A NEW *HERPSILOCHMUS* ANTWREN (AVES: THAMNOPHILIDAE) FROM NORTHERN AMAZONIAN PERU AND ADJACENT ECUADOR: THE ROLE OF EDAPHIC HETEROGENEITY OF *TERRA FIRME* FOREST

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ABSTRACT.—*Herpsilochmus gentryi*, the Ancient Antwren, is described from northern Amazonian Peru and from one locality in southeastern Ecuador. As for several other recently described birds, the new species was first identified by voice. *Herpsilochmus gentryi* is restricted to two structurally distinct kinds of *terra firme* forest, growing on nutrient-poor, podzolic and quartzitic soils; its distribution is almost entirely edaphically controlled. Morphological and vocal comparisons strongly indicate a sister relationship with *H. stictocephalus* of the widely disjunct Guianan region. Both species are sympatric with sister taxa of parallel geographic disjunction in the *H. sticturus* complex. However, the degree of syntopy in the two regions is different. We suggest that the more limited overlap of *H. gentryi* with *H. sticturus dugandi* is a function of higher habitat mosaicism resulting from Andean orogeny and fluvial perturbance in Amazonian Peru than on the relatively stable and uniform Guianan shield. *Herpsilochmus gentryi* is common within its habitat, but the habitat itself is naturally rare and patchily distributed. Construction of a road through these ancient and fragile habitats near the city of Iquitos has led to a dramatic increase in habitat destruction over just the last 10 years. Integration of satellite imagery and aerial photographs with multidisciplinary ground-truthing of soil types, and botanical inventories by teams from the University of Turku, has shown that *terra firme* landscape heterogeneity is high in Peruvian Amazonia, and at least some distinctive habitats, such as those of *H. gentryi*, are readily mapped. Both the history and destiny of *H. gentryi* exemplify how the deterministic effects of local edaphic conditions on phytogeographic and, by extension, bird distribution, define an integral role for these factors in conservation initiatives, and in revealing biogeographic patterns. *Received 16 September 1997, accepted 2 February 1998.*

OVER THE COURSE of several years of field work along the Tigre, Corrientes, and Pucacuro rivers in northwestern Loreto, Peru, we (Alvarez 1994, Alvarez and Whitney unpubl. data) documented an exceptionally diverse avifauna, including several species not previously known from the country. An integral aspect of this work was the recording of vocalizations. In September 1994, Whitney listened to some of Alvarez's recordings, mostly of unseen canopy birds. Among them, he identified one song of an undescribed species of *Herpsilochmus* antwren, diagnosing it as most closely related to *H. stictocephalus* (Todd's Antwren) of the widely disjunct Guianan region. In late January 1995, we mounted a brief expedition up the Tigre in search of the new *Herpsilochmus*. This work resulted in the tape-recording of several

individuals and the collection of two adult males of the new antwren, which proved to be common in the canopy of one type of *terra firme* forest. Subsequent collections of both sexes and different age classes by Alvarez, and tape recordings of a larger sample of individuals by both of us, have significantly augmented our knowledge of the new bird's distribution (even to the edge of the city of Iquitos). In addition, David J. Stejskal has recently documented with tape recordings the occurrence of the new species at Kapawi Ecological Reserve along the Río Pastaza a short distance into Ecuador.

Examination of the material at hand, study of a pertinent selection of museum specimens and tape recordings, and extensive field experience with the genus *Herpsilochmus* throughout its wide range, convinces us that this distinctive antwren is best described as a new species. Its description, with a discussion of its intrageneric and ecological relationships, follows.

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Herpsilochmus gentryi sp. nov.
Ancient Antwren

Holotype.—Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (hereafter MUSM), No. 17679, adult male from the left bank of the middle Río Tigre, 03°44'S, 74°32'W, across the river from the village of P. J. Lores, approximately 260 m elevation, Department of Loreto, Peru, collected 23 January 1995 by José Alvarez Alonso, tape-recorded by Bret M. Whitney. Voice specimen archived at Library of Natural Sounds (hereafter LNS), Cornell Laboratory of Ornithology, Ithaca, New York, LNS No. 79049.

Assignment to Herpsilochmus *Cabanis 1847.*— *Herpsilochmus gentryi* is a typical member of the genus *Herpsilochmus*, closely similar to other members in size, overall proportions, plumage pattern, and degree of sexual dichromatism. However, generic characteristics of the morphometrics and plumages of *Herpsilochmus* Cabanis 1847 have not been described diagnostically. Cabanis's original description of two sentences (translated from German) provided only a cursory comparison with three other genera: "Like the previous species, also a connecting link between *Thamnophilus* and *Formicivora* and to a degree a small reiteration of *Thamnophilus*. Distinguishes itself sufficiently from *Dysithamnus* by the strongly graduated tail and brighter plumage, from *Thamnophilus* by the more delicate and not laterally compressed bill, and from *Formicivora* by a stronger [broader?] bill not laterally compressed near the tip as well as by narrower tail feathers and brighter plumage." Modern descriptions offer little improvement. A better diagnosis is desirable for objective allocation of a new species to the genus.

Herpsilochmus comprises a conservative minimum of 16 (B. Whitney pers. obs.) described and undescribed species-level taxa, all of which are small birds not exceeding 13 cm in overall length. The following diagnosis applies to all known populations in the genus (few individual measurements outside these ranges): wing chord, 45 to 64 mm; tail, 34 to 60 mm; tarsus, 15 to 21 mm; length of culmen from base, 15 to 20 mm; body mass probably does not exceed 12.5 g (data from Cory and Hellmayr 1924, Davis and O'Neill 1986, and personal examination of specimens). Adult males of all species have a semi-glossy black forehead (spotted in two species) and crown (spotted in one species). Crowns of adult females and subadults of both sexes usually are spotted, streaked, or with some rufous tones. All have the crown bordered by a contrasting, pale superciliary; a black line through or posterior to the eye; strongly graduated tail; extensive white tips on all but the central pair of rectrices (outer rectrices often mostly white); conspicuous pale spots on the tips of the wing coverts; a white border (usually conspicuous) on the distal margins of the scapular feathers; a semi-concealed, white interscapular patch; dark iris; grayish lower mandible; bluish-gray legs and toes; soles of feet usually yellow. Additionally, all species forage primarily in the upper strata of forest/woodland habitats in association with mixed-species flocks of other insectivores and, sometimes, frugivores and nectarivores.

Diagnosis of Herpsilochmus gentryi *sp. nov.*— Differs from all congeners by entirely yellow underparts (shared only by some subspecies of *H. axillaris* [Yellow-breasted Antwren], which, however, are appreciably paler), facial region, and superciliary stripe (cover, Fig. 1A). Further distinguished by plumage from its presumed sister species, *H. stictocephalus* (Fig. 1B), by absence of pale spots on the forecrown of males; slightly different distribution of pale spotting on the crown of females (that of the new species is described in detail below); orangish frontal feathers of females and immatures (black in *stictocephalus*); more extensive black in the preocular region and mantle; and presence of a continuous, whitish margin on at least one web (usually the inner, or proximal) of at least one of the two central rectrices of both sexes as opposed to three to four oblong spots on the outer web (and wholly dark inner web), the typical pattern on the central rectrices of *H. stictocephalus* (tail patterns not visible in Fig. 1). Morphometrically, the new species has the tail averaging about 2.5 mm shorter, bill averaging 0.6 mm longer, and body mass about 2 g heavier, than *H. stictocephalus* (sexes for each combined, because measurements overlap extensively; Table 1).

Diagnosis: Voice.—Loudsongs (following Willis 1967) of all *Herpsilochmus* species are about 2 s in duration and consist of a variably paced series of notes that, for almost all species, is characterized by a slight rise in frequency through the first few notes. The song of *H. gen-*
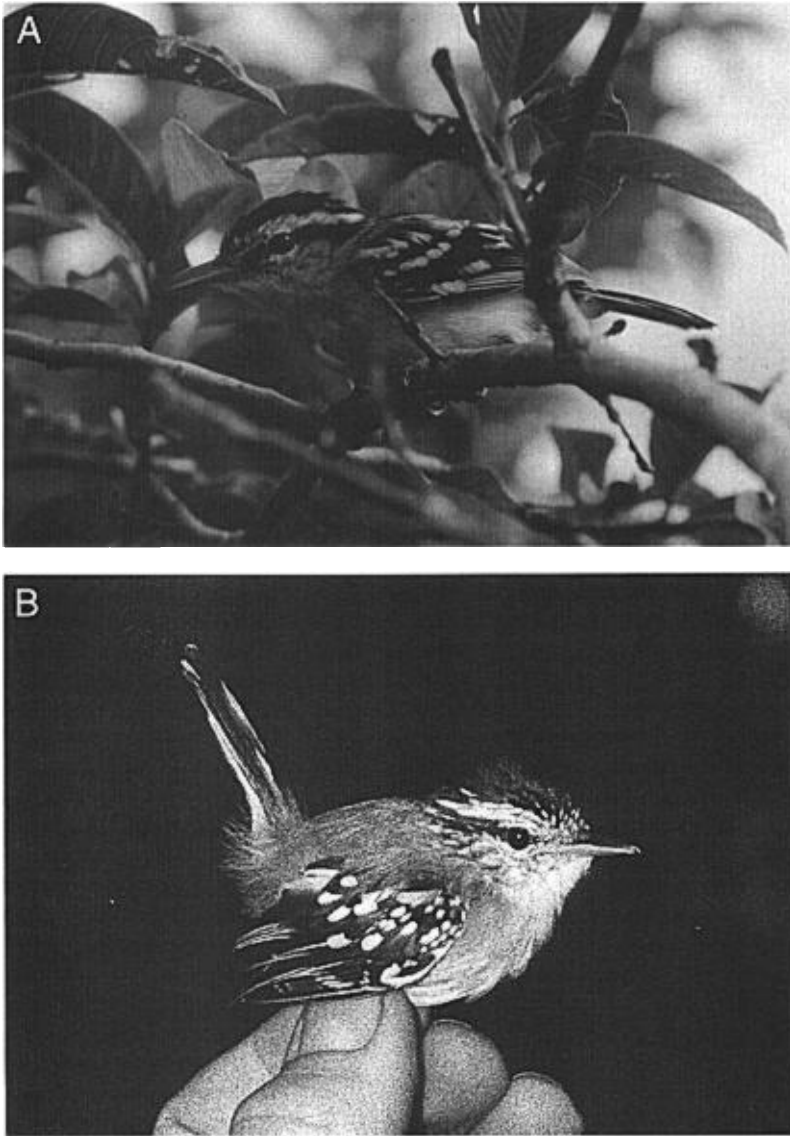
FIG. 1. (A) Adult male *Herpsilochmus gentryi* sp. nov., Ancient Antwren, from the middle Río Tigre, Loreto, Peru. (B) Its presumed sister species, *H. stictocephalus*, Todd's Antwren, is restricted to Guianan forests, ca. 1,700 km to the northeast. Photos by José Alvarez Alonso (A) and Bret M. Whitney (B).

