The Condor 98:547–556

GENETIC DIFFERENTIATION AND TAXONOMY IN THE HOUSE WREN SPECIES GROUP[1]

ROBB T. BRUMFIELD[2] AND A. P. CAPPARELLA
Department of Biological Sciences, Illinois State University, Normal, IL 61790

Abstract. The current taxonomic status of the *Troglodytes aedon* (House Wren) species group was evaluated by examining levels and patterns of isozyme differentiation. Traditionally, three major taxonomic groups of continental House Wrens have been recognized: (1) *aedon* (Northern House-Wren); (2) *brunneicollis* (Brown-throated Wren); and (3) *musculus* (Southern House-Wren). The isozyme data were converted to genetic distances and analyzed using UPGMA, Distance Wagner, Fitch-Margoliash, "minimum-evolution," and neighbor-joining algorithms. In addition, a cladistic frequency parsimony analysis (FREQPARS) was performed. All of these methods revealed that the Northern House-Wren and the Brown-throated Wren are sister taxa. There was little genetic differentiation (average Nei's $D = 0.010$) among the seven subspecies of the Southern House-Wren analyzed. Average genetic distances between the Southern House-Wren, the Northern House-Wren, and the Brown-throated Wren are higher than any values reported for intraspecific variation in Nearctic birds, and are comparable to levels of divergence between other Nearctic and Neotropical species. Although the current taxonomy considers the three forms members of a single species, we recommend re-elevating the three groups to species status based on the genetic differences that indicate the three are distinct evolutionary "units." We propose a vicariant hypothesis for the divergence of the Northern House-Wren and the Brown-throated Wren.

Key words: *Aves; Troglodytidae;* Troglodytes aedon; *House Wren; genetic variation; isozymes; systematics; historical biogeography.*

INTRODUCTION

With breeding populations distributed from southern Canada to southernmost South America, *Troglodytes aedon* (House Wren) has the largest latitudinal breeding range of any native passerine in the New World. Despite its large range, *T. aedon* exhibits surprisingly little morphological and plumage variation. Although 30 subspecies (20 continental, 10 insular) are currently recognized (Paynter 1960), most of these were diagnosed based on subtle differences in plumage shade, amount of barring on the flanks, and minor variations in wing-to-tail proportions (Paynter 1957). For example, Chapman and Griscom (1924) stated that most characters used to diagnose the South American forms differ so subtly that researchers working independently on the same material would probably not reach the same taxonomic conclusions. They attributed the small degree of variation among these forms to either an evolutionary constraint on plumage and morphology, or recent dispersal into the majority of the areas they now inhabit.

Previous taxonomic studies of *T. aedon* have concentrated on plumage and morphological characters to assess genetic relatedness. The purpose of this study is to evaluate genetic differentiation within the *aedon* species group based on patterns of isozyme differentiation among available continental populations of the Northern House-Wren (*T. a. aedon, T. a. parkmanii*), the Brown-throated Wren (*T. a. brunneicollis*), and the Southern House-Wren (*T. a. inquietus, T. a. albicans, T. a. audax, T. a. puna, T. a. tecellatus, T. a. rex,* and *T. a. chilensis*) (Paynter 1960).

TAXONOMIC HISTORY

Throughout the taxonomic history of the House Wren, three major continental groups have been consistently recognized: *T. aedon* (breeds from southern Canada to southern United States and northern Baja California, Mexico), *T. brunneicollis* (breeds from southeastern Arizona to Oa-

[1] Received 6 December 1995. Accepted 13 May 1996.
[2] Present Address: Laboratory of Molecular Systematics, National Museum of Natural History, Smithsonian Institution MRC 534, Washington, DC 20560, and Department of Zoology, University of Maryland, College Park, MD 20746, e-mail: brumfld@onyx.si.edu

xaca and west-central Veracruz, Mexico), and *T. musculus* (breeds from eastern Oaxaca, Mexico to Tierra del Fuego, Chile). Several other well differentiated insular forms occur, but their analysis was beyond the scope of this study. The island forms, although problematic, should be considered in a full revision of the House Wren complex.

In the first taxonomic review of the genus, Oberholser (1904) recognized *aedon, brunneicollis,* and *musculus* as distinct species based on plumage differences. He recognized a fourth species, *T. peninsularis* (coastal Yucatán), as the connection between *aedon* and *musculus* because of its intermediate plumage. Despite its geographic proximity to *aedon* and *musculus, brunneicollis* was not considered the connection between the two because of its distinctly different plumage. Oberholser (1904) considered the subspecies of *brunneicollis* described by Sharpe (1881), *T. b. rufociliatus* (highlands of Chiapas, Mexico to north central Nicaragua), as more closely related to the *T. solstitialis* (Mountain Wren) species group of the montane regions of South America to southern Central America, and recognized it as a distinct species, *T. rufociliatus* (Rufous-browed Wren).

Ridgway (1904) also recognized *aedon, brunneicollis, musculus,* and *rufociliatus* as distinct species based on morphological and plumage characters. *Troglodytes aedon* was diagnosable from *musculus* by its tail being five-sixths as long as its wing, *brunneicollis* from *aedon* and *musculus* by its distinct superciliary stripe and distinctly barred flanks, and *rufociliatus* from the other three forms by its tail being less than three-fourths as long as the wing.

