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SYSTEMATIC REVISION AND BIOGEOGRAPHY OF THE *HERPSILOCHMUS PILEATUS* COMPLEX, WITH DESCRIPTION OF A NEW SPECIES FROM NORTHEASTERN BRAZIL

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ABSTRACT.—Study of vocalizations of *Herpsilochmus* antwrens in northeastern Brazil revealed that the traditional *H. pileatus* complex is comprised of not two but three species-level taxa. We show that the systematics and biogeography of the group have been based on an unnamed species that has been called *H. pileatus* for most of this century. Here, we name this "new" species and conclude that its several morphological and vocal distinctions clearly set it apart from other members of the complex. True *H. pileatus*, as determined through comparison of the lectotype with recently collected specimens and from the distribution of recordings, is confined to southern coastal Bahia. Morphological and vocal analyses suggest that *H. pileatus* and *H. atricapillus* are each other's closest relatives. We provide a simple key to diagnostic plumage and mensural characters to permit identification of museum specimens. An extensive series of specimens demonstrated that *H. atricapillus* includes two male morphs. Geographic overlap of pure morphs in southern Goiás, and the existence of some apparent intermediates in this general area, suggest secondary contact of two weakly differentiated populations, perhaps along complex habitat gradients. Analysis of recordings of *H. atricapillus* disaggregated geographically and by male morph revealed no diagnostic (by criteria of Isler et al. [1998]) variation within that species, although average measures of overall pace and pace of three sections of loudsongs differed between the morphs by approximately 20%, which we interpret as another indication of incipient differentiation. Revision of the *Herpsilochmus pileatus* complex provides a case in point for the fundamental role in conservation of both field and taxonomic research and demonstrates the importance of examination of type specimens and inclusion of topotypical samples (whether anatomical, biochemical, or tape recordings) in studies of taxonomy and systematics. *Received 7 September 1999, accepted 11 January 2000.*

RESUMO.—O estudo de vocalizações dos *Herpsilochmus* do nordeste do Brasil revelou que o tradicional complexo *H. pileatus* nesta região compreende não dois mas três táxons ao nível de espécie. É demonstrado que tanto a sistemática quanto a biogeografia do grupo tem sido baseada numa espécie inominada chamada de *H. pileatus* na maior parte deste século. É dado nome a esta "nova" espécie e conclui-se que seus vários atributos distintivos de morfologia e vocalizações a colocam claramente à parte dos outros membros do complexo. O verdadeiro *H. pileatus*, como determinado através da comparação do lectótipo com espécimes recentemente coletados, e da distribuição das gravações, é confinado a região costeira do sul da Bahia. Análises morfológicas e vocais indicam um relacionamento muito próximo entre *H. pileatus* e *H. atricapillus*. Uma chave simples de caracteres diagnósticos da plumagem e relativos as medidas é fornecida para permitir a identificação de espécimes em museus. Uma ampla série de espécimes demonstrou que *H. atricapillus* inclui dois morfos de macho. A sobreposição geográfica dos morfos puros no sul de Goiás e a existência de alguns aparentes intermediários nessa mesma região, sugere um contato secundário de duas fracamente diferenciadas populações, talvez ao longo do complexo gradiente de hábitats. Análise de gravações de *H. atricapillus* dissociada geograficamente, por morfos dos machos e por sexo, não revelou diferenças diagnósticas (segundo critérios de Isler et al. [1998]) dentro da espécie.

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No entanto, as médias do andamento total e das três seções do canto foram aproximadamente 20% diferente entre os morfos, as quais são interpretadas como sendo outra indicação de diferenciação incipiente. A revisão do complexo *Herpsilochmus pileatus* chama a atenção para o papel fundamental da pesquisa taxonômica e de campo nas questões conservacionistas, e demonstra a importância do exame dos espécimes tipo e a inclusão de amostras topotípicas (sejam estas anatômicas, bioquímicas ou gravações) em estudos taxonômicos ou sistemáticos.

WITH ITS current contingent of nearly 200 species, the Thamnophilidae (typical antbirds) ranks among the numerically most important families of Neotropical birds. The genus *Herpsilochmus* comprises a conservative minimum of 16 closely related species-level taxa. Species diversity in the genus is highest in eastern Brazil south of the Amazon River, but most taxa from this region are represented by few specimens that are scattered in various museums. This circumstance, together with the close morphological similarity of some taxa (especially in adult males), has hampered understanding of species-level relationships. As is the case with numerous other problems in Neotropical ornithology, careful attention to vocalizations has permitted the only significant recent advance in resolution of species limits and relationships.

Our new specimens and tape recordings have revealed the identity and distribution of the type species of the genus, *Herpsilochmus pileatus*, and an unnamed parapatric species that is widespread in the interior of the region. This "new" species has been treated in all pertinent literature under the name *pileatus*. Furthermore, its morphological similarity to and geographic overlap with *H. atricapillus* has resulted in acceptance of a close relationship (either as a subspecies or allospecies) to that taxon (e.g. Davis and O'Neill 1986, Sibley and Monroe 1990).

Here, we describe this unnamed species, provide a detailed description of *H. pileatus* (Lichtenstein 1823), map the distributions of these taxa from documented points of occurrence, and discuss relationships based on interpretation of morphological, vocal, and ecological data. We propose to name the new species:

Herpsilochmus sellowi sp. nov.
Whitney and Pacheco
Caatinga Antwren (Chorozinho-da-caatinga in Portuguese)

Holotype.—Museu Paraense Em'lio Goeldi (MPEG) 54039, adult male from about 2 km east of Boa Nova, Bahia, Brazil (14°22'S, 40°10'W), at 760 m; collected 1 September 1992 by J. F. Pacheco, prepared by L. P. Gonzaga. Tape recorded by J. F. Pacheco, Library of Natural Sounds (LNS), Cornell Laboratory of Ornithology 79060; Arquivo Sonoro Elias P. Coelho (ASEC), Universidade Federal do Rio de Janeiro JFP 054/10; and Isler inventory JFP 6:02 to 07.

Diagnosis: Morphology.—A lightly built thamnophilid most clearly allied with *Herpsilochmus* as the genus was characterized by Whitney and Alvarez (1998). Males distinguished from all congeners by a combination of bill width at anterior edge of nares less than 3 mm, wing chord 43 to 50 mm, tail 44 to 51 mm, and narrow rectrices with central ones less than 5 mm wide and entirely black (lacking white lateral edging or spotting, although pale apical fringe may be present; see Table 1, cover). Females distinguished by the above characters and by unique crown pattern (see below). Further distinguished from parapatric *H. pileatus* and sympatric (locally syntopic) *H. atricapillus* by narrower and shorter bill and by short, relatively indistinct postocular streak and absence of conspicuous preocular spot (both well defined and blackish in *H. pileatus* and *H. atricapillus*; this usually hard to judge in specimens, but see cover). The sympatric (locally syntopic) *H. pectoralis* (Pectoral Antwren) is readily identified by the black pectoral patch in males and the orange head of females and immatures. *Herpsilochmus rufimarginatus* (Rufous-winged Antwren), also locally syntopic, is distinguished in all plumages by the conspicuously rufous-edged remiges.

Diagnosis: Voice.—Loudsong (following Willis 1967) immediately separable from those of all congeners by uniformly rapid pace without change in duration of individual notes or tonality (although there is a steady rise and fall in frequency and amplitude, which are shared by several other species). Loudsong of *H. axillaris* (Yellow-breasted Antwren) of subtropical forests on the east slope of the Andes is per-

TABLE 1. Morphometrics (see text for details of measurements) of three species of *Herpsilochmus* antwrens, including two morphs (and intermediates between them) of male *H. atricapillus*. Values are $\bar{x}$, with range and n in parentheses.

Sex	Bill width (mm)	Culmen (mm)[a]	Wing chord (mm)[b]	Tail (mm)	Body mass (g)
			H. sellowi		
Male	2.8 (2.7–2.9, 5)	14.3 (13.6–14.9, 7)	47.8 (45.3–50.0, 8)	48.3 (44.1–50.8, 6)	8.0 (1)
Female	2.7 (2.6–2.9, 5)	14.1 (13.4–14.7, 5)	47.3 (43.8–49.8, 5)	49.9 (47.7–50.8, 4)	7.3 (7.0–7.5, 2)
Sex unknown	2.7 (1)	14.6 (1)	45.5 (1)	48.0 (1)	—
			H. pileatus		
Male	3.7 (2)	16.9 (16.5–17.2, 2)	48.7 (48.2–49.2, 2)	(41.8–45.3, 2)[c]	9.3 (1)
Female	3.5 (1)	16.2 (1)	47.4 (1)	42.7 (1)[c]	8.5 (1)
			H. atricapillus		
Male[d]	3.5 (3.1–3.8, 71)	15.8 (14.2–17.8, 61)	52.1 (48.5–55.9, 75)	56.2 (51.9–60.0, 57)	9.1 (7.0–12.0, 40)
Female	3.4 (3.0–3.9, 46)	15.6 (14.7–17.3, 44)	51.0 (48.2–55.1, 45)	56.3 (52.0–60.2, 30)	8.9 (7.0–12.0, 35)
			***H. atricapillus* (gray morph)**		
Male	3.5 (3.2–3.8, 26)	15.3 (14.4–17.8, 22)	51.6 (48.5–55.7, 29)	55.4 (51.9–60.0, 22)	10 (7.5–12.0, 8)
			***H. atricapillus* (white morph)**		
Male	3.4 (3.1–3.8, 37)	15.5 (14.2–16.5, 34)	52.2 (49.0–55.9, 37)	56.3 (52.9–59.8, 27)	8.9 (7.0–11.0, 26)
			***H. atricapillus* (intermediate)**		
Male	3.4 (3.1–3.7, 8)	15.9 (15.1–16.8, 7)	53.6 (52.0–56.6, 9)	58.0 (55.2–59.5, 8)	9.2 (8.2–11.0, 6)

[a] From base at skull.
[b] Both wings usually measured, but longer measurement included here.
[c] Central rectrices estimated to be within 4 mm of fully grown of smallest individual.
[d] Entire sample of males (including both morphs and intermediates).

haps the most similar, but it rises abruptly in frequency and amplitude, is of higher frequency overall, and has a different tonal quality. Some calls also are highly distinctive (vocalizations described in detail below).

Distribution.—Patchily from southern coastal Rio Grande do Norte, southern Ceará, and central Maranhão south through the interior of Bahia east to near Jeremoabo (10°02′S, 38°11′W), Lamarão (11°45′S, 38°55′W), Jaguaquara (13°41′S, 39°30′W), and Boa Nova (14°22′S, 40°10′W), thence west to northwestern Minas Gerais (known as far south as Mocambinho [15°05′S, 44°00′W]); a disjunct (?) population in the serra do Cachimbo of Pará (Fig. 1). Occurs mostly between 500 and 900 m elevation and also near sea level in Rio Grande do Norte.