TABLE 1. Measurements of selected species of *Herpsilochmus* antwrens. Values are $\bar{x}$, with range and n in parentheses.

Taxon	Culmen (mm)[a]	Wing chord (mm)	Tail (mm)	Body mass (g)
H. gentryi	16.2 (15.5–16.8, 11)	48.6 (46.8–50.2, 10)	36.6 (35.3–38.5, 9)	10.6 (10.2–11.0, 6)
H. stictocephalus	15.6 (14.8–16.5, 13)	47.9 (46.9–49.6, 13)	39.0 (35.8–41.6, 13)	8.8 (7.8–9.6, 11)
H. sticturus sticturus	15.7 (13.0–17.3, 11)	46.6 (43.0–48.5, 11)	35.7 (34.3–36.8, 9)	9.0 (8.9–9.2, 3)
H. sticturus dugandi	16.0 (15.2–17.1, 4)	49.7 (47.9–52.0, 5)	37.1 (35.4–39.1, 5)	10.3 (9.3–11.3, 4)
H. axillaris aequatorialis	16.0 (15.2–17.1, 4)	52.6 (51.4–53.9, 4)	48.0 (47.2–48.8, 4)	11.6 (10.2–13.0, 2)

[a] Measured from base at skull.

TABLE 2. Loudsong measurements[a] of *Herpsilochmus gentryi* and *H. stictocephalus*. Values are $\bar{x}$, with range in parentheses.

Taxon	Total no. of notes	No. notes in first 0.5 s	Peak frequency (PF) 4th note	ΔPF, 4th to final note
H. gentryi	17.4 (13.3–21.3)	6.9 (5.7–8.0)	2.5 (2.3–2.7)	0.3 (0.1–0.5)
H. stictocephalus	13.2 (10.7–15.0)	4.3 (4.0–5.0)	2.7 (2.6–2.9)	1.0 (0.7–1.3)

[a] Three songs (usually the first three) from each of 10 individuals were measured and averaged. Means and ranges reflect combined measures of 10 individuals. Recordings listed above in "*Specimens examined: Voice.*"

tryi is typical in these respects. Full songs are readily distinguishable aurally and spectrographically from all congeners except *H. stictocephalus*. The similar songs of these two species (only male songs analyzed to date) may be diagnostically identified, especially when several successive songs of any individual are considered, by at least two characters: (1) number of notes in the first 0.5 s ($\bar{x}$ = 4.3 for *gentryi* vs. 6.9 for *stictocephlaus*), and (2) the change in frequency between the fourth and final notes ($\bar{x}$ = 0.95 kHz for *gentryi* vs. 0.26 kHz for *stictocephalus*; Table 2). Calls of *Herpsilochmus gentryi* may be differentiated from homologous calls of *H. stictocephalus* on the basis of note structure and tonality, although mobbing vocalizations are quite similar. A larger sample of calls is highly desirable.

Distribution.—Highly patchy, in upland forest on nutrient-poor soils north of the Marañón River, primarily in northern Loreto, Peru (Fig. 2). Known from as far east as the southern edge of the city of Iquitos, Peru (ca. 03°57'S, 73°24'W), thence west along the major rivers Marañón, Tigre, Corrientes, and Pucacuro. In Ecuador, thus far known only from southeastern Pastaza Province on the left bank of the Río Pastaza at the Kapawi Ecological Reserve (ca. 02°35'S, 76°53'W). Undoubtedly occurs more widely in this general region, wherever habitat requirements (see below) are met, perhaps especially in the unexplored Tigre/Nanay interfluvium. The *terra firme* avifauna of southern Amazonian Ecuador also is quite poorly known.

Description of holotype.—See cover and Figure 1A. Alphanumeric color designations determined from direct comparison to the Munsell soil color chart (1994). Crown from base of bill posterior to occiput entirely deep, semi-glossy black. Loral region and coterminous, 2.5-mm wide superciliary stripe clear yellow, closest to 5Y 8/6. Terminal 6 mm of superciliary slightly wider (ca. 3.5 mm) and whitish. Preocular
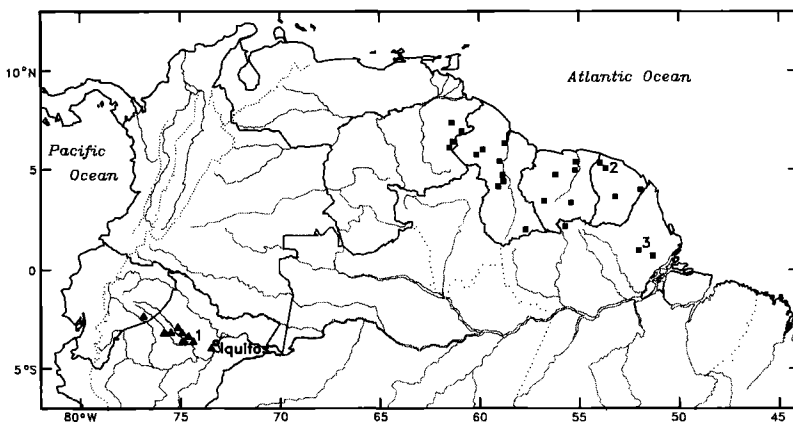

FIG. 2. Distribution of *Herpsilochmus gentryi* sp. nov. in northern Peru and southeastern Ecuador (triangles), and *H. stictocephalus* (squares). Occurrence at all points was documented with specimens and/or tape recordings. Numbers are: (1) Lores, type locality of *Herpsilochmus gentryi*; (2) Tamanoir, French Guiana, type locality of *H. stictocephalus*; (3) Serra Grande and Serra do Navio, Amapá, Brazil, where occurrence of *H. stictocephalus* recently confirmed with tape recordings by J. F. Pacheco and A. Whittaker, respectively. Range disjunction of the presumed sister taxa is ca. 1,700 km.

stripe to near base of bill and 2.5-mm wide postocular stripe, to a point about 12 mm posterior to orbit, same deep black as crown. Facial region, including auriculars, same yellow as anterior portion of superciliary, this color extending posteriorly around the end of the postocular stripe to meet the superciliary. Tiny feathers on side of neck same yellow, but with olivaceous fringes, imparting slightly duskier appearance to this region. Nuchal region generally olive (5Y 5/4), but gray feather bases and black tips or fringes on some feathers contribute to a mixed appearance. Most feathers of mantle and back same deep black as crown; some lateral feathers black with olive margins, wholly gray (5Y 6/1), or gray with blackish tips. Thus, nuchal region olive mixed black, and mantle and middle back black mixed olive and gray, exact appearance depending on position of individual feathers. Feathers of back overlie and mostly conceal a large, black-and-white patch (in Thamnophilidae, often denoted "interscapular patch"). Individual feathers of interscapular patch white on proximal webs, sometimes with black tips on these webs, and either entirely black on distal webs or with white bases. Feathers of lower back and rump greatly elongated (some >30 mm) and silky in texture, generally gray with olive or black subterminal bands and gray tips such that overall color of rump is blackish mixed olive and gray. Uppertail coverts black with whitish shafts and terminal fringes.

Underparts mostly yellow, essentially concolor with facial and superciliary regions (slightly brighter than 5Y 8/6), this color most saturated along midline from chin to vent. A few tiny feathers of throat more whitish. Sides of breast distinctly olivaceous (nearest 5Y 5/4); somewhat elongated feathers of flanks subtly grayer. Tail graduated, with outermost pair of rectrices about half as long as the central (longest) pair and entirely white, except base of proximal web (hidden by undertail coverts) black. White tips on successive pairs of rectrices decreasing in size from outermost to innermost such that undertail appears mostly white with irregular black spots showing between overlying white tips. Central rectrices (growing in) black, lacking white tips, but marked with continuous (i.e. not broken into spots) white lateral fringes appearing, in dorsal aspect, as thin white stripes along midline of

black tail. Central rectrices differ in amount of white edging: upper rectrix bears considerably wider white fringe on proximal web; lower rectrix has most conspicuous fringe on outer (exposed) web. Wing coverts same deep black as crown and most of back, each feather marked with a conspicuous yellowish or, less commonly and apparently randomly, clear white tip, more extensive on distal web. Light tips on tiny feathers at bend of wing and on lesser wing coverts appear as scattered spots, but arrangement of light tips on median and greater coverts more regular, imparting two well-defined wing bars. Scapulars sharply bicolored, black on proximal and yellowish white on distal webs, forming a conspicuous yellowish-white stripe overlying proximal ends of wing bars. Bend of wing same yellow as breast. Primary coverts black with minute pale fringes on distal webs. Alula black with contrasting yellowish margin on distal web reaching tip. Remiges blackish (more brownish toward tips owing to oxidation and wear) with tiny whitish fringes on distal webs and wider, yellowish margins on proximal webs (hidden on closed wing). Tertials blackish with weak olive tinge, marked with conspicuous yellowish-white margins on distal webs, coterminous with similarly yellowish-white margins on scapulars. Soft parts in life: iris dark brown; upper mandible blackish with grayish tomia, lower mandible grayish, slightly darker away from midline; legs and feet bluish gray, feet with yellow-orange soles.