In an analysis of House Wrens, Chapman and Griscom (1924) recognized *aedon, brunneicollis,* and *musculus* as species, and elevated *T. m. tecellatus* (southern Peru to northern Chile) to species status because it was allopatric from the forms north and south of it. Although they recognized the intermediacy of *peninsularis* between *aedon* and *musculus,* they reduced *T. peninsularis* to a subspecies of *musculus* because "it possesses no character that one or more races of *musculus* does not have." Because they did not consider *rufociliatus* a House Wren, it was not analyzed.

Hellmayr (1934) recognized *aedon, brunneicollis,* and *musculus* as species. He reduced *tecellatus* to a subspecies of *musculus* because individual variation in the plumage of *tecellatus* overlapped with the forms north and south of it (Hellmayr 1932). Because *T. m. peninsularis* was intermediate in plumage between *T. musculus* and *T. aedon,* he was tempted to consider the two conspecific, but did not because the southern breeding limits of *aedon* were unknown. Hellmayr (1934) saw no specimens of *rufociliatus,* but he considered it to be the bridge between *brunneicollis* and *solstitialis,* and thought the three forms might best be considered a single species.

In the most recent detailed taxonomic treatment of House Wrens, Paynter (1957) found that the characters used by Ridgway (1904) to distinguish *aedon, brunneicollis,* and *musculus* were not useful because of intra-taxonomic variation. Paynter (1957, 1960) reduced *brunneicollis* to a subspecies of *aedon* based both on clinal convergence in plumage characters and interbreeding reported by Marshall (1956). Although interbreeding between *aedon* and *musculus* had not been documented, Paynter (1957) also reduced *musculus* to a subspecies of *aedon* because if *brunneicollis* (the most easily diagnosable form) hybridized with *aedon,* then *musculus* (not consistently diagnosable from *aedon*) must be conspecific as well. However, this was accepted only tentatively by Binford (1989) and was rejected by Miller et al. (1957). Paynter (1960) subsumed *peninsularis,* the form recognized by Oberholser (1904) as the connection between *aedon* and *musculus,* into *intermedius,* the most northern subspecies of the former Southern House-Wren. The current AOU checklist (1983) agrees with Paynter, but notes that species limits within the House Wren complex are not well understood.

Paynter (1957) removed *rufociliatus* from other House Wrens based on the sympatry of *musculus* and *rufociliatus* in El Salvador, and placed it as a subspecies of *T. solstitialis.* Despite this, *T. rufociliatus* is currently considered a full species by some (AOU 1983, Sibley and Monroe 1990). Others, like Hellmayr (1934), considered *rufociliatus* and *brunneicollis* members of the *solstitialis* complex (Griscom 1932, Phillips 1986). All authors have considered *aedon* and *musculus* distinct relative to the *solstitialis* group.

In the most recent taxonomic treatment (Paynter 1957), the former Northern House-Wren consists of an eastern and western North American subspecies, nominate *aedon* and *parkmanii.* Although both subspecies breed north to southern Canada, their southern breeding limits differ. *T. a. aedon* occurs south only to northeastern Ten-

TABLE 1. Collecting localities for *Troglodytes* specimens used in this study. Acronyms and sample sizes for taxa appear in parentheses. Specimen numbers in parentheses after localities refer to frozen tissue inventory number.

Taxon	Collecting locality
Northern House-Wren	
T. aedon aedon (AEDO: 19)	ILLINOIS: McLean Co.; Money Creek Twp. (T25N, R3E, S4), ca. 5 mi. WNW Lexington (ISU 1–6, 8–11, 39, 40, 57, 97, 99, 103, 105, 107, 108).
T. a. parkmanii (PARK: 1)	MEXICO: Jalisco; Sierra de Manatlán, Puerto de los Mazos (FMNH MEX331).
Brown-throated Wren	
T. a. brunneicollis (BRUN: 3)	MEXICO: Michoacan; Pico de Tancitaro, 3 km N Zirimondiro (FMNH MEX161, 170, 189).
Southern House-Wren	
T. a. albicans (ALBI: 1)	ECUADOR: prov. Pichincha; Mindo (ANSP 12082).
T. a. audax (AUDA: 1)	PERU: depto. Lambayeque; Las Pampas, km 885 Pan-Am Hwy. (LSUMZ 5192).
T. a. chilensis (CHIL: 7)	CHILE: prov. Magallanes; Brunswick Peninsula, near mouth of Río Santa Maria, ca. 2 km S San Juan (ISU 362–367); Tierra del Fuego, ca. 18 km by road E Porvenir (ISU 368).
T. a. inquietus (INQU: 1)	PANAMA: prov. Bocas del Toro; Isla San Cristobal, Bocatorito (USNM 362).
T. a. puna (PUNA: 1)	PERU: depto. Pasco; Playa Pampo, 8 km NW Cushi, 2,100 m (LSUMZ 8087).
T. a. rex (REX: 5)	BOLIVIA: depto. Santa Cruz; 21 km S Catarata Arco Iris (LSUMZ 14769, 14837, 14864, 14873, 14875).
T. a. tecellatus (TECE: 2)	PERU: depto. Arequipa; Cerro de los Cantire, 5 km E Chala, 425 m (LSUMZ 3844); La Bodega, 8 km E Atico, sea level (LSUMZ 3912).
Outgroup	
T. troglodytes (TROG: 1)	ILLINOIS: McLean Co.; Normal (ISU 197)

