases. However, *genibarbis* possesses an introductory phrase that may be the functional equivalent of that present in the more distantly related *Cantorchilus* group. At present we do not know if the repertoire of these phrases is associated in a non-random fashion with the cyclic component of the song. None of the other *Pheugopedius* wrens appears to use a second form of male phrase in such a way; *mystacalis* and *fasciatoventris* do have a similar repertoire of male calls but in these cases we found no evidence of such a clear link to the duet songs.

An intriguing possibility is that the songs of *genibarbis*, *mystacalis* and *fasciatoventris* may represent transitional stages towards the duet form shown by *Cantorchilus* wrens. The members of the latter group (along with *euophrys*) possess the most complex and temporally-coordinated duets. The alternations between the sexes occur with almost no overlapping, an impressive feat considering the rapidity of the interchanges with very short latencies between phrases. Furthermore, these birds show the greatest similarity in male and female phrase structure (see Appendix). Recent single-species

studies of 'Thryothorus' wrens have concluded that duetting and chorus singing in this group most likely represent a largely cooperative enterprise (Mann et al., 2003, 2006b; Mennill, 2006; Logue et al., 2008). Both temporal coordination of duets and sexual convergence in song contributions might then be predicted to develop as species evolve social and breeding systems in which the roles of pair members converge more generally. Informal observations during the present study did suggest that strongly affiliative behavior such as allopreening occurs more often in *Cantorchilus* wrens, and pair members of this group appear especially prone to duetting while perched side-by-side. Ahumada (2001) also found affiliative behaviour to be stronger in *leucotis* (*Cantorchilus*) than in *rufalbus* (*Thryophilus*). We would predict that *genibarbis*, and to a lesser extent perhaps *mystacalis* and *fasciatoventris*, are intermediate between other *Pheugopedius* and *Cantorchilus* in terms of the degree of cooperation and coordination of activities shown by pair members.

Within *Cantorchilus* the two species which phylogenetic analysis suggests are least closely related to the rest, *thoracicus* and *leucopogon*, also sing very differently to others in the group (singing style 9, Table 4). Both species, clearly closely related to one another, share two distinct forms of male song, the 'hoot song' and a series of more complex phrases. In *thoracicus*, at least, only the latter type of song was used during duets. It is curious that we failed to record duetting, or indeed any female song, from *leucopogon*, despite the great similarity in male vocalizations, and despite working twice with this species. O. Jahn (pers. commun.), while performing a song bird census at Playa de Oro, Ecuador, believes that he heard duetting from *leucopogon*, so perhaps we were unfortunate enough to have been at both sites at times when female song is suppressed or completely absent. Certainly some pairs were attending recently fledged young when we were working in Panama, so other activities may have taken precedence over song. However, although the frequency of duetting does vary seasonally to some extent in other wrens (e.g., Levin, 1996; Marshall-Ball, 2003), female song contributions do not usually disappear completely. Brewer (2001) knew of no reference to duetting in *leucopogon*, and two field guides covering part of its range also make no mention of it (Hilty & Brown, 1986; Ridgely & Greenfield, 2001), so, if not entirely absent, it does appear to be rare.

The final outlier within *Cantorchilus* is *superciliaris* (singing style variable, 4, 6 and 7, Table 4), with a song structure atypically lacking consis-

tency. What appeared to be its equivalent of the introductory phrase was incorporated with great regularity in the antiphonal, cyclic part of the song, and many duets, possibly as a direct consequence of this, showed considerable overlapping of phrases.

Conclusions and future directions

By combining detailed song analysis with our phylogenetic data, we have identified several species in the group '*Thryothorus*' where song diverges from that of near relatives. Closer study of such cases may help one to identify selective forces that have led to such divergence. At this stage there is very little information available on life histories, ecology and behavior for most species within the group, so any suggestions concerning such selection pressures are necessarily tentative.

