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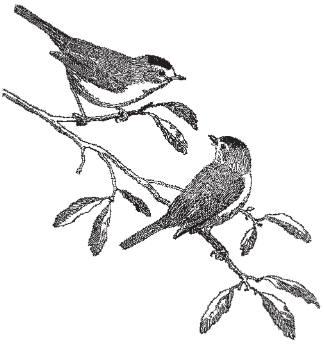

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SPECIES LIMITS IN ANTBIRDS (THAMNOPHILIDAE): THE SCALE-BACKED ANTBIRD (*WILLISORNIS POECILINOTUS*) COMPLEX

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ABSTRACT.—The geographic range of the Scale-backed Antbird (*Willisornis poecilinotus*) encompasses Amazonia. Seven currently defined subspecies are distinguished from one another by diagnostic plumage characters except for one pair. Six pairs of subspecies are apparently parapatric and lack a known barrier to intergradation in at least a portion of their contact zone; yet confirmed hybrids are known only for one pair in one location. An analysis of >350 recordings, however, found vocal differences among them insufficient to recommend elevating subspecies to the species level with one exception. Populations in southeastern Amazonia should be considered a distinct species, *Willisornis vidua* (Hellmayr), Xingu Scale-backed Antbird, on the basis of their distinct loudsongs, raspy call series, and contact calls. Within the widespread *Willisornis poecilinotus*, Common Scale-backed Antbird, the remaining instances of parapatry without extensive intergradation provide a focus for future fieldwork to define interrelationships in contact zones and mechanisms of species recognition that may be sustaining them on independent evolutionary paths. *Received 15 May 2010. Accepted 9 September 2010.*

The Scale-backed Antbird (*Willisornis poecilinotus*) (Cabanis 1847), a widespread Amazonian complex, occupies a unique place in thamnophilid antbird evolution. Scale-backed Antbirds, as described in detail by Willis (1982), primarily forage over or near army ant swarms, but their morphology directed early taxonomists (Ridgway 1911, Cory and Hellmayr 1924) to place them in the genus *Hylophylax* with species that were not obligate ant-followers. Willis (1982) and other observers (e.g., Zimmer and Isler 2003) noted that Scale-backed Antbirds did not look or behave like other *Hylophylax* species, but it remained for a molecular study (Brumfield et al. 2007) to demonstrate that Scale-backed Antbirds evolved in the clade of army ant-following birds distant from *Hylophylax* species in the phylogenetic tree. The genus *Dichropogon* had been erected earlier (Chubb 1918) for the complex, but Agne and Pacheco (2007) found the name *Dichropogon* was preoccupied by a genus of asilid flies and proposed the new generic name of *Willisornis* in honor of Edwin O'Neill Willis, who had contributed so much to the understanding of the complex as well as other thamnophilid species.

Seven subspecies have been recognized (Peters 1951, Zimmer and Isler 2003). Almost all are readily distinguished by plumage features, primarily in females. Substantial differences in female plumage led Hellmayr (1929) to include the complex in his seminal study of geographic

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forms that present more well-marked characters in females than in males, variation which he termed heterogynism. In temporal order, the seven subspecies are *W. p. poecilinotus* (Cabanis 1847), *W. p. griseiventris* (von Pelzeln 1869), *W. p. lepidonotus* (Sclater and Salvin 1880), *W. p. vidua* (Hellmayr 1905), *W. p. nigrigula* (Snethlage 1914), *W. p. duidae* (Chapman 1923), and *W. p. gutturalis* (Todd 1927). Together they populate the Amazonian lowlands (Fig. 1).

In the years since these subspecies were described, ornithological surveys in Amazonia have expanded our knowledge of their distribution and have produced a large number of vocal recordings from throughout their range. Vocal characters afford a relevant ''yardstick'' (*sensu* Mayr and Ashlock 1991) for estimating reproductive isolation and species status of sympatric and allopatric populations of suboscine passerines (Isler et al. 1998, Johnson et al. 1999, Baptista and Kroodsma 2001, Helbig et al. 2002, Remsen 2005). Recently obtained data provide an opportunity to reevaluate the taxonomic status of *Willisornis* populations based on geographic relationships among plumage-defined subspecies, and on the extent to which vocal differences among these subspecies support species status.