Description of holotype.—See cover. Alphanumeric color designations determined through direct comparison with Munsell soil color charts (1994). Plumage fresh and unworn. Crown semiglossy black, this color extending posteriorly to include center of nape; some lateral feathers above orbits with whitish distal webs. Nasal tufts and a few tiny feathers near base of bill with whitish tips. Crown bordered by conspicuous superciliary stripes, whitish in loral and supraloral regions posterior to slightly behind eyes, becoming subtly grayer and blending into medium-gray (Gley chart 2: 5/5PB) sides of neck. Narrow postocular streak (ca. 2 mm wide and 4 mm long) blackish. Subocular and auricular regions same whitish as anterior superciliary and similarly becoming grayer posteriorly. Mantle and lateral areas of back same medium-gray as sides of neck. Scapulars medium-gray, distal webs mostly blackish with a whitish fringe, widest just anterior to tip. Middle back dominated by a semi-concealed, loosely integrated, interscapular patch: anterior feathers with white bases and blackish tips on inner webs, outer webs medium-gray; posterior feathers longer (to 20+ mm) and silvery-white with broad (ca. 7 mm), sharply contrasting black tips. Thus, middle back mixed gray, black, and white, appearing irregularly blotched, pattern varying with handling of the specimen. Rump feathers medium-gray tinged ochraceous at tips; uppertail coverts medium-gray. Chin and throat silvery-whitish (a few grayish feather bases showing through). Breast and belly whitish along midline, becoming subtly grayer laterally. Flank feathers loosely

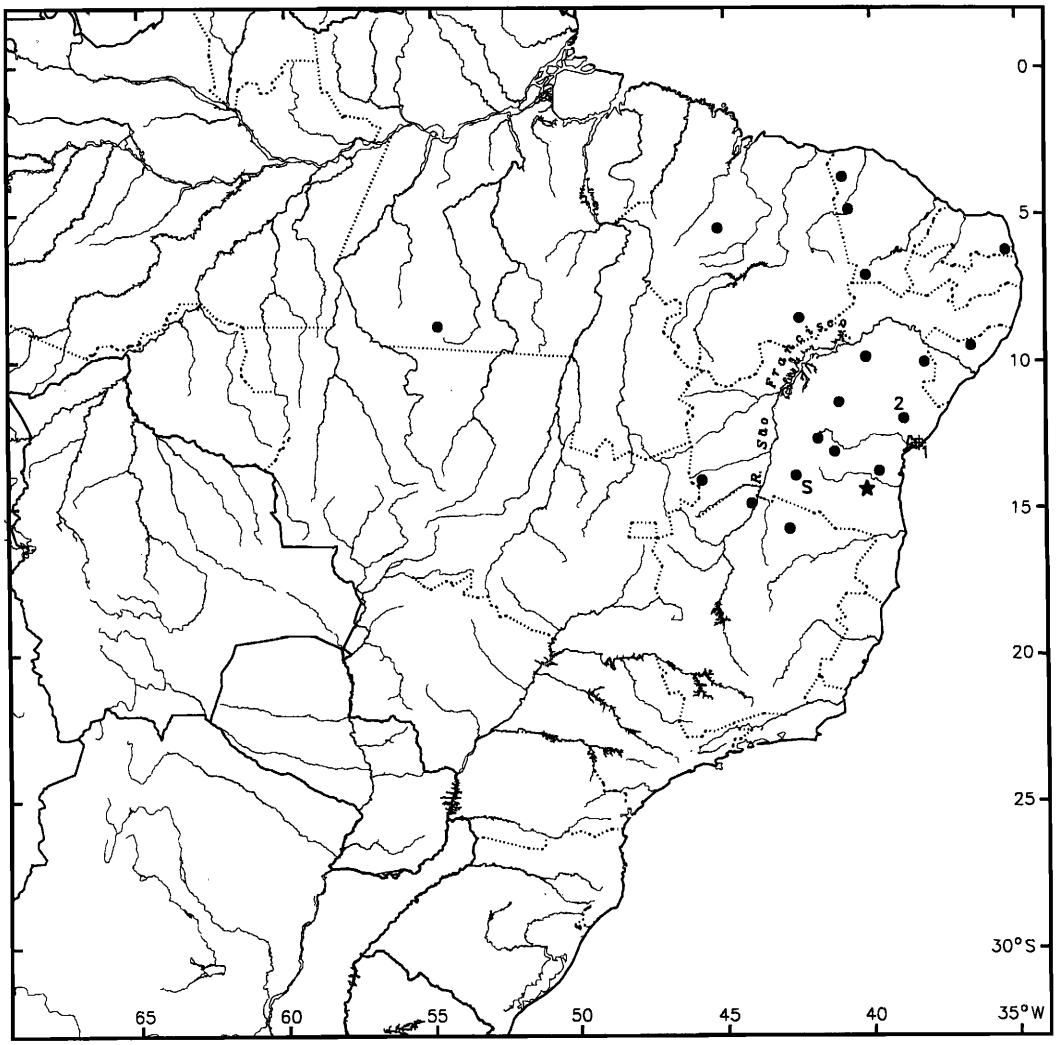

FIG. 1. Distribution of *Herpsilochmus sellowi* from documented (specimen or tape recording examined) points of occurrence. Star marks the type locality of Boa Nova, Bahia. Dotted lines mark Brazilian state boundaries. Numbers are cities in the state of Bahia: (1) Salvador, and (2) Lamarão. An "s" beside a point on this and other maps indicates a sight record. Localities and sources for points on all maps are available from the senior author.

integrated and greatly lengthened (to 25+ mm), whitish or grayish, the distal several mm tinged dull ochraceous (10YR 7/6), this color intensifying slightly posteriorly and including the lower belly between the legs and the undertail coverts.

Tail and wing not in molt. Tail strongly graduated (outer rectrices ca.34 mm vs. central rectrices 50.0 mm), appearing in dorsal aspect entirely blackish or blackish with white edges, and, from below, mostly white with blackish center line and subterminal blotches. Outermost pair of rectrices almost entirely white (a thin strip of blackish on margin of proximal web at base); next pair entirely white on distal webs and black on basal one-half of proximal webs (extent and distribution of black differing appreciably on the two feathers). Amount of white on successively longer rectrices decreasing and concentrated toward feather tips, such

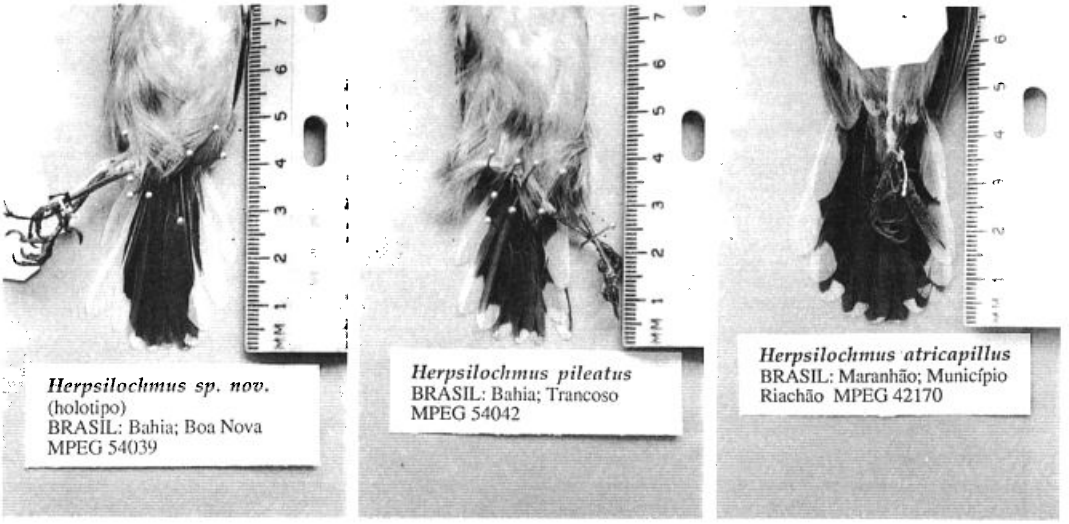

FIG. 2. Ventral tail patterns of some *Herpsilochmus* antwrens from northeastern Brazil. Left, *H. sellowi*. Center, *H. pileatus*. Both tail length and the graduation maximum (see Appendix 1) are much shorter than in the other taxa. Right, *H. atricapillus*.

that black bases (most extensive on proximal webs) are largely concealed by white areas of overlying feathers. Central rectrices entirely blackish with minute grayish or brownish tips (see Fig. 2 for exact extent and pattern of black and white on rectrices).

FIG. 3. Female specimens of *H. pileatus* (left) and *H. sellowi* (right) for comparison of crown patterns and bill size. *Herpsilochmus sellowi* lacks discrete white marks on the crown (buffy feather tips impart a weakly mottled pattern) and has a relatively delicate bill. The crown and bill of female *H. atricapillus* are closely similar to those of *H. pileatus*.

Upperwing coverts semiglossy black, each feather marked with a white tip (on lesser wing coverts, white usually concentrated on distal web), forming conspicuous wing bars on the median and greater coverts. Alula black with white distal margin and tip. Primary coverts black with minute white apical margins. Remiges blackish-brown, primaries bearing narrow white fringes on distal webs, increasing in extent from outermost (which is essentially unmarked) to innermost; secondaries with weak grayish margins. Innermost secondaries with fairly conspicuous white distal margins (shortest innermost ones, concealed by longer feathers of back, are entirely dull bownish). Irides brown, maxilla black, mandible gray, tarsi and feet light gray, soles yellow.

Measurements of holotype.—Bill width at anterior edge of nares 2.7 mm; bill depth at anterior edge of nares 3.4 mm; culmen from anterior edge of nares 8.3 mm; culmen from base (at skull) 14.3 mm; wing chord 46.7 mm; tail 50.0 mm; tarsus 17.8 mm; body mass 8.0 g.

Description of allotype (female).—MPEG 54040. See cover and Figure 3 (right side). Plumage fresh and unabraded. Crown feathers black-centered with dull-buff apical margins, dark center invading buffy margin slightly along shaft, imparting an overall weakly dappled effect. This pattern more concentrated on fore-

head to midcrown, becoming faint posteriorly, such that hindcrown is mostly blackish. A weakly contrasting line of tiny lateral crown feathers bordering pale supercilium mostly dull-buffy. Loral region mixed buffy and whitish, merging posteriorly with superciliary stripe. Supercilium whitish in orbital region, returning to buffy a few mm posterior to orbit. Periorbital area whitish, contrasting weakly with suborbital and auricular region and poorly defined dusky postocular stripe. Nape mixed black and medium-gray, individual feathers with black centers and weakly contrasting medium-gray margins. Mantle dull olive-gray (5Y 5/1-2), this color carrying weakly through the sides of the neck and mid-back, becoming subtly grayer posteriorly. Scapulars brownish, margined dull-buffy. Interscapular patch as in holotype but overall less-well defined, especially posteriorly; at least a few small, white patches visible without raising any feathers. Rump feathers medium-gray with distinct dull-buffy tips, which, however, because of the weak structure and loose integration of these feathers, does not produce any striking pattern. Uppertail coverts medium-gray.