Measurements of holotype.—Wing chord, 47.8 mm; tail, 36.1 mm (central rectrices nearly fully grown); culmen from base (at skull), 16.1 mm; culmen from anterior edge of nares, 9.3 mm; bill depth at anterior edge nares, 3.9 mm; bill width at anterior edge nares, 4.2 mm; tarsus, 17.5 mm; body mass 10.2 g.

Description of female.—Adult (skull 100% ossified) female MUSM No. 17686. Differs most clearly from holotype, and males in general, by crown deep black with conspicuous spots, somewhat more concentrated anteriorly. Tiny feathers of forecrown, anterior to orbits, with orangish (nearest 10YR 6/8) centers and margins and blackish tips. Posterior to forecrown, most crown feathers with two yellowish-white or white marginal spots, one on each web opposite each other, and black centers and tips. Some feathers have only one marginal spot,

and those toward posterior sides of crown are wholly deep black. Spots also vary somewhat in size such that overall pattern of spotting is irregular. Feathers of facial region and auriculars with minute dusky fringes, imparting weakly mottled effect. Breast, especially at sides, slightly darker than holotype, some feathers weakly tinged olive-yellow or "bronzy" (nearest 2.5Y 6/8). White interscapular patch greatly reduced, and middle back slightly grayer. Otherwise, plumage and soft parts similar to holotype. Measurements: wing chord, 49.0 mm; tail (fully grown), 37.2 mm; culmen from base (at skull), 15.5 mm; culmen from anterior edge nares, 8.9 mm; bill depth at anterior edge nares, 3.9 mm; bill width at anterior edge nares, 4.0 mm; tarsus, 16.7 mm; body mass unknown.

Description of juvenile.—Male (skull 60 to 70% ossified) MUSM No. 17684. Superciliary less well defined, especially anteriorly, than either holotype or adult female described above. Like adult female, tiny forecrown feathers with orangish centers and margins and blackish tips. Crown less deeply black than adult and marked with large, irregularly sized and spaced whitish blotches, appearing less distinctly spotted than adult female. Posterior to forecrown, feathers have much whitish on proximal webs and blackish on distal webs, but those in center of crown have whitish spots on opposite margins as in adult female. Further differs from adults in having more olive in upperparts. White interscapular patch present, less extensive than in holotype, but well developed in comparison with adult female. Rectrices more pointed than those of adults. Central rectrices grayish (darker above than below) with an oblong, blackish blotch on distal portion of proximal web. White lateral margin on proximal web as in adults, but white lacking on distal margins. Central rectrices also with minute, white tips. Otherwise, plumage like that of adult female described above, and soft parts as in adults. Measurements: wing chord, 48.5 mm; tail (fully grown), 34.2 mm; culmen from base (at skull), 16.2 mm; culmen from anterior edge nares, 9.5 mm; bill depth at anterior edge of nares, 4.2 mm; bill width at anterior edge nares, 4.1 mm; tarsus, 17.3 mm; body mass unknown.

Specimens examined: Skins.—Only specimens measured are listed. Plumages of males and fe-

males of all other described species and subspecies of *Herpsilochmus* were compared superficially. Standard measurements for most taxa are available in Cory and Hellmayr (1924) and Davis and O'Neill (1986), although we note that published measurements for individual specimens may vary appreciably. *Herpsilochmus gentryi*: Peru, Loreto, seven males and five females (MUSM Nos. 17679 to 17687, 17702 to 17704). *Herpsilochmus stictocephalus*: French Guiana, one male (Academy of Natural Sciences of Philadelphia [ANSP] No. 65398); Guyana, five males and eight females (American Museum of Natural History [AMNH] Nos. 125610, 805679; ANSP 11 specimens uncatalogued). *Herpsilochmus sticturus sticturus*: Guyana, six males and one female (AMNH Nos. 490657, 805675; ANSP Nos. 50993, 50994, and three specimens uncatalogued); Venezuela, Bolívar, one male and three females (AMNH Nos. 490657, 490659, 323769, 323770). *Herpsilochmus sticturus dugandi*: Ecuador, Napo, one male (ANSP No. 169739); Peru, Loreto, three males and one female (MUSM, two skins and one in alcohol uncatalogued; Louisiana State University Museum of Natural Science [LSUMZ] No. 128512); Amazonas, one female (LSUMZ No. 92402). *Herpsilochmus axillaris aequatorialis*: Ecuador, Zamora-Chinchipe, two males and two females (ANSP Nos. 176845, 176846, 184693, 185467).

Specimens examined: Tape recordings.—At least three recordings of all described species and almost all subspecies of *Herpsilochmus* were compared aurally to *H. gentryi*. The restricted set of recordings compared and measured spectrographically (Table 2) is listed below. Data for recordings reproduced as figures are provided in the corresponding legends. All recordings by Bret Whitney unless otherwise indicated. *Herpsilochmus gentryi*: Peru, Loreto, upper ríos Corrientes and Tigre downstream to Iquitos, 10 (one by J. Alvarez). *Herpsilochmus stictocephalus*: Venezuela, Bolívar, two (Paul Schwartz, LNS uncatalogued); Guyana, two; Suriname, five (one by Tom Davis, LNS 25222); Brazil, Amapá, one (A. Whittaker). All of the authors' recordings, and most of the other recordings listed here, have been or will be archived at the Library of Natural Sounds at the Cornell Laboratory of Ornithology, Ithaca, New York.

Etymology.—It is with great pleasure that we name this small, canopy-inhabiting antwren in honor of the late Alwyn H. Gentry, one of the

most gifted and productive field botanists of all time. Beyond his legendary stature as a field man, however, Dr. Gentry was a great systematist and phytogeographer, whose many published works have clearly guided the thinking of a generation of students of Neotropical biodiversity and conservation, including us. His early (1981) paper on the edaphic specialization of some *Passiflora* species was seminal in demonstrating the deterministic role of edaphic heterogeneity in understanding Amazonian biodiversity. Indeed, the local distribution of *Herpsilochmus gentryi* is apparently dictated almost entirely by edaphic control of the woody plant community. Finally, Dr. Gentry spent a great deal of time in the Iquitos region, and had a special interest in the white-sand plant communities of northern Peru (see Conservation below). His influence will be pervasive in conservation planning in most areas of the Neotropics forever. The English name Ancient Antwren derives from our postulation of the new species' divergence from ancestral stock perhaps several million years before present. Of necessity, our hypothesis of the vicariant events involved in its differentiation will be presented elsewhere.

REMARKS

Variation in the type series.—The type series consists of 12 specimens. In addition to the two males and one female described above, there are five adult males (including MUSM No. 17704 in alcohol), three adult females, and one subadult female. Among adult males, there is little appreciable variation from the holotype (apparent differences in back patterns are due to individual arrangement of feathers); three show minute whitish tips on the central rectrices, and MUSM No. 17682 shows no white on the central rectrices, but these feathers are only half-grown on this specimen, which might obscure the usual pattern of white lateral fringes. MUSM No. 17683 appears to have a little more black in the preocular area, but we suspect that variability of this feature is reflected more in preparation of the skins than by true individual variation. It seems best to refer to the cover illustration and Figure 1A for a clear depiction of the amount of black in the preocular region of *H. gentryi*. One of the adult females (MUSM No. 17703) is like MUSM No. 17686, described above. MUSM No. 17702 varies from these in

having a more weakly spotted crown, but this appears to be due to more extensive feather wear. The remaining adult female (MUSM No. 17685) is noticeably darker brownish olive or "bronzy" (nearest 2.5Y 5/6) across the breast and sides of the neck, and most of the whitish feathers in the posterior portion of the superciliary stripe are margined with this color. Additionally, the yellow in the middle of the lower breast and belly is of a deeper chroma (nearest 5Y 8/8). The subadult female (MUSM No. 17687) had a skull 80 to 90% ossified and pointed rectrices like those of the juvenile male described above. Plumage of the head and body appears to be fresh and not in molt. The wing and tail are somewhat worn but not in molt. The crown is similar to that of the adult female but is less spotted owing to reduced pale marginal spots on the individual feathers; the forecrown is also less weakly tinged orangish. Otherwise, its plumage is like that of the adult female described above. Thus, this specimen may have undergone a postjuvenal molt of the head and body, but not the flight feathers. Regardless, the crown is much less heavily spotted or blotched than the juvenile male described above.