The necessity of a good phylogeny is perhaps best illustrated by comparing *Thryophilus sinaloa* and *Pheugopedius felix*. These species are frequently sympatric, occupying the same habitat, and indeed often have overlapping territories (as do many other species), yet only the latter demonstrates well-developed duetting: in this case, the song seems more linked to phylogenetic relationships (reflected here in their generic classification) than to broad-level ecological factors such as climate or vegetation. However, although relatedness *per se* no doubt does explain much of the song similarity between congeners, it remains possible that more subtle ecological traits are shared more closely within members of each genus, whatever the broad habitat type, and such factors may play a more direct role on constraining song form. Although a detailed analysis is beyond the scope of this paper, it is possible that members of a particular genus tend to share similar foraging behavior, which in turn may impose constraints on intra-pair spacing, the relative roles of the pair members in territorial and reproductive duties, and hence on the form of the acoustic signals that they produce.

This argument was used by Ahumada (2001), in his study of *rufalbus* and *leucotis*. He suggested that the frequent ground foraging amongst leaf litter of pair members of *rufalbus* imposed limitations on the time they could spend in close proximity and, thus, on their duetting capabilities, whereas no such constraints applied to species that gleaned prey within the shrub layer, such as *leucotis*. Certainly, all *Thryophilus* species spend much of their foraging time on, or very close to, the ground, in contrast to members of

Cantorchilus, which all tend to search within the shrub layer (Brewer, 2001, pers. obs.). Interestingly, informal observations of *superciliaris*, which does not consistently show the high level of duet coordination possessed by its nearest relatives, suggested that it might be more similar to *Thryophilus* than *Cantorchilus* in its foraging behaviour. It should be noted that some *Campylorhynchus* wrens do perform well-coordinated duets despite generally foraging on the ground. Anecdotal observations, however, suggest that bouts of singing and foraging may be more temporally separated in these birds.

This study has addressed the song characteristics of members of the traditional genus '*Thryothorus*', but exhaustive comparisons have not been possible. For example, a more subtle look for differences in repertoire sizes would be worthwhile. Large discrepancies in the size of male and female song samples, and of sample sizes between different species, have precluded more definitive conclusions about how repertoires vary across the group and between the sexes (see Appendix). It is often assumed that tightly coordinated duetting can arise as a consequence of the convergence of male and female roles in regard to, for example, territorial defence (e.g., Wickler, 1980). As the functions of the vocalizations of the two sexes converge, it might be assumed that the respective phrase repertoires would also become more similar, both in terms of the form of the phrases and the number of phrase-types present. This study has provided broad support for both of these assumptions (consider, for example, the extreme cases of the male and female *ludovicianus* vocalizations, compared to those of a *Cantorchilus* duetter); however, it is not clear whether the pattern holds true at a finer level. Finally, the present study set out to address the different forms of duet present within the genus '*Thryothorus*', with the intention of identifying transitional evolutionary stages in duet complexity and precision within this all-inclusive group. Given that we now know that the taxon is paraphyletic, it is clear that the form of the songs of other closely related genera (e.g., *Cinnycerthia*, *Cyphorhinus*, *Henicorhina*, *Uropsila*) must also be examined, if the picture of song evolution in the group is to be fully understood.

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Appendix

Detailed song phrase descriptions

Although this study has focused on how the newly described genera of '*Thryothorus*' wrens show variation in the frequency and patterning of song duetting, it is also appropriate to include descriptions of the structural characteristics of the phrases comprising these duets. In an evolutionary sense the two are connected, as selection pressures leading to rapid, precise, antiphonal male–female songs are likely also to select for phrases which are relatively short, consistent in duration and with salient timing cues. Conversely, phrase structure characteristics may impose constraints on the degree of song coordination possible within a particular species. Certain structural features of individual song phrases have been included in the main part of the manuscript, where they relate directly to duet format. Here we provide a more thorough description of phrase structure, followed by an account of repertoire size, across the four genera.

