

A Summary of Evidence for Female Song, Vocal Duetting and Cooperative Breeding in Species of the Family Certhiidae (*sensu* Sibley & Ahlquist 1990)

Note to Readers

Throughout the text, accounts of species with particularly poor observational data (often no more than a mention of occurrence) are marked with asterisks (*). This survey first appeared as Appendix F of my dissertation (Barker, F.K. 1999. The evolution of cooperative breeding in *Campylorhynchus* wrens: a comparative approach. [Ph.D. Dissertation](#), University of Chicago). **Although the data presented here have not been comprehensively updated since 1999, I recently added a number of references (especially on *Thryothorus*) that have been sitting on my desk for some time. There are more (e.g., some work on *Cistothorus*) that need adding, which I will hopefully get to soon. As before, if you notice particularly egregious errors, misinterpretations, or omissions, I would be happy to hear of them.**

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Introductory Comments

The following is a general literature review of the evidence for female song, vocal duetting, and cooperative breeding in the the avian family Certhiidae (*sensu* Sibley & Ahlquist 1990). The intent of this review is to make the most accurate estimate possible, given available published accounts, of the frequency and taxonomic distribution of these traits within the two families. This information can then be used in the inference of patterns of behavioral evolution within the Certhiidae, using the Sittidae as an outgroup. These families are sister taxa according to DNA-DNA hybridization studies (Sibley & Ahlquist 1990, Sheldon and Gill 1997), making comparison of behavioral traits between the two families critical to determination of character polarity within the Certhiidae.

In the course of conducting this review, it became immediately apparent that the distribution of behavioral information on species in these groups is highly biased toward North American and European species. Admittedly, this pattern is not unexpected, but nevertheless highlights the severe need for basic descriptive natural history work on a large number of species. An obvious consideration is the issue of "negative evidence." Unlike morphological characters, behavioral characters are expressed only transiently, and therefore the issue of temporal sampling becomes important. For this reason, the caveat "absence of evidence is absence of evidence, not evidence of absence" must be rigorously adhered to in behavioral character analysis. Based upon this argument, the stringency of criteria for assigning a state of "absence" to a species for a given behavioral character must be much higher than for assignment of "presence" (assuming that such discrete assignments can even be made). I have attempted to assess qualitatively the degree of confidence which can be placed in the assignment of character states to species, taking into account the frequency of observation of species in the wild, and the types of studies which have been made of given species (field observations, recordings, observations in captivity, studies of banded populations). Character state assignments which I do not consider strongly supported by published information have been highlighted with a ? after the assignment. Additionally, summaries of the frequency of behaviors within genera are likewise highlighted if the estimates are based on uncertain state assignments.

A second vital issue is the criteria used for assignment of character states. In the case of female song and duetting, basic definitions are problematic. The concept of "song" was developed primarily in the context of seasonally territorial, often migratory north temperate species, and application of the concept to some groups is controversial. This is especially apparent for the Polioptiline genera *Ramphocaenus* and *Microbates*. Vocalizations of the other taxa included in this review seem generally to fit the classical definitions of "songs" and "calls." Additionally, definitions of "duetting" are variable, and there is likely a continuum between "typical" male-only song, song in both sexes, and temporally coordinated duetting behavior (Farabaugh 1982). Following Farabaugh (1982), I have taken a catholic approach to female song and duetting, and have included all reports of simultaneous female and male vocalizations as potential duets. Where evidence was available, I have noted where duetting appears to be on the simultaneous or the antiphonal ends of the scale of temporal coordination between males and females (S/A; Farabaugh 1982). In agreement with Farabaugh's (1982) observation in her general review, usage of these terms in the literature reviewed here is extremely variable, with different authors often applying one term or the other to vocalizations of the same populations of a single species. Additionally, I have made some indication of the degree of similarity between male and female song by designating species as monophonic or diphonic (M/D). Both of these designations are in brackets following the duetting designation. Regarding cooperative breeding, definitions are less controversial, but the evidential burden is greater. I have recognized a continuum of observations suggesting the presence of this behavior, in increasing order of certainty. This continuum, roughly speaking, is as follows: year-round sociality (usually found in groups), mixed flocks of adults and young with more than two adults, dependent young attended by more than two adults. One step beyond this last is the observation of multiple adults caring for young (e.g. nest defense or feeding nestlings), which is the defining criterion for cooperative breeding (Brown 1987). Naturally, the observation of this behavior in banded populations must be taken as even stronger evidence for the presence of cooperative breeding.

Subfamily Certhiinae

Genus *Certhia* (6 species, female song:0[?], duetting:0[?], cooperative breeding:0[?])

familiaris: This and the next two species are extremely well known, especially in terms of their vocalizations (e.g. Thielcke 1962). Available data (Baker 1932, Witherby et al. 1938, Ali and Ripley 1983, Roberts 1992, and see especially Cramp and Perrins 1993) indicate the absence of female song, duetting, and cooperative breeding. (FS=0, D=0, CB=0)

americana: As for the other well-known *Certhia* species, neither female song nor helpers at the nest seem to be present in this species (Bent 1948, Davis 1978). (FS=0, D=0, CB=0)

brachydactyla: There is no evidence for female song or helpers in this well-characterized species (data summarized in Cramp and Perrins 1993). (FS=0, D=0, CB=0)

himalayana: This and the following two species are poorly known. Available data indicate behavioral similarity to more well-known members of the genus (Baker 1932, Ali and Ripley 1983, Roberts 1992, Harrap and Quinn 1995). (FS=0?, D=0?, CB=0?)

nipalensis: See comments under *himalayana* (Baker 1932, Ali and Ripley 1983, Harrap and Quinn 1995). (FS=0?, D=0?, CB=0?)

discolor: See comments under *himalayana* (Baker 1932, Ali and Ripley 1983, Harrap and Quinn 1995). (FS=0?, D=0?, CB=0?)

