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COMPARATIVE ANALYSIS OF THE VOCALIZATIONS OF *HYLORCHILUS* WRENS[1]

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Abstract. Analysis of variation in the main song and in other characters of *Hylorchilus* wrens, together with biogeographic considerations, support the recent suggestion that the genus consists of two species, Sumichrast's Wren (*H. sumichrasti*) and Nava's Wren (*H. navai*). The evidence also challenges the proposal that the Canyon Wren (*Catherpes mexicanus*) is this genus' closest relative. The song characteristics shared by the two separate species of *Hylorchilus* suggest that the song of their common ancestor included abrupt changes in pitch, pauses between syllables, and frequent use of syllables lasting more than 0.35 sec. These are exactly the opposite of what would be expected if the Canyon Wren were their closest relative (sister-group). It is suggested that the Canyon Wren-like characteristics of the song of one of the species are due to convergence. Thus the closest relative of *Hylorchilus* wrens remains to be found.

Key words: Troglodytidae, Hylorchilus, *Mexico, vocalizations, ancestor reconstruction.*

For 100 years after its description in 1871, Sumichrast's Wren (*Hylorchilus sumichrasti*) was known only from a small area of central Mexico. In 1969–1971, a disjunct population discovered in western Chiapas and extreme southeastern Veracruz, far to the east of previously known localities, was described as a new subspecies (*H. s. navai*) based mainly on differences in plumage coloration and size (Crossin and Ely 1973). However, the described differences in measurements between the eastern and western forms (Crossin and Ely 1973, Phillips 1986) were based on a small sample size and indicate large overlap in measurements.

Previous studies of the vocalizations of this genus have led to two interesting proposals. First, it was claimed that *Hylorchilus* is the sister-group of the Canyon Wren (*Catherpes mexicanus*) based upon the resemblances between their songs, calls, and motor patterns (Hardy and Delaney 1987). Then, with the discovery of the widely different song and call of *Hylorchilus* wrens from Chiapas, it was proposed to raise the eastern form to the rank of species (Atkinson et al. 1993). This proposal has important consequences for conservation, because the two separate species would have very small ranges (Collar et al. 1992).

Vocalizations available for previous studies consisted of a few recordings from the opposite ends of the range of the genus, separated by a gap of nearly 400 km (Hardy and Delaney 1987, Atkinson et al. 1993). Recordings are now available from intermediate localities spanning the entire range of the genus (Fig. 2 and 3) and these recordings enable a comparative analysis of the evolution of vocalizations in the genus. This new information supports treatment of the two forms of *Hylorchilus* as separate species. It also suggests that the Canyon Wren-like song of some populations of one of the species has arisen convergently, and therefore does not support a sister-group relationship between this genus and *Catherpes*.

The genus *Hylorchilus* is apparently restricted to humid tropical forest growing over limestone boulders ("karstic terrain") between 75 and 1,000 m above sea level (Collar et al. 1992). Its range follows a basically east-west strip of "tropical karst forest" in the humid lowlands of southeastern Mexico. However, this strip is broken by a 100 km gap between the karst area of central Veracruz-Oaxaca (regions 1–2 in Fig. 1) and that of southern Veracruz-Chiapas (regions 3–4).

METHODS

Recordings and observations of 10–30 males of *Hylorchilus* wrens were obtained opportunistically from each of the four regions of tropical karst forest (Fig. 1) between 1991 and 1996. Recordings were made at different times of day, although the majority were between 08:00 and 12:00. Earlier recordings were made with Sony TCM-81, Realistic CTR-67, and Panasonic mini cassette-recorders. Recordings in 1996 were made with a Marantz PMD221 cassette-recorder with ProCo matching transformer and Sennheiser ME88/K3U shotgun microphone (equipment lent by the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York). Sonograms reproduced here were chosen to represent the largest possible range of variation and were made by Dorn Cox (Fig. 2) and Kathy Dunsmore (Fig. 3) of the Library of Natural Sounds using Canary 1.2.1 software. Other sonograms studied were made by Santiago Jesús Pérez Ruíz of the Centro de Instrumentos of the Universidad Nacional Autónoma de México. Sonograms are arranged geographically from west to east (an exception is Fig. 3A, which is from east of the source of Fig. 3B and 3D).

