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PHYLOGENETIC PATTERNS IN MONTANE *TROGLODYTES* WRENS[1]

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Abstract. Phylogenetic studies based on mitochondrial DNA sequences of 10 species of wrens in *Troglodytes* and related genera suggest a new hypothesis of relationships for the group. The Winter Wren (*T. troglodytes*) and the anomalous Timberline Wren (*Thryorchilus browni*) are distantly related to the remainder of *Troglodytes*. The latter group divides into a tropical montane group and a northern/lowland group that includes the northernmost two montane taxa (*T. rufociliatus, T. brunneicollis*). Erection of the genus *Nannus* for the Winter Wren is proposed. Song evolution in the complex has involved either convergent derivation or retention of primitive song types in distant lineages.

Key words: mtDNA sequences, Nannus, *phylogeny,* Troglodytes, wrens.

North American ornithologists are well-acquainted with the relatively simple song of the House Wren (*Troglodytes aedon*), in contrast to the long and complex song of the Winter Wren (*T. troglodytes*). Recent field work in the mountains of southern Mexico and El Salvador brought two of us into contact with the Rufous-browed Wren (*T. rufociliatus*); we were struck by the extreme similarity of its song with that of Winter Wrens. Further examination of *Troglodytes* song variation, in which two major song types were noted (Fig. 1), motivated the study reported herein. Songs of Northern and Southern House Wrens (*T. aedon* and *T. musculus,* respectively) and Brown-throated Wrens (*T. brunneicollis*) have long trills, whereas Winter, Rufous-browed, Ochraceus (*T. ochraceus*), and Mountain (*T. solstitialis*) Wrens all have longer, more varied songs largely lacking trills.

Our working hypothesis was that Winter Wrens might share a close phylogenetic relationship with the montane tropical forms of *Troglodytes,* representing an early lineage separate from the lowland forms. The only previous phylogenetic study of the genus did not include taxa critical to testing this hypothesis (Brumfield and Capparella 1996). Furthermore, morphometric studies of the entire genus by one of us (Escalona-Segura 1995) did not lead to firm conclusions regarding the evolutionary history of *Troglodytes.* For these reasons, we undertook a test of our hypothesis based on studies of mitochondrial DNA sequences.

METHODS

Tissue samples are listed in Table 1. One or two representatives of each mainland taxon that has at some point been considered as a species were included for analysis, as well as the enigmatic Timberline Wren (*Thryorchilus browni,* at times placed in *Troglodytes*) and outgroup taxa (White-breasted Wood-Wren *Henicorhina leucosticta,* Pinyon Jay *Gymnorhinus cyanocephalus*). Use of single or few individuals to represent taxa in phylogenetic analyses based on mitochondrial DNA sequence data follows Moore and DeFilippis