Genus *Salpornis* (1 species, female song:0[?], duetting:0[?], cooperative breeding:0[?])

silonotus: This species is relatively poorly known, but despite morphological differences between it and *Certhia*, its behavior seems in general very similar (Stark 1900, Baker 1932, Priest 1936, Bannerman 1948, Ali and Ripley 1983, Ginn et al. 1989, Harrap and Quinn 1995). (FS=0?, D=0?, CB=0?)

Subfamily **Polioptilinae**

Genus *Microbates* (2 species, female song:2[?], duetting:0[?], cooperative breeding:0[?])

collaris: Sick (1993), who describes the vocalization of the species, makes no mention of duetting. However, the vocalization pattern of this species seems similar to that of its congener (see below). Oniki and Willis (1979) followed one nest (and observed several others) of this species in detail and made no note of helpers at the nest. (FS=1?[M], D=1?[A?], CB=0?)

cinereiventris: Farabaugh (1982) lists this species as duetting based upon unpublished data of E.S. Morton. On the other hand, Stiles et al. (1989), though they describe the vocalizations of this species, make no mention of duetting. Species in this genus may follow a pattern similar to that found in the closely related genus *Ramphocaenus* (below). The only observation of breeding is by Kiff (1977) who noted only the presence of an unaccompanied pair. (FS=1?[M], D=1?[A?], CB=0?)

Genus *Ramphocaenus* (1 species, female song:1, duetting:0, cooperative breeding:0[?])

melanurus: Skutch (1960, 1968) makes no mention of duetting in the species (subspecies *rufiventris* and *melanurus*), following extensive observations of courtship and nesting. Nor again is such behavior mentioned in Stiles et al. (1989). On the other hand, Sick (1993) suggests the presence of a female call potentially coordinated with a similar male vocalization. Belcher and Smooker (1936) similarly describe a trilling call of the given by individuals of the species, noting that it is given by both sexes, but without noting coordination between the sexes. Farabaugh (1982) lists the species as duetting, based upon the description of Ridgely 1976 (subsp. *rufiventris*, see Ridgely and Gwynne 1989), which reads: "Usually in pairs, frequently calling back and forth to each other with a distinctive clear musical trill usually only on one pitch, sometimes rising in intensity and then softening towards the end..." Skutch's observations (1960, 1968) revealed no evidence of supernumeraries. (FS=1[M], D=1?[A?], CB=0?)

Genus *Polioptila* (11 species, female song:0[?], duetting:0[?], cooperative breeding:0[?])

caerulea: Root (1969), who observed several color-banded pairs, as well as other pairs in contiguous habitat, found no indication of duetting. This observation is supported by Ellison (1992), who specifically states that female song is absent in this species. No observation of helping at the nest has been made. (FS=0, D=0, CB=0)

californica: Intense observation of a single pair (Woods 1928), as well as more general observations of this species' behavior (Atwood 1988, Howell and Webb 1995) indicate the absence of female song and nest helpers. (FS=0, D=0, CB=0)

melanura: Available observations of this species' behavior (Atwood 1988, Howell and Webb 1995) indicate the absence of female song and nest helpers. (FS=0, D=0, CB=0?)

**lembeyei*: This species is poorly represented in the literature. Bond (1985) describes the song of this species as "loud and more melodious than that of the Blue-grey Gnatcatcher," but

- makes no mention of duetting or female song. Nesting behavior is undocumented, but probably similar to that of other members of the genus. (FS=0?, D=0?, CB=0?)
- nigriceps*: This species is fairly well known vocally, but behavioral observations are limited (Atwood 1988, Howell and Webb 1995). Available data indicate similarity to *californica* and *melanura*. (FS=0, D=0, CB=0?)
- albiloris*: This species appears relatively poorly known behaviorally. Available observations (Stiles et al. 1989, Howell and Webb 1995) do not indicate the presence of female song or nest helpers. (FS=0?, D=0?, CB=0?)
- plumbea*: Skutch (1960) makes no mention of duetting or helpers at the nest, following extensive observations of courtship and nesting. This is supported by other published accounts (Marchant 1960, Hilty and Brown 1986, Stiles et al 1989, Howell and Webb 1995). (FS=0, D=0, CB=0)
- **lactea*: This and the following three species are the most poorly known members of the genus, and little published information is available on their behavior. The account of Ridgely and Tudor (1989) does not indicate the presence of female song or regular occurrence of nest helpers. Additionally Willis and Bosso (1997), in the first description of the nest of this species, also give a brief description of the behavior and vocalizations of a single pair of this species without mentioning coordinated vocalizations. (FS=0?, D=0?, CB=0?)
- **guianensis*: The brief description of Meyer de Schauensee and Phelps (1978) gives no indication of female song or cooperative breeding. (FS=0?, D=0?, CB=0?)
- **schistaceigula*: The account of Hilty and Brown (1986) only gives a description of one call, without mentioning the song. Available data do not indicate the presence of cooperative breeding in this species. (FS=0?, D=0?, CB=0?)
- **dumicola*: Sick (1993) gives an extended description of song types and patterns in this species, but makes no mention of duets. Available data do not indicate the presence of cooperative breeding. (FS=0?, D=0?, CB=0?)