The Carolina wren, *ludovicianus*, and the species/sub-species *albinucha* (known as the white-browed wren) both belong to the genus *Thryothorus*. Their songs, in the conventional sense, are limited to males (see Figure 2). These male phrases consist of loud, rapid trills, produced at a rate of 3–5 per second with each component of the trill usually consisting of 3–4 complex notes. Individual notes generally show at least one sharp frequency inflection, with the whole phrase regularly covering a broad frequency range from approx. 2 kHz to

over 6 kHz. It is not known whether *albinucha* songs, although clearly very similar to those of more northern *ludovicianus*, are different in their fine characteristics.

The chatter vocalization occasionally produced by female *ludovicianus* in association with male song phrases comprises a very rapid series of broadband, click-like notes. We have very little data on the range of variation found in these calls (in the samples we obtained the notes were produced at approx. 30 per second and the duration of the vocalization varied from 0.42 to 1.44 s). We did not encounter such calls in *albinucha*.

Songs of members of the genus *Thryophilus* are depicted in Figure 3. Male phrases from *sinaloa*, *pleurostictus* and *rufalbus* have several features in common: all begin with some relatively quiet introductory notes, usually a mixture of clicks, whistles and hoots (tonal notes) followed by a distinctive sequence (or, less commonly, two sequences) of repeated notes, forming a trill or rattle. The songs of all three often end with a single inflected note, which is usually at a higher frequency than the rest of the song, and is often emphatic. In many regards, the songs of these wrens show most contrast between *sinaloa* and *rufalbus*, with *pleurostictus* being somewhat intermediate. The introductory, trill and terminal notes of *sinaloa* all tend to be higher-pitched (some notes reaching 8 kHz), and cover a greater frequency range (bandwidth may be up to 5 kHz), than the corresponding notes of the other two species. Chevron, or tick-shaped trill notes appear to be more common in this species. At the other extreme, *rufalbus* songs are pitched at the lowest frequency (all song components are usually below 3 kHz) and the notes are almost exclusively flat and tonal, with the overall effect being ethereal and flute-like. Males of both *sinaloa* and *pleurostictus* may sometimes break their usual singing pattern to produce compound songs consisting of two linked phrases (described also for these species by Brown & Lemon, 1979 and Molles & Vehrencamp, 1999, and for *Pheugopedius fasciatoventris* by D.M. Logue, pers. commun.).

In *sinaloa*, the female songs were at least as varied as those of males in terms of the number of different syllables present (Figure 3C), but were produced with reduced amplitude. Also, and most notably, they usually lacked the emphatic trill component. Although we found female songs in this species to contain as many syllable types as those of males, Brown and Lemon (1979) found them to be shorter and simpler; they also noted that females usually sing in close proximity to the nest. We did not encounter female songs in *pleurostictus*, but Molles & Vehrencamp (1999) describe them as being lower in amplitude than those of males and with trills lacking in consistency. Both sexes in *rufalbus* produce somewhat similar songs although, at a fine level, those of females tend to have fewer repeated elements in the trill component, are often quieter, and the overall song frequency is a little higher than in males (Figure 3F and G). A more detailed description of *rufalbus* song is given in Mennill & Vehrencamp (2005), where the authors report that a small proportion of songs are shared between the sexes. A recent study (Valderrama et al., 2007) has shown that the fourth member of this genus, *nicefori*, although having a very similar song to *rufalbus*, tends to produce shorter phrases, with fewer syllables and syllable types, and with the trill and terminal frequency components at higher frequency.

Figure 4 depicts spectrograms for members of the genus *Pheugopedius*. In the main text, discussion was divided to cover 'typical' singers for this genus and then the outliers, and the same format will be followed here. The eight species with the characteristic *Pheugopedius* song form are *fasciatoventris*, *atrogularis*, *felix*, *rutilis*, *sclateri*, *maculipectus*, *coraya* and *mystacalis*. In two of this group, *felix* and *coraya*, the male phrase, but not the female phrase, ended with a trill (consisting of 2–13 repeated notes in *coraya*, mean of 5.1, and 2–6 repeated notes in *felix*, mean of 2.7). In *sclateri*, the male song phrase typically ended with just

two identical notes, and again the female had no such repeats. The only species in which both sexes possessed a trill was *atrogularis*, but this feature was longer in the male (mean 7.9 notes, max 17) than in the female (mean 3.1 notes, max 9). The other four species (*fasciatoventris*, *rutilis*, *maculipectus* and *mystacalis*) did not produce phrases containing trills (Table 3). Female *sclateri* regularly (63% of all duets sampled), and female *rutilus* and *felix* occasionally, alternated a repeated phrase with each single phrase produced by their partner.