nessee, whereas *T. a. parkmanii* breeds south to at least northern Baja California and southeastern Arizona (Phillips 1986). Paynter (1960) retained three forms of the former Brown-throated Wren. The taxon *cahooni* is restricted to the Sierra Madre Occidental, *compositus* to the Sierra Madre Oriental, and nominate *brunneicollis* to mountains south of the Trans-Volcanic Belt. Paynter (1960) recognized 15 continental forms of the former Southern House-Wren, with populations distributed throughout Central and South America from sea level to over 4000 meters in the Andes (Ridgely and Tudor 1989).

METHODS AND RESULTS

Specimens and collecting localities of the ten subspecies examined are presented in Table 1. The taxa in this study were chosen based on availability in frozen tissue collections. In addition to specimens from the frozen tissue collection of the Illinois State University Museum (ISU; Normal), tissue specimens were provided by the frozen tissue collections of the following institutions (in decreasing order of amount borrowed): Louisiana State University Museum of Zoology (LSUMZ; Baton Rouge), Field Museum of Natural History (FMNH; Chicago), Academy of Natural Sciences (ANSP; Philadelphia), and the United States National Museum of Natural History (USNM; Washington, DC). The individual of *T. a. parkmanii* used in this study was collected in Mexico, and probably represents a wintering bird that breeds north of Mexico. Because there are no consistently diagnosable differences between *T. a. parkmanii* and *T. a. aedon,* the possibility that this individual may represent a wintering *T. a. aedon* cannot be rejected.

Only a few individuals were available for most of the Neotropical taxa. However, Gorman and Renzi (1979) found that as long as the number of loci examined is high, one or a few individuals per taxon will provide robust estimates of genetic

distances. Because the allele frequencies are either near zero or one and there is low heterozygosity, the sample size problem discussed by Archie et al. (1989) should be minimized. Samples of heart, liver, and muscle were taken within 3 h of death and stored in liquid nitrogen (−196° C). Tissue homogenates were prepared by grinding equal amounts of heart, liver, and pectoral muscle in 1 ml of distilled water. The mixture was spun in a Beckman J2-21 centrifuge (JA-14 rotor) at 7,000 rpm for 35 min, and the resulting supernatant frozen (−80° C) for subsequent electrophoretic experiments. Buffer conditions, running conditions, and buffer recipes are available on request. All gels were 12% starch. Each locus was scored on at least two different buffer types to minimize hidden variation (Hackett 1989).

Twenty-four enzyme systems representing 33 presumptive loci were resolved. Enzymes were assayed using procedures outlined by Harris and Hopkinson (1976) with slight modifications. Fifteen enzymes were monomorphic and fixed for the same allele across all taxa examined: Adenylate kinase (EC 2.7.4.3), creatine kinase (EC 2.7.3.2), erythrocyte acid phosphatase (EC 3.1.3.2), esterase-napthyl propionate substrate-3 (EC 3.1.1.1), glutamate dehydrogenase (EC 1.4.1.3), glutamate-oxaloacetate transaminase-2 (EC 2.6.1.1), malate dehydrogenase-1 and 2 (EC 1.1.1.37), malic enzyme-1 and 2 (1.1.1.40), nicotinamide adenine dinucleotide phosphate diaphorase (1.6.4.2), leucyl-alanine dipeptidase-2 (EC 3.4), phosphoglucomutase-2 (EC 2.7.5.1), pyruvate kinase (EC 2.7.1.40), and superoxide dismutase-2 (EC 1.15.1.1). Aconitase-1 and 2 (EC 4.2.1.3), esterase-napthyl propionate substrate-2 (EC 3.1.1.1), α-glycerol phosphate dehydrogenase (EC 1.1.1.8), and purine nucleoside phosphorylase (EC 2.4.2.1) were eliminated from the analysis due to inconsistent or uninterpretable banding patterns.

PAUP (Swofford 1993; the edition used was a prerelease version of PAUP* 4.0) was used to find the optimal tree under the "minimum-evolution" criterion of Rzhetsky and Nei (1992) and the neighbor-joining algorithm (Saitou and Nei 1987). BIOSYS-1 (Swofford and Selander 1981) was used to compute genetic distances (Rogers 1972, Nei 1978), estimate Distance Wagner trees (Farris 1972) using the "multiple addition criterion" of Swofford (1981), and to derive a UPGMA phenogram (Sneath and Sokal 1973). PHYLIP 3.5c (Felsenstein 1993) was used to generate unrooted FITCH (Fitch and Margoliash 1967) networks.