Subfamily **Troglodytinae**

Genus ***Donacobius*** (1 species, female song:1, duetting:1, cooperative breeding:1)

atricapillus: Fuertes (1913), and Skutch (1968) describe simultaneous duetting in this species. This observation has been confirmed by Kiltie and Fitzpatrick (1984), who also documented the presence of cooperative breeding in a banded population of the species. (FS=1[M?], D=1[S], CB=1)

Genus ***Campylorhynchus*** (13 species, female song:12, duetting:12, cooperative breeding:12[?])

chiapensis: Skutch (1960) describes simultaneous duetting in the species, as does Selander (1964). However, the recording of Hardy and Coffey (1996; hereafter H&C) seems to represent tightly-coordinated antiphonal duetting. Selander (1964) made extensive observations of nest helpers in this species. (FS=1[M], D=1[A], CB=1)

griseus: Ridgely and Tudor (1989) describe simultaneous duetting in the species, well demonstrated in H&C's recording. Cooperative breeding is extremely well-documented in this species, from the work of Rabenold (e.g., 1990). (FS=1[M], D=1[A], CB=1)

rufinucha: Skutch (1960) and Stiles and Skutch (1989) describe simultaneous duetting in the species from Costa Rica. Selander (1964) describes very similar behavior in Mexican representatives of the species, and this behavior is apparent in H&C's recording. The

- presence of helpers at the nest has been documented in this species by Joyce (1993). (FS=1[D], D=1[S], CB=1)
- jocosus*: Selander (1964) describes simultaneous duetting in this species (confirmed by pers. obs.), but H&C's recording does not provide an example. Additionally, both Selander (1964) and Farley (1996) confirm the presence of nest helpers in this species. (FS=1[D], D=1[S], CB=1)
- gularis*: Selander (1964) reports duetting in this species, though it is not clear of what type: H&C's recording of this species contains only call notes. Selander's (1964) observations of this species did not indicate the presence of supernumeraries, but the work of Farley (1996) demonstrates their regular occurrence. (FS=1[D?], D=1[S?], CB=1)
- yucatanicus*: Zimmerman (1957) describes simultaneous duetting in this species in detail (confirmed, pers. obs), though H&C's recording does not provide an example. Groups of three have been observed just prior to breeding (pers. obs.), and the presence of supernumeraries during breeding is likely but not confirmed. (FS=1[D], D=1[S], CB=1?)
- brunneicapillus*: Anderson and Anderson (1973), who have conducted the most extensive studies of *brunneicapillus* behavior, give no indication of duetting in the species. They observed one instance of a member of an earlier clutch feeding a member of a later clutch, but generally parental aggression towards mature offspring seems to preclude helping at the nest. (FS=0, D=0, CB=0)
- zonatus*: Skutch (1935, 1960; Stiles and Skutch 1989) describes simultaneous duetting in the species from observations in Guatemala and Costa Rica, as does Selander (1964) for Mexico. This is well demonstrated in H&C's recording. Helpers at the nest have been confirmed by the observations (in Guatemala, and Costa Rica) of Skutch (1935, 1960), as well as those of Selander (in Mexico; 1964). (FS=1[M], D=1[S], CB=1)
- megalopterus*: Selander (1964) describes the song of this species as nearly identical to that of the previous, thus indicating simultaneous duetting (confirmed, pers. obs.). H&C's recording is a collection of superimposed individual call notes. Helpers at the nest have been observed (confirmed by collection, pers. obs.) in this species. (FS=1[M], D=1[S], CB=1)
- fasciatus*: Ridgely and Tudor (1989) describe simultaneous duetting in the species, well demonstrated in H&C's recording. Nest helpers have been confirmed in this species by study of a banded population (Rabenold 1990, pers. comm.). (FS=1[M], D=1[S], CB=1)
- nuchalis*: This is the most thoroughly studied species of the genus. Duetting has been studied in detail, including playback experiments to test for pair recognition (Wiley and Wiley 1977; well demonstrated in H&C's recording). The occurrence of cooperative breeding in this species is well documented (e.g. Rabenold 1990). (FS=1[M], D=1[S], CB=1)
- turdinus*: Ridgely and Tudor (1989), and Sick (1993) indicate that members of this species commonly duet simultaneously, though this is not apparent in H&C's recording. This species is commonly found in groups, and helpers at the nest are likely (R.H. Wiley, pers. comm.). (FS=1[M?], D=1[S?], CB=1?)
- albobrunneus*: Farabaugh (1982) designates this species as a duetter. Additionally, Ridgely and Tudor (1989) describe simultaneous duetting in the species, and this behavior is apparent in H&C's recording. Scant observations of this species suggest that it is usually found in groups, and that helpers at the nest are likely (e.g. Wetmore et al. 1984). (FS=1[M], D=1[S], CB=1?)

Genus *Odontorchilus* (2 species, female song:0[?], duetting:0[?], cooperative breeding:0[?])

**cinereus*: This species is poorly known. Ridgely and Tudor (1989) give no indication of duetting, an observation supported by H&C's recording (though it is not certain that this represents territorial song). Absence of female song certainly has not been demonstrated. Virtually no information on breeding exists, certainly no mention of helpers at the nest. (FS=0?, D=0?, CB=0?)