Breeding and molt.—Specimens in the type series were collected in early December (one adult male in alcohol; no data on molt or reproductive condition as yet), late January (three adult males), late February (one juvenile male and two adult females), mid-April (one adult female), late June (one adult female), and mid-August (one adult male and one subadult female). With the exception of the April and June 1996 females, all specimens were collected within a single annual cycle (1995 calendar year). This is important in that variation within the series resulting from differential seasonality (for example, duration or severity of wet/dry periods) or undocumented variability in resource abundance, is kept to a minimum. The effects of such factors on the reproductive activities of Neotropical birds are almost completely unknown. A juvenile male (skull 60 to 70% ossified) in the final stage of completing growth of its central rectrices was collected on 23 February and almost certainly had fledged in that month. A subadult female (skull 80 to 90% ossified) with minute ova and fresh head and body plumage but worn, juvenal wing and tail, was collected on 10 August. It seems rea-

sonable to presume that this bird also fledged in February or March. Another less substantial observation, but one that lends support to the above evidence of a nesting period early in the year, is that we frequently observed family groups of three or four individuals (including one or two juveniles) foraging with mixed-species flocks in mid-April. The single adult female from that period (16 April 1996) was not in molt (crown feathers appear worn) and was accompanied by at least two other individuals, probably the mate and one offspring; reproductive condition of this specimen, and of the female taken in late June 1996, is unknown. Two adult females collected 22 and 23 February differed from each other in molt and reproductive condition. One was in replacing its back, breast, wing, and tail feathers, and its largest ovum measured 4 × 4 mm. The other was not molting, but its outer rectrices were severely abraded, and its largest ovum measured 1 × 1 mm. Both of these females might have been nesting or have recently completed nesting. The three adult males taken 22 to 27 January were replacing their rectrices, and one also showed light body molt. Testes of these birds measured 1 × 1, 3.5 × 1, and 3.5 × 2 mm, respectively. Again, we suspect that molt and gonadal development imply a postbreeding condition, but we suppose that these data also could be interpreted as indicating a prebreeding condition. The single adult male taken on 10 August showed no sign of molt and had testes measuring 2 × 1 mm; it probably was not in high breeding condition. Data on molt and breeding condition are rather difficult to interpret. In this case, the sketchy data suggest that *H. gentryi* fledged young between January and March, at least, during the 1995 annual cycle.

Habitat: Fluvial perturbance and mosaicism.— *Herpsilochmus gentryi* is virtually restricted to two general classes of *terra firme* forest growing on nutrient-poor (extensively leached; Anderson 1981), podzolic and quartzitic soils. In fact, in some places soil is almost nonexistent, the sandy ground instead being covered with a thin layer of organic material (humus) and networks of thin, springy, tree roots. In Peru, the local peoples' names for the two most important forest types inhabited by *H. gentryi* are convenient for discussion of them: "*irapayal*" and "*varillal*." In many *irapayales*, canopy height averages more than 40 m, and tree

crowns generally are interlocking. Arboreal epiphytes, especially bromeliads, are rare, perhaps owing to the (our perceived) abundance of small-leaved trees in the upper strata, the relatively open canopies of which exacerbate the desiccating effect of the sun. In the understory, the small (2 to 3 m) palm *Lepidocaryum tenue* ("*irapay*," Palmae or Arecaceae) grows in profusion, forming such a conspicuous and culturally significant feature that this habitat is known locally as *irapayal* (Fig. 3A). Tuomisto and Ruokolainen (1994) reported that *Lepidocaryum tenue* was the only species of palm they found in sandy-soil forest at Mishana, on the Río Nanay near Iquitos. Among the emergent trees in *irapayales* are *Anacardium giganteum* ("sacha casho"), family Anacardiaceae; *Brosimum guianensis*, *B. utile*, and *Clarisia biflora* ("machinga," "chingonga," and "capinuri de altura" respectively), family Moraceae; *Iryanthera tricornis* ("pucuna caspi"), family Myristicaceae; *Aspidosperma excelsum* and *Macoubea guianensis* ("remo caspi de altura" and "loro micuna," respectively), family Apocinaceae; *Anthodiscus pilosus* ("boton caspi"), family Caryocaceae; *Cariniana decandra* ("papellilo"), family Lecythidaceae; *Buchenavia viridiflora* ("largatillo de altura"), family Combretaceae; and *Batesia floribunda* and *Hymenaea oblongifolia* ("huayruro colorado" and "azucar huayo," respectively), family Fabaceae.

Where nearly pure white sands occur, the forest is considerably lower in stature and plant species diversity (Encarnación 1985, Ruokolainen and Tuomisto 1993, Tuomisto and Ruokolainen 1994, Ruokolainen et al. 1995), with average and more-or-less uniform canopy height often lower than 25 m and relatively few trees greater than about 40 cm diameter at breast height (dbh). Density of tree growth is, however, significantly higher than on more nutrient-rich, clayey soils (Tuomisto and Ruokolainen 1994). Most of the trees are less than 20 cm dbh and have narrow canopies. This is *varillal* (or "*chamizal*"), so named for the highly variable size of tree trunks (Fig. 3B). Anderson (1981) suggested the term "Amazon caatinga," with appropriate modifiers, for this and related physiognomically simple, white-sand habitats in Amazonia. In most *varillales* near Iquitos, *Lepidocaryum* is absent, and palms are generally in low density (Tuomisto and Ruokolainen 1994); melastomes and scattered dense patches
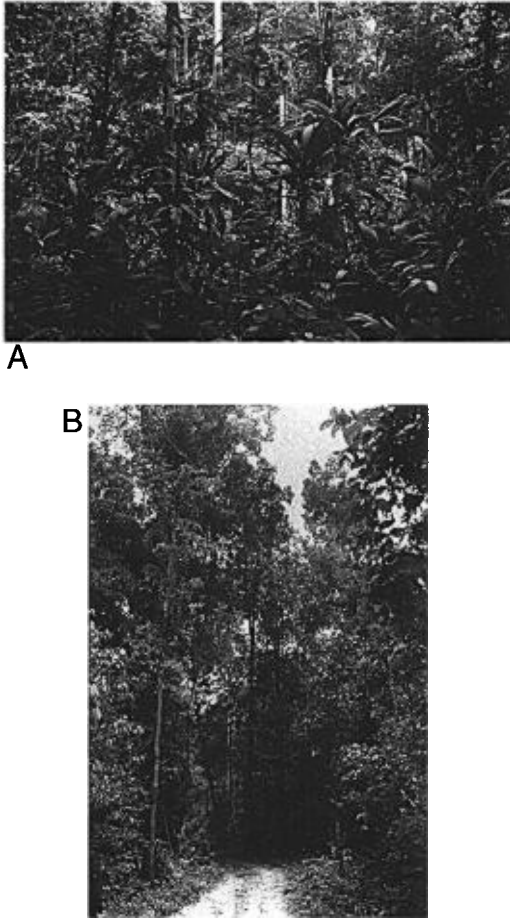
FIG. 3. Two principal habitats of *Herspilochmus gentryi* in northern Loreto, Peru. (A) Understory of tall *terra firme* forest on extensively weathered, nutrient-poor soil. This is an *irapayal*, a forest type distinguished by local peoples on the basis of abundance of the palm *Lepidocaryum tenue* ("irapay"); numerous individuals are visible in the photograph. (B) *Terra firme* forest on nearly pure white sand overlying a compacted, podzolic, soil with poor drainage, known as *varillal*. Canopy height generally is uniform and averages less than about 25 m; canopies of most trees are narrow, and most trunks are less than 20 cm dbh. Tree species composition, canopy height, and density of tree growth in Iquitos-area *varillales* seem to vary with edaphic conditions. Both photos taken at km 24–25 on the highway between Iquitos and Nauta, by J. Alvarez A.

Iquitos (the same areas in which *H. gentryi* is common) were Fabaceae, Lauraceae, Sapotaceae, and Myrtaceae, and that, relative to 19 other study sites on somewhat more nutrient-rich soils, Annonaceae and Apocynaceae were predominant in *varillales*. Dominant canopy trees in two general types of *varillales* near Iquitos are: (1) well-drained *varillales*: *Pachira brevipes* ("punga de varillal"), family Bombacaceae; *Macrolobium gracile* and *Macrolobium* sp. ("santo caspi" and "pashaco de varillal," respectively; the former also in other *varillales*), family Fabaceae; *Terstroenia klugiana* ("colorete caspi"), family Theaceae; and (2) poorly drained *varillales*: *Mauritia carana* and *Euterpe catinga* ("aguaje de varillal" and "huasai de varillal," respectively), family Palmae or Arecaceae (in northern Peru, these palms are virtually restricted to *varillales*); *Dicymbe* sp. ("boa caspi"), *Parkea igneifolia* ("goma pashaco"), and *Parkea velutina* ("cutana pashaco"), family Fabaceae; *Meteniusa tessmaniana* ("sacha humari"), family Icacinaceae; *Mezilaurus* sp. ("itauba de varillal"), family Lauraceae; *Virola pavonis* ("caupuri cumala"), family Myristicaceae; *Caraipa tereticaulis* and *Caraipa jaramilloi* ("aceite caspi de varillal" for both), family Clusiaceae; and *Pouteria* sp. ("quinilla blanca"), family Sapotaceae. We have observed some subtly different *varillal* forests near Iquitos with at least some elements of the avifauna apparently distinctive; *H. gentryi* is present in all of them.

In southeastern Pastaza Province, Ecuador, *H. gentryi* inhabits tall (canopy height >40 m) *terra firme* forest a few km inland from the banks of the Río Pastaza (only left-bank *terra firme* has been inventoried to date). There it occurs on the highest, driest hills. Surface soil on these hills is less obviously sandy than farther east in Peru, although the local Achuar people informed Whitney (December 1997) that the soil a short distance beneath the surface was quite sandy. *Lepidocaryum tenue* is uncommon, and Whitney observed no large patches of it. Palm diversity and density are high, which probably indicates a higher clay content on the surface here than in most *irapayales* and, especially, *varillales* nearer Iquitos (cf. Tuomisto and Ruokolainen 1994).