A cladistic analysis was performed using the FREQPARS method (Swofford and Berlocher 1987). FREQPARS implements a parsimony method for polymorphic character data that assigns (for any given tree) a set of ancestral allele-frequency arrays that minimize the total amount of frequency change implied by the reconstruction, with change measured in terms of Manhattan distance between nodes (the "MANAD" criterion). The FREQPARS analysis of phylogenetically informative loci was performed using a technique available in PAUP* 4.0 (Berlocher and Swofford in press) that obtains an exact solution to the "MANOB" criterion of Swofford and Berlocher (1987), which is a good approximation to the "MANAD" criterion. MANOB requires that allele-frequency arrays assigned to each internal node of the tree (hypothetical ancestral taxa) be chosen from the set of allele-frequency arrays observed in the terminal taxa. In this analysis, each unique allele-frequency array is treated as a character-state, and "step-matrices" are created in which the cost of transformation between any pair of states is the Manhattan distance between the allele-frequency arrays represented by the two states. Because of the low amount of genetic differentiation within *musculus* (average Nei's $D = 0.018$), all populations were pooled to obtain better allele frequency estimates. To root the phylogenetic trees, one individual (ISU 197) of *T. troglodytes* (Winter Wren) was scored. This outgroup was chosen because it is a House Wren congener for which frozen tissue was available.

LEVELS AND PATTERNS OF GENETIC DIFFERENTIATION

Thirty-three presumptive loci were resolved (Tables 2 and 3); 16 of these (52%) were variable within or among the ingroup taxa. Thirteen loci were variable within the Northern House-Wren ($n = 20$), five loci were variable within the Brown-throated Wren ($n = 3$), and 10 loci were variable within the Southern House-Wren ($n = 18$). Differences in the number of variable loci are probably due to varying sample size among the three groups. The genetic distance between the two subspecies of Northern House-Wren is very low (Nei's $D = 0.022$). Because Nei's (1978) genetic distance revealed a relatively low level of differentiation among the seven forms of *musculus*

TABLE 2. Allele frequencies at 18 variable loci. Acronyms for taxa are in Table 1. Alleles coded by their relative mobility from the origin; "a" is most anodal. The following loci were monomorphic and fixed for the same allele in all taxa: AK, CK, EAP, EST-NP3, GLUD, GOT2, MDH1, MDH2, ME1, ME2, NADPH, PEP-LA2, PGM2, PK, SOD2. LSUMZ 14769 (REX) not scored for EST-NP1. One additional individual from Illinois (ISU 109) scored for LDH.

	AEDO	PARK	BRUN	TECE	AUDA	PUNA	ALBI	REX	INQU	CHIL	TROG
ADA	a (0.026) c (0.868) d (0.106)	c	c	c	c	c (0.500) e (0.500)	c (0.500) e (0.500)	b (0.100) c (0.800) e (0.100)	c	c (0.929) d (0.071)	c
EST-MA	b (0.053) c (0.947)	c	c (0.667) d (0.333)	c	c	c	c	c	c	c	a (0.500) b (0.500)
EST-NP1	b	b	b (0.833) c (0.167)	b	b	b	b	a (0.125) b (0.750) c (0.125)	b	b	b
FUM	a	a (0.500) b (0.500)	a	a	a	a	a	a	a	a	a
GDA	a	a	a	a	a	a	a	a	a	a	b
GOT1	a	a	a	a	a	a	a	a (0.900) b (0.100)	a	a	a
GPT	b	b	b	b	b	b	b	b	b	a (0.100) b (0.900)	a
GSR	b	b	b	b	b	b	b	b	b	b	a
ICD1	a (0.316) b (0.658) c (0.026)	b	a (0.500) b (0.500)	b	b	b	b	b	b	b	b
ICD2	a (0.763) b (0.237)	a (0.500) b (0.500)	a (0.333) b (0.667)	a	a	a	a	a (0.900) b (0.100)	a (0.500) b (0.500)	a (0.714) b (0.286)	a
LDH	b (0.150) c (0.850)	c	c	b	b	b	b	a (0.100) b (0.900)	b	a (0.214) b (0.786)	d
MPI	a (0.947) b (0.053)	a	a	b	b	b	b	b	b	b	c
PEP-LA1	a (0.026) b (0.974)	b	b	a (0.250) b (0.750)	b	b	b	b	b	b	b
PEP-LGG	b	b	a	a	a	a	a	a	a	a	a
PGD	a (0.026) b (0.974)	b	b	b	b	b (0.500) c (0.500)	b	b	b	b	b
PGI	a (0.053) b (0.947)	b	b	b	b	b	b	b	b	b	a
PGM1	a (0.974) b (0.026)	a (0.500) b (0.500)	a (0.833) b (0.167)	a	a	a	a (0.500) b (0.500)	a	a	a	a
SOD1	a (0.026) b (0.974)	b	b	b	b	b	b	b	b	b	b

TABLE 3. Genetic distances (Nei 1978, below diagonal; Rogers 1972, above diagonal) for taxa analyzed in this study. Acronyms for taxa defined in Table 1.