**branickii*: This species is somewhat better known than the previous species, but still few data are available. Ridgely and Tudor (1989) suggest similar behavior to *cinereus*, but details unknown. H&C's recording of the species gives no indication of duetting, but absence of female song has not been demonstrated. Details of breeding unknown; however, the species is described as generally solitary or in pairs (Ridgely and Tudor 1989), suggesting absence of long-term social bonds typical of cooperative species. (FS=0?, D=0?, CB=0?)

Genus *Salpinctes* (1 species, female song:0, duetting:0, cooperative breeding:0)

obsoletus: No source indicates duetting in this species, despite intensive observation (e.g. Kroodsma 1975), including banding of a number of pairs (Merola 1995). This latter study made no reference to the existence of female song. This species generally observed as solitary individuals or in pairs, with no indication of nest helpers. (FS=0, D=0, CB=0) [Merola (1995): 5(n=2); nest=rock crevice, lined]

Genus *Catherpes* (1 species, female song:1, duetting:1, cooperative breeding:0[?])

mexicanus: Jones and Dieni (1995) indicate the presence of female song in the species, describing it as "rarer and usually shorter." They further describe courtship vocalizations as overlapping calls and songs from both male and female, with the female typically giving buzzes of various types in response to male song. "Female song is rare, and females usually respond to males with the Location Call," which is described as a "loud, metallic buzz." These descriptions seem to fit the definition of simultaneous duetting, with an asymmetry in degree of overlap. Jones and Dieni (1995) report that nest helpers have not been reported in this species. (FS=1[D], D=1[S], CB=0)

Genus *Hylorchilus* (2 species, female song:2[?], duetting:2[?], cooperative breeding:0[?])

sumichrasti: Hardy and Delaney (1987), Collar et al. (1992), Atkinson et al. (1993), and Gómez de Silva (1997) describe solitary, unduetted song in this and the following species. However, recent observations by Pérez-Villafañá et al. (1999; see also Gómez de Silva et al. 2004) indicate the presence of female-specific song in *H. sumichrasti*, which is often expressed in concert with the male vocalization, in a fashion similar to that noted for *Catherpes*. No mention has been made of helpers in this species, though there are few details on breeding other than nest descriptions. (FS=1[D], D=1[S], CB=0?)

navai: Behavior and appearance similar to *sumichrasti*: which see. Recently, vocal duets have been reported for this species, as previously observed in *H. sumichrasti* (Gómez de Silva et al. 2004). (FS=1, D=1, CB=0?)

Genus *Cinnycerthia* (4 species, female song:4[?], duetting:4[?], cooperative breeding:4[?])

unirufa: Ridgely and Tudor (1989; also Fjeldsa and Krabbe 1990) describe duetting in the species, shown quite well to be simultaneous duetting by H&C's recording. Regarding the possibility of nest helpers, no observations are available for the species, though Parker

et al. (1985) indicate close behavioral similarity to the following species, and it is generally described as being found in groups (though generally smaller than in *peruana*, Ridgely and Tudor 1989). This suggests that helpers at the nest may be present. (FS=1[D], D=1[S], CB=1?)

peruana superspecies: Ridgely and Tudor (1989) do not indicate duetting in the species complex, while they give detailed account of duetting in *unirufa*. On the other hand, Fjeldsa and Krabbe (1990) clearly indicate the presence of simultaneous duetting in members of the complex. The generally close behavioral similarity between *peruana* and *unirufa* and H&C's recording support the latter conclusion. Ridgely and Tudor (1989) note that this species is commonly found in large groups (up to 20), suggesting strong sociality. Gochfeld (1979) and Graves (1980) both indicate that this species has helpers at the nest, though only Gochfeld describes a group (seven birds plus one incubating) attending an active breeding nest. Though no specific references were found, the members of the other two recently elevated species in this complex (*olivascens* and *fulva*: Brumfield and Remsen 1996) are likely to be simultaneous duetters with nest helpers as in the closely-related *peruana*. (FS=1[D], D=1[S], CB=1)

Genus *Cistothorus* (4 species, female song:1[?], duetting:1[?], cooperative breeding:0[?])

platensis: This species has been studied systematically, though not as extensively as *palustris* (see below). These studies, including some of banded birds (e.g., Verner 1965, Kroodsma and Verner 1978, Burns 1982) have found no evidence of female song, duetting or cooperative breeding in this species. On the other hand, this species has an extremely wide distribution extending from northern North America to extreme southern South America, and the sedentary South American populations are not well known behaviorally. It is possible that these populations could differ significantly from the migratory North American population. (FS=0, D=0, CB=0)

meridae: Generally, this species is poorly known, and the presence of female song, duetting, and cooperative breeding cannot be excluded. In fact, D. Kroodsma (pers. comm.), based upon recent field observations, suggests the possibility that this species is a simultaneous duetter. (FS=1?[D], D=1?[S], CB=0?)

apolinari: This species, though existing fairly close to populated areas in Colombia seems to be poorly known behaviorally, perhaps in part due to severe population declines throughout its range. Hilty and Brown (1986; and Fjeldsa and Krabbe 1990) describe the species as being found in "loose colonies," though it is unclear whether or not these aggregations have any social structure or significance. Current data cannot exclude the possibility of female song, infrequent duetting, or cooperative breeding. (FS=0?, D=0?, CB=0?)