RESULTS

The calls of *Hylorchilus* wrens in regions 1 and 2 are identical to one another but differ markedly from calls of birds in regions 3 and 4 (Fig. 2). In regions 1 and 2, both a hoarse "chuck" or a squealing "wheeo" may be made by the same individual, whereas the call of

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birds from regions 3 and 4 is a very different metallic "tink." The time between successive calls also is clearly different between regions 1–2 and 3–4 (Fig. 2), as is plumage coloration and pattern (e.g., see Howell and Webb 1995, Plate 49). These observations suggest a divergence which parallels the range gap between areas 2 and 3 and reinforces the suggestion that two allopatric species are involved.

There is much between- and intra-individual variation in the number of syllables per song. For example, Howell and Webb (1995) mentioned long and short songs from regions 1 and 2. However, such variation seems to fall within well-defined limits. Particularly, the duration of syllables, frequency range and pattern of the songs are similar within each region. Thus all variants shown here are presumably homologous in the broad sense of the word. Songs are made often and throughout the day.

The longer songs most prevalent in region 1, but also occurring in the east of region 2, comprise a very short rising series of syllables followed by a longer descending series (see sonograms in Hardy and Delaney 1987 and Atkinson et al. 1993). The pitch goes from 2,300 to 4,000 Hz or more in the rising portion, and then descends to 900–1,500 Hz. The descending portion is essentially composed of five or (usually) more repeated syllables, usually given with no pause between them. In the descending portion, syllables are either V-shaped or have a marked down-slurred portion and last less than 0.35 sec. This is the song that was likened to that of a Canyon Wren by Hardy and Delaney (1987).

The song in region 3 closely resembles the song in region 4 (Fig. 3D–3F and sonograms in Atkinson et al. 1993). In both cases, songs are composed of syllables of long duration as compared with the long songs of regions 1 and 2, frequently lasting more than 0.3 sec; adjacent syllables usually alternate in pitch (i.e., syllables do not form rising or descending series) and lie mostly within the 1,000 to 3,000 Hz frequency band, seldom reaching 4,000 Hz, whereas the long

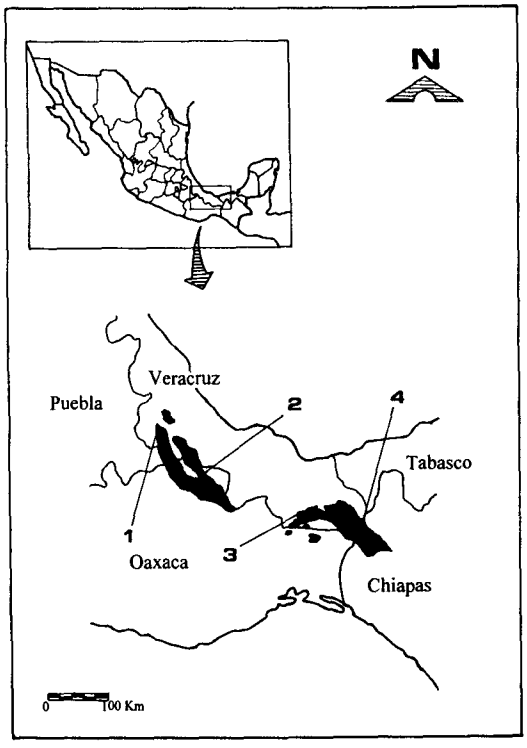

FIGURE 1. Distribution of *Hylorchilus* wrens (modified from Gómez de Silva, unpubl. data). Numerals indicate the four regions referred to in this article.