	AEDO	PARK	BRUN	TECE	AUDA	PUNA	ALBI	REX	INQU	CHIL	TROG
AEDO	*****	0.063	0.081	0.118	0.112	0.136	0.135	0.118	0.113	0.105	0.257
PARK	0.022	*****	0.091	0.144	0.136	0.167	0.136	0.147	0.121	0.130	0.284
BRUN	0.039	0.052	*****	0.124	0.116	0.146	0.136	0.118	0.101	0.110	0.249
TECE	0.091	0.125	0.088	*****	0.008	0.038	0.038	0.028	0.023	0.028	0.216
AUDA	0.090	0.123	0.087	0.000	*****	0.030	0.030	0.021	0.015	0.020	0.208
PUNA	0.107	0.144	0.106	0.016	0.015	*****	0.030	0.042	0.045	0.048	0.238
ALBI	0.106	0.126	0.100	0.016	0.015	0.016	*****	0.042	0.045	0.048	0.238
REX	0.088	0.120	0.080	0.001	0.001	0.012	0.012	*****	0.030	0.026	0.225
INQU	0.092	0.116	0.073	0.008	0.008	0.024	0.024	0.005	*****	0.018	0.223
CHIL	0.084	0.112	0.072	0.003	0.003	0.018	0.018	0.000	0.002	*****	0.213
TROG	0.271	0.309	0.254	0.233	0.231	0.255	0.255	0.234	0.243	0.223	*****

analyzed (average Nei's $D = 0.010 \pm 0.008$; range 0.000–0.024), all samples of *musculus* were pooled in order to calculate average genetic distances among the three major groups. The individual of *T. a. parkmanii* was not used in this calculation of average genetic distance because as a wintering bird, its taxonomic status remains uncertain. Nei's (1978) genetic distance between *aedon* and *musculus* was 0.087; between *aedon* and *brunneicollis* was 0.039; and between *brunneicollis* and *musculus* was 0.078.

Using Rogers' (1972) distance measure, all of the distance analyses resulted in the same topology as the most-parsimonious FREQPARS tree (see below). The most-parsimonious "minimum-evolution" tree (0.322 steps) was the same length as that found using the neighbor-joining algorithm (Saitou and Nei 1987). The UPGMA analysis of all taxa revealed that the seven forms of *musculus* cluster together, and that *aedon* and *parkmanii* are sister taxa. *Brunneicollis* is the sister group to the Northern House-Wren group. The Distance Wagner and FITCH trees also showed *aedon* and *brunneicollis* as sister taxa, but had different topologies among the forms of *musculus*. Given the small sample sizes and small genetic variation among the forms of *musculus*, we consider relationships within this group unresolved.

FREQPARS searches that implement the "MANOB" criterion are not guaranteed to find all optimal trees. In this analysis, however, "MANOB" perfectly approximated the more optimal "MANAD" criterion, as evidenced by the fact that all possible rooted topologies were analyzed. The FREQPARS analysis with all *musculus* taxa pooled found a single most-parsimonious tree (14.57 steps) that united *aedon* and *brunneicollis* as sister taxa (Fig. 1). This sister relationship is supported by the synapomorphic alleles ICD1[a] and MPI[a]. LDH[c] may represent a synapomorphy for *aedon* and *brunneicollis*; however, the outgroup taxon did not polarize the character states at this locus (Table 2). We do not interpret LGG[a] as a synapomorphy uniting *brunneicollis* and *musculus*. Instead, the fixed difference between these two groups and *aedon* represents an *aedon* autapomorphy based on the presence of an "a" allele in the outgroup, *T. troglodytes*. One thousand random addition (10 reps) bootstrap replicates (Swofford 1993) resulted in 91% support for the *aedon-brunneicollis* clade (Fig. 1). House Wren relationships based on this analysis are, however, weakly supported by the isozyme data. The longest tree (i.e., the least-parsimonious) was only $15.324 - 14.570 = 0.754$ steps longer, equivalent to only 0.377 amino acid substitutions. Increasing both the number and geographic representation of *brunneicollis* samples will be necessary to provide a more robust phylogeny using this method.

DISCUSSION

HISTORICAL BIOGEOGRAPHY

The northern limit of *brunneicollis* coincides roughly with the northern limit of pine-oak woodland (Marshall 1957, Binford 1989), a distinct vegetational association found in the Sierra Madre of Mexico north to central Arizona (Brown 1982). The biogeographic significance of this