palustris: Numerous intensive banding studies of this species have been performed, and its song has been extensively recorded (e.g., Verner 1965, 1975; Kroodsma and Verner 1987). Kroodsma and Verner (1997) provide a summary of the extensive research (both field and laboratory) that has been done on the species. None of the published behavioral accounts of this species indicate the presence of duetting, female song, or cooperative breeding. (FS=0, D=0, CB=0)

Genus *Thryomanes* (2 species, female song:1[?], duetting:1[?], cooperative breeding:0)

bewickii: A number of studies of this species have been performed, including studies of song (Kroodsma 1973, 1974, 1985), and behavioral studies of banded populations (Kennedy and White 1996). Kennedy and White (1997) summarize research on this species. None

of these studies indicate the presence of duetting, female song, or cooperative breeding. (FS=0, D=0, CB=0)

sissonii: Howell and Webb (1995) indicate that the female countersings with the male, "contributing gruff chatters." This behavior is similar to that of Central and South American species of *Troglodytes*, and indeed Howell and Webb place this species in that genus, rather than in *Thryomanes* as in standard systematic treatments. Published observations of the species are too few to exclude the possibility of cooperative breeding. (FS=1?[D], D=1?[S?] CB=0?)

Genus *Ferminia* (1 species, female song:0[?], duetting:0[?], cooperative breeding:0[?])

cerverai: The few available sources (Bond 1985, Garrido 1985, Collar et al. 1992) do not indicate duetting, though behavioral details are extremely sketchy for this extremely rare species. H&W's recording does not seem to suggest duetting. The paucity of data on this species cannot exclude the presence of female song, and certainly the possibility of cooperative breeding cannot be excluded. (FS=0?, D=0?, CB=0?)

Genus *Thryothorus* (27 species, female song:27[?], duetting:26[?], cooperative breeding:0[?])

Generally, wrens of the genus *Thryothorus* appear to be fairly well known in terms of duetting behavior, but most species lack detailed information on breeding behavior. The most well studied species in the group are those found in Central America, due largely to the efforts of Alexander Skutch. Recently, Central American *Thryothorus* have been studied in detail as a model system for understanding duetting behavior in birds. This research has expanded the natural history data available for many species, and hopefully will continue to do so. Even so, details of breeding behavior of many species, and of general behavior in many South American species, remain to be described. Based upon the few published observations available for members of the genus, I have assumed the presence of duetting and the absence of cooperative breeding for all members of the genus, as above adding a ? where this assignment is made on few or no data.

spadix: Hilty and Brown (1986) indicate duetting in the species. H&C's recording suggests antiphonal duetting. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)

atrogularis: Stiles and Skutch (1989) indicate antiphonal duetting in the species, an observation confirmed by Hartshorne (1973), and Brown and Lemon (1979). The duet is either too tightly organized to detect or not present in H&C's recording of the species. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)

fasciatoventris: Farabaugh's (1982) work shows the presence of simultaneous duetting in this species, though H&C's recording doesn't seem to be an example. The latter possibly antiphonal duetting, as is suggested for the species by Hilty and Brown (1986). Logue and Gammon (2004) have studied a banded population of this species, confirming duetting behavior, in which there is at least some song overlap between pair members. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)

eisenmanni: Ridgely and Tudor (1989; and Fjeldsa and Krabbe 1990) indicate antiphonal duetting similar to *euophrys*, but H&C's recording clearly indicates simultaneous duetting. The latter conclusion is clearly supported by sonograms in Parker and O'Neill (1985),

- though they describe the song as antiphonal. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[S], CB=0?)
- euophrys*: Parker and O'Neill (1985), Hilty and Brown (1986), Ridgely and Tudor (1989), and Fjeldsa and Krabbe (1990) describe antiphonal duetting in the species, well-demonstrated by H&C's recording. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- genibarbis*: Hilty and Brown (1986), Ridgely and Tudor (1989), and Fjeldsa and Krabbe (1990) describe antiphonal duetting in the species, also noted in passing by Sick (1993). This observation is supported by H&C's recording. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- mystacalis*: H&C's recording clearly indicates antiphonal duetting in the species, as described in the closely related species *genibarbis*. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- coraya*: Meyer de Schauensee and Phelps (1978), Brown and Lemon (1980), Hilty and Brown (1986), and Ridgely and Tudor (1989) describe duetting in the species, and H&C's also indicates slightly overlapping antiphonal duetting. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- felix*: Grant (1966) describes this species as an antiphonal "vocalizer," though he suggests that males use distinctive song types for duetting ("contact calls") and for territorial display. Brown and Lemon (1979, 1980) clearly state that *felix* are antiphonal duetters, though at low frequency (20% of male song was duetted, it is unclear if female song is restricted to duetting). H&C's recording may be an example of antiphonal duetting. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- sinaloa*: Grant (1966) seems to describe both *felix* and *sinaloa* as antiphonal "vocalizers", but indicates that he did not record the sharing of "contact calls" between pairs of *sinaloa*. Brown and Lemon (1979, 1980) clearly state that duetting is absent in *sinaloa*, though they do report the presence of female song, infrequently expressed. H&C's recording seems to be of a lone individual. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=0, CB=0?)
- maculipectus*: Hilty and Brown (1986) and Stiles and Skutch (1989) indicate antiphonal duetting in this species. This is supported by Brown and Lemon (1979, 1980): perhaps the simplicity of the song precludes easy detection of duetting in H&C's recording. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- **sclateri*: Ridgely and Tudor (1989) do not note the presence of duetting in this species, though they do suggest vocal and behavioral similarity to *rutilus*, indicating antiphonal duetting. Available data do not indicate the presence of cooperative breeding. (FS=1?[M?], D=1?[A?], CB=0?)
- rutilus*: Farabaugh's work (1982) demonstrates the presence of antiphonal duetting in this species, an observation supported by Slud (1964), Brown and Lemon (1979, 1980), Hilty and Brown (1986), Ridgely and Tudor (1989), Stiles and Skutch (1989), Skutch (1960, 1981), and Ridgely and Gwynne (1989) though it is difficult to detect in H&C's recording. Skutch (1960, 1981) describes nesting behavior of several pairs, both during nest construction and brood care, and makes no mention of supernumeraries. (FS=1[M], D=1[A], CB=0?)
- nigricapillus*: Slud (1964), Brown and Lemon (1980), Farabaugh (1982), Wetmore et al. (1984), Hilty and Brown (1986), Stiles and Skutch (1989) and especially Levin (1996 a,b)