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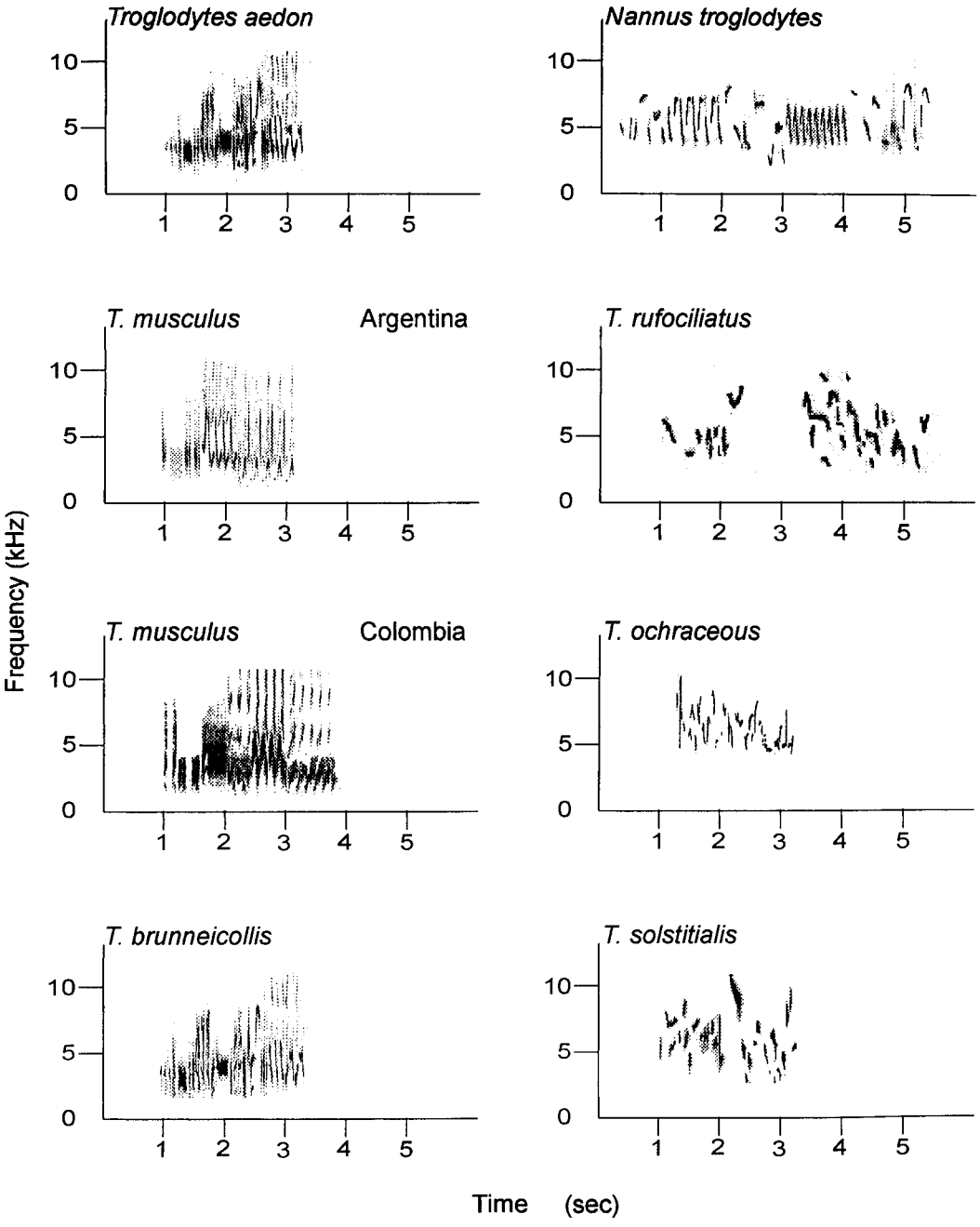

FIGURE 1. Sonograms for representative *Troglodytes* and *Nannus* wren taxa examined in this study.

(1997), based on low levels of within-taxon sequence variation.

Genomic DNA was extracted from each sample using Qiamp tissue extraction kits available from Qiagen (Valencia, California). A 534 base pair (bp) portion of the ND2 gene was chosen for study, given the excellent resolution provided by this gene for species- and generic-level questions in other applications (Rice, unpubl. data). This segment was amplified using conventional thermal-cycling techniques, with a thermal profile of denaturing at 95°C for 30 sec, annealing at 55°C for 30 sec, and extension at 70°C for 90 sec (Kocher

TABLE 1. Tissue samples used in this study.

Species		Locality	Collection[a]	Tissue number	GenBank accession number
Winter Wren	*Troglodytes troglodytes*	Illinois	FMNH	1785	AF104975
		Illinois	FMNH	1778	AF104976
Northern House Wren	*T. aedon*	Illinois	FMNH	1815	AF104979
		Illinois	FMNH	1783	AF104980
Southern House Wren	*T. musculus*	Oaxaca, Mexico	MZFC	uncat.	AF104978
Brown-throated Wren	*T. brunneicollis*	Oaxaca, Mexico	MZFC	OMVP213	AF104973
Rufous-browed Wren	*T. rufociliatus*	Chiapas, Mexico	MZFC	BMM607	AF104977
Ochraceous Wren	*T. ochraceus*	Cartago, Costa Rica	LSU	19926	AF104982
Mountain Wren	*T. solstitialis*	Pasco, Peru	LSU	8178	AF104981
Tepui Wren	*T. rufulus*	Amazonas, Venezuela	LSU	7395	AF104983
Timberline Wren	*Thryorchilus browni*	Cartago, Costa Rica	LSU	19924	AF104974
White-breasted Woodwren	*Henicorhina leucosticta*	Loreto, Peru	KU	814	AF104972
Pinyon Jay	*Gymnorhinus cyanocephalus*	Baja California, Mexico	FMNH	1667	AF104971

[a] FMNH = Field Museum of Natural History, MZFC = Museo de Zoología of Universidad Nacional Autónoma de México, LSU = Louisiana State University Museum of Natural Science, KU = University of Kansas Natural History Museum.