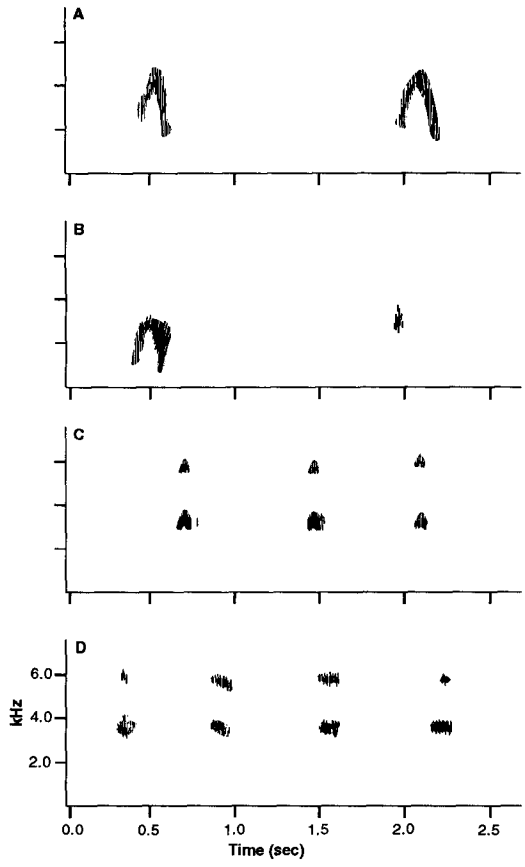

FIGURE 2. Calls of *Hylorchilus* from different regions. Note the different structure and inter-call length between *H. sumichrasti* (A–B) and *H. navai* (C–D). *H. sumichrasti*: "wheeo" calls from (A) region 1, recorded 1.5 km south of Amatlán, Veracruz (18°50′N, 96°55′W), and (B) region 2, recorded at Cerro de Oro, Oaxaca (18°01′N, 96°01′W). *H. navai*: metallic "tink" calls from (C) region 3, taped by Steve N. G. Howell near the bridge over Río Chalchijapan, Veracruz (17°13′N, 94°45′W), and (D) region 4, taped by Adam Kent near the mouth of Río La Venta in the Reserva Especial de la Biosfera Selva El Ocote, Chiapas (17°02′N, 93°48′W).

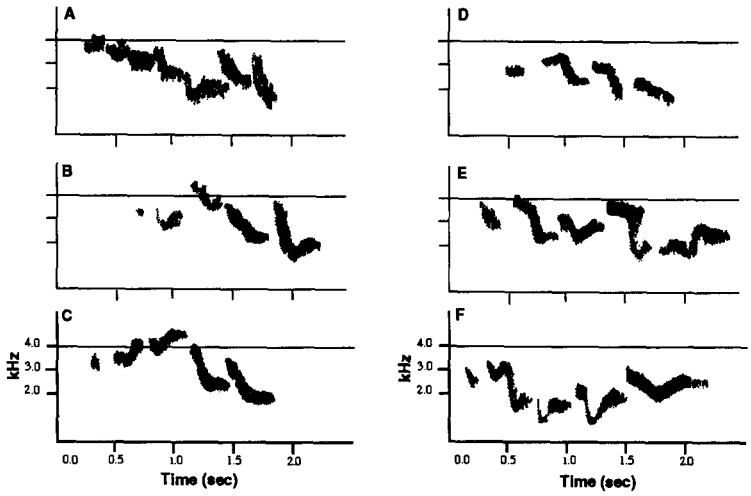

FIGURE 3. Songs of *Hylorchilus* from regions 2, 3 and 4. *Hylorchilus sumichrasti*: (A) region 2: 2 km south of Bethania, Oaxaca (17°56′N, 96°01′W); (B) and (C) possibly a single individual, region 2: Cerro de Oro, Oaxaca (18°01′N, 96°01′W). *Hylorchilus navai*: (D) and (E) different individuals, region 3: Poblado Nueve, Veracruz (17°20′N, 94°27′W). (F) Region 4: at or near type locality (16°56′N, 93°48′W).

songs of regions 1 and 2 have many portions above 3,000 Hz and even some that rise above 4,000 Hz. Additionally, in regions 3 and 4 there usually are pauses and/or abrupt changes in pitch between syllables. This observation also agrees well with a hypothesis of divergence caused by the existence of a gap between areas 2 and 3 and with the suggestion that two allopatric species are involved. The vocal differences are far greater than between other closely related species of wren, such as between the wood-wrens *Henicorhina leucophrys* and *H. leucosticta* (Hardy and Coffey 1991, S. N. G. Howell, pers. comm.; pers. observ.)

Short songs from regions 1 and 2, previously poorly known, suggest that although there are important differences between the songs of the two taxa, the situation is more complex than suggested by Atkinson et al. (1993). These short songs (Fig. 3A–3C) appear intermediate between the long songs from the same regions and the songs from regions 3 and 4. These songs resemble region 1–2 long songs in the pattern of syllables sometimes forming a descending series (Fig. 3A), the prevalence of repeated, down-slurred syllables and their frequency range (many syllables between 3,000 and 4,000 Hz). On the other hand, these shorter songs resemble region 3–4 songs in the longer duration of syllables and the pauses and abrupt changes in pitch between syllables.