The highly localized distribution of *H. gentryi* may be better understood by integrating some causal abiotic environmental factors. *Irapayales* and *varillales* are relatively rare habitats,

of pteridophytes (also common in *irapayales*) predominate in the understory, and herbaceous plants are rare.

Ruokolainen et al. (1995) found that the most speciose tree families in three *varillales* near

FIG. 4.   River terrace on the middle Río Tigre, Lo-reto, Peru. Light-colored, nutrient-poor, sandy alluvium predicts presence of an *irapayal*. Lower-lying forest near and on the river floodplain (left side of photograph) is on silt-laden, relatively nutrient-rich soil, and is the preferred habitat of *H. sticturus dugandi* in this region. In such situations, the congeners are narrowly syntopic. Photo by Bret M. Whitney, January 1995.

persisting mostly on the highest *terra firme* in the region. Their patchy distribution, throughout Amazonia, is dictated entirely by edaphic conditions (Anderson 1981, Encarnación 1985, van der Werff 1992, Tuomisto and Ruokolainen 1994, Ruokolainen et al. 1997). They grow only on deeply weathered, nutrient-poor (podzolic or quartzitic) soils, varying in plant species composition and canopy height depending on drainage and other factors (e.g. Poulsen and Tuomisto 1996). Contemporary distribution of these soil types in northwestern Amazonia has been determined by fluvial perturbance (e.g. sediment recycling, river channel migration, avulsions, etc.) in the tectonically active Andean forelands (Salo et al. 1986, Räsänen et al. 1987, Räsänen et al. 1992). For example, white sands in the Iquitos arch area probably have been recycled several times before Plio-Pleistocene deposition on (now *terra firme*) terraces (Räsänen et al. 1992, 1993). Because the high sand content promotes groundwater flow, erosion of these uplands is by rainwater surface denudation (Räsänen et al. 1990, Puhakka et al. 1992), a very slow process. Along the major rivers Marañón and Tigre, *irapayales* and *varillales* are usually limited in extent to a few square kilometers or less, with *irapayales* occurring mostly on bluffs (Fig. 4). Therefore, these special habitats may be viewed as relatively old and particularly stable islands within the *terra firme* surrounded by lower-lying forest types on

more nutrient-rich, clayey soils, some of which are *terra firme* and some of which are seasonally flooded (Kalliola et al. 1992). Indeed, the nutrient-poor soils on which special plant communities and such birds as *H. gentryi* depend contribute highly distinctive elements to a complex mosaic of climax forest habitats. Many of these forest types are identifiable with digital satellite imagery and occur in a patchwork of steep environmental gradients (Tuomisto et al. 1995). The remarkable (but largely unstudied) heterogeneity of habitats in western Amazonia has had a deterministic role in the relatively high species-packing of birds and other organisms in this region.

Behavior and ecology.—*Herpsilochmus gentryi* foraged in the uppermost strata of the forest which, in many *irapayales*, is more than 40 m above ground. The birds were so difficult to observe through the various layers of vegetation in the midstory and subcanopy that it took us three days of constant effort to collect the first specimens. *Herpsilochmus gentryi* usually spent several minutes in individual (especially emergent) tree crowns, moving among branches rather deliberately with short (usually several cm at a time) hops and flutters and occasional short flights. The birds frequently flicked their wings shallowly and rapidly out from the sides, but performed no obvious tail motions, except when mobbing a predator. In these instances, observed at least twice, the birds flicked their wings more forcefully, and periodically snapped their tail upwards about 30° above the normal, nearly horizontal, position. Our scanty observations of foraging behavior were gathered mostly in *varillales*, where lower canopy heights occasionally allowed us to observe the birds as low as about 15 m. Many foraging maneuvers were observed, virtually all of which were "near-perch" reaches and gleans of small arthropods (e.g. caterpillars and moths) from live foliage and thin branches, almost always in the outer quarter (near the periphery) of tree crowns. We observed no manipulative dead-leaf searches. The only other maneuvers we recorded were a few brief lateral or downward flutters in pursuit of fleeing or falling prey items. Because of the severe angle of observation, the distances involved, and the rapidity of most maneuvers, we were unable to determine from which surfaces most prey were sought or secured.

Herpsilochmus gentryi is an inveterate member of mixed-species canopy flocks. Regular associates in these flocks include *Piaya melanogaster* (Black-bellied Cuckoo), *Capito niger* (Black-spotted Barbet), *Lepidocolaptes albolineatus* (Lineated Woodcreeper), *Myrmotherula menetriesii* (Gray Antwren), *Zimmerius gracilipes* (Slender-footed Tyrannulet), *Ornithion inerme* (White-lored Tyrannulet), *Myiopagis gaimardii* (Forest Elaenia), *M. caniceps* (Gray Elaenia), *Tolmomyias assimilis* (Yellow-margined Flycatcher), *T. poliocephalus* (Gray-crowned Flycatcher), *Pachyramphus marginatus* (Black-capped Becard), *Hylophilus hypoxanthus* (Dusky-capped Greenlet), *Tachyphonus cristatus* (Flame-crested Tanager), *Euphonia rufiventris* (Rufous-bellied Euphonia), *Tangara chilensis* (Paradise Tanager), *T. schrankii* (Green-and-gold Tanager), and *T. callophrys* (Opal-crowned Tanager); one or more nectarivorous species (e.g. dacnis and honeycreepers) usually were present as well. Canopy flocks were sometimes augmented by species from understory guilds.

In a few localities along the Río Tigre we documented the syntopy of *H. gentryi* and *H. sticturus* (Spot-tailed Antwren; the disjunct western subspecies, *dugandi*, is sometimes considered a full species). In this region, *H. sticturus* inhabits seasonally flooded forest and *terra firme* on more nutrient-rich soils. Where these edaphically maintained habitats meet the nutrient-poor soils supporting *irapayales* and *varillales*, perhaps creating more-or-less linear ecotones, the two species can coexist. Populations from source habitats presumably provide sufficient overflow to permit these morphologically and (apparently) ecologically similar canopy antwrens to narrowly occupy habitats that appear to be suboptimal (they are certainly less preferred) for either of them (e.g. Pulliam 1988). At the Kapawi Ecological Reserve in Pastaza Province, Ecuador, the two species apparently do not occur in the same forest types (B. Whitney pers. obs.). *Herpsilochmus gentryi* appears to be absent from seasonally flooded and "transition" habitats, which are inhabited by *H. sticturus*. Farther south, in lowland forests at the eastern foot of the Cordillera de Cutucú (near Miazal, Morona-Santiago Province), *H. gentryi* appears to be entirely absent, and *H. sticturus* is fairly common in both seasonally flooded and *terra firme* habitats, replaced above about 600 m in the Cutucú by *H. rufimarginatus*

(Rufous-winged Antwren; B. Whitney pers. obs.).

The nominate form of *H. sticturus* is found almost entirely on quartzitic soils on the northern half of the Guianan shield (B. Whitney pers. obs.). There it is widely (although not always) syntopic with and regularly present in mixed-species flocks in the canopy with *H. stictocephalus* (B. Whitney pers. obs., R. S. Ridgely and M. B. Robbins pers. comm.). *Herpsilochmus stictocephalus* is almost certainly the sister species to *H. gentryi* (see below), just as *dugandi* is to nominate *sticturus*. In both disjunct areas of their distributions, the sister species appear to be ecologically and behaviorally quite similar (they certainly occupy the same foraging guild), and it seems reasonable to suggest that competition has, at some level, dictated their partitioning of ecological space. However, we suspect that the discordant degree of syntopy observed in the two discrete areas of distribution also could have been influenced by differences in the physical environment. The relatively dynamic recent paleohistory and resultant high habitat mosaicism of northwestern Amazonia have not only promoted species packing (e.g. Salo 1986; no other area of the planet holds as many species of birds), but also have resulted in variably continuous populations of a single species by generating relatively sharp and frequent ecological gradients. Thus, *H. gentryi* and *H. sticturus dugandi* occupy neighboring habitats of patchy distribution, relatively rarely occurring together. That they do coexist, albeit only along narrow ecotones, demonstrates their ability to partition ecological space within habitats, just as their sisters do on a more widespread scale in the Guianas. This situation should not be viewed as an example of Endler's (1982) hypothesis that modern ecological variance is sufficient to allow genetically distinct populations of closely related birds to evolve in parapatry, nor of Smith et al's. (1997) postulation that rainforest ecotones may be centers for speciation. It appears that the *sticturus* and *stictocephalus* groups stem from separate branches within *Herpsilochmus*, and we suspect that both competition and spatial constraints of the environment have been operative in permitting and maintaining the observed variable degree of syntopy between them.