Male phrases in this group of eight species were on average significantly longer than those of females, measured in terms of both the number of notes present (Table 3) and the phrase duration (see also Logue et al., 2007, for detailed account of differences in *fasciatoventris*). The songs of female *coraya* and *sclateri* were actually slightly more diverse than those of the males, in terms of the average number of note-types present per phrase (Table 3), although the repeated notes in the male phrases meant that the latter still tended to be longer.

The songs of all eight species included a variety of tonal and frequency-modulated whistles. Female phrases tended to be pitched slightly higher than those of males (for example, the maximum frequency reached in each phrase, on average, was significantly higher for four of the species; see Table 3) and they typically contained notes that covered a broader frequency range. In these species there was usually a distinct sex difference in the form of the first note within each phrase. In males, this note was generally either a tonal whistle, or a slight up-sweep or down-sweep. The frequency of this note varied from species to species, at around 3–4 kHz in *felix* and down to around 2 kHz or lower in *fasciatoventris* and *mystacalis*. The first note of female phrases across the eight species had a tendency to show greater frequency modulation and was usually pitched higher than was the case for males. *Mystacalis* and *fasciatoventris* also possess a second set of phrases produced by the male, which do not appear to be closely tied to the duet. Those of *mystacalis* comprised either one or two sharply inflected notes, rising from approx. 800 Hz to 2–3 kHz. The *fasciatoventris* phrases consisted of an initial rasping or rattling harmonic note covering a wide frequency band, followed by two low frequency notes (usually below 2 kHz), both of which were typically frequency-modulated and with the second lower pitched than the first.

Moving on to *Pheugopedius* species with less typical songs, *genibarbis* have song phrases used in their duets which resemble those of *coraya*, with the male phrase, but not that of the female, beginning with a drawn-out tonal note or slight down-sweep, followed by a trill or rattle. The introductory phrases produced by *genibarbis* consisted of one or two rasping down-slurred and drawn-out harmonic notes followed by a trill or rattle, typically comprising 3–6 repeated components.

Both sexes in *euophrys* possess repertoires of two types of song phrase, although those within a sex are so strongly linked that they may be best described as a single song type (A–C in males, B–D in females) within which the appropriate half of the other sex's song is inserted. All four phrases contain just 2–3 short-duration notes, each with sharp frequency modulations (tonal notes are absent in this species). Both male phrases extend across a 1–4 kHz range, whereas the female B phrase typically covers a broader frequency range (1–6 kHz) than the D phrase (1–3 kHz). For further details of individual phrase structure see Mann et al. (2005). The notes present in *eisenmanni* songs resemble those of *euophrys*. Other characteristics of the phrase structure in this species will be given in a future publication (data not shown).

Our small sample of recordings of *spadix*, the final *Pheugopedius* species, all consisted of a series of repeated five or six-note phrases, most of which tended to decline in frequency

through the course of the phrase (Figure 4T). The notes were, typical of the genus, a mixture of mostly frequency-modulated whistles, with occasional tonal notes. Within this small sample, there was no obvious tendency for the first note in particular to be tonal. None of the notes were repeated to form a trill, which raises doubts about this species being conspecific with *atrogularis* (a possibility mentioned in Brewer, 2001).