et al. 1989). Extension time was lengthened 4 sec each cycle for 35 cycles. ND2 primers (H-6313: 5′-CTCTTATTTAAGGCTTTGAAGGC-3′ and L-5757: 5′-GGCTGAATRGGMCTNAAYCARAC-3′) were developed by M. Sorenson (pers. comm.; H and L refer to heavy and light strands, respectively, and numbers indicate relative position of primers on reference chicken sequence, Desjardins and Morais 1990). Amplified product was purified on a low-melt (1%) NuSieve GTG agarose gel (FMC BioProducts; Rockland, Maine) electrophoresed for 45 min at 85–95 volts; bands containing target products were excised from the gel, and DNA recovered using Qiaquick spin columns (Qiagen). Finally, purified product was amplified using one primer (heavy or light), and sequenced with an ABI Prism Automated Sequencer (Model 310). The thermal profile for both primer systems was denaturing at 96°C for 10 sec, annealing at 50°C for 5 sec, and extension at 60°C for 4 min, repeated for 25 cycles. Negative controls were used at each step to test for reagent contamination.

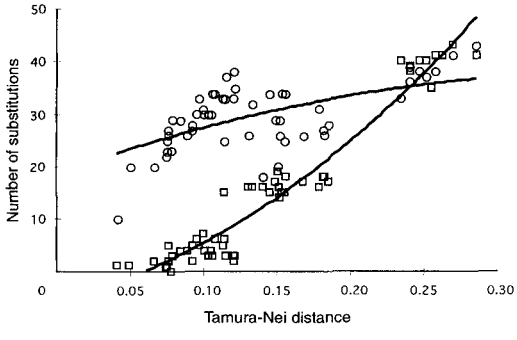

FIGURE 2. Third-position saturation curves for ND2 sequences, showing second-order polynomial fitted curves. Transitions are depicted with open circles, and transversions with open squares.

Numbers of variable and phylogenetically informative molecular characters, as well as numbers and classes of transitions and transversions, were calculated using MEGA 1.01 (Kumar et al. 1993). Rather than using percent sequence divergence as a distance measure to assess saturation, we used the Tamura-Nei Distance, which considers percent base composition for each individual, and is thus more robust than sequence divergence measures (Kumar et al. 1993). All sequences were deposited in GenBank (Table 1).

Phylogenetic trees were estimated based on sequence data using the exhaustive search procedure of PAUP (version 3.1.1, Swofford 1991), an approach guaranteed to identify shortest trees. Support for particular branches in resulting hypotheses was assessed using the branch-and-bound character bootstrapping algorithms in PAUP with 500 replicate searches, and counts of unreversed synapomorphies.

RESULTS

BIOCHEMICAL PATTERNS

Examination of sequences from the ND2 region revealed no insertions or deletions. Of the 534 base pairs examined, 215 were variable and 85 were phylogenetically informative. Partitioning bases by coding position revealed that 132 third position sites were variable, 60 of which were phylogenetically informative. At first and second positions, 61 (18 informative) and 22 (7 informative) sites, respectively, were variable.

Saturation of sequence substitutions was not detected either in the overall analysis or partitioning by coding position (Fig. 2). However, given the small size of the data matrix, we conducted exploratory analyses with different transition:transversion weighting schemes (0:1, 1:1, 2:1, 5:1, and 10:1) and outgroup taxa (*Henicorhina leucosticta* and *Gymnorhinus cyanocephalus*). These tests suggested that the topology de-

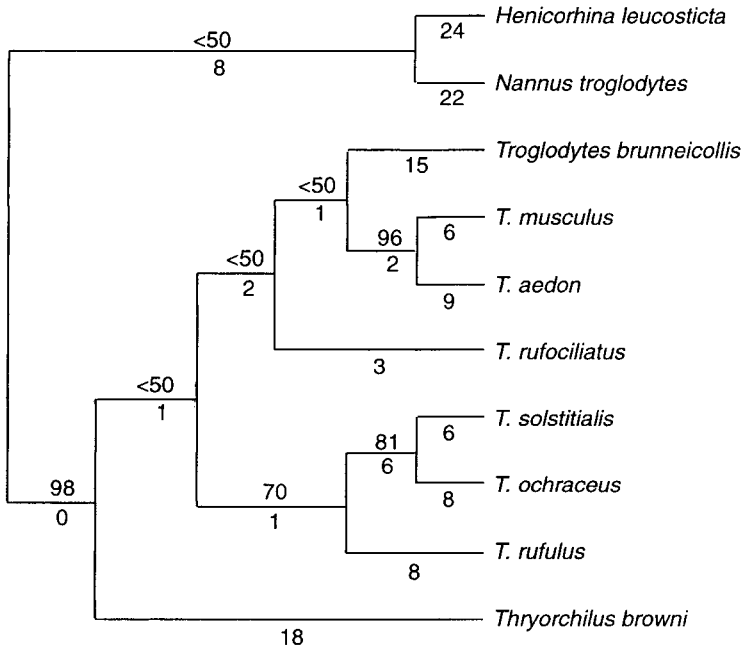

FIGURE 3. Cladogram showing the most parsimonious tree derived from analyses of sequences of the ND2 gene for montane *Troglodytes* wrens. Numbers above each node indicate bootstrap support, and those below each node are numbers of unreversed synapomorphies; those for terminal taxa represent numbers of autapomorphic base pairs.