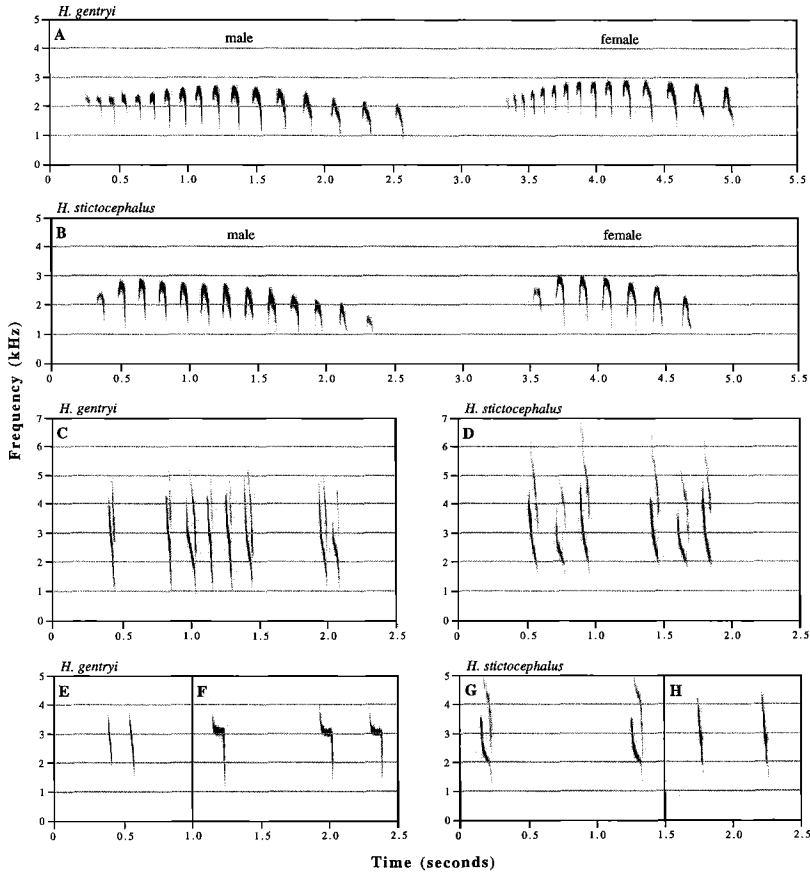*Vocalizations.*—The loudsong of *H. gentryi* is

FIG. 5. Sound spectrograms of presumed sister taxa in the *Herpsilochmus stictocephalus* complex for comparison with each other and with spectrograms presented in Figure 6. (A) Loudsongs of male and female *Herpsilochmus gentryi* sp. nov. (Peru, Loreto, 10 km by road SW of Iquitos at "Varillal," 14 April 1996). (B) Loudsongs of male and female *H. stictocephalus* (Suriname, Brownsberg Nature Reserve, 23 October 1995). Songs of the two species are remarkably similar aurally and spectrographically, but that of *H. gentryi* starts faster, shows less overall change in frequency, and typically comprises more notes than that of *H. stictocephalus*. (C) Mobbing vocalizations (attention directed at predator) of male and female *H. gentryi*; male gives the more bisyllabic notes (same data as A, but different birds). (D) Mobbing vocalizations (attention directed at predator) of male and female *H. stictocephalus*; male gives the more bisyllabic notes (Venezuela, Bolívar, date unknown; Paul A. Schwartz). (E) "Chup" pair-contact call of *H. gentryi* (Peru, Loreto, upper Río Tigre near "Liborio," 22 January 1995). (F) "Tink" or "Tyink" of *H. gentryi* that may serve as alarm or heightened awareness call (same recording as E). (G) The most common call of *H. stictocephalus*, perhaps a pair-contact call homologous to E of *H. gentryi* (same data as D). (H) Another, less common, call of unknown context of *H. stictocephalus* (Brazil, Amapá, Serra do Navio, date unknown; Andrew Whittaker). All recordings except D, G, and H by Bret M. Whitney.

a lightly rising and falling series of about 13 to 21 (average about 17) notes of similar structure and tonality, being loudest through the middle section, and slowing slightly throughout, most conspicuously through the terminal third. Notes appear as inverted "hairpin" traces on spectrograms, often slightly broader, and more sharply peaked, through the final two or three

notes. The loudest notes, those in the center section of the song, are also of highest frequency, usually peaking at approximately 2.7 kHz (Fig. 5A). The foregoing applies especially to male songs; female songs are quite similar, but usually are composed of fewer notes and are at a slightly higher frequency. Some measurements of unsolicited, male loudsongs are pre-

sented in Table 2. After tape playback (especially within the first minute or so), birds sometimes delivered abnormally long (more notes) songs which, however, fell well within ranges of natural songs in other respects.

We have identified three kinds of calls. A "chup" note, when delivered singly, appears to serve as a pair-contact vocalization. It is given while routinely foraging (Fig. 5E) and often is delivered in a couplet as individuals fly short distances between perches. A more bisyllabic call is used in the context of mobbing a predator (such as a snake or pygmy-owl). Both sexes may deliver it in a highly agitated manner (Fig. 5C). The third call is a highly distinctive, ringing "tink" or "tyink" note (Fig. 5F). We have not been able to determine its context, but we suspect that it serves as an alert or heightened-awareness call.

Systematic relationships.—*Herpsilochmus*, comprising 13 currently recognized species, perhaps is the most clearly monophyletic group of more than five species in the Thamnophilidae presently considered to be congeneric. Males of most members are whitish or pale grayish below. Two species are fairly extensively pale yellow, one of which (*H. rufimarginatus*) also has extensive rufous in the remiges and a solid rufous crown in the female, both of which are unique features in the genus. Therefore, it seems reasonable to suggest that yellow underparts and rufous primaries are derived characters. *Herpsilochmus gentryi* is brighter yellow ventrally than any of the other species and is the only one with a yellow facial/superciliary region. A traditional plumage comparison would probably suggest a close relationship to *H. axillaris*, because both species are extensively yellow below, and they share an extensively spotted crown (also rare in the genus) in the females. Furthermore, *H. axillaris aequatorialis* occurs in geographical proximity, but at higher elevations on the east slope of the Andes, and thus might be interpreted as an elevationally parapatric sister taxon. However, if the strong yellow in the face and underparts of *H. gentryi* is viewed as the ancestral grayish white, its male plumage is more nearly approached by those of *H. atricapillus* (Black-capped Antwren) and *H. stictocephalus*. It should be noted, however, that male plumages of *Herpsilochmus* species are weakly differentiated; females are much more readily identifiable. Again, consid-

ering the yellow of *H. gentryi* as grayish white reveals that its female plumage also is more similar to that of *H. atricapillus* (which shares the orangish frontal feathers) and of *H. stictocephalus* than to any other member of the genus. Beyond their conspicuously similar head plumages, the buffy breastband characteristic of females of *H. stictocephalus* (and extensively buffy underparts of *H. atricapillus*) finds its match in the "bronzy" one (an overlay of yellow on buff?) of *H. gentryi*. Morphometrics of the two species, presented in Table 1, seem to reflect greater differentiation. Most notably, *H. gentryi* is a heavier bird, and is proportioned somewhat differently from *H. stictocephalus*, averaging slightly shorter in the tail and longer in the bill.

Vocalizations have not been considered in any arrangement of *Herpsilochmus* (cf. Davis and O'Neill 1986). However, recent studies (e.g. Stein 1963, Pierpont and Fitzpatrick 1983, Braun and Parker 1985, Whitney 1994, Pacheco and Gonzaga 1995, Whitney et al. 1995 a, b, Cohn-Haft 1996, Isler et al. 1997, Zimmer 1997) have shown that vocalizations are particularly informative in suggesting species limits and relationships in suboscine groups, including thamnophilid antbirds. The loudsong of *H. axillaris aequatorialis* is not closely similar to that of *H. gentryi*. Although the general rise and fall in frequency (typical of the genus) and individual note shapes (closed hairpins) bear some resemblance, the song of *H. axillaris aequatorialis* is a thin, rapid series, about twice as fast as that of *H. gentryi*, and is about 1 kHz higher in frequency through the center section (cf. Fig. 5A with Fig. 6D). The other species of *Herpsilochmus* with yellow underparts, *H. rufimarginatus*, also occurs nearby, at the base of the Andes (subspecies *frater*). It is even more vocally distinct from *H. gentryi* than is *H. axillaris aequatorialis*, having a short, structurally complex, two-parted loudsong (cf. Fig. 5A with Fig. 6E).

Likewise, *H. sticturus dugandi* is strongly differentiated vocally from *H. gentryi*. Its loudsong is an accelerating (rather than decelerating) series of nearly vertical chopping notes, audibly and spectrographically quite different from that of *H. gentryi* (cf. Fig. 5A with 6B). The songs of the two subspecies of *H. sticturus* are closely similar in all respects (Fig. 6A and B; some apparent differences in these spectrograms may be due to recording quality), as are
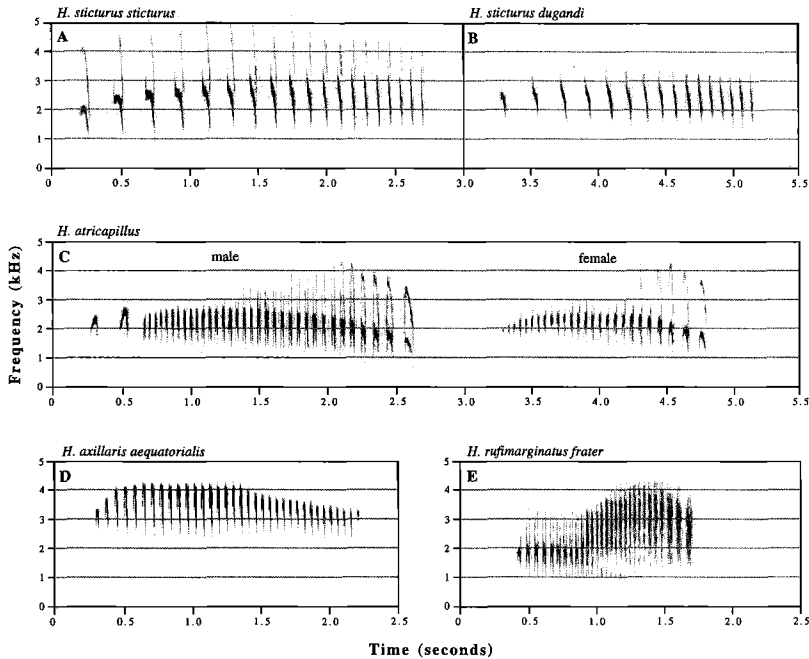
FIG. 6.   Sound spectrograms of loudsongs of selected other taxa in *Herpsilochmus*, mostly from near type localities. (A) *H. sticturus sticturus* (Guyana, Potaro-Siparuni region, Iwokrama Forest Reserve, 24 June 1997). (B) *H. sticturus dugandi* (Ecuador, Sucumbios, Cuyabeno Forest Reserve, 1 August 1992). Apparent subtle differences in A and B may be due, in part, to relatively poor quality of B. (C) *H. atricapillus* (Brazil, Bahia, Boa Nova, 9 November 1993). (D) *H. axillaris aequatorialis* (Ecuador, Napo, W Loreto on Volcán Sumaco, 1 January 1990; LNS 47276). (E) *H. rufimarginatus frater* (Ecuador, Napo, lower Volcán Sumaco, 14 January 1991; LNS 50990). All recordings by Bret M. Whitney.