- indicate antiphonal duetting in the species, strongly supported by H&C's recording of subspecies *castaneus*. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A], CB=0?)
- semibadius*: Farabaugh (1982), Wetmore et al. (1984) and Stiles and Skutch (1989) indicate antiphonal duetting in the species, perhaps too tightly organized to be detected in the recording by H&C. Skutch (1960, 1981) reports observations of a number of breeding pairs of this species, with no indication of supernumeraries. However, somewhat unusual for a member of this genus, he notes that *semibadius* are most often found in groups of 3-4, which he attributed to a protracted breeding season and extended parental care. (FS=1[M], D=1[A], CB=0?)
- **leucopogon*: This species appears poorly known even for a tropical *Thryothorus*. Ridgely and Gwynne (1989) describe the song of the species, and fail to mention the presence of duetting. Wetmore et al. (1984), and Hilty and Brown (1986) both fail to describe the song of this species. No data are available on breeding behavior, though Wetmore et al. (1984) noted observation of a pair constructing a nest. (FS=1?[M?], D=1?[A?], CB=0?)
- thoracicus*: H&C's recording strongly suggests antiphonal duetting, an observation supported by Skutch's (1972) suggestion, Brown and Lemon's (1980) and Farabaugh's (1982) designation, Slud's (1964) and Stiles and Skutch's (1989) more detailed descriptions, and the brief reference given by Ridgely and Gwynne (1989). Skutch (1972) reports observations of a single breeding nest, at which he found no evidence of supernumeraries. (FS=1[M], D=1[A], CB=0?)
- pleurostictus*: Stiles and Skutch (1989), and Howell and Webb (1995) do not mention duetting, and Brown and Lemon (1979, 1980) clearly state its absence in the species. Intensive studies of banded populations (Molles and Vehrencamp 1999; 2001a,b) show that only males produce tonal song in this species, with females chattering or trilling, often in association with male singing during territorial disputes, as has been noted for *T. ludovicianus*. Available data do not indicate the presence of cooperative breeding. (FS=1[D], D=1[S], CB=0?)
- ludovicianus*: Farabaugh (1982) and Shuler (1965) describe the combination of female chatter and male song as a duet (simultaneous), and Haggerty and Morton (1995) indicate that while overlap between the two vocalizations is not complete for either sex, female chatter occurs most often in association with male song; H&C's recording provides no example. Haggerty and Morton's (1995) review of numerous studies of this species, including some study of banded populations, suggests the absence of cooperative breeding. (FS=1[D], D=1[S], CB=0)
- rufalbus*: Farabaugh (1982) demonstrates simultaneous duetting in this species, also observed by Stiles and Skutch (1989) and Ahumada (2004), and amply illustrated in H&C's recording. Hilty and Brown (1986) describe the song of this species as antiphonal, indicating that they use the term as a synonym for duetting. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[S], CB=0?)
- **nicefori*: Basically nothing is published on this species. As either a subspecies of *rufalbus* or a close relative, this species is probably a simultaneous duetter. Available data do not indicate the presence of cooperative breeding. (FS=1?[M?], D=1?[S?], CB=1?)
- modestus*: Skutch (1960, also Stiles and Skutch [1989]; see also Worth 1939, Slud 1964, Farabaugh 1982, and Wetmore et al. 1984) precisely describes antiphonal duetting in this species, which is apparent in H&C's recording. Duet structure and repertoire size have

been studied in detail by Mann et al., who describe precisely-timed antiphonal duets, with males having two repertoires: one of starting phrases (also used in solo song) and another of duet phrases (Mann et al. 2003; see also Marshall-Ball and Slater 2004). Skutch (1960) reported limited observations of two nests, where he never saw both members of a pair, let alone possible supernumeraries. (FS=1[M], D=1[A], CB=0?)

leucotis: Farabaugh (1982) shows this species to be an antiphonal duetter, apparent in H&C's recording. Also recorded as antiphonal in Skutch (1968), Wetmore et al. (1984), Hilty and Brown (1986), Sick (1993), and studied intensively by Ahumada (2001) and Gill (2003). Gill (2004) gives the first report of cooperative breeding from this species. Only four individuals of 41 followed displayed natal philopatry through their parents' next breeding attempt, and while these individuals sang and contributed to dormitory nest construction, only one fed individuals of the new clutch. Cooperative breeding thus appears rare in at least one population of the species (Panamá). (FS=1[M], D=1[A], CB=1)

**superciliaris*: Ridgely and Tudor (1989, p. 81) only describe song of this species as "...fast and very rollicking, with phrases so run together that the effect is sometimes quite warbled," giving no indication of duetting behavior. However, the behavior of this species is likely similar to that of its probable close relative, *leucotis*. Available data (e.g. Marchant 1960) do not indicate the presence of cooperative breeding. (FS=1?[M?], D=1?[A?], CB=0?)