veloped herein was robust to a variety of analytical techniques and warranted detailed examination. All members of the same species had identical sequences, so only one representative per taxon was used in subsequent analyses. Because choice of outgroup had little qualitative effect on tree topologies, all further analyses were carried out with the White-breasted Wood-Wren as the sole outgroup.

PHYLOGENETIC PATTERNS

Exhaustive searches of the molecular data set resulted in a single most parsimonious tree of 256 steps; consistency index (CI) = 0.724, homoplasy index (HI) = 0.276, retention index (RI) = 0.398, rescaled consistency index (RC) = 0.288, $g_1 = -0.881$ (Fig. 3). The skew of the tree length histogram suggests that the shortest tree indeed contains significant phylogenetic signal ($P < 0.01$; Hillis and Huelsenbeck 1992). Hence, we continued interpreting and exploring its implications.

The shortest tree did not support the monophyly of the genus *Troglodytes*. Rather, the Timberline Wren was placed as sister to most *Troglodytes*, and weak support existed for a sister relationship of White-breasted Wood-Wren and Winter Wren. The genus *Troglodytes* minus Winter Wren was supported as a monophyletic lineage by one unreversed synapomorphy.

Within the main *Troglodytes* lineage, two major clades were supported, one consisting of what has previously been called the House Wren complex (Northern and Southern House Wrens, Brown-throated Wren) plus Rufous-browed Wren (supported by two unreversed synapomorphies), and the other clade including the Mountain, Ochraceous, and Tepui Wrens (*T. rufulus*; Fig. 3). Within the House Wren complex, Northern and Southern House Wrens were well-supported as sister taxa, with Brown-throated Wren forming the sister lineage. Unexpectedly, but supported by two unreversed synapomorphies, Rufous-browed Wren also was placed with the House Wrens, although this species has long been placed with, or even considered conspecific with, Mountain Wrens of Central and South America (Paynter 1957). Within the other major lineage, Mountain and Ochraceous Wrens were sister taxa, with Tepui Wren as sister species. This result suggests that the two lowland House Wrens were derived from within the 'montane wren' lineage.

DISCUSSION

The historical hypothesis developed herein is based on a single-gene lineage, and thus must be interpreted with some caution. Although support for nodes was not always strong, at least one unreversed synapomorphy was present for all nodes except one, suggesting that the hypothesis was supported by available data. Implications of this hypothesis for understanding the taxonomy and evolutionary patterns in songs of the group are discussed below.

Our results differ from those of Brumfield and Capparella (1996) regarding the relationships of the Northern and Southern House Wrens and the Brown-throat-

ed Wren. Brumfield and Capparella (1996), using isozyme data, concluded that the Northern House Wren and Brown-throated Wren are sister taxa, and that the Southern House Wren is their sister taxon. Based on ND2 sequences, we found that the Northern and Southern House Wrens are sister taxa, with the Brown-throated Wren as sister. The conflict between the two hypotheses is illuminated by forcing the Brumfield and Capparella (1996) hypothesis onto our data set, which increased tree length by nine steps. Brumfield and Capparella (1996) did have more individuals per species sampled and better geographic representation of species. However, the allozyme results can be confusing, given the distant nature of the outgroup used (Winter Wren), the polymorphic nature of the characters used, and the small number of taxa represented. Hence, we suspect that the hypothesis presented herein will turn out to be better supported than that of Brumfield and Capparella (1996), but such a result must await further study of additional character suites.

TAXONOMIC IMPLICATIONS

Our tree suggests several points on which wren taxonomy needs revision. Some previous researchers placed the Timberline Wren within *Troglodytes* (e.g., Paynter and Vaurie 1960). Because of its placement basal to *Troglodytes* and its highly autapomorphic nature (18 unique bases; Fig. 3), it is unlikely to represent the sister taxon to *Troglodytes*. The diversity of outgroup taxa in the present study was insufficient to address this issue. Further investigations of wren systematics by colleagues (F. K. Barker, unpubl. data) will clarify this question.