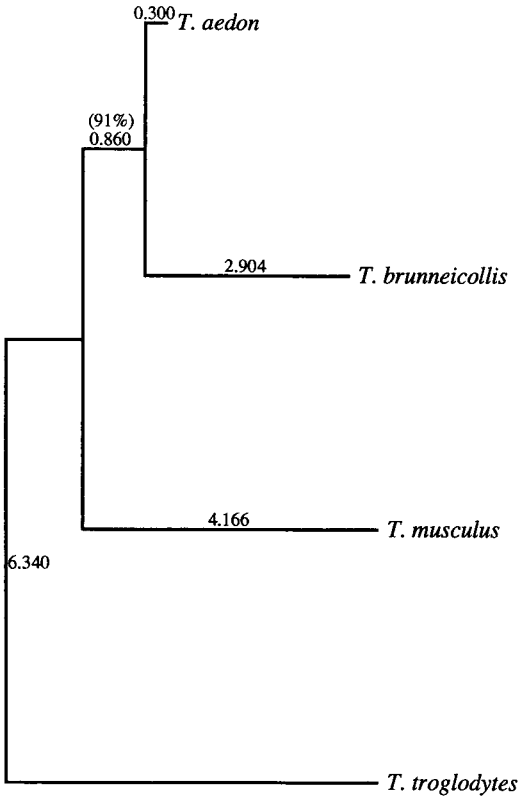

FIGURE 1. Most-parsimonious tree (14.57 steps) of *Troglodytes aedon* (House Wren) relationships based on parsimony analysis of allele-frequency data from isozyme loci (FREQPARS). Tree is rooted to *T. troglodytes* (Winter Wren). Branch lengths reflect amount of allele-frequency change (measured as Manhattan distances) between each pair of nodes. Bootstrap support is presented (in parentheses) for the *aedon-brunneicollis* clade. Relationships depicted in this tree are identical to those found using distance algorithms.

geographic region has been recognized previously for birds (Marshall 1957). Many Mexican taxa restricted to pine-oak woodland have their northern breeding limit in this region (Escalante et al. 1993). Similarly, many North American species restricted to high elevations have their southern limit in this region (Phillips et al. 1964). For example, of 17 passerines restricted to coniferous (pine, fir) and pine-oak woodland in the Rincon mountains of Arizona (Marshall 1956), 43% (eight) have differentiated taxa that meet in this region. This may be the result of a large-scale vicariant event that isolated populations in this area.

The Miocene uplift of the Sierra Madre Occidental contributed to the Tertiary trend towards a drier climate in the American Southwest (Maldonado 1964). At the time of the uplift, the Sonoran desert was covered by sclerophyll woodland and thorn forest (Axelrod 1983), indicating a milder climate than at present. At that time, forests at higher elevations of the Sierra Madre presumably supported House Wren populations. During the Pleistocene, milder climates associated with glacial periods resulted in an elevational lowering of montane vegetation. Analysis of packrat (*Neotoma*) middens show that pinyon-juniper woodlands existed throughout the Sonoran and Chihuahuan Deserts (Van Devender and Spaulding 1983). The glacials, which lasted approximately 100,000 years, thus produced a corridor for dispersal of Mexican highland forms into the southwestern United States (Fa and Morales 1993). During interglacials, which lasted 10,000 to 20,000 years, the woodlands were replaced by desert vegetation that prevented gene flow between populations restricted to montane vegetation. Although this cyclical pattern of elevational vegetation shifts has only been documented as far back as the Wisconsinan, this basic pattern likely existed during earlier glacial periods.

Based on this vicariant hypothesis, the Northern House-Wren was originally restricted to vegetation associated with higher elevations (e.g., pine-oak woodland, aspen). Because this vegetation is also found at higher latitudes, regardless of elevation, the House Wren was able to disperse northward and, once in the northern latitudes, eastward. Its ancestral distribution may have resembled that of species currently restricted to montane vegetation (e.g., *Junco hyemalis* [Slate-colored Junco], *Spinus pinus* [Pine Siskin]).

The fact that the Southern House-Wren's northern limit occurs near the Isthmus of Tehuantepec suggests that historical marine transgressions may have resulted in the divergence of it from the *aedon-brunneicollis* ancestor (Maldonado 1964). Before any vicariant hypotheses are proposed, however, the putative status of *musculus* as sister taxon to the *aedon-brunneicollis* clade needs to be examined. Griscom (1932), Hellmayr (1934), and Phillips (1986) suggested that *brunneicollis* is a latitudinal replacement of *T. rufociliatus*. If this is true, *rufociliatus* would be the sister taxon to the *aedon-brunneicollis* group, making the currently recognized

House Wren species group polyphyletic. This is further complicated by the fact that *T. rufociliatus* has been traditionally thought to represent the most northern form of the *T. solstitialis* species complex, a lineage that, except for *T. rufociliatus,* has never been considered part of the House Wren clade. Clearly, future analyses of the House Wren species complex should include representatives of all these forms.

TAXONOMY

Average levels of allozyme differentiation among congeneric species differ drastically in Nearctic and Neotropical birds. Within the few genera of Neotropical birds examined, genetic distances (Nei 1978) average 0.177 (range 0.080–0.302; Hackett and Rosenberg 1990). Genetic distances within genera of Nearctic birds averaged 0.044 (range 0.0078–0.1267; Barrowclough 1980). The genetic distance values between populations of the Southern House-Wren and both the Northern House-Wren (Nei's $D = 0.087$) and the Brown-throated Wren (Nei's $D = 0.078$) are higher than any of the values reported for intraspecific variation in Nearctic birds (Barrowclough 1980), and are as high as those reported between many congeneric species in the Neotropics (Hackett and Rosenberg 1990). *Aedon* and *brunneicollis* also show a level of divergence (Nei's $D = 0.039$) higher than any reported values of intraspecific variation in Nearctic birds (Barrowclough 1980).