**guarayanus*: Ridgely and Tudor (1989) indicate similarity to the closely related species *leucotis*, which would suggest antiphonal duetting. Available data do not indicate the presence of cooperative breeding. (FS=1?[M?], D=1?[A?], CB=0?)

longirostris: Sick (1993) describes duetting in this species, though it is unclear whether antiphonal or simultaneous. Ridgely and Tudor (1989) indicate similarity to the closely related species *leucotis*, which would suggest antiphonal duetting. This is supported by H&C's recording of the species. Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A?], CB=0?)

**griseus*: Ridgely and Tudor's (1989) description of the song makes no indication of the presence of duetting in this species, nor does the song on H&C's tape seem to be a duet. No data are available on breeding behavior. (FS=1?[M?], D=1?[A?], CB=0?)

Genus ***Troglodytes*** (9 species, female song:4[?], duetting:2[?], cooperative breeding:0[?])

troglodytes: Extensive observation and recording of this species, including banding studies (e.g., Armstrong 1955, Kroodsma 1980, Evans and Burn 1995), have yielded no evidence of duetting, though female song seems to exist, very rarely expressed. Supernumeraries have not been observed. (FS=1[D], D=0, CB=0)

aedon: Extensive observation and recording of this species, including banding studies (e.g., Kendeigh 1941, Drilling and Thompson 1991, Johnson and Albrecht 1993) have failed to detect evidence of duetting in this species. However, Johnson and Kermott (1990) describe female song from one population, rarely expressed. Supernumeraries have not been observed. (FS=1[D], D=0, CB=0)

brunneicollis: Howell and Webb (1995) make no mention of duetting behavior in the species, an observation confirmed by my own experience with the species (D.F. and Guerrero, Mexico). However, it is not known whether female song is expressed in this species as in the former. Though much less well known than its close relative *aedon*, helpers at the nest have not been observed in the species. (FS=0?, D=0, CB=0?)

musculus: Skutch (1960; also Haverschmidt 1952, Farabaugh 1982, Stiles and Skutch 1989) describes simultaneous duetting in the species, the female having a trill or chatter sung "...chiefly in response to her mate." The situation sounds similar to that found in *Thryothorus ludovicianus*. Skutch (1960, 1983) describes in detail one case of alloparental care from this species which occurred when offspring from an early clutch helped feed with members of a later. However, Skutch noted (1983) that this occurrence must be extremely rare in the species, for he never again observed it in many years of observation of the species. Supporting this suggestion, Freed's (1986) observations of a banded population of this species in Panama failed to yield any report of nest helpers. (FS=1[D], D=1[S], CB=0)

ochraceus: Skutch (1960), in his brief note on observations of this species, described the song as "modest" but gave no indication of the extent of female vocalization nor of the occurrence of duets. He detected no evidence of helpers at the nest. (FS=0?, D=0?, CB=0?)

rufociliatus: Skutch (1960) indicates that both sexes of this species sing typical song, but is somewhat unclear on the point of duetting. His comment "...as I tried to follow the pair to their roost, I heard them singing..." would seem to indicate a duet, probably simultaneous. On the other hand, he gives no indication of the presence of helpers at the nest in the species. (FS=1?[D?], D=1?[S?], CB=0)

**monticola*: This species is poorly known. Available data do not indicate presence of female song, duetting, or cooperative breeding (Ridgely and Tudor 1989). (FS=0?, D=0?, CB=0?)

solstitialis: Skutch (1960) described the song as similar to *ochraceus*, but again gave no indication of duetting or the possibility of female song, an observation supported by the description of Ridgely and Tudor (1989). He detected no evidence of cooperative breeding. (FS=0?, D=0?, CB=0?)

**rufulus*: This species is poorly known. Available data do not indicate presence of female song, duetting, or cooperative breeding (Ridgely and Tudor 1989). (FS=0?, D=0?, CB=0?)

Genus *Thryorchilus* (1 species, female song:0[?], duetting:0[?], cooperative breeding:0[?])

**browni*: The song of this species has been described by Worth (1939), Slud (1964), and Hartshorne (in Wetmore et al. 1984), none of whom noted duetting behavior. However, observations to date have been extremely limited, so duetting remains a possibility, and certainly the absence of female song cannot be asserted as yet. Given that even vocal data are sketchy, breeding data are even worse, and the possibility of supernumeraries cannot be excluded. (FS=0?, D=0?, CB=0?)

Genus *Uropsila* (1 species, female song:1, duetting:1, cooperative breeding:0?)

leucogastra: Sutton (1948) describes this species as a duetter, specifically not antiphonal. I am not certain that his definition of antiphonal is the same as employed here, and his description of the song is not detailed enough to judge. Lacking other evidence, this species should be considered a simultaneous duetter. The species is not well-known enough to establish the absence of nest helpers, but it is generally described as being found in pairs, inconsistent with status as a regularly social wren. (FS=1[M], D=1[S?], CB=0?)