METHODS

Populations were based on geographic ranges of currently defined subspecies with two further subdivisions. Vocalizations of *lepidonotus* were divided into recordings obtained below and above 800 m elevation based on preliminary molecular analysis of J. M. Bates (pers. comm.). Vocalizations of *griseiventris* were allocated to populations east and west of the Rio Madeira because the Rio Madeira is a major barrier to gene flow in understory birds (Isler et al. 2007a, b; Burney and Brumfield 2009).

Specimens were examined at the Louisiana State University Museum of Natural Science (LSUMZ), the Museo Paraense Emilio Goeldi (MPEG), the Museo de Zoologia, Universidade de São Paulo (MZUSP), and the National Museum of Natural History, Smithsonian Institution (USNM) with additional data provided by staffs of the American Museum of Natural History (AMNH), the Carnegie Museum of Natural History (CM), the Colección Ornitológica Phelps (COP), and the Field Museum of Natural History (FMNH). Measurements of bill width, depth, and length (at nares) and tarsus, tail, and wing chord were taken with MAX-CAL electronic digital calipers, which were also used to measure the length of the white interscapular patch at the center of the back. Colors were recorded by comparison with Munsell Soil Color Charts (Kollmorgan Instruments Corp., New Windsor, NY, USA), and English color names used in verbal plumage descriptions were adapted from these charts. We developed a locality-based map (Fig. 1) of the geographic distribution of each subspecies based on sites listed in museum inventories, sites referenced in the literature, and sites of vocal recordings.

Tape and digital recordings of vocalizations were compiled from our own inventories, from unarchived contributions of other individuals, and from the Macaulay Library (ML, Cornell Laboratory of Ornithology, Ithaca, NY, USA). We examined 358 recordings (Appendix). We reviewed the documentation of recordings to identify the number and gender of individuals vocalizing. RAVEN, Version 1.3 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA) was used to make a spectrogram of every vocalization type delivered by each individual on every recording. All clearly delineated spectrograms were examined visually for characters (e.g., note shape) that might distinguish a population. Spectrograms shown in figures were selected to express typical measurements (e.g., the mean number of notes in loudsongs) and were made by exporting RAVEN files into CANVAS, Version 9.0.4 (ACD systems, Victoria, BC, Canada).

Vocal characteristics obtained for loudsongs were: (1) number of notes, (2) duration, (3) pace, (4) change of pace, (5) note shape, (6) change in note shape, (7) note length, (8) change in note length, (9) interval length, (10) change in interval length, (11) frequency (nadir, peak, and max), and (12) change in frequency. The nadir is the lowest point in the tracing of a note; peak the highest point; and maximum frequency is measured at the point of highest intensity in the note. Measurements were taken of the initial, central (in time), and terminal notes and their associated intervals. Characteristics obtained for calls were fewer as they contained fewer notes. We required pairs of measurements expressing diagnostic characters to have correlation coefficients <0.80 given the possibility that some characters might be linked by common ancestry.

Quantitative measures were obtained from spectrograms projected on a 43-cm screen using