Chin and throat whitish, merging indistinctly with weakly buffy breast. Remainder of underparts washed dull-buff or dull-ochraceous, this color intensifying slightly posteriorly and becoming purest and brightest (10 YR 7/6) in the lower flanks and lower belly (but remaining a decidedly pale hue throughout). Tail and wing not in molt. Tail as described for holotype except outermost rectrices with slightly more black at bases of proximal webs, and pale tips on central rectrices barely perceptible. Wing as described for holotype, but black and blackish-brown areas more brownish, and all white feather tips and margins duller. Pattern on inner secondaries mirrors that of holotype, but margination wider on distal webs and tips. Soft parts as described for holotype. Bill width at anterior edge of nares 2.7 mm; bill depth at anterior edge of nares 3.2 mm; culmen from anterior edge of nares 8.0 mm; culmen from base (at skull) 14.1 mm; unflattened wing chord 48.2 mm; tail 50.5 mm; tarsus 17.6 mm; body mass 7.5 g.

Specimens examined: Skins.—Measurements of listed birds are in Table 1 (all specimens were measured by B. Whitney). Two morphs of male *H. atricapillus*, and intermediates between them, are listed separately; all females are listed together. A list of *H. atricapillus* specimen numbers may be obtained from the senior author on written request.

Herpsilochmus sellowi, Brazil: Maranhão, two males (Field Museum of Natural History [FMNH] 63533 and 63534); Ceará, female (FMNH 63517); Pernambuco, sex unknown (American Museum of Natural History [AMNH] 243024); Bahia, four males and four females (MPEG 54039 [holotype] and 54040 [allotype]; AMNH 243020, 243021, 243023, 243026, 243042, 490646). These 12 specimens comprise the type series. Three specimens (Museu de Zoologia da Universidade de São Paulo [MZUSP] 38503 [male], 38504 [female], and a female in alcohol collected by M. Bornschein but not yet accessioned) are not to be considered paratypes.

Herpsilochmus pileatus, Brazil: Bahia, two males and one female (MPEG 54042, 54043; AMNH 5381). We examined color photographs of the lectotype of *H. pileatus* (Museum für Naturkunde der Humboldt-Universität zu Berlin [MNHB] 2993).

Hepsilochmus atricapillus (white morph, all males), Brazil: Bahia (11), Tocantins (1), Minas Gerais (1), São Paulo (4), Distrito Federal (1), Goiás (11), Mato Grosso (2); Bolivia: Santa Cruz (8).

Herpsilochmus atricapillus (gray morph, all males), Brazil: Maranhão (15), Piauí (1), Ceará (6), Alagoas (2), Bahia (3), Goiás (2).

Herpsilochmus atricapillus (intermediate between gray and white morphs, all males), Brazil: Bahia (1), Minas Gerais (2), São Paulo (1), Goiás (3), Mato Grosso do Sul (2). One additional adult male from Goiás was measured but not scored to morph.

Herpsilochmus atricapillus (females), Brazil: Maranhão (10), Piauí (1), Ceará (1), Bahia (18), Minas Gerais (3), São Paulo (1), Goiás (13), Mato Grosso (1); Bolivia: Santa Cruz (3).

Specimens Examined: Tape recordings.—See Table 2. All recordings are in the library of Phyllis and Morton Isler; only five recordings (all of *H. atricapillus*) are institutionally archived, but almost all will be archived by the individual recordists. Many recordings feature more than one individual and more than one type of vocalization. Other recordings were of sufficiently good quality to confirm taxon identification

TABLE 2. Measurements of loudsong characteristics[a] of three species of *Herpsilochmus* antwrens, including gray and white morphs of *H. atricapillus*.[b] Values are $\bar{x} \pm$ SD, with range and n in parentheses.[c]

Character	*H. sellowi*	*H. pileatus*	*H. atricapillus*	*H. atricapillus* (gray)	*H. atricapillus* (white)
Number of notes	55.6 ± 6.7 (43.5–71.0, 32)	24.5 ± 3.8 (14.5–30.3, 22)	27.4 ± 0.3 (15.0–41.0, 101)	—	—
Duration (s)	2.2 ± 0.3 (1.6–2.9, 32)	2.2 ± 0.3 (1.5–2.6, 22)	1.8 ± 0.3 (0.8–2.5, 101)	—	—
Peak frequency[d]	2.7 ± 0.2 (2.4–3.0, 32)	2.1 ± 0.1 (1.9–2.3, 22)	2.3 ± 0.2 (1.7–3.0, 97)	—	—
Overall pace	25.6 ± 3.1 (19.3–30.4, 32)	11.0 ± 0.8 (9.2–12.1, 22)	15.7 ± 2.0 (10.4–19.8, 101)	16.9 ± 1.4 (14.3–19.1, 23)	13.3 ± 1.6 (10.4–16.8, 25)
Pace section 1	25.3 ± 3.4 (17.9–30.0, 32)	7.9 ± 1.2 (6.1–11.2, 22)	20.6 ± 2.5 (14.6–25.6, 101)	22.4 ± 1.9 (17.8–25.6, 23)	17.5 ± 1.4 (14.2–20.0, 25)
Pace section 2	24.6 ± 3.3 (17.8–29.3, 32)	13.4 ± 1.1 (11.2–15.3, 22)	16.0 ± 2.2 (9.5–20.5, 101)	17.1 ± 1.7 (13.0–19.6, 23)	13.4 ± 1.8 (8.9–17.1, 25)
Pace section 3	26.9 ± 2.8 (21.1–31.9, 32)	11.8 ± 1.1 (9.7–13.3, 22)	10.1 ± 1.9 (5.8–14.3, 101)	10.6 ± 1.9 (6.5–14.9, 23)	8.8 ± 1.8 (5.3–12.6, 25)
Change of pace					
Section 1/2	1.0 ± 0.02 (1.0–1.1, 32)	0.6 ± 0.1 (0.5–0.9, 22)	1.3 ± 0.1 (1.2–1.7, 101)	—	—
Section 1/3	0.9 ± 0.1 (0.8–1.0, 32)	0.7 ± 0.1 (0.5–1.1, 22)	2.1 ± 0.3 (1.5–3.1, 101)	—	—
Section 2/3	0.9 ± 0.1 (0.8–1.0, 32)	1.2 ± 0.1 (1.0–1.3, 22)	1.6 ± 0.2 (1.3–2.2, 101)	—	—
Note length (ms)					
Second note	18 ± 3 (13–27, 32)	44 ± 7 (33–64, 22)	20 ± 3 (13–30, 101)	—	—
Middle note	21 ± 3 (17–30, 32)	32 ± 3 (25–38, 22)	27 ± 4 (17–44, 101)	—	—
Penultimate note	17 ± 2 (14–20, 32)	36 ± 5 (30–49, 22)	47 ± 9 (25–73, 101)	—	—

[a] Terminology and methodology follow Isler et al. (1998). See text for discussion of diagnostic characters in pairwise species comparisons. Complete data sets for all measures are available from Phyllis and Morton Isler.

[b] No characters were diagnostic between morphs, but measures of pace are presented to show ranges and means (see text).

[c] Sample sizes are numbers of individuals recorded (after loudsongs of individuals were averaged to minimize effects of intraindividual variation).

[d] Defined as the highest frequency of the note at the most intense (loudest) point in the song, which for these species is toward the middle of the song.

but were not measured for the vocal analysis (because spectrograms had poor resolution or were unavailable when vocalizations were measured) and thus are not included in this list. Restricted samples of two morphs of *H. atricapillus* are listed separately. Recordists other than the authors are listed in the Acknowledgments; a list of recordings by recordist and locality is available from the senior author.

Herpsilochmus sellowi, Brazil: Rio Grande do Norte (2), Ceará (13), Bahia (30), Minas Gerais (1).

Herpsilochmus pileatus, Brazil: Bahia (20).

Herpsilochmus atricapillus (excluding restricted samples of morphs), Brazil: Rio Grande do Norte (2), Ceará (26), Pernambuco (1), Alagoas (6), Tocantins (1), Minas Gerais (11), São Paulo (2), Mato Grosso do Sul (1), no location (1). Paraguay, Amambay (3); Bolivia: Santa Cruz (9), Chuquisaca (1); Argentina: Jujuy (1).

Herpsilochmus atricapillus (white morph), Brazil: Distrito Federal (7), Goiás (15).

Herpsilochmus atricapillus (gray morph), Brazil: Bahia (29).

Etymology.—Friedrich Sellow (1789–1831) was a German who came to Brazil in 1814 to collect natural history specimens. In the latter half of 1815, Sellow met Prince Maximilian Wied-Neuwied at G. H. Baron von Langsdorff's home in Rio de Janeiro, and in August of that year he set off with Wied to collect specimens. After four months in the company of Wied, and nearly a year alone, mostly in Espírito Santo collecting specimens for Langsdorff, Sellow continued north along the coast into Bahia. Between December 1816 and May 1818, he shipped some 1,604 specimens of birds from Salvador (the city was at that time known as Bahia) to Berlin, where they were received by M. H. K. Lichtenstein, then director of the MNHB. Lichtenstein and others described a number of new species from Sellow's material, among them *Myiothera* (= *Herpsilochmus*) *pileata*, and such spectacular birds as *Campephilus robustus* (Robust Woodpecker) and *Aratinga auricapilla* (Golden-capped Parakeet). In 1831, Sellow drowned in the Rio Doce of Minas Gerais at the age of 42. We have chosen to name this new antwren in recognition of Friedrich Sellow's important collections of natural history specimens from eastern Brazil, which numbered approximately 5,457 birds, 263 mammals, 110,000 invertebrates, 12,500 plants, and 2,000 geological samples (most of the above information from Stresemann [1948]).

The English name Caatinga Antwren refers to the fact that the new species is largely restricted to this biome. With clarification and modification of the nomenclature, taxonomy, and distribution of the members of the *Herpsilochmus pileatus* complex (see below), it seems least confusing to give the new name Bahia Antwren to the endemic *H. pileatus*. Black-capped Antwren, the long-standing name for *H. atricapillus*, should be maintained.

REMARKS

Variation in the type series.—The type series comprises 12 specimens (listed above): seven males, four females, and one sex unknown. Among males, the only appreciable difference is in the amount of dull ochraceous in the posterior underparts. This color reaches it greatest extent in the holotype and another specimen (which is much older, and somewhat faded) from the same locality (Boa Nova, in southern Bahia). It is slightly less noticeable in one from Lamarão, and there is no trace of the color in the other males. Whether this variation is individual or has a geographical restriction or tendency we cannot judge from the small series at hand. It also seems possible that feather wear and oxidation from the intense sunshine in the region occupied by *H. sellowi* could cause this weak hue to fade to the point of obsolescence. We have noted in the field, however, that the dull ochraceous of the posterior underparts seems most conspicuous in the southern birds (particularly around Boa Nova, where the color can appear darker than in the holotype). Birds in northern and western Bahia and southern Ceará look essentially whitish (concolor with upper belly and throat) in the field during the same months of the year. Compared with the holotype, AMNH 243042 has a slightly more extensive black area on the proximal web of the outer rectrix (only one is present).