Genus *Henicorhina* (3 species, female song:3, duetting:3, cooperative breeding:0[?])

leucosticta: Skutch (1960) described antiphonal duetting in the species, an observation supported by Meyer de Schauensee and Phelps (1978) and Farabaugh (1982). H&C's recording of the species sounds more like a simultaneous duet. Stiles and Skutch (1989; p. 359-360) contradict this information by indicating that, while female song is present in *leucosticta*, the species does not participate in duets (*contra* Fitzpatrick et al.'s comment under *leucoptera*). Wetmore et al.'s (1984) description is ambiguous regarding the presence of duetting, despite a detailed description of the song. Skutch (1960) reports observations of five nests of this species, and found no evidence for the presence of supernumeraries. (FS=1[M], D=1[A?], CB=0?)

leucophrys: Skutch (1940, 1960; also Slud 1964, Farabaugh 1982, Wetmore et al. 1984, Stiles and Skutch 1989) describes simultaneous duetting in the species. Ridgely and Tudor (1989) describe antiphonal duetting in the species, possibly supported by H&C's recording. Skutch (1960) reports observation of one nest, at which he found no evidence for supernumeraries. (FS=1[M], D=1[A?], CB=0?)

leucoptera: Fitzpatrick et al. (1977) indicate that this species engages frequently in duets, "during which each bird repeated its own motif in syncopation with the other...", which I take to describe antiphonal song. "This habit is well known in the other two *Henicorhina* species...." Available data do not indicate the presence of cooperative breeding. (FS=1[M], D=1[A?], CB=0?)

Genus *Microcerculus* (5 species, female song:0[?], duetting:0, cooperative breeding:0[?])

As is typical for data on tropical wren biology, most of what is known of this genus comes from studies of its Central American representatives (the *philomela/luscinia* species pair). The South American species, judging from the literature, appear almost unknown behaviorally. In general, it does not appear that song in this genus is duetted with sufficient frequency for it to have been detected, though the possibility of female song cannot be excluded. Breeding data on species of the genus are extremely few, but make no suggestion of cooperative breeding, a conclusion supported by descriptions of members of the genus generally being seen as solitary individuals.

philomela: Stiles (1983), who studied this species and the following in detail, makes no mention of duetting, nor do Slud (1958), or Hardy and Delaney (1987), nor again is it indicated by H&C's recording. Absence of female song has not been demonstrated. No data are available on breeding behavior. (FS=0?, D=0, CB=0?)

luscinia: See comments under *philomela*. (FS=0?, D=0, CB=0?)

**marginatus*: This species is poorly known. Available data do not indicate presence of female song, duetting, or cooperative breeding (Ridgely and Tudor 1989). (FS=0?, D=0?, CB=0?)

**ustulatus*: This species is poorly known. Available data do not indicate presence of female song, duetting, or cooperative breeding (Ridgely and Tudor 1989). (FS=0?, D=0?, CB=0?)

**bambla*: This species is poorly known. Available data do not indicate presence of female song, duetting, or cooperative breeding (Ridgely and Tudor 1989). (FS=0?, D=0?, CB=0?)

Genus *Cyphorhinus* (3 species, female song:2[?], duetting:2[?], cooperative breeding:1[?])

Neither Hilty and Brown (1986) nor Ridgely and Tudor (1989) describe South American members of the genus *Cyphorhinus* as duetters, though descriptions and recordings of the species from Central America (e.g. Hardy and Coffey 1996) clearly indicate that the song of *phaeocephalus* is frequently duetted. It is unclear whether all members of the genus are duetters or not. *Phaeocephalus* and *aradus* are both described as being typically encountered in groups. This fact, in combination with their apparent communal use of dormitory nests (Skutch 1960) suggests that both (probably all) species should be examined closely for the presence of cooperative breeding.

**thoracicus*: Published accounts of this species are scarce to nonexistent. A description of the song by Fjeldsa and Krabbe (1990) makes no mention of duetting. The song of this species is very simple, and inference of duetting or its lack from available taped evidence alone is impossible. No data are available on breeding behavior. (FS=0?, D=0?, CB=0?)

phaeocephalus: Skutch (1960; also Howell 1957, Slud 1964, Farabaugh 1982, Stiles and Skutch [1989]) describes antiphonal duetting in the species, though this was not suggested for the species in Ridgely and Tudor (1989). Further, Wetmore et al. (1984) make no mention of duets, despite a detailed description of the song. In agreement with the former sources, antiphonal duetting is strongly indicated by H&C's recording. Skutch (1960) observed one breeding nest, at which he found only an unaccompanied pair. However, his description of this species indicates that it is typically found in groups, and he notes that it uses communal roosts, as in other cooperative members of the family. Recent field studies of this species have confirmed the presence of helpers at the nest (T. Robinson, pers. comm.). (FS=1[M], D=1[A], CB=1) [Skutch (1960): 2(n=2); nest=retort (r=2-8f); dormitory/communal]

**arada*: Ridgely and Tudor (1989) indicate similarity to *phaeocephalus*, suggesting antiphonal duetting: the song on H&C's recording does not appear to be a duet. Available data do not indicate presence of cooperative breeding (but see account of *phaeocephalus*). (FS=1?[M?], D=1?[A?], CB=0?)

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