their respective plumages, and it seems clear that they are indeed sisters. Although the two are sometimes considered separate species (e.g. Ridgely and Tudor 1994:257–258), specimens are rare in collections, and the question of their relationship has not been analyzed. Measurements presented in Table 1 suggest that *H. s. dugandi* is a larger bird (no or minimal overlap in wing chord, tail length, and mass), and loudsong characteristics point to distinctions that merit careful analysis beyond the scope of this paper.

We are confident that *H. stictocephalus* and *H. gentryi* are sister species. This is phenotypically expressed most clearly by vocalizations. Comparisons of vocalizations are provided in Table 2 and Figure 5. Loudsongs are strikingly similar in pace or rhythm, frequency, structure of individual notes, and tonality; in other words, they sound very much alike. No other member of the genus is nearly so vocally similar to *H. gentryi*. We sought to quantify differences in the loudsongs of *H. stictocephalus* and *H. gentryi*

with spectrographic analysis. We selected a sample of 10 recordings of unsolicited (i.e. no tape playback), almost certainly male songs of each species, made spectrograms of and measured the first three clear songs, and then averaged this sample for each individual (for one individual of each species, only two songs were averaged). Means and ranges for each species in Table 2 therefore reflect the sample of 10 individuals, with some attempt to control for variation within individuals. We counted the total number of notes, and the number of notes in the first 0.5 s, of each of the three songs, measured the peak frequency (PF) of the fourth note and the terminal note, and calculated the change in peak frequency (ΔPF) between these two notes.

Although we were far from exhaustive in terms of the number of potentially informative characters measured, this analysis identified two diagnostically different attributes of loudsongs of *H. stictocephalus* and *H. gentryi*. First, ranges for the number of notes delivered in the

first 0.5 s of the song did not overlap. Individuals were remarkably consistent in this character; only 4 of the 20 birds varied one song. These were all *H. gentryi,* and we suspect that this was owing more to some difficulty in counting (seeing) the quiet notes at the beginning of songs than real variation within individuals. The slower, louder *H. stictocephalus* was easier to measure, and no individuals varied number of notes in the first 0.5 s, consistently delivering either four or five notes. Ranges for ΔPF likewise showed no overlap. Moreover, the song of *H. gentryi* attained its PF later, toward the middle, confirming that its song is delivered on an overall steadier frequency than that of *H. stictocephalus,* which reaches its PF early then falls off steadily. Finally, it was generally true that several unsolicited songs of an individual *H. gentryi* averaged between 15 and 18 notes, whereas songs of *H. stictocephalus* typically comprised 12 to 14 notes. Only one individual *H. gentryi* overlapped with the sample of *H. stictocephalus* in total number of notes. Additionally, as can be seen in comparison of Figures 5C and D, mobbing vocalizations of *H. gentryi* and *H. stictocephalus* are closely similar. Homologous vocalizations of the taxa in Figure 6 are distinctly different (*H. axillaris aequatorialis* is unknown to us).

Although it appears that *H. gentryi* and *H. stictocephalus* are each other's closest relatives, parallels in plumage (within the sexes) and loudsong of *H. atricapillus* (Fig. 6C; compare with Fig. 5A and B, which differ primarily in being more slowly paced) suggest that this sister-pair represents the *atricapillus* complex north of the Marañón/Solimões/Amazon. Relationships within the *atricapillus* group (south of the Amazon River) were discussed by Davis and O'Neill (1986).

Conservation.—*Herpsilochmus gentryi* is a common bird and such an inveterate singer (singing fairly regularly even during nonbreeding periods) that it is among the most conspicuous members in its community. Much more important than the observation that *H. gentryi* does not seem to be threatened in its habitat, however, is the fact that the habitat itself is rare and patchily distributed. As long ago as 1976, before local satellite maps or aerial photographs were available, and before the region came under the current threat of destruction, Gentry (1977) recognized the uniqueness

of the sandy-soil forests in the Iquitos area. He wrote, "Less well-known is the occurrence of similar but less extensive white sand areas in northern Amazonian Peru. These low productivity ecosystems are extremely slow to regenerate (Janzen 1974) and even a relatively low intensity of disturbance has destroyed most of their natural vegetation in the Iquitos vicinity. There seems to be a certain amount of plant endemism in the Peruvian white sand areas, although most of the species are widespread ones characteristic of similar regions in southern Venezuela and northern Brazil. While not in any immediate danger, the totally distinct biota of these regions—even some mammals are endemic to them—makes them important from the conservation viewpoint. Special care must be taken to include such areas among those eventually to be designated as preserves or sanctuaries."

It is clear that these habitats need to be identified and their distribution mapped as accurately as possible. But a problem arises at the outset in defining "Amazon caatinga" (of Anderson 1981) and its various, possibly gradational, forms. An attempt needs to be made to identify those features that characterize these little-known habitats. Both abiotic and biotic parameters, such as edaphic conditions (e.g. sand content, drainage, soil pH, and other characteristics), plant associations, vegetation structure, even avifaunal assemblages could be measured and described in a standardized manner to allow comparison of discrete areas.

Humid lowland Amazonia has been treated as a largely homogeneous expanse comprised of only a few phytogeographic units (e.g. Prance 1989, Duivenvoorden and Lips 1995, Stotz et al. 1996), such as upland or *terra firme* forest (with a small number of obviously different patchy habitats, like bamboo tracts, and isolated sand campinas and vine forests sometimes singled out) and seasonally flooded forest (sometimes subdivided into poorly defined *várzea* and *igapó* or "whitewater" and "blackwater," and palm swamps). More than a decade ago, however, Salo et al. (1986) emphasized that fluvially controlled habitat mosaicism within *terra firme* forest has been the most important factor contributing to the high diversity of the general *terra firme* biota in Amazonian Peru. *Terra firme* mosaicism was illustrated clearly by Tuomisto et al. (1994, 1995).

The latter study examined satellite images of Amazonian Peru covering areas of 185 × 185 km to estimate landscape heterogeneity. In each of the approximately 30 images, they conservatively identified between 21 and 54 biotopes (habitats) and noted that a 30-km long transect typically crossed four biotopes. Botanical inventories (e.g. Gentry 1981, 1988, Young and León 1989, van der Werff 1992, Tuomisto and Poulsen 1996, Poulsen and Tuomisto 1996) have provided a finer resolution, focusing on the importance of edaphic habitat specialization of plant communities. Up to the present, however, a key role for edaphic characteristics in differentiation of habitats has not been incorporated in discussions of diversity or composition of Neotropical bird assemblages. Edaphic heterogeneity undoubtedly has contributed more to the unparalleled species richness of northwestern Amazonia than has been recognized previously.

Failure to consider soil and forest heterogeneity (beyond flooded vs. non-flooded terrain) resulted in the recent opening of a paved road for colonization and the clearing of much land near Iquitos in the mistaken belief that the reasonably arable soils at the head of the road were typical of the whole area. Costs of the project have run to approximately 45 million dollars. Over the past few years, after the road was in place, it became clear that the region is mostly covered in nutrient-poor soil not suitable for any kind of agriculture or livestock (Dourojeanni 1990, Ruokolainen and Tuomisto 1993, pers. obs.). Unfortunately, this is precisely the area of *varillales* and *irapayales* on which *H. gentryi* and numerous other equally habitat-restricted organisms are dependent. Because the road is new and paved, people are increasingly establishing homesteads. Consequently, *varillales* are being clearcut for a variety of uses. There is great hope that a proposed reserve, to be called Allpahuayo-Mishana, encompassing some 27,000 ha of *variallales, irapayales*, and other *terra firme* habitats and palm swamps near Iquitos, soon will be established by the Peruvian government. More remote points in the distribution of *H. gentryi* along the Río Tigre are currently under little anthropogenic pressure. The single known locality in Ecuador seems reasonably well protected within the new "Kapawi Ecological Reserve," and it is

likely that *H. gentryi* occurs more widely in this general region of the country.

The lesson we have taken from our research on the speciation and distribution of *H. gentryi* is that we must now attempt to conduct inventories of birds with greater attention to environmental gradients and spatial patterns. In this regard, it is imperative that all ornithologists conducting inventories carry global positioning systems and record coordinates to as fine a resolution as available as close to inventory sites as possible. Satellite imagery offers promising potential for revelation of habitat mosaicism, identification and mapping of many specific habitats, and orientation of field inventories. Conservation dollars should be channeled to multidisciplinary efforts to reveal the distribution of specific "classes" of soils and forests in Amazonia. As we understand more about the phenomenon of phytogeographic edaphic specialization, high-quality inventories of birds, as some of the easiest organisms to assess quickly in the Neotropics, may help direct field work in other disciplines. Gradually, we will gain important new insights on the biogeography of plants and animals in this most biologically diverse region on earth.