The female specimens vary little from the allotype, although AMNH 243026, which also is in fresh plumage, has a blacker crown with fewer and grayer feather edges (forehead is similarly buffy). The single specimen of unknown sex (AMNH 243024) is in worn plumage. The crown is blackish with indistinct (probably abraded) buff feather edges. The

back shows more gray (less olivaceous tinge) than any of the other females, approaching the males. Perhaps it is a subadult male. Morphometrics of males and females overlap extensively (Table 1).

Habitat.—Herpsilochmus sellowi was listed as a *caatinga* endemic by Parker et al. (1996; appearing in their databases as *H. pileatus*), a designation with which we generally agree. The *caatinga* was adequately characterized, for the purposes of this paper, by Rizzini et al. (1988:162) as "a mosaic of both xerophytic and deciduous vegetation . . . composed predominantly of woody species mixed with a large number of prickly, succulent cacti and spiny, rigid-leaved bromeliads, along with many annual species . . . plant components vary greatly in relative number of individuals depending on substrate and local climate, thus affording the *caatinga* many facies." Above about 500 m, woodlands are semideciduous or evergreen (known as *brejo* in northeastern Brazil) owing to greater and more regular precipitation and slightly cooler temperatures (Andrade-Lima 1982).

Another woodland habitat, rich in vines and huge terrestrial bromeliads and known as *mata-de-cipó* ("vine" forest; Maack 1962), occurs in southern Bahia between about 700 and 1,000 m. *Herpsilochmus sellowi* is concentrated in the enclaves of semideciduous woodland and scrub of the *caatinga,* being absent from the most humid forests and the lowest, driest sectors. It also occurs along ecotones with *cerrado* in western Bahia, and taller deciduous forest in northern Minas Gerais. At Tibau do Sul in southern coastal Rio Grande do Norte, *H. sellowi* occurs in restinga woodland (so classified by Salgado et al. [1981]). The habitat in the serra do Cachimbo of southern Pará where *H. sellowi* has been collected is not definitely known. Among the most abundant trees and shrubs in all habitats in which *H. sellowi* is common, especially in the lower elevation areas, are various species in the family Leguminosae. We have frequently observed *H. sellowi* foraging in Leguminosae, and it may be that the presence of some species of trees in this family is an important aspect of the habitat.

Behavior and ecology.—Herpsilochmus sellowi forages in the middle and upper strata of the woodland and scrub it inhabits, but where scrubby growth is dense, it may occur in vegetation less than 2 m tall. Typical attacks are near-perch maneuvers such as reaches and gleans, and we have observed almost no hangs (see Remsen and Robinson 1990:146–148). They frequently hitch (see Whitney and Pacheco 1994) upward in vine tangles and other dense vegetation, investigating foliage and bark for arthropods and not paying special attention to dead foliage. Members of pairs usually forage within about 5 m of each other but occasionally are separated by several trees. Shallow and irregular movements of the wings and tail are almost constant, but these do not appear to be distinctive; the tail is rarely cocked higher than about 30° above the plane of the back unless birds are scolding or mobbing, involved in interspecific interactions (chases, displacement behaviors), or otherwise excited.

Schubart et al. (1965) analyzed stomach contents of the two above-mentioned specimens from Cachimbo in southern Pará, identifying fragments of Orthoptera, Hemiptera, and Coleoptera (Curculionidae), among other insects. Nothing is known of nesting habits. Under his account for *H. p. pileatus* (i.e. *H. sellowi*), H. Snethlage (1928:705) described two young birds as near fledging in February (apparently near Várzea Formosa, Ceará) but did not mention having collected adults or young, or having seen a nest. An adult female collected near Mocambinho, Minas Gerais, on 2 February 1997 by M. Bornschein (preserved in alcohol and not yet deposited in a museum) had undeveloped gonads and was not in molt.

Herpsilochmus sellowi usually forages in mixed-species flocks of insectivores (flock associates vary with locality). In some areas, these include other species of *Herpsilochmus.* Syntopy is greatest with *H. atricapillus* and has been documented with direct field observations and tape recordings at Tibau do Sul, Rio Grande do Norte; in the Chapada do Araripe of southern Ceará; at Jequié (K. Zimmer recordings) and Boa Nova in southeastern Bahia; and near Mocambinho, Minas Gerais (M. Bornschein pers. comm.). These two species (FMNH 63534 [*sellowi*] and 63535 [*atricapillus*]) also were collected at Barra do Corda, Maranhão, on 22 and 27 September 1927, respectively, but apparently in different habitats (Snethlage 1928:705). *Herpsilochmus sellowi* also occurs with *H. pectoralis* near Tibau do Sul (the only locality we know of where syntopy of three

species of *Herpsilochmus* has been documented), near Morro do Chapéu, and about 25 km west of Jeremoabo, Bahia. Finally, we found *H. sellowi* with *H. rufimarginatus* in *mata-de-cipó* near Jaguaquara and at the interface of drier and more humid woodland near Ibicoara, Bahia (although not yet in the same mixed-species flocks). *Herpsilochmus rufimarginatus* is absent at Boa Nova where *H. sellowi* and *H. atricapillus* coexist, but it occurs just a few km to the east in more humid Atlantic Forest not inhabited by the other species. Along the coast of southern Bahia, *H. pileatus* and *H. rufimarginatus* are syntopic in forest on sandy soil about 18 km west of Porto Seguro and near Trancoso. Microhabitat preferences and niche partitioning among syntopic antwrens are not obvious and are worthy of study.

TAXONOMIC HISTORY AND GEOGRAPHIC DISTRIBUTION OF THE *HERPSILOCHMUS PILEATUS* COMPLEX

Since erection of the genus *Herpsilochmus* Cabanis, 1847 and publication of Sclater's (1858) *Synopsis of the American Ant Birds* (Part II), the unity of *Herpsilochmus* has been recognized universally. The type species of *Herpsilochmus* is *Myiothera* (= *Herpsilochmus*) *pileata* (Lichtenstein 1823), from "Bahia." The lectotype (designated by E. Stresemann on one of the specimen labels) is housed in the MNHB; we hereby formally recognize this specimen as the lectotype. Lack of a more precise locality of collection for the type, coupled with the fact that this important specimen apparently has not been examined with specimens of presumably related species of *Herpsilochmus*, has contributed to the polemical nomenclatural and taxonomic history of *H. pileatus* and its presumed closest relatives and to the misinterpretation of the geographic distribution of these taxa.

Hellmayr (1908) considered the described species *pileatus*, *atricapillus*, and *motacilloides* to be geographic representatives "more properly designated by trinomials." Based on five males (which did not include the type) and one female (only one of the six with locality more precise than "Bahia"), Hellmayr (*in* Cory and Hellmayr 1924) restricted the distribution of *H. p. pileatus* to "Eastern Brazil, coast district of state of Bahia." The single definite locality among this (1924) series was Lamarão, which Hellmayr stated to be "near the city of Bahia" (Bahia is now known as Salvador, on the coast). Lamarão actually is about 140 km northwest of Salvador (Paynter and Traylor 1991) and is about the same distance inland from the coast. A few years later, after examination of additional specimens, Hellmayr (1929:373) concluded that nominate *pileatus* ranged "from Bahia north to Ceará and thence through northern Piauhy west to central Maranhão." He summarized the distribution of *H. p. atricapillus* (Cory and Hellmayr 1924:374) by saying: "replaces the preceding race [nominate *pileatus*] in central Brazil, its range extending northward to northwestern Bahia (Rio Preto) and the extreme south of Piauhy and Maranhão."

Zimmer (1932) accepted Hellmayr's treatment of *atricapillus* as a subspecies of *pileatus*, but referred to specimens from eastern Brazil as "puzzling." Naumburg (1939), diagnosing specimens of *Herpsilochmus* collected in eastern Brazil by Emil Kaempfer, adopted without reservation Hellmayr's identification of the Lamarão specimen as typical of *H. p. pileatus*, and, in comparison with this specimen, assigned three Kaempfer skins (one male and two females) from Barra do Rio Grande (some 560 km west-northwest of Salvador at the confluence of the rios Grande and São Francisco) to *pileatus*. She also accepted as *pileatus* specimens from Villa Nova (= Bonfim; one male and two females; MZUSP 7237, 7271, 7272) cited by Pinto (1932). Naumburg's (1939) recommendation of species-level status for *H. pileatus* and *H. atricapillus* was not adopted by Peters (1951) or Meyer de Schauensee (1966, 1970), who continued to treat them as subspecies, but it was resurrected by Davis and O'Neill (1986) and followed by Sibley and Monroe (1990), Sick (1993, 1997), Ridgely and Tudor (1994), and Parker et al. (1996).

Through study of extensive tape recordings of vocalizations of *Herpsilochmus* in northeastern Brazil, we suspected that three species-level taxa occurred in the traditional "*pileatus* complex." We examined photographs of the lectotype of *Herpsilochmus pileatus* kindly sent from the MNHB. The original label bears the name "Sello" (= Sellow; this spelling variation was noted by Papavero [1971:56] in the following passage: ". . .Friedrich Sellow (or Sello) was born on 12 March 1789. . ."). Papavero's (1971) map (fold-out number 8), based on Sellow's

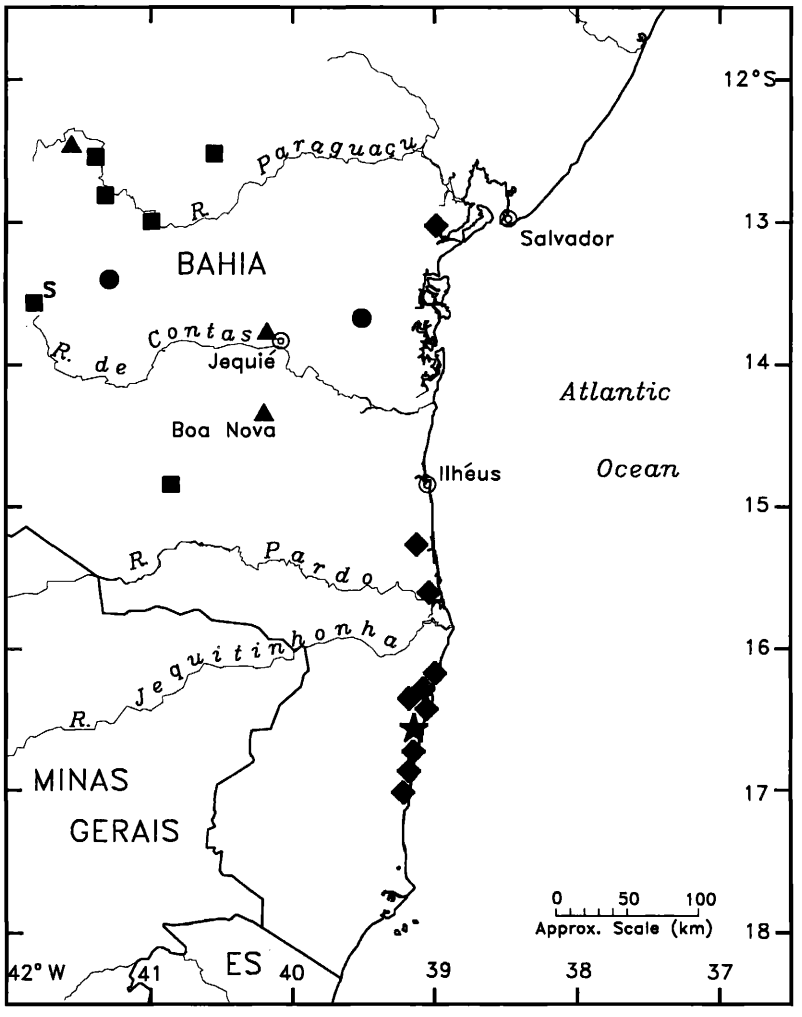

FIG. 4. Southeastern Bahia showing area of sympatry of *H. sellowi* (dots) with *H. atricapillus* (squares) and parapatry of these species with *H. pileatus*. Triangles indicate three localities where syntopy of *H. sellowi* and *H. atricapillus* has been confirmed. Entire known range of *H. pileatus* (diamonds) is shown on map; star marks Trancoso, the proposed type locality for *H. pileatus*.

itinerary (Stresemann 1948), shows that Sellow's travels in Bahia were restricted to the immediate coast south of the city of Salvador. Thus, the type of *Herpsilochmus pileatus*, collected by Sellow and described by Lichtenstein, must have been taken somewhere in southern coastal Bahia.