The taxonomic history of House Wrens presented above highlights the controversy concerning the phylogenetic relationships and taxonomic status of the three major continental House Wren groups. Several factors have catalyzed this controversy. First, the two forms that look the most similar superficially (Northern and Southern House-Wren) are allopatric and, based on isozymes, are not sister taxa. Secondly, two forms that look very different (Northern House-Wren and Brown-throated Wren) are known to hybridize (Marshall 1956).

Paynter's (1957) merger of *aedon* and *brunneicollis* was based on clinal convergence of plumage characters and reports of three hybrid nests between *T. aedon* and *T. brunneicollis* at a site in southeastern Arizona (Marshall 1956). Spectrograms of the primary song of the Brown-throated Wren (the subspecies analyzed was *T. a. cahooni*) and the Northern House-Wren are more similar to each other than are the two Northern House-Wren subspecies (Lanyon 1960). Based on this result, Lanyon concluded that "difference in song" cannot be used to elevate *aedon* and *brunneicollis* to species status. Unfortunately, there have been no comparative vocalization analyses between nominate *aedon* and nominate *brunneicollis,* the forms analyzed in this study. Because there is no indication that nominate *brunneicollis* sings like *cahooni,* future analysis of vocalizations may find differences that support the genetic divergence between these forms.

The high level of genetic divergence between *aedon* and *brunneicollis,* including a fixed difference at LGG, indicates that the two have been on separate evolutionary trajectories, and are therefore good phylogenetic species. We therefore recommend re-elevating the Northern House-Wren and the Brown-throated Wren to phylogenetic species status. We note as a caveat that our *brunneicollis* samples were collected far from the contact zone with *aedon,* and are not the subspecies that contacts *aedon* in southeastern Arizona. In the contact zone the presence of steep plumage character clines (Marshall 1956) as well as the discontinuity of appropriate habitat (Lanyon 1960) suggest that gene flow is restricted between *aedon* and *brunneicollis.* Until more detailed genetic analyses of the hybrid zone are performed, we are hesitant to consider the two biological species.

The northern breeding limit of the Southern House-Wren in Central America is in Oaxaca, Mexico, where it has been found at the margins of tropical semideciduous forest and lower reaches of cloud forest (Binford 1989). Because *musculus* is geographically isolated from *aedon* (AOU 1983) and apparently elevationally isolated from *brunneicollis* (Binford 1989), Paynter (1957) used morphology to infer whether they could potentially interbreed. He argued that because *musculus* was more morphologically similar to *aedon* than to *brunneicollis,* they would probably interbreed. Differences are apparent in the vocalizations of *aedon* and *musculus,* with Ridgely and Tudor (1989) noting that the Southern House-Wren in Ecuador gives a very different call note from the Northern House-Wren. Ridgely and Gwynne (1989) suggested that the Southern House-Wren's song in Panama is "less raspy" than the Northern House-Wren's. In Costa Rica, the Southern House-Wren's song is described as "more prolonged and varied" than the Northern House-Wren's (Stiles and Skutch 1989).

Fixed and strong allele frequency differences between the Southern House-Wren and both the Northern House-Wren and the Brown-throated Wren contribute to a high level of genetic divergence that indicates the former represents a distinct evolutionary unit. Although northernmost *musculus* were not examined due to unavailable material, the fact that Panama birds (*inquietus,* the farthest north available) were as differentiated from both *aedon* and *brunneicollis* as Chilean birds (*chilensis,* the farthest south available) suggests the lack of an effect of geographic distance on genetic distance. Based on the genetic and vocalization differences, we recommend re-elevating the Southern House-Wren as a phylogenetic and biological species.

ACKNOWLEDGMENTS

We thank the many skilled field workers who collected samples, and Mike Braun, Scott Lanyon, Town Peterson, Van Remsen, Mark Robbins, Fred Sheldon, and Bob Zink for providing them to us. C. F. Thompson and two anonymous reviewers made valuable comments on the manuscript.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds, 6th ed. Am. Ornithol. Union, Washington, DC.

ARCHIE, J. W., C. SIMON, AND A. MARTIN. 1989. Small sample size does decrease the stability of dendrograms calculated from allozyme-frequency data. Evolution 43:678–683.

AXELROD, D. I. 1983. Paleobotanical history of the western deserts, p. 113–129. *In* S. G. Wells and D. R. Haragan [eds.], Origin and evolution of deserts. Univ. of New Mexico Press, Albuquerque.

BARROWCLOUGH, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. Auk 97:655–668.

BERLOCHER, S. H., AND D. L. SWOFFORD. In press. Searching for phylogenetic trees under the frequency parsimony criterion: an approximation using generalized parsimony. Syst. Biol.

BINFORD, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Ornithol. Monogr. 43:1–418.

BROWN, D. E. 1982. Madrean evergreen woodland, p. 59–65. *In* D. E. Brown [ed.], Biotic communities of the American southwest-United States and Mexico. Univ. of Arizona Press, Tucson.

CHAPMAN, F. M., AND L. GRISCOM. 1924. The House Wrens of the genus *Troglodytes.* Bull. Amer. Mus. Nat. Hist. 50:279–304.