LITERATURE CITED

ALVAREZ A., J. 1994. Abundancia y diversidad de especies de aves en los ríos Tigre y Corrientes. M.S. thesis, Universidad Nacional de la Amazonía Peruana, Iquitos.

ANDERSON, A. 1981. White sand vegetation of Brazilian Amazonia. Biotropica 13:199–210.

BRAUN, M. J., AND T. A. PARKER III. 1985. Molecular, morphological, and behavioral evidence concerning the taxonomic relationships of "*Synallaxis*" *gularis* and other synallaxines. Pages 333–346 in Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithological Monographs No. 36.

COHN-HAFT, M. 1996. Why the Yungas Tody-Tyrant (*Hemitriccus spodiops*) is a *Snethlagea*, and why it matters. Auk 113:709–714.

CORY, C., AND C. E. HELLMAYR. 1924. Catalogue of birds of the Americas. Field Museum of Natural History Zoological Series 13, Part 3.

DAVIS, T. J., AND J. P. O'NEILL. 1986. A new species of antwren (Formicariidae: *Herpsilochmus*) from Peru, with comments on the systematics of other members of the genus. Wilson Bulletin 98:337–352.

DOUROJEANNI, M. 1990. Amazonia Que hacer? Centro de Estudios Téologicos en la Amazonia, Iquitos, Peru.

DUIVENVOORDEN, J. F, AND J. M. LIPS. 1995. A landecological study of soils, vegetation, and plant diversity in Colombian Amazonia. Tropenbos Series No. 12.

ENCARNACIÓN, F. 1985 Introducción a la flora y vegetación de la Amazonia peruana: Estado actual de los estudios, medio natural y ensayo de una clave de determinación de las formaciones vegetales en la llanura amazónica. Candollea 40:237–252.

ENDLER, J. A. 1982. Pleistocene forest refuges: Fact or fancy? Pages 641–657 in Biological diversification in the tropics (G. T. Prance, Ed.). Columbia University Press, New York.

GENTRY, A. H. 1977. Endemic plant species and habitats of Ecuador and Amazonian Peru. Pages 136–149 in Extinction is forever (G. T. Prance and T. Elias, Eds.). New York Botanical Garden, New York.

GENTRY, A. H. 1981. Distributional patterns and an additional species of the *Passiflora vitifolia* complex: Amazonian species diversity due to edaphically differentiated communities. Plant Systematics and Evolution 137:95–105.

GENTRY, A. H. 1988. Patterns of plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75:1–34.

ISLER, M., P. ISLER, AND B. WHITNEY. 1997. Biogeography and systematics of the *Thamnophilus punctatus* complex. Pages 355–381 in Studies in Neotropical ornithology honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithological Monographs No. 48.

KALLIOLA, R., J. SALO, M. PUHAKKA, M. RAJASILTA, T. HÄME, R. NELLER, M. E. RÄSÄNEN, AND W. DANJOY-ARIAS. 1992. Upper Amazon channel migration: Implications for vegetation perturbance and succession using bitemporal Landsat MSS images. Naturwissenschaften 79:75–79.

MUNSELL®. 1994. Soil color charts, revised edition. Macbeth Division of Kollmorgan Instruments Corporation, New Windsor, New York.

PACHECO, J. F, AND L. P. GONZAGA. 1995. A new species of *Synallaxis* of the *ruficapilla/infuscata* complex from eastern Brazil (Passeriformes: Furnariidae). Ararajuba 3:3–11.

PIERPONT, N. J., AND J. W. FITZPATRICK. 1983. Specific status and behavior of *Cymbilaimus sanctaemariae*, the Bamboo Antshrike. Auk 100:645–652.

POULSEN, A. D., AND H. TUOMISTO. 1996. Small-scale to continental distribution patterns of Neotropical pteridophytes: The role of edaphic preferences. Pages 551–561 in Pteridology in perspective (J. M. Camus, M. Gibby, and R. J. Johns, Eds.). Royal Botanic Gardens, Kew, United Kingdom.

PRANCE, G. 1989. American tropical forests. Pages 99–132 in Ecosystems of the world 14B. Tropical rain forest ecosystems: Biogeographical and ecological studies (H. Leith and M. J. A. Werger, Eds.). Elsevier, Amsterdam, The Netherlands.

PUHAKKA, M., R. KALLIOLA, M. RAJASILTA, AND J. SALO. 1992. River types, site evolution and successional vegetation patterns in Peruvian Amazonia. Journal of Biogeography 19:651–665.

PULLIAM, H. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

RÄSÄNEN, M. E., R. KALLIOLA, AND M. PUHAKKA. 1993. Mapa geoecológico de la selva baja peruana: Explicaciones. Pages 207–216 in Amazonia Peruana: Vegetación húmeda tropical en llano subandino (R. Kalliola, M. Puhakka, and W. Danjoy, Eds.). Amazon Project of the University

of Turku (PAUT and ONERN), Jyväskylä, Finland.

RÄSÄNEN, M. E., R. NELLER, J. SALO, AND H. JUNGER. 1992. Recent and ancient fluvial deposition systems in the Amazonian foreland basin. Geological Magazine 129:293–306.

RÄSÄNEN, M. E., J. SALO, H. JUNGNERT, AND L. PITTMAN. 1990. Evolution of the western Amazon lowland relief: Impact of Andean foreland dynamics. Terra Nova 2:320–332.

RÄSÄNEN, M. E., J. SALO, AND R. KALLIOLA. 1987. Fluvial perturbance in the western Amazon basin: Regulation by long-term sub-andean tectonics. Science 238:1398–1401.

RIDGELY, R. S., AND G. TUDOR. 1994. The birds of South America, vol. 2. University of Texas Press, Austin.

RUOKOLAINEN, K., A. LINNA, AND H. TUOMISTO. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. Journal of Tropical Ecology 13:243–256.

RUOKOLAINEN, K., AND H. TUOMISTO. 1993. La vegetación de terrenos no inundables (tierra firme) en la selva baja de la Amazonia peruana. Pages 139–153 in Amazonia Peruana: Vegetación húmeda tropical en el llano subandino (R. Kalliola, M. Puhakka, and W. Danjoy, Eds.). Amazon Project of the University of Turku (PAUT and ONERN), Jyväskylä, Finland.

RUOKOLAINEN, K., R. VÁSQUEZ, O. PHILLIPS, R. ORTIZ, AND L. REBATA. 1995. Tree species distributions in Peruvian rain forests: Correlation with satellite image patterns and edaphic factors. Reports from Department of Biology, No. 50, University of Turku, Turku, Finland.

SALO, J., R. KALLIOLA, I. HÄKKINEN, Y. MÄKINEN, P. NIEMELÄ, M. PUHAKKA, AND P. COLEY. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322:254–258.

SMITH, T. B., R. K. WAYNE, AND M. W. BRUFORD. 1997. A role for ecotones in generating rainforest biodiversity. Science 276:1855–1857.

STEIN, R. C. 1963. Isolating mechanism between populations of Traill's Flycatchers. Proceedings of the American Philosophical Society 107:21–50.

STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER III, AND

D. K. MOSKOVITS. 1996. Neotropical birds: Ecology and conservation. University of Chicago Press, Chicago.

TUOMISTO, H., A. LINNA, AND R. KALLIOLA. 1994. Use of digitally processed satellite images in studies of tropical rain forest vegetation. International Journal of Remote Sensing 15:1595–1610.

TUOMISTO, H., AND A. POULSEN. 1996. Influence of edaphic specialization on Pteridophyte distribution in Neotropical rain forests. Journal of Biogeography 23:283–293.

TUOMISTO, H., AND K. RUOKOLAINEN. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in Amazonian rain forest. Journal of Vegetation Science 5:25–34.

TUOMISTO, H., K. RUOKOLAINEN, R. KALLIOLA, A. LINNA, W. DANJOY, AND Z. RODRIGUEZ. 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.

VAN DER WERFF, H. 1992. Substrate preference of Lauraceae and ferns in the Iquitos area, Peru. Candollea 47:11–20.

WHITNEY, B. M. 1994. A new Scytalopus tapaculo (Rhinocryptidae) from Bolivia, with notes on other Bolivian members of the genus and the magellanicus complex. Wilson Bulletin 106:585–614.

WHITNEY, B. M., J. F. PACHECO, P. R. ISLER, AND M. L. ISLER. 1995b. Hylopezus nattereri (Pinto 1937) is a valid species (Passeriformes: Formicariidae). Ararajuba 3:37–42.

WHITNEY, B. M., J. F. PACHECO, AND R. PARRINI. 1995a. Two species of Neopelma from southeastern Brazil and diversification within the Neopelma/Tyranneutes complex: Implications of the subspecies concept for conservation. Ararajuba 3: 43–53.

WILLIS, E. O. 1967. Behavior of Bicolored Antbirds. University of California Publications in Zoology Vol. 79.

YOUNG, K. R., AND B. LEÓN. 1989. Pteridophyte species diversity in the central Peruvian Amazon: Importance of edaphic specialization. Brittonia 41:388–395.

ZIMMER, K. 1997. Species limits in Cranioleuca vulpina. Pages 849–864 in Studies in Neotropical ornithology honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithological Monographs No. 48.

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