Cantorchilus spectrograms are shown in Figure 5. Two closely-related species in this genus, *thoracicus* and *leucopogon*, each possess two distinct forms of male song. In *thoracicus*, one song type was a repertoire of a repeated sequence of phrases, usually consisting of 2–4 notes (mean 2.7 ± 0.53 SD) in the 1–3 kHz range. Most of these notes were sharply frequency-modulated, but some tonal notes were also present. The song usually started quietly, with the first few phrases showing an increase in amplitude. Up to 20 or so repeats of the same phrase were present within a single song, each separated by approx. 0.3 s. Female phrases were similar in the number of notes, their duration and note structure to the complex phrases of the males, although they tended to reach a higher frequency (Table 3). The second male song type was quite different, although it also showed a pattern of repeats, with a quiet start before full amplitude was reached. In this case the components were single, short, low frequency (approx. 2 to 2.5 kHz), rather pure-tone 'hoots' (of which, again, each bird possesses several varieties). Up to 28 hoots, each separated by approx. 0.5 s, occurred in a single sequence.

The complex songs of male *leucopogon* again consisted of repeated 2–4 note phrases (mean 2.26 ± 0.54 SD), increasing in amplitude through the song. The notes were also structurally similar in form to those of *thoracicus*, although the phrases were typically at a higher frequency, ranging from 2–4 kHz. Hoot songs in *leucopogon* were also similar in form to those of *thoracicus*, but again they tended to be at a higher frequency (3–4 kHz). We failed to encounter female song in *leucopogon*.

The remainder of the *Cantorchilus* wrens that we focused on in this study typically show a singing style which we define as $I(AB)_n$, with male producing the introductory (I) phrase and the B-phrase, and with the female producing the A-phrase. The A and B-phrases of this group of wrens were typically much shorter in duration than the duet phrases of *Pheugopedius* wrens, and comprised very few notes. For *leucotis* and *modestus zeledoni*, the male 'phrases' were usually just a single note, whereas 2–3 notes (and occasionally four) were the norm for *nigricapillus*, *semibadius* and *m. modestus*. The female phrases also usually consisted of 1–3 notes, with just one again being most common for *leucotis*. In contrast to the *Pheugopedius* group, in *Cantorchilus* wrens it was common for female phrases to contain a greater number of note-types than male ones (Table 3). A clear trill (a series of up to 8 repeated notes) was only present in male *nigricapillus* (Figure 5E and F), leading to this species being the only *Cantorchilus* member in which males had the longer song phrases (Table 3). Males of *m. modestus* frequently gave a repeat of the last note in the phrase (Figure 5H), but there was still no significant difference between the sexes in overall phrase length.

As with *Pheugopedius*, female phrases in *Cantorchilus* tended to contain notes reaching a higher maximum frequency (Table 3), with the exception of *semibadius*, where no sex difference was found in this measure. Most of the notes in *Cantorchilus* songs were sharply frequency-modulated, and various forms of chevron were common. Only male *nigricapillus* occasionally incorporated a tonal note.

The form of the introductory phrase differed markedly between species. In *leucotis* it was a fast trill of 2–10 notes (mean 4.8) mostly in the 4–7 kHz range (Figure 5J). Some *nigricapillus* phrases were also fast trills, but at a lower frequency (generally 1–2 kHz; Figure 5E).

Other *nigricapillus* introductory 'phrases' were either single low frequency whistles, containing both a frequency-modulated and tonal component, or were much more complex and consisted of multiple trills, covering a wide range of frequencies (Figure 5F). Male *semibadius* used single (or, rarely, up to three) sharply frequency-modulated notes covering a wide frequency band (1.5 to 4–6 kHz; Figure 5G). The introductory phrases of the two *modestus* sub-species both comprised a series of high-pitched notes (4–8 kHz), most of which were sharply frequency-modulated (Figure 5H and I). Compared to *m. zeledoni*, *m. modestus* had an average of slightly more notes in the phrase (mean 5.74 rather than ca. 4), but had a shorter phrase duration (because each note was briefer and the interval between notes was considerably less). A further difference was that the *m. modestus* phrase lacked the repeated middle note typical of *m. zeledoni*.