ESCALANTE, P. P., A. G. S. NAVARRO, AND A. T. PETERSON. 1993. A geographic, ecological, and historical analysis of land bird diversity in Mexico, p. 281–307. *In* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: origins and distribution. Oxford Univ. Press, New York.

FA, J. E., AND L. M. MORALES. 1993. Patterns of mammalian diversity in Mexico, p. 319–361. *In* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: origins and distribution. Oxford Univ. Press, New York.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106:645–668.

FELSENSTEIN, J. 1993. PHYLIP (Phylogenetic Inference Package) version 3.5c. Distributed by author. Depart. of Genetics, Univ. Washington, Seattle.

FITCH, W. M., AND E. MARGOLIASH. 1967. Construction of phylogenetic trees. Science 155:279–284.

GORMAN, G. C., AND J. RENZI, JR. 1979. Genetic distance and heterozygosity estimates in electrophoretic studies: effects of sample size. Copeia 1979:242–249.

GRISCOM, L. 1932. The distribution of bird-life in Guatemala. Bull. Am. Mus. Nat. Hist. 64:1–439.

HACKETT, S. J. 1989. Effects of varied electrophoretic conditions on detection of evolutionary patterns in the Laridae. Condor 91:73–90.

HACKETT, S. J., AND K. V. ROSENBERG. 1990. Comparison of phenotypic and genotypic differentiation in South American antwrens (Formicariidae). Auk 107:473–489.

HARRIS, H., AND D. A. HOPKINSON. 1976. Handbook of electrophoresis in human genetics. North-Holland Publishing, Amsterdam.

HELLMAYR, C. E. 1932. The birds of Chile. Field Mus. Nat. Hist. Zool. Ser. 19:1–472.

HELLMAYR, C. E. 1934. Catalogue of birds of the Americas and the adjacent islands. Field Mus. Nat. Hist. Zool. Ser. 13:1–531.

LANYON, W. E. 1960. Relationship of the House Wren (*Troglodytes aedon*) of North America and the Brown-throated Wren (*Troglodytes brunneicollis*) of Mexico. Proc. Int. Ornithol. Congr. 12:450–458.

MALDONADO, M. K. 1964. Geohistory and paleogeography of Middle America, p. 3–32. *In* R. C. West [ed.], Handbook of Middle American Indians, Vol. 1. Univ. of Texas Press, Austin.

MARSHALL, J. T., JR. 1956. Summer birds of the Rincon Mountains, Saguaro National Monument, Arizona. Condor 58:81–97.

MARSHALL, J. T., JR. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pacific Coast Avifauna 32.

MILLER, A. H., H. FRIEDMANN, L. GRISCOM, AND R. T. MOORE. 1957. Distributional check-list of the birds of Mexico. Part 2. Pacific Coast Avifauna 33.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

OBERHOLSER, H. C. 1904. A review of the genus *Troglodytes.* Proc. U.S. Natl. Mus. 27:197–211.

PAYNTER, R. A. 1957. Taxonomic notes on the new world forms of *Troglodytes.* Breviora 71:1–15.

PAYNTER, R. A. 1960. Check-list of birds of the world, Vol. 9. Harvard Univ. Press, Cambridge, MA.

PHILLIPS, A. R. 1986. The known birds of North and Middle America, Part 1. Denver Mus. Nat. Hist, Denver, CO.

PHILLIPS, A., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. of Arizona Press, Tucson.

RIDGELY, R. S., AND J. GWYNNE. 1989. A guide to the birds of Panama. Princeton Univ. Press, Princeton, NJ.

RIDGELY, R. S., AND G. TUDOR. 1989. The birds of South America: the oscine passerines. Univ. of Texas Press, Austin.

RIDGWAY, R. 1904. The birds of North and Middle America. Bull. U.S. Natl. Mus 3:1–801.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics. Univ. Texas Publ. 7213:145–153.

RZHETSKY, A., AND M. NEI. 1987. A simple method for estimating and testing minimum-evolution trees. Mol. Biol. Evol. 9:945–967.

SAITOU, N., AND M. NEI. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4:406–425.

SHARPE, R. B. 1881. Catalogue of the birds of the British Museum 6:1–420.

SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, CT.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman, San Francisco.

STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Comstock Publ., Ithaca, NY.

SWOFFORD, D. L. 1981. On the utility of the distance Wagner procedure, p. 25–43. *In* V. A. Funk and D. R. Brooks [eds.], Advances in cladistics, Vol. 1. New York Botanical Gardens, New York.

SWOFFORD, D. L. 1993. PAUP: phylogenetic analysis using parsimony, version 3.1. Computer program distributed by Illinois Natural History Survey, Champaign, IL.

SWOFFORD, D. L., AND S. H. BERLOCHER. 1987. Inferring evolutionary trees from gene frequencies under the principle of maximum parsimony. Syst. Zool. 37:271–290.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72:281–283.

VAN DEVENDER, T. R., AND W. G. SPAULDING. 1983. Development of vegetation and climate in the southwestern United States, p. 131–156. *In* S. G. Wells and D. R. Haragan [eds.], Origin and evolution of deserts. Univ. of New Mexico Press, Albuquerque.