A male (and a female) *Herpsilochmus* species, tape recorded and collected by Buzzetti near Trancoso (on the southern coast of Bahia about 400 km south of Salvador) on 21 September 1997 closely matches the lectotype in plumage and overall morphological aspect (most importantly in having a large bill; very short tail; and gray chest, sides, and flanks), and we are confident that these three specimens represent true *H. pileatus*. A good sample of tape recordings of *H. pileatus* and other *Herpsilochmus* taxa in northeastern Brazil establishes that *H. pileatus* is restricted to the coastal region of Bahia from the vicinity of Baia de Todos os Santos (near Salvador) south at least to Barra do Caí (ca. 17°S; Fig. 4). We suggest Trancoso, Bahia (16°35'S, 39°06'W), as a precise type locality for *Herpsilochmus pileatus*.

Having established the identity and geo-

graphic distribution of *H. pileatus*, we examined most of the specimens listed by Cory and Hellmayr (1924) and Hellmayr (1929). It is clear that Hellmayr's series for *H. p. pileatus* included mostly *H. sellowi* and a few *H. atricapillus*. The Lamarão specimen proved to be a male *H. sellowi*. It was principally this misidentification that set the stage for the long-standing confusion of *sellowi* as *pileatus*. Although Cory and Hellmayr (1924) examined the type of *pileatus* in Berlin, it is unlikely that it was directly compared with the rest of Hellmayr's series (he did not include measurements of it in the 1924 paper), which was scattered mostly in several European museums. We suspect that some of the skins from "Bahia" he examined in the Naturhistorisches Museum (Vienna) and the Natural History Museum (formerly British Museum [Natural History]) represent true *H. pileatus*, but we have not seen these specimens. Aside from the lectotype and the recent MPEG pair mentioned above, the only other specimen of *H. pileatus* we have located is a male collected by Wied (locality "Brasilien" = Brazil). This specimen (AMNH 5381) was inexplicably labeled the "type of *Formicivora pileata* Wied" (corrected in August 1998; M. LeCroy pers. comm.). We have confirmed that all three of the Kaempfer specimens from Barra do Rio Grande included in Naumburg's (1939) series of *H. pileatus* are *H. sellowi*. Similarly, two specimens from Cachimbo in southern Pará (MZUSP 38503 and 38504), identified as *H. pileatus atricapillus* by Pinto and Camargo (1957) and as *H. pileatus* by Stotz et al. (1997), also are *H. sellowi*. The three specimens from Bonfim proved to be *H. atricapillus*.

Appendix 1 is a simple key to the specimen identification of the three similar species of *Herpsilochmus* discussed in this paper: *sellowi*, *pileatus*, and *atricapillus*. Their distributions are mapped in Figures 1, 4, and 5 from confirmed (specimens or tape recordings) points of occurrence. Detailed plumage descriptions of male and female *H. pileatus* are provided in Appendix 2.

SYSTEMATICS OF THE *HERPSILOCHMUS PILEATUS* COMPLEX

Morphology.—Davis and O'Neill (1986) discussed taxonomy and systematics of *Herpsilochmus* based on morphology and inferences from geographic distributions. They focused especially on systematics of the *H. pileatus* complex, supporting Naumburg's (1939) elevation of *H. atricapillus* to species rank and concluding that nominate *pileatus*, *atricapillus*, *motacilloides* (Creamy-bellied Antwren), and *parkeri* (Ash-throated Antwren) are the closest relatives of each other. Although Davis and O'Neill (1986) stopped short of suggesting that these four taxa comprised a superspecies, they were cited as the source in the classification by Sibley and Monroe (1990) of the four taxa as allospecies. Davis and O'Neill (1986: figure 3) mapped the distributions of members of their *H. pileatus* complex but showed no members reaching the coast of eastern Brazil, and apparently they included only the localities Bonfim and Barra do Rio Grande for *H. pileatus*.

Morphological analysis alone could be interpreted as supporting the "*pileatus* complex" of Davis and O'Neill (1986), although their analysis included *H. sellowi* but not true *H. pileatus*. We propose, however, that the significantly narrower and shorter bill (one-way ANOVA, sexes combined; $P < 0.0005$ for *H. sellowi* vs. *H. pileatus* and *H. atricapillus*; see Table 1); the narrow rectrices, lacking whitish lateral edging (or spots) on the central pair; and the unique crown pattern of females (together with other less-diagnostic differences) serve to set *H. sellowi* distinctly apart from other members of this aggregate. Male plumages of true *H. pileatus* and *H. atricapillus* are remarkably similar; females differ principally in extent and saturation of buffy wash on the underparts. The distribution of white on the rectrices (Fig. 2), tail length (Table 1) and degree of graduation of the tail (Appendix 1) of the two species are dramatically different.

Morphological variation within H. atricapillus.—Examination of approximately 120 specimens of *H. atricapillus* revealed significant, apparently non-clinal plumage variation in the extent of gray in the underparts of males. Each specimen was scored as "gray," "white," or "intermediate" without noting the locality of collection. When the distributions of these morphs were mapped (Fig. 5), it became apparent that males from the northern and eastern parts of the range south to central and southeastern Bahia and eastern Minas Gerais were grayish on the throat, breast, and sides

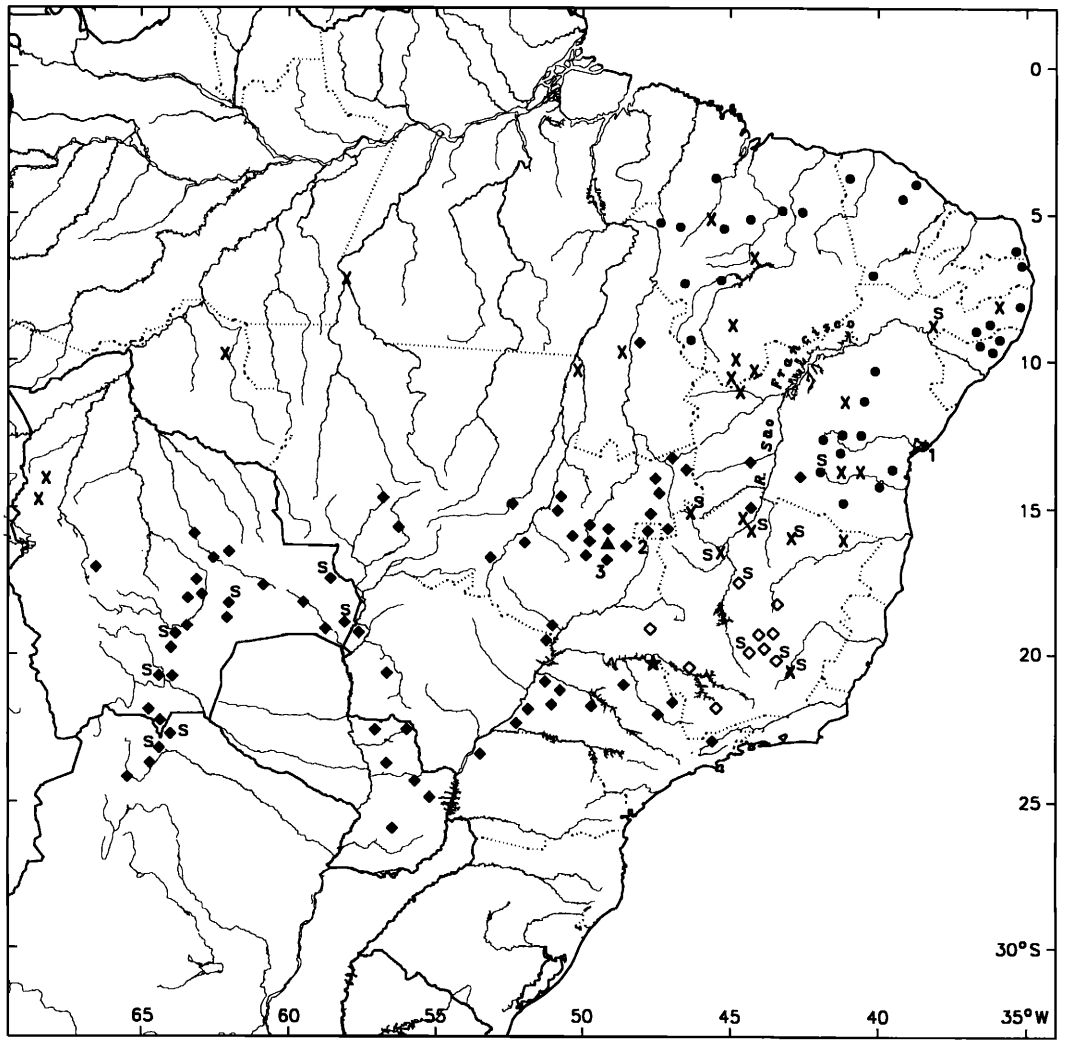

FIG. 5. Distribution of *H. atricapillus* showing approximate ranges of two male morphs. Black dots denote where gray morph has been confirmed; black diamonds denote where white morph has been confirmed and, in far western and southern parts of range, is also presumed; white diamonds denote morph unknown (either because no adult male examined or no specimen examined), but considered more likely white morph; and "x" denotes where specimens have not been examined and species are undetermined. Because of widespread sympatry of *H. atricapillus* with *H. sellowi* in northeastern Brazil, all unexamined specimens and undocumented reports of any members of the complex from this region are considered unidentified. Specimens and recordings from Rondônia, Brazil, and La Paz, Bolivia, which are under further study (see text), also are mapped as species undetermined. The single black triangle in southern Goiás marks "Nerópolis," where both gray and white morphs have been collected (see text for discussion of some apparent intermediates from this region). A star marks the type locality of *H. atricapillus*. Numbers indicate the cities of (1) Salvador, (2) Brasilia, and (3) Goiânia.