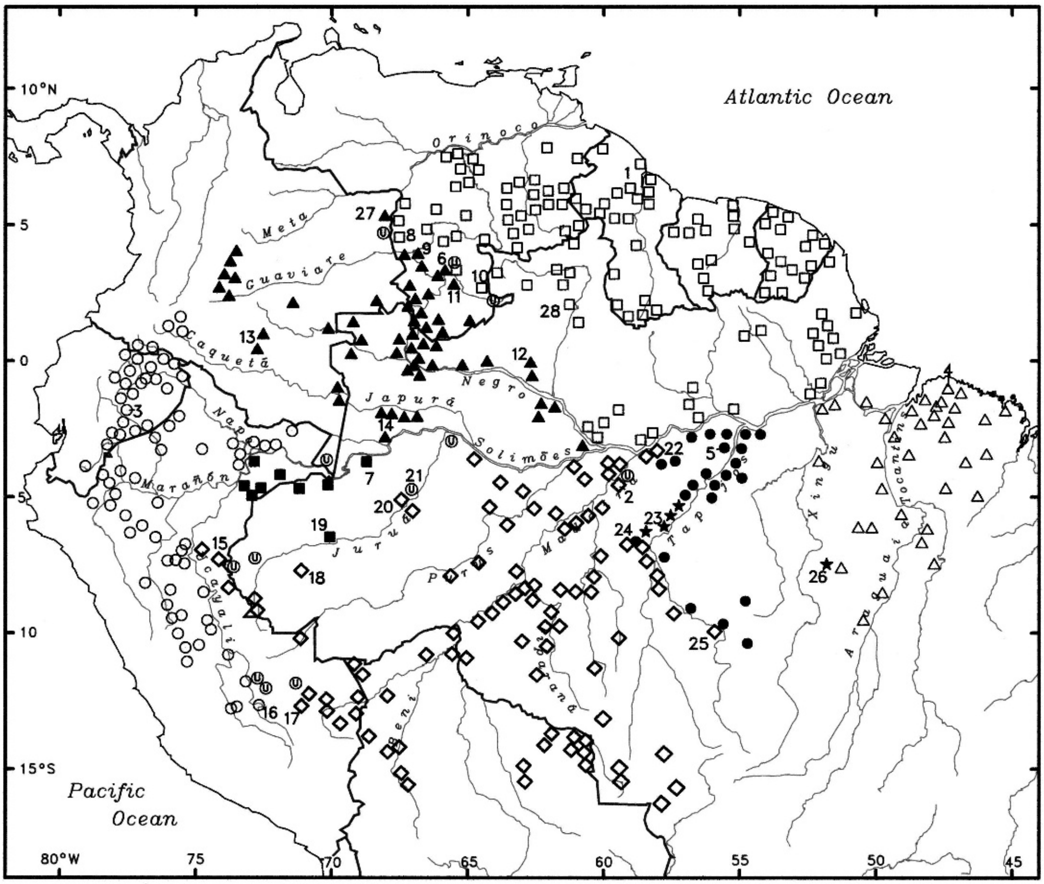

FIG. 1. Geographic ranges of *Willisornis* populations. Symbols represent the occurrence of taxa within small geographic sectors (Isler 1997). Open square = *poecilinotus*; solid triangle = *duidae*; open circle = *lepidonotus*; solid square = *gutturalis*; open diamond = *gutturalis*; solid circle = *nigrigula*; open triangle = *vidua*; star = two subspecies occur in sector; U surrounded by a circle = subspecies not identified. Type localities and locations are as mentioned in text. (1) ''British Guiana'' (exact locality unknown; type locality of *poecilinotus*). (2) Borba, Amazonas, Brazil (04° 24′ S, 59° 35′ W; type locality of *griseiventris*). (3) Sarayacu, Pastaza, Ecuador (01° 44′ S, 77° 29′ W; type locality of *lepidonotus*). (4) Igarapé Açu, Pará, Brazil (01° 07′ S, 47° 37′ W; type locality of *vidua*). (5) Boim, Pará, Brazil (03° 00′ S, 55° 27′ W; type locality of *nigrigula*). (6) Cerro Duida, Amazonas, Venezuela (03° 25′ N, 65° 40′ W; type locality of *duidae*). (7) São Paulo de Olivença, Amazonas, Brazil (03° 27′ S, 68° 48′ W; type locality of *gutturalis*). (8) Caño Usate, Amazonas, Venezuela (04° 25′ N, 67° 48′ W). (9) Campamento Manaka, Amazonas, Venezuela (03° 57′ N, 67° 05′ W). (10) Río Putaco, Amazonas, Venezuela (02° 50′ N, 64° 25′ W). (11) Ocamo, Amazonas, Venezuela (02° 48′ N, 65° 14′ W). (12) Demini Camp, Rio Demini, Amazonas, Brazil (00° 02′ S, 62° 48′ W). (13) Sierra de Chiribiquete, Caquetá, Colombia (00° 56′ N, 72° 42′ W). (14) Tonantins, Amazonas, Brazil (02° 47′ S, 67° 47′ W). (15) Divisor; Loreto, Peru (07° 12′ S, 73° 53′ W). (16) Kiteni, Cuzco Peru (12° 20′ S, 72° 50′ W). (17) Cordillera de Pantiacolla, Madre de Dios, Peru (12° 40′ S, 71° 13′ W). (18) Santa Cruz, Rio Eiru, Amazonas, Brazil (07° 30′ S, 70° 49′ W). (19) Eirunepé, Amazonas, Brazil (06° 40′ S, 69° 52′ W). (20) Reserva Uakarai, Amazonas, Brazil (05° 26′ S, 67° 17′ W). (21) Carauarí, Amazonas, Brazil (04° 52′ S, 66° 54′ W). (22) Region of the Rio Canumã, Amazonas, Brazil. (23) Jacareacanga, Amazonas, Brazil (06° 27′ S, 57° 54′ W). (24) Rio Sucunduri near BR 230, Amazonas, Brazil (06° 46′ S, 59° 07′ W). (25) Alta Floresta, left bank Rio Teles Pires (09° 50′ S, 55° 54′ W) and Rio Cristalino, right bank (09° 36′ S, 55° 56′ W), Mato Grosso, Brazil. (26) Riozinho, Area Indigena Kayapó, Pará, Brazil (~ 08° 00′ S, 52° 00′ W). (27) Bosque de Guaipé, Vichada, Colombia (05° 18′ N, 67° 57′ W). (28) Vicinal Aporui, 12 km north of Caracarai, Roraima, Brazil (01° 59′ N, 61° 45′ W).