The taxonomic affinities of the Rufous-browed Wren have long been unclear. Ridgway (1904) considered it as a member of the House Wren group. Hellmayr (1934), having not seen specimens, placed it as transitional between the Brown-throated Wren and montane forms to the south, and hypothesized that the group formed a single species. Others have considered it as separate from the House Wren group, placing it with Ochraceous and Mountain Wrens (Oberholser 1904, Chapman and Griscom 1924, Paynter 1957). Our molecular results placed it close to the House Wrens; although bootstrap support for this hypothesis was not high, two unreversed synapomorphies were present. This result indicates that the Rufous-browed Wren is a latitudinal replacement of the Brown-throated Wren (Griscom 1932, Hellmayr 1934, Phillips 1986); its status as a species, however, given marked differences in song and plumage, is not in doubt.

Finally, our results suggest that *Troglodytes*, as currently defined, is polyphyletic. Exhaustive searches under varied assumptions all indicated that the Winter Wren is not part of the clade including other *Troglodytes* wrens examined in this study, which is somewhat surprising given our initial hypothesis that the Winter Wren and Rufous-browed Wren would be sister taxa! This revised view of the phylogenetic placement of Winter Wrens argues for its placement in a separate genus. Because the type species of *Troglodytes* is *T. aedon* (Paynter and Vaurie 1960), the remainder of the species presently placed therein should remain *Troglodytes*. An available genus for the Winter Wren is *Nannus* (after Billberg 1848 in Paynter and Vaurie 1960), so we suggest its use for Winter Wrens. We suggest that the remainder of the species analyzed herein (*aedon, musculus, brunneicollis, rufociliatus, ochraceus, solstitialis,* and *rufulus*), and by inference the insular "House Wrens" *T. tanneri, T. beani,* and "*Thryomanes*" *sissonii,* be retained as members of the genus *Troglodytes*.

SONG EVOLUTION

The hypothesis that motivated this study—that Winter Wrens form a sister lineage to the montane tropical *Troglodytes* wrens—was clearly falsified by the molecular data. This result suggests that song evolution in the group has been complex, and that song characters should be used with caution when formulating or supporting systematic hypotheses. Nowhere is this more obvious than in "House" wrens, in which insular forms have derived songs strikingly different from those of mainland populations. Surprisingly similar songs either evolved independently in Winter Wrens and the montane tropical *Troglodytes,* or are the primitive song type for a broad lineage of wrens.

Troglodytes (excluding *Nannus*) divides clearly into two lineages. One includes the southern montane tropical forms, all of which have the complex "Winter Wren" song. The other has Rufous-browed Wren placed basally ("Winter Wren" song) to the lowland forms plus Brown-throated Wren (trilled song). This arrangement suggests that the trilled song was derived from the "Winter Wren" song, forming a synapomorphy defining the House Wren + Brown-throated Wren lineage.

LOWLAND VS. MONTANE HABITATS

The *Troglodytes* assemblage represents two broadly distributed complexes of lowland (*aedon* and *musculus*) and montane (*brunneicollis, rufociliatus, ochraceus, solstitialis, rufulus*) habitats in close apposition altitudinally throughout much of the Americas. An interesting question is the pattern of invasion of lowlands or highlands—(1) a montane clade nested within lowland forms would indicate lowland origin and a single invasion of highlands, (2) a lowland clade nested within highland forms would indicate highland origin and a single invasion of the lowlands, and (3) a series of sister relationships of lowland and montane forms would indicate independent invasions of different latitudinal bands. The results of our study strongly supported the second hypothesis. The two lowland forms (sister taxa) were nested within four hierarchical levels of montane taxa, suggesting that the pattern of invasion was into the lowlands from the highlands.

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DISPERSAL AND POPULATION STRUCTURE IN THE EUROPEAN STARLING[1]

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Abstract. Dispersal in birds can be estimated in several ways, including the use of banding data and the indirect use of genetic data. This study uses both of these to estimate dispersal and genetic population structure in the European Starling (*Sturnus vulgaris*) in North America. Banding data imply that natal dispersal is quite high, and this finding is supported by the observed rapid colonization of North America. Genetic data, based on allozyme allele frequencies from populations in Virginia, Vermont, Colorado, and California, are consistent with a species with large demes and high rates of dispersal.

Key words: dispersal, European starling, population structure, Sturnus vulgaris.

Natal dispersal allows for the exchange of individuals among existing populations and provides individuals to colonize new areas. Thus, this process is integrally associated with the genetic structure of populations. Unfortunately, it is often very difficult to make direct and accurate estimates of natal dispersal. Banding data have offered important insights into both seasonal movements and dispersal. An alternative is the use of

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