(often appearing weakly mottled or streaked) and whitish on the belly. Males from western and southern Bahia and northern Minas Gerais (west of the serra do Espinhaço) south at least through northern São Paulo and west through southern Tocantins, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, and Bolivia west to the foothills of the Andes, were white below and lacked the grayish wash on the throat and breast (see cover). White birds also

tended to have expanded areas of white in the tail and a light buffy wash on the lower flanks and undertail coverts (rare in gray birds); these characters may be individually variable. Likewise, female plumage variation (most evident in the intensity of buff in the underparts, with white-morph birds generally the whitest below) seems best explained by individual variability. One-way ANOVA of males of both morphs of *H. atricapillus* (see Table 1) revealed no significant differences in morphometrics or body mass. There were no significant differences in morphometrics or body mass between the sexes of *H. atricapillus* except for wing chord, which was longer for males than females ($P < 0.005$, $n = 75$ males, 45 females).

Among 76 male specimens from five museums, nine were judged intermediate. These were like the white morph but with a slight grayish tinge on the sides of the breast. Seven were collected from the rather restricted area of southwestern Bahia, northwestern Minas Gerais, south-central Goiás, and northern São Paulo (the other two were from Bonito, Mato Grosso do Sul). Given sympatry of the morphs in part of this area (see below), this is the region where intermediates would be most expected. However, 24 other specimens from most of the same localities were scored unambiguously; all but two (see below) were white morphs. No intermediates were found among the many specimens from north or east of the serra do Espinhaço. These observations are consistent with the hypothesis of secondary contact of two weakly differentiated populations of *H. atricapillus* in east-central Brazil.

The situation in southern Goiás invites a closer focus. Of 16 specimens from this area, 11 were white morphs, two were gray morphs, and three were among the intermediates. The two gray birds (MPEG 44585, 44586) were collected near Nerópolis ("Fazenda Dois Irmãos"), about 30 km north of Goiânia. This penetrates the southern perimeter of the white-morph specimen distribution in Goiás, and white birds have been collected within 50 km to the east and west, near Trindade and Goiânia. Furthermore, one of the specimens scored as intermediate (FMNH 344506; judged probably white with the annotation "not bright; feathers lightly soiled?") also was collected at "Nerópolis."

Secondary contact of the two morphs implied by overlap of collecting localities for "pure" morphs (i.e. no cline) and the local concentration of apparent intermediates might be explained by the significant habitat heterogeneity in this region. Southern Goiás encompasses rather sharp ecological gradients between semideciduous woodland and *cerrado* (see Magnago et al. 1983: figure 4.7) and is further complicated by many linear breaks of gallery forest and the westernmost influence of the more-humid Atlantic Forest. White morphs are widespread in semideciduous woodland (B. Whitney pers. obs.). We have not located gray birds in the field in southern Goiás, but this morph occurs almost exclusively in evergreen (i.e. relatively few trees drop all their leaves annually) forest and woodland farther north and east. Secondary contact of two populations of *H. atricapillus* may have been permitted through habitat shifts controlled by such abiotic factors as long-term variation and stability of mean annual rainfall, mean annual temperature, and edaphic conditions. The two morphs also occur fairly close together in the Tocantins / Piauí border region, which is poorly known ornithologically.

Vocalizations.—Measurement and analysis of vocalizations of *H. sellowi, H. pileatus,* and *H. atricapillus* followed the terminology and methodology of Isler et al. (1998) and were performed by Phyllis and Morton Isler. Measurements were taken of 461 loudsongs of 165 individuals from 107 recordings. Measures of multiple loudsongs of individuals were averaged to provide means for individuals before inclusion in the analyses. The sample of *H. atricapillus* loudsong recordings initially was disaggregated by geography and morph (explained above). To reduce ambiguity of morph identification, samples were restricted to southeastern Bahia (Jequié and Boa Nova; gray birds) and southern Goiás (all birds identified visually in the field) and the Distrito Federal (white birds). The sample of *H. atricapillus* was taken as a whole for the interspecific analysis. Although female songs of all three species often sound slightly higher in frequency than those of males, no diagnosable differences were found between the sexes, so they were combined for the vocal analysis.

In the following descriptions of each species' vocalizations, we define "rattles" as compris-

ing several structurally similar notes delivered in bursts of variable duration; they are usually delivered in repetitive sequences. *Herpsilochmus* rattles are analogous to rattles in the *Thamnophilus punctatus* complex, as defined by Isler et al. (1997). Functions of some other vocalizations have not been determined with a reasonable degree of certainty.

The male loudsong of *H. sellowi* is a steady series of closely spaced notes of uniform structure and tonality ($\bar{x}$ = 56 notes in 2.2 s, n = 32). The series rises and falls gently in frequency and amplitude, maintaining a frequency of about 3 kHz (mean peak frequency = 2.7 kHz, n = 32) for most of its duration (Table 2, Fig. 6A). There are two basic types of rattles or rattle-like calls. The one used to mob or scold predators such as snakes and Ferruginous Pygmy-Owls (*Glaucidium brasilianum*; vocal imitation of this species is sufficient to elicit the call) consists of pairs or repetitions of up to about six unmodulated notes sounding like *iip* or *wiip* (Fig. 7A). Proximity of a quiet observer (mild threat) does not elicit this call. Another rattle-like call comprises a rapidly paced series of sharp, hairpin-shaped notes usually introduced by a different, slightly longer note, the whole call lasting about 1 s and often rising in frequency (Fig. 7B). An individual may deliver several variations of this vocalization in sequence.

The loudsong of *H. pileatus* begins with four to seven notes separated by successively shorter intervals merging into a regularly and more closely spaced series ($\bar{x}$ = 25 notes in 2.2 s, n = 22), the whole song characterized by essentially uniform note structure. The song rises and falls gently in frequency and amplitude, maintaining a frequency of about 2 kHz (mean peak frequency 2.1 kHz, n = 22) for most of its duration. Comparing first and second and first and third sections, the loudsong accelerates in pace (Table 2, Fig. 6B). We have 10 recordings of rattles; two variations are illustrated in Figures 7C and D. The one shown in Figure 7C is given frequently; it is closely similar to and apparently given in the same context as the mobbing/scolding calls of *H. gentryi* (Ancient Antwren) and *H. stictocephalus* (Todd's Antwren) shown in Whitney and Alvarez (1998: figures 5C and D). The most frequently heard call is a single, modulated *greep* that is repeated at irregular intervals in a pair-contact context (Fig. 7G).

The loudsong of *H. atricapillus* begins with one or two (rarely three) introductory notes of individually variable frequency and duration distinctly separated from and of different structure than the rest of the notes in the song. The main series of closely spaced notes usually lasts less than 2 s ($\bar{x}$ = 27 notes in 1.8 s, n = 101) and maintains a frequency of slightly more than 2 kHz before falling off at the end. Comparing first and second and first and third sections (not including the introductory notes in the first section), the loudsong decelerates in pace (Table 2, Fig. 6C). We noted two types of rattles. The one illustrated in Figure 7E is heard commonly and functions primarily (but perhaps not exclusively) to scold or mob potential predators. It is the only rattle among the taxa studied that shows multiple, clearly visible overtones in spectrograms. The other rattle or rattle-like vocalization (Fig. 7F) is represented in our sample by only three recordings. The call heard most frequently is a single, modulated *greep* repeated at irregular intervals in a pair-contact context (Fig. 7H). An unmodulated single *chup* or *chip* call (Fig. 7I), although heard fairly commonly in the field, is represented in the sample by only 10 recordings. It is sometimes delivered repetitively and interspersed with modulated calls, being given in an excited, heightened awareness context, and also is given regularly as individuals fly between trees.

Table 2 provides an overview of loudsong characters measured and results for each species and the morphs of *H. atricapillus* (complete data sets available from P. and M. Isler). Following Isler et al. (1998), in the following comparisons, "diagnosable" means that differences in pairwise species comparisons were significant at the 97.5 percentile and would remain so even if n were equal to 30 or more (sample sizes for each species provided in Table 2). The loudsong of *H. sellowi* is highly distinctive and is diagnosable from those of *H. pileatus* and *H. atricapillus* in at least five characters: number of notes (more in *sellowi*); pace (overall pace and pace of all sections slower in *pileatus*; pace of section 3 slower in *atricapillus*); change of pace (nearly constant pace in *sellowi*); note length; and structure of individual notes (essentially narrow mirror images of the other species' notes). This