default settings of RAVEN 1.3 (Charif et al. 2008), except the display was set to smooth, overlap was adjusted from 50 to 93.7% depending on recording quality, and contrast was adjusted according to recording intensity with care taken to retain all elements of the vocalization. Cursor measurements were typically at scales of 0.07 sec/cm and 0.6 kHz/cm. A concern that voices of males and females might differ as in some other thamnophilid species (e.g., Isler et al. 2002, 2007a) dictated that the analysis initially distinguished recordings of males and females. Unfortunately, individuals in the *Willisornis* complex often vocalize from beneath dense cover, and many recordings did not identify either male or female. Consequently, the analysis proceeded in an iterative fashion, aggregating samples when results did not indicate differences between males and females or between those identified and unidentified to gender. For example, we compared samples of male loudsongs of populations (except *gutturalis*, whose recording inventory of male vocalizations was insufficient) before adding samples of recordings of females and those unidentified to gender. Sample sizes cited reflect number of individuals, not number of vocalizations measured.

Diagnostic differences had to be discrete, non-overlapping character states that have the potential for unambiguous signal recognition (Isler et al. 1998, 1999). Ranges of samples of continuous variables could not overlap, and the likelihood that ranges would not overlap with larger sample sizes was estimated by requiring the means ($\bar{x}$) and standard deviations (SD) of the population with the smaller set of measurements (*a*) and the population with the larger set of measurements (*b*) to meet the test:

$$\bar{x}_a + t_a SD_a \leq \bar{x}_b - t_b SD_b$$

where t_i = the *t*-score at the 97.5 percentile of the *t* distribution for $n - 1$ degrees of freedom.