DISCUSSION

Plumage coloration (Crossin and Ely 1973, Howell and Webb 1995) and vocalizations reveal a clear-cut difference between the two forms of *Hylorchilus* from opposite sides of the habitat gap that is found between regions 2 and 3 (Fig. 1). This gap coincides with the northern or southern limit of a large number of plant species, including trees and herbs (Wendt 1989, 1992), indicating that it is an effective barrier that has significantly limited biological interchange between the two sides, although it is unknown how long ago this gap originated (Wendt 1992). These observations support the conclusion of Atkinson et al. (1993) and Howell and Webb (1995) that the two forms should be treated as separate species, *H. sumichrasti* and *H. navai.*

There are certain similarities between short songs of *H. sumichrasti* and the songs of *H. navai* (syllables often lasting more than 0.3 sec, pauses and abrupt changes in pitch between syllables). The simplest explanation for the existence of these similarities is direct inheritance from a common ancestor; therefore, these similarities are probably shared primitive character-states (symplesiomorphies) that have been retained from before the vicariant isolation of the two species by formation of the gap. Furthermore, these same character-states are more widespread in wrens, being found also in *Henicorhina* and *Thryothorus* for example (Hardy and Coffey 1991, pers. observ.), and thus seem to be plesiomorpic for a more inclusive clade in the phylogeny.

Hardy and Delaney (1987) based their conclusion of the sister-group relation of *H. sumichrasti* and *Catherpes mexicanus* largely on the observation that their songs are very different from those of most other wrens. Those authors interpreted this difference from other wrens as a true homology uniting these two species (a synapomorphy). Those authors were not aware of either the song of *H. navai* or the short songs of *H. sumichrasti,* both of which are here suggested to be plesiomorphic with respect to the long song of *H. sumichrasti* for the reasons given in the previous paragraph. Now that these songs are known, I hypothesize that the long song of *H. sumichrasti* is uniquely derived (autapomorphic) and thus any resemblance to the song of *C. mexicanus* can be attributed to convergence (homoplasy). An alternative is that *C. mexicanus* was

derived from *H. sumichrasti* after the latter's "invention" of the long song, but this alternative is implausible in view of the large number of unique specializations (autapomorphies) of *Hylorchilus* (see below).

Of the other characters which have been put forward to support the sister-group relationship between *Catherpes mexicanus* and *Hylorchilus,* the call of *H. sumichrasti* indeed somewhat resembles the call of *C. mexicanus* (see Fig. 2 in Hardy and Delaney 1987), although it differs in being of lower pitch and having an elongate down-slurred portion. The call of *H. navai,* however, more closely resembles one of the calls of the White-breasted Wood-Wren *Henicorhina leucosticta* (described as "a bright, metallic *peenk* or *biink*" in Howell and Webb 1995). Several hours of observation in the field support the mention by Hardy and Delaney (1987) that the "mewing call" of *C. mexicanus* has no homologue in *Hylorchilus.*

The "bouncing crouch" motion while calling or singing, shared by *Catherpes* and *Hylorchilus,* may actually be a plesiomorphy because it is shared with several other genera of wrens such as *Troglodytes, Thryothorus* and *Henicorhina* (pers. observ.). These other wrens make similar motions, especially when excited. Additionally, the alarm call of *H. sumichrasti* is a staccato chatter similar to the alarm calls of the aforementioned wrens except, apparently, *C. mexicanus.*

There are several other differences between *Catherpes* and *Hylorchilus,* some of which are clearly specializations of the latter genus. For example, they differ in clutch size and egg color (see Bangs and Peters 1927 for eggs of *Hylorchilus*), tail length, shape and number of feathers (Crossin and Ely 1973), shapes of wing and of individual flight feathers (Ridgway 1904, Atkinson et al. 1993), arrangement of tarsal scutes (contra Ridgway, the anterior tarsus is nearly booted in *Hylorchilus,* whereas it is scutellate in *Catherpes* as in most wrens), and other morphological details (Nelson 1897, Ridgway 1904). Most of these are autapomorphies of *Hylorchilus* insofar as *Catherpes* shares the primitive character-states with other wrens.

The rock-loving habit is the final character-state "uniquely shared" by *Catherpes* and *Hylorchilus,* but it also is possessed by the Rock Wren *Salpinctes obsoletus,* which more closely resembles *Catherpes* in many characters (e.g., clutch size, egg color and pattern on upperparts). Therefore, there remains no unequivocal character-state to inform us as to which wren is *Hylorchilus'* closest relative.

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