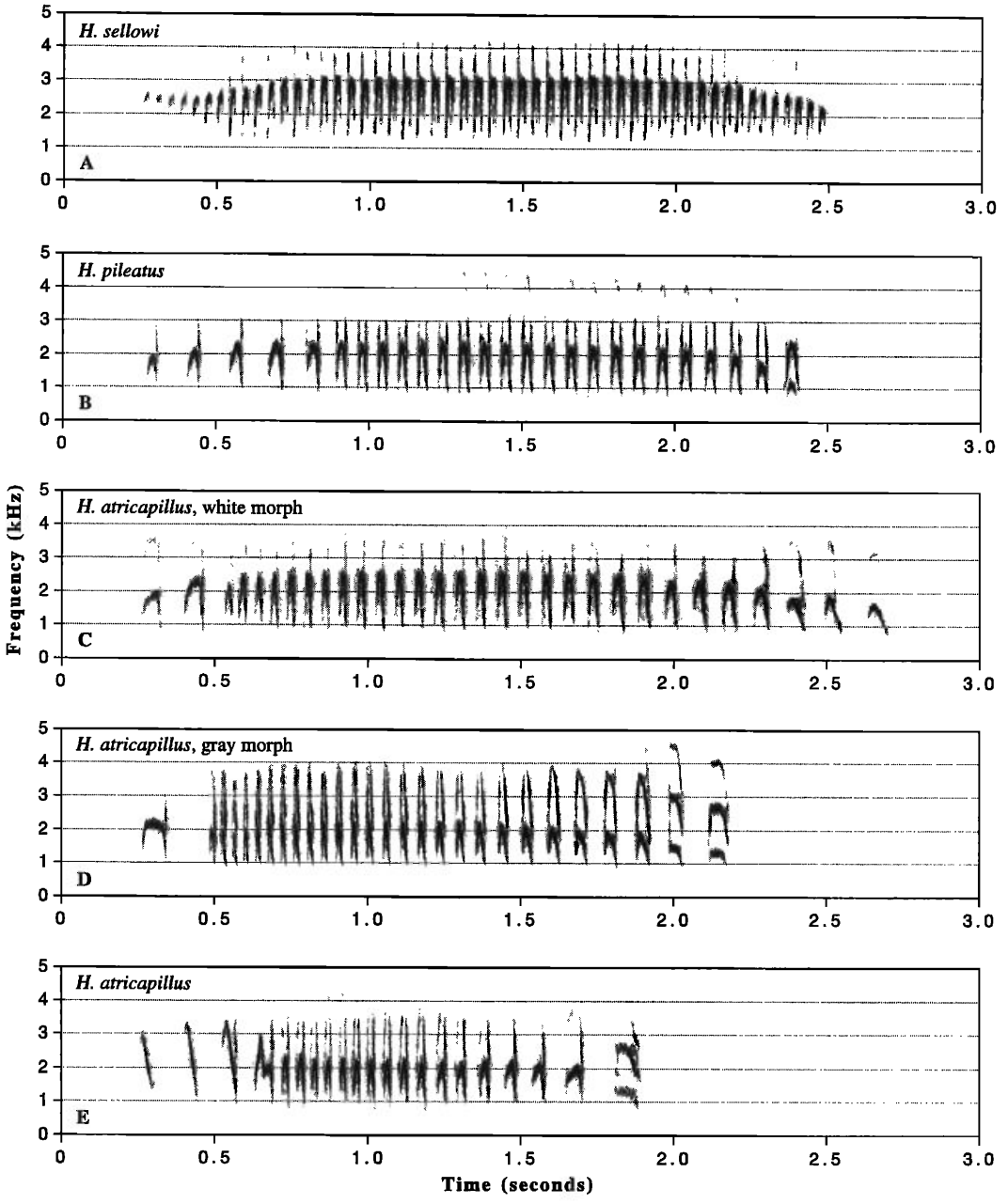

FIG. 6. Loudsongs of some *Herpsilochmus* antwrens from northeastern Brazil selected to illustrate mean differences. Quantitative, diagnostic, interspecific differences are described in the text from measurements presented in Table 2. (A) *H. sellowi*; Isler BMW 122:09; Chapada do Araripe, Ceará, 25 February 1996; recordist B. Whitney. (B) *H. pileatus*; Isler MISC 3:11; near Trancoso, Bahia, 20 September 1997; recordist D. R. C. Buzzetti. (C) *H. atricapillus*, white morph; Isler BMW 159:19; Parque Ecológico Ulysses Guimarães, Goiás, 21 June 1998; recordist B. Whitney. (D) *H. atricapillus*, gray morph; Isler JFP 6:09; near Boa Nova, Bahia, 30 August 1992; recordist J. F. Pacheco. (E) *H. atricapillus*, aberrant loudsong (see text); Isler KJZ 46:13; near Jequié, Bahia, January 1996; recordist K. J. Zimmer.

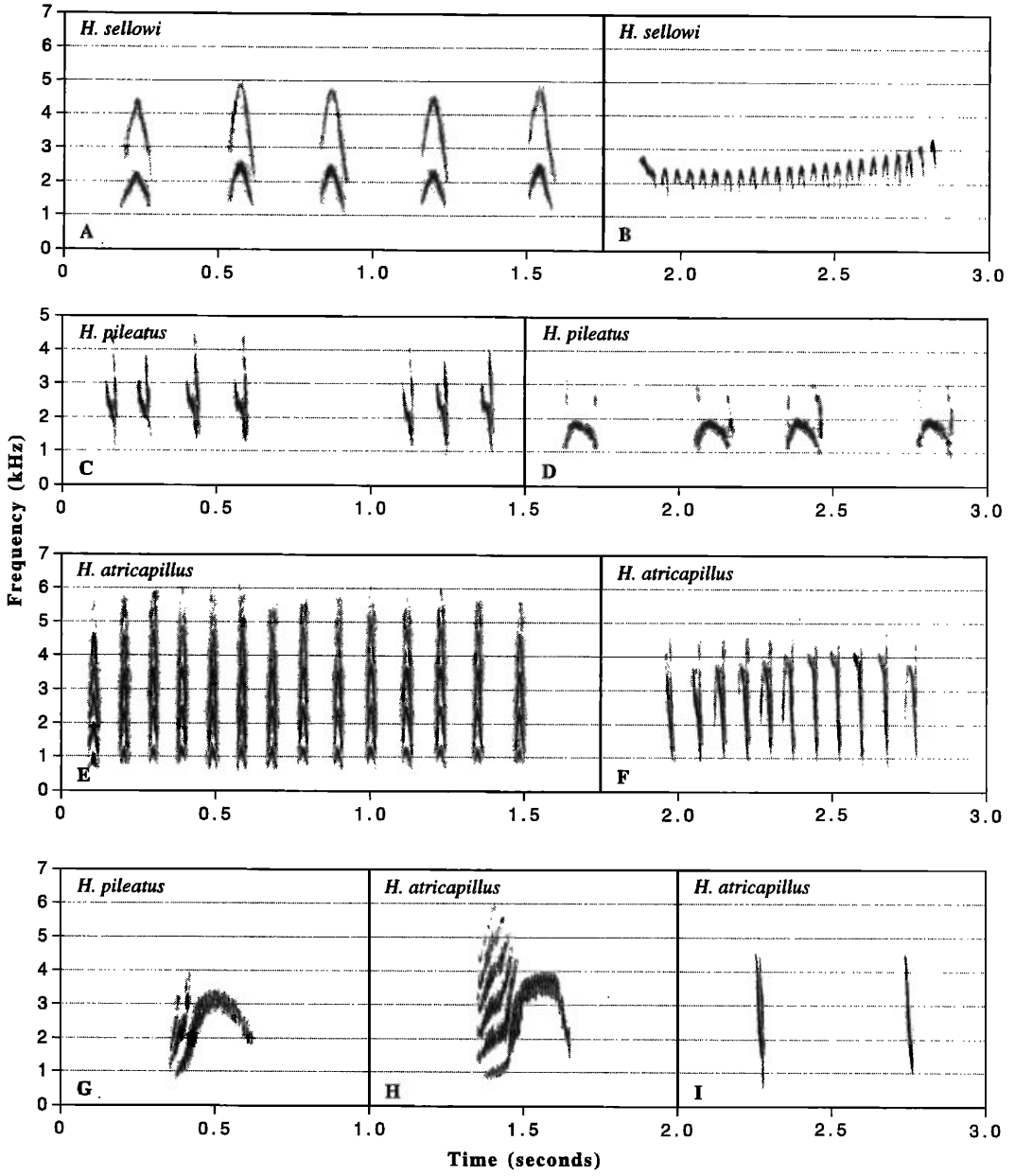

FIG. 7. Rattles and other frequently delivered calls of some *Herpsilochmus* antwrens from northeastern Brazil. Behavioral contexts of these vocalizations are discussed in the text. (A) *H. sellowi* rattle; Isler JFP 6:07; near Boa Nova, Bahia, 30 August 1992; recordist J. F. Pacheco. (B) *H. sellowi* rattle-like call; Isler BMW 91:05; 40 km North Manga, Minas Gerais, 11 November 1994; recordist B. Whitney. (C) *H. pileatus* rattle; Isler MISC 3:11; near Trancoso, Bahia, 20 September 1997; recordist D. R. C. Buzzetti. (D) *H. pileatus* rattle-like call; Isler MISC 3:26; near Canavieiras, Bahia; recordist R. Parrini. (E) *H. atricapillus* rattle, given by both morphs; Isler BMW 123:20; near Boa Nova, Bahia, 7 March 1996; recordist B. Whitney. (F) *H. atricapillus* rattle-like call; same data as (E). (G) *H. pileatus* modulated *greep* call; Isler MISC 3:27; near Canavieiras, Bahia; recordist R. Parrini. (H) *H. atricapillus* modulated *greep* call; this call is indistinguishable from that of *H. pileatus*; Isler BMW 67:12; near Boa Nova, Bahia, 10 November 1993; recordist B. Whitney. (I) *H. atricapillus* unmodulated *chup* or *chip* call; Isler BMW 68: 11; near Boa Nova, Bahia, 10 November 1993; recordist B. Whitney.

is easy to understand when the songs are heard together; *H. sellowi* sounds nothing like the others. The rattles of *H. sellowi* also are highly distinctive, although the individual unmodulated notes of *H. sellowi* (Fig. 7A) and of *H. pileatus* (Fig. 7D) bear resemblance. The loudsongs of *H. pileatus* and *H. atricapillus* sound much more alike, primarily owing to close similarity in structure and tonality of individual notes, and much more similar pace.

In the analysis, loudsongs of *H. pileatus* were considered to lack introductory notes and, because the introductory notes of *H. atricapillus* were individually variable as mentioned above, loudsongs of that species were measured without the introductory notes. Loudsongs of the two species were diagnosable, then, by lack of introductory notes in *H. pileatus*; pace (section 1 was slower in *pileatus*); change of pace (as described above, *pileatus* accelerated and *atricapillus* decelerated); and note length (second note of *pileatus* was longer, although of similar structure). Diagnostic differences would be altered in important ways if the loudsong of *H. pileatus* were considered to have introductory notes and the introductory notes of *H. atricapillus* were included in the analysis. For example, the *H. pileatus* loudsong shown in Figure 6B could be interpreted as having five introductory notes ahead of the main series. Inclusion of the introductory notes of *H. atricapillus* would probably shift most or all differences between that species and *H. pileatus* to the first third of the loudsong, the latter two-thirds of their songs showing close similarities in these and other measures. Rattles of *H. pileatus* and *H. atricapillus* are quite different, but the modulated, single-note call of the two species is remarkably similar both aurally and spectrographically.

We found no diagnosable variation between the samples of loudsongs of gray (n = 25) and white (n = 23) morphs of *H. atricapillus*. However, we documented mean differences in the overall pace and pace of each section of the loudsongs: gray birds averaged 21% faster than white birds overall, and 22%, 22%, and 17% faster through each of the three sections (introductory notes excluded from analysis). Average loudsongs of white and gray morphs are illustrated in Figures 6C and D, respectively. The unmodulated, single-note *chup* call, recorded from several individuals in the sample of gray morphs, was not recorded in the white morphs; rattles appear to be indistinguishable. Diagnosable differences in pace of loudsongs were demonstrated by Isler et al. (1998) to be among the most important vocal characters separating thamnophilid taxa at the species level. We suspect that the average pace differences of gray and white morphs of *H. atricapillus* reflect incipient speciation. A less-rigorous statistical analysis and interpretation of the above data could result in judgement of subspecies or even species status for the *H. atricapillus* morphs, but we believe that the Isler et al. (1997, 1998) criteria allow a more conservative and evolutionarily accurate perspective on differentiation at the species level. The gray morph may merit recognition as a subspecies, but we hesitate to name it based on a brief overview and so few characters.

Finally, the aberrant loudsong illustrated in Figure 6E, which was delivered consistently by an individual *H. atricapillus* at Jequié, Bahia, is unique in the sample of 165 individuals. This example emphasizes that vocalizations of a single individual should not form the basis for judgements of taxonomic divergence.

Systematics summary and origins.—Substitution in the traditional *H. pileatus* complex of true *H. pileatus* for *H. sellowi* has the effect of maintaining the nomenclatural status quo of the recent taxonomic literature, although geographic distributions and relationships of the revised membership have required significant clarification. *Herpsilochmus sellowi* is a highly distinctive species, both morphologically and vocally, and we recognize that a reasonable argument could be made for its generic separation. However, pending biochemical analysis of the Thamnophilidae, we prefer that it be maintained in *Herpsilochmus*. It is sympatric with four species of *Herpsilochmus* (including *H. longirostris* [Large-billed Antwren] near Correntina, Bahia [B. Reinert pers. comm.], and probably in northern Minas Gerais, pers. comm.).

Morphological and vocal analyses of all members of *Herpsilochmus* (Whitney and Alvarez 1998, this paper) indicate that *H. pileatus* and *H. atricapillus* are each other's closest relatives. Although differentiation of these two essentially parapatric species may be relatively recent, we are confident that their evolutionary destinies are independent. A more recent (dif-

ferentiation only incipient) genetic rift in interior eastern and central Brazil, perhaps across the serra do Espinhaço, seems to have given rise to the gray and white morphs of *H. atricapillus.* The evolutionary record in this case is obscured by apparent secondary contact and lack of diagnostic vocal markers, which we suspect is another indication of relatively incipient differentiation. We concur with Davis and O'Neill (1986) that the *H. pileatus* complex should embrace *H. motacilloides* and *H. parkeri.* Whitney and Alvarez (1998) suggested that the allospecies *H. stictocephalus* and *H. gentryi* are the closest relatives of the *H. pileatus* complex north of the Amazon, Solimões, and Marañon rivers, another judgement with which we agree. Indeed, the *H. pileatus* lineage has had a long and genetically fragmented evolutionary history.

Preliminary examination of specimens and tape recordings of the *Herpsilochmus* population in northeastern Rondônia, Brazil (Stotz et al. 1997), suggests that it is distinctive. It is under further study by its discoverers. Another poorly known population conspecific with or closely allied to *H. atricapillus* inhabits dry forest at about 900 m elevation in the valley of the Río Tuichi in La Paz, Bolivia (Pearman 1993, Perry et al. 1997). It also is under further study (Pearman 1993).

Conservation.—The "arboreal" *caatinga* inhabited by *H. sellowi* and many other endemic organisms has suffered recent and widespread clearing and burning. Furthermore, grazing by goats effectively inhibits regeneration of most woody *caatinga* plants. The *mata-de-cipó* is inhabited by a high proportion of globally threatened species (Gonzaga et al. 1995, Whitney 1996). We know of no patches of undisturbed *mata-de-cipó,* and none of it is officially protected. Fortunately, *H. sellowi* seems reasonably adaptable to habitat disturbance, but overall it must be considered a rare species. Even worse off is *H. pectoralis,* which is more dependent on the presence of intact woodland and has become extirpated or quite rare in most of its former range.

Although it is presently common in many localities, *H. pileatus* is restricted to the narrow band of *restinga* (low stature, sandy soil) woodland and coastal forest of southern Bahia, occurring only a short distance inland. At least 40% of coastal forest plant species in southern Bahia are endemic to this region (Thomas et al. 1998). According to the quarterly newsletter "Bahia Invest: Tourism" (year 4, number 14; published by the Department of Culture and Tourism of Bahia), the first of a series of large-scale resort developments was initiated in September 1998 near Trancoso, with a budget of 150 million dollars. These resorts and the associated airstrips, roads, and other infrastructure will take a heavy toll of the environment in the coming decade.

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APPENDIX 1. Key to specimen identification of *Herpsilochmus pileatus, H. atricapillus,* and *H. sellowi.* Bill widths measured at the anterior edge of the nares. Tail measurements apply to fully grown (at most slightly abraded), normally closed tails. Measure tail length from the point where central rectrices enter skin to the tip. It is necessary to carefully part the feathers of the rump and uppertail coverts to obtain a clear view of this point. The distance from the tip of the shortest (outer) pair of rectrices to the tip of the longest pair (central, sometimes matched by one or more adjacent pairs) of rectrices we define as the "graduation maximum," modified from "graduation" of Baldwin et al. (1931: figure 127). One rectrix of a pair may be slightly longer than its counterpart (especially with outer rectrices); in this case, measure from / to the tip of the longer one to obtain a value maximum as close as possible to the fully grown condition (i.e. it is not always possible to determine whether rectrices that appear to be completely grown truly are). Width at the approximate midpoint of the central rectrices is obtained from naturally arranged feathers (i.e. barbs regularly interlocking, vanes not sleeked or flattened). Note that juvenile birds not fully developed can show measurements below the thresholds in this key. The cover and Figures 2 (tail patterns) and 3 (female heads) may aid in identification of individual specimens and provide reference for the appearance of "discrete, whitish marks [crown]" of females. Mensural thresholds for *H. pileatus* were determined from a sample of two males and one female (female crown and breast from one specimen augmented by field observations); a larger sample could result in slight adjustments of some of the elements of this key but probably would not alter its diagnostic utility. See Table 1 for selected measurements for each species.

1a Bill width less than 3.0 mm; wing chord 50 mm or less; tail less than 52 mm (usually less than 51 mm); central rectrices less than 5 mm wide at midpoint and entirely black with or

without pale apical fringes; female crown lacking discrete, whitish marks ..... *H. sellowi*

1b Bill width greater than 3.0 mm; central rectrices more than 5 mm wide at midpoint (often exceeding 6 mm) and having narrow, whitish lateral fringes and (almost always) small, white tips; female crown with discrete, whitish marks 2

2a Tail less than 47 mm; graduation maximum less than 17 mm (less than 15 mm may be typical); female lacking distinct ochraceous wash on breast (weak tinge with grayish wash may be typical) ..... *H. pileatus*

2b Tail greater than 52 mm (perhaps very rarely as short as 51 mm and usually 54 to 60 mm); graduation maximum greater than 17 mm (usually 20 to 25 mm); female with distinct ochraceous wash on breast, usually pervading most of underparts and sides of head (rarely lacking a distinct wash, appearing mostly whitish) ..... *H. atricapillus*

APPENDIX 2. Description and distribution of *Herpsilochmus pileatus* (Lichtenstein, 1823). We have located only four specimens (three males and one female) of *H. pileatus*, including the lectotype in the MNHB. Several points of occurrence are documented with tape recordings. We suggest Trancoso, Bahia (16°35'S, 39°06'W), as the precise type locality.

Adult male

See cover. MPEG 54042 is described. Color designations from direct comparison with Munsell soil color charts (1994). Plumage fresh and unabraded. Crown (except for a few minute whitish feathers near base of bill) deep, semiglossy black. Loral region (including nasal tufts) and coterminous superciliary stripe bordering and sharply contrasting with crown, white, widest (to about 3.5 mm) and becoming slightly grayish behind eye. Preocular spot (at anterior edge of eyering) and 2.3-mm wide postocular stripe to a point about 11 mm posterior to orbit same deep black as crown. Facial region same whitish as superciliary stripe, merging posteriorly with grayer sides of neck. Entire upperparts from nape to rump medium-gray (Gley chart 2: 5/5PB) with hint of black-and-white feathers of interscapular patch (most are white with black tips most extensive on distal vane) barely showing through (pattern varies with handling of specimen). Throat whitish (feathers with lightly grayish tips), essentially concolor with facial and superciliary regions. Breast slightly darker gray (whitish feather centers contribute to a weakly mottled effect), especially at sides, which are nearly as dark as sides of neck and back, this hue continuing posteriorly through flanks. Center of belly whitish (palest area of underparts), returning to grayish through undertail coverts. No indication of yellow or buff in flanks or undertail. Central rectrices (only one present) about 4 mm short of fully grown; rest of tail fully grown. Tail weakly graduated, with outer rectrices about 14 mm shorter than central pair (estimated length of central rectrices), all others within about 5 mm of length of central pair. Outer rectrices white with black bases (ca. ⅓ of feather), black most extensive on proximal vanes. White tips on successive pairs decreasing from outermost to innermost. Central rectrix with only a minute white spot at tip, but with distinct white edges, most conspicuous on proximal margin (see Fig. 2 for extent and pattern of black and white on rectrices). Wing coverts same deep-black as crown, each feather marked with a conspicuous white tip, more extensive on distal vane. 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 tricolored, gray on proximal vanes, and black with a contrasting white margin on distal vanes, forming a conspicuous white stripe overlying proximal ends of wing bars. Bend of wing white, greater primary coverts blackish. Alula black with contrasting white margin on distal vane reaching tip. Remiges blackish with narrow but conspicuous whitish fringes on distal vanes. Inner secondaries black, marked with conspicuous white margins on distal vanes, coterminous with white-margined scapulars. Iris dark brown; upper mandible blackish with grayish tomia, lower mandible grayish; legs and feet bluish-gray, color of soles not recorded. Selected measurements included in Table 1.

One other male, AMNH 5381, is available for direct comparison. Although this specimen was collected more than 165 years before MPEG 54042, its wing and tail were more abraded at the time of collection, and it was obviously prepared for display in a case (legs wired and bent, glass eyes), there is only a slight indication of fading of the plumage (black areas somewhat "flat," lacking semiglossy effect of fresh specimen, but not foxed toward brownish). It matches the above description quite closely. Its complete, fully grown tail (tip of right outer rectrix missing) has a graduation maximum of 14.2 mm. Color photographs of the lectotype of *H. pileatus* are closely similar in proportions and plumage features to the above two males. Preparation for mounting of the lectotype and AMNH 5381 is so remarkably similar as to suggest that these two specimens from the 1830s were prepared by the same hand.

Adult female

See cover and Figure 2 (left side). MPEG 54043, the only specimen known to us, is described. Plumage fresh and unabraded. Tiny feathers of forecrown black with light buff (2.5Y 7/6) tips, imparting a weakly streaked effect. Crown deep black with irregularly scattered, short but conspicuous whitish streaks or spots formed by white distal margins of some feathers. Loral region (including nasal tufts) same light buff as forecrown, blending posteriorly into whiter superciliary stripe and facial region. Preocular spot and postocular stripe same deep black as crown. Sides of neck and entire upperparts same medium-gray (Gley chart 2: 5/5PB) as male described above only slightly duller. Throat and malar region creamy-white, appearing weakly mottled owing to black feather bases and white tips. Breast grayish with a weak overlay of buff (nearest 5Y 7/3, but limited extent of this hue makes chart matching especially difficult); sides, flanks, and undertail coverts concolor but slightly paler. Center of belly whitish. Tail as in male described above, but black more extensive on outer rectrices (covering more than the basal half of the feather); graduation maximum 13.5 mm (central rectrices within ca. 2 mm of fully grown). Wings and soft parts as described for male above. Selected measurements included in Table 1.

Distribution

Herpsilochmus pileatus is known only from the coastal, sandy-soil forests of Bahia south of the city of Salvador and Baia Todos os Santos (northernmost point ca. 25 km by road north of Valença: 13°01'S, 38°59'W) south at least to Barra do Caí (ca. 17°00'S, 39°10'W; Fig. 4).