A similar test could not be used for ratios which were not normally distributed. Thus, we used a non-parametric bootstrap simulation to examine statistical significance. We compared Difference Between Means (DBM) of the two taxa being analyzed and two groups of generated data of the same sample sizes. The method generated 10,000 sample population pairs, with replacement, and compared the DBM between the two compared species to the distribution of DBMs of the simulated populations. The result was distributed normally, and significance was assigned according to the rules of this distribution.

We recommend species status under the Biological Species Concept (BSC) for populations that differed diagnostically in both vocalizations and morphology. We accepted current subspecies definitions as reflecting diagnostic morphological differences described in the literature (Cory and Hellmayr 1924, Zimmer 1934, Ridgely and Tudor 1994, Zimmer and Isler 2003) after finding them to be consistent in large series of specimens examined at major museums. Vocal differences were considered diagnostic if the analysis revealed three or more diagnostic characters following the ''yardstick'' developed by Isler et al. (1998). For brevity, we use subspecies names to reference populations.

RESULTS

Subspecies differed from their geographic neighbors by at least one diagnostic plumage character in every instance (100% diagnosable) with the exception of *duidae* and *lepidonotus*, and apparent hybrids between *poecilinotus* and *duidae*. We examine the biogeography of parapatric populations after reporting the results of vocal analyses.

Vocalizations

Vocal repertoires of *Willisornis* populations include five principal vocal types: (1) *loudsongs*, (2) *contact calls*, (3) *chirrs*, (4) *raspy series*, and (5) *other calls*. *Softsongs* were recorded too infrequently to be useful in the analysis.

Loudsongs.—All subspecies deliver a series of long, upslurred notes separated by shorter intervals, the series generally rising in pitch (Fig. 2). Individual variation of loudsong characteristics within populations was high. For example, of 37 loudsongs analyzed for *poecilinotus*, nine contained 3–5 notes, 11 contained 6–8 notes, 13 contained 9–11 notes, and four contained 12–15 notes. The unusually large variability could not be related to gender or age in our samples. No diagnosable differences in loudsongs were found between populations as a consequence of the large within-population variability with one exception. Notes of *nigrigula* and *vidua* were frequency-modulated in an even pattern, whereas such modulation was erratic or lacking in loudsong notes of the other subspecies (Fig. 2). Differences in note shape allowed perfect allocation of loudsong recordings to the two groups, and

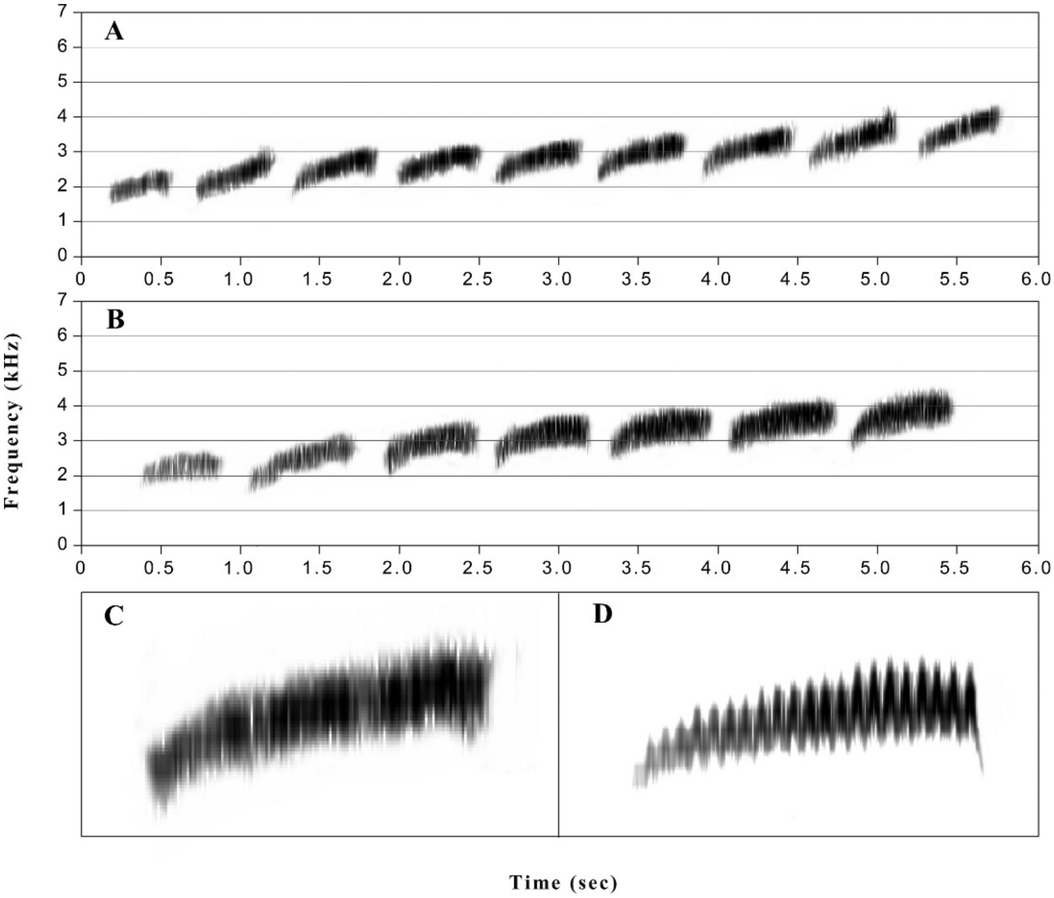

FIG. 2. Loudsongs of *Willisornis* populations. Nomenclature follows recommendations of this paper. Acronyms for recording archives in Appendix. (A) *W. p. lepidonotus*, Kapawi Lodge, Pastaza, Ecuador (ISL BMW 157:001). (B) *W. v. nigrigula*, km 209 on BR 230 south of Itaituba, Pará, Brazil (ISL BMW 226:002). (C) *W. p. lepidonotus*, Kapawi Lodge, Pastaza, Ecuador (ISL BMW 157:001). (D) *W. v. vidua*, Caxiuanã, Pará, Brazil (ISL BMW 109:022). Magnified notes are expanded 3× on frequency axis, 4× on time axis.

differences in quality were apparent in the field and laboratory to the human ear.

Differences in loudsong characteristics among other populations did not meet our criteria as diagnostic, but when values were plotted geographically, distributional patterns emerged that may prove relevant to future species-level analysis. For example, frequency measures of the first note of *poecilinotus* loudsongs (37 individuals) were higher pitched than those of *duidae* (18 individuals), and ranges barely overlapped. When these frequency characters were mapped geographically, the extreme examples of each population occurred at considerable geographic distance from the contact zone, and loudsongs recorded closest to the contact zone (although only 2 individuals of each taxon) differed substantially.

Similar differences were found between *duidae* and *lepidonotus* loudsongs with *duidae* notes delivered at lower frequencies and a slower pace. For example, the mean of the lowest frequency of the central note of *duidae* was 1,948 Hz (range = 1,332–2,177, SD = 242, n = 18), whereas that of *lepidonotus* was 2,302 Hz (range = 2,177–2,678, SD = 128, n = 24), but the difference did not meet our significance test. Plotting frequency and pace geographically did not suggest a tendency for *duidae* loudsongs either to diverge or converge clinally with *lepidonotus*, although recordings are needed from the region where these populations are likely to come into contact. No significant

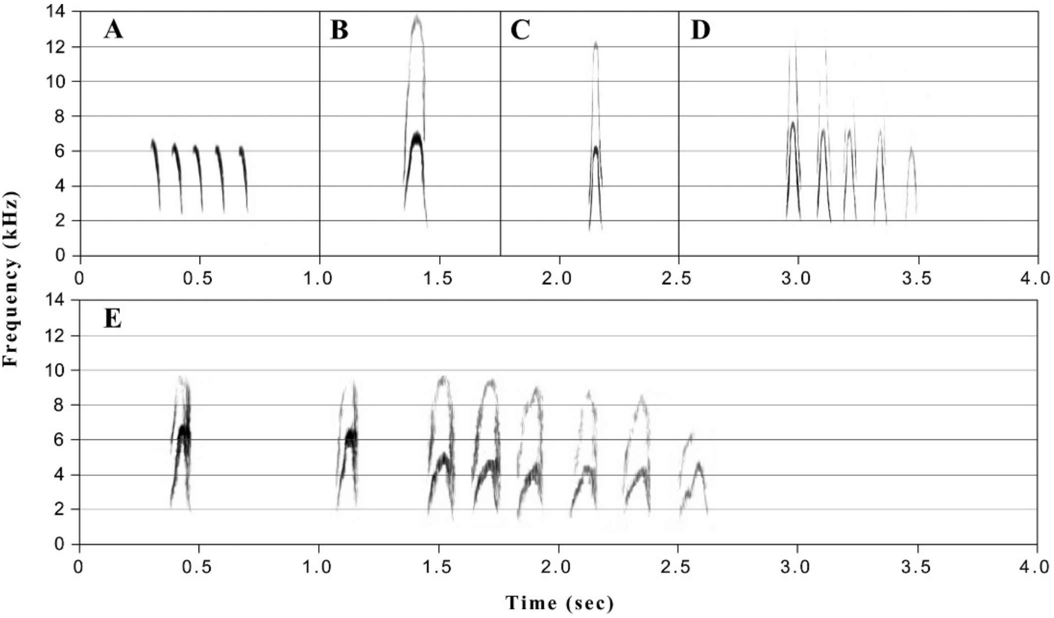

FIG. 3. Contact calls of *Willisornis* populations. Nomenclature follows recommendations of this paper. Acronyms for recording archives in Appendix. (A) *W. v. nigrigula*, Jacareacanga, Pará, Brazil (ISL BMW 219:065). (B) *W. p. poecilinotus*, Reserva Ducke, Amazonas, Brazil (ISL BMW 131:020). (C) *W. p. griseiventris*, Prainha Nova, Amazonas, Brazil (ISL BMW 196:028). (D) *W. p. griseiventris*, Explorer's Inn; Madre de Dios, Peru (ML 35547). (E) *W. p. duidae*, Parque Nacional Natural Chiribiquete, Caquetá, Colombia (ISL MAR 006:033).

differences were found with regard to elevational differences within *lepidonotus*, even though a small sample of higher elevation loudsongs tended to be higher pitched and faster.

Initial notes of *griseiventris* loudsongs in general were lower-pitched than the equivalent *lepidonotus* notes, but loudsongs of the westernmost population of *griseiventris*, nearest the range of *lepidonotus*, were highest in frequency and closest to notes of *lepidonotus*, suggesting clinality. We identified no differences in *griseiventris* loudsongs east and west of the Rio Madeira.

Contact Call.—These calls consist of abrupt notes given when flying between perches as well as when perched. They differed diagnosably between what we termed a *twitter,* which is found only in the repertoires of *nigrigula/vidua,* and a *psit,* which is delivered only by the remaining populations (Fig. 3). The *twitter* is a short (2–16, typically 3–5), high-pitched series of clear, almost tinkling, musical notes (Fig. 3A) Each note bends slightly downward in frequency; the series descends slightly in frequency; and intervals between notes with rare exceptions lengthen slightly (typically from 60 to 75 millisec, extremes 34 and 112 millisec). Notes, especially the initial note, often start with a small hook (Fig. 3A). In contrast, the *psit* note was shaped like an inverted U or V, usually sounding lower-pitched and harsher to the human ear than the *twitter*. The *psit* was typically given singly (Fig. 3B and C), but occasionally in short series that usually decreased in frequency, sometimes dramatically so (Fig. 3D and E).

The duration of the *psit* call varied among populations. The mean length in northern lowland populations (*poecilinotus*, *duidae*, and lowland *lepidonotus*) was 0.093 sec (range = 0.071–0.118, SD = 0.0120, n