The song of *superciliaris* was found to be atypical, with the $I(AB)_n$ pattern less discernable. The separate descriptions of the three components given below must, therefore, be regarded as somewhat tentative. I-phrase notes occurred between 2–4 kHz and were sharply frequency modulated, with more than one switch in frequency. The presumed B-phrases began with one, or two, high frequency but descending trills made up of sharply frequency-modulated chevrons or down-sweeps, that started at 6–8 kHz, dropping to 3–4 kHz (Figure 5M and N). The trills contained 2–8 notes (mean 4.8 ± 2.14 SD). These phrases ended with 2–3 louder, frequency-modulated notes in the 1–4 kHz range, with the last note usually reaching the lowest frequency found in the whole phrase. The female phrases contained 4–6 elements (mean 4.60 ± 0.63 SD), with each having a different structure and usually containing at least two sharp frequency modulations. In contrast to the male phrase, the last note, or sometimes the penultimate note, reached the highest frequency.

Repertoire size amongst 'Thryothorus' wrens

Although we recorded a large sample of songs from several pairs of each study species, it was unlikely that we encountered the full phrase repertoire for many individuals. Females in particular, due to their much lower song rates, will have been under-sampled and so comparing the repertoire size of the two sexes was difficult. Likewise, in *Cantorchilus* wrens, it was not easy to deduce whether there was a similar repertoire size for all three components of the songs, since the rates of the three differed substantially. Thirdly, we had very different sample sizes of songs across species, so precluding accurate assessment of variation between them.

For the purpose of this study, however, some general conclusions about repertoires can be made. Morton (1987) found a repertoire size of 32 for male *ludovicianus* (genus *Thryothorus*) and our estimate of 24.5 songs (range 20–28) for *albinucha* suggests a similar number in this taxon. In the genus *Thryophilus*, we found an average of 22.2 songs per male (range 20–27) for *sinaloa* and Molles & Vehrencamp (1999) found a mean of 19.7 songs per male (range 15–24) for *pleurostictus*. The latter was considerably higher than the average of only 11.8 (range 9–14) songs we identified per male in our Mexican population of the same species. Although we sampled between 328–717 songs for five males, our regular use of playbacks probably led to an underestimate of this measure. Molles & Vehrencamp (1999) and Trillo & Vehrencamp (2005) have shown that male *pleurostictus* use more consecutive repeats of phrases during playback, therefore revealing their repertoire more slowly. These authors demonstrate that *pleurostictus* oscillates between different singing styles, sometimes switching rapidly between song types (singing with immediate variety) and sometimes using

many repeats of the same song before switching (eventual variety). The same singing pattern, of mixing immediate and eventual variety, applies also to *sinaloa* (Brown and Lemon, 1979; pers. obs.), but it is not obviously present in other *Thryothorus*, where eventual variety is the norm.

We do not have useful data on female repertoire size for either *sinaloa* or *pleurostictus* since our sample sizes are too small. Males of the other member of *Thryophilus*, *rufalbus*, appear to possess fewer songs in their repertoire than males of *sinaloa* and *pleurostictus*. Mennill & Vehrencamp (2005) found *rufalbus* males to have an average of 10.8 songs (range 6–14), while females had a significantly lower average of 8.5 songs (range 4–11). These figures are similar to those from two pairs for which we had a large data set ($N > 300$ songs), where there were 9 songs for each sex in one case, and 11 for the male and 8 for the female in the other.

Within *Pheugopedius*, males for which we had a reasonably large data set (200–1500 songs) usually revealed 20–30 different phrase types, with a maximum in *felix* of 40. Female repertoire sizes more often ranged between 15–22 phrase types, with *felix* again having the maximum number (34). The *Cantorchilus* wrens follow a similar pattern, with 15–30 versions of the cyclic duet components present for most pairs, along with a similar number of introductory phrases possessed by each male. Females again appeared to have slightly smaller repertoires, although this is by no means certain, as fewer female songs were generally sampled per pair. In *nigricapillus* and *semibadius*, but not in other species, fewer *I* phrases were identified compared to *A* and *B* phrases, despite considerably more sampling of the former. Larger samples of songs would be required than we were able to obtain to determine whether significant differences are present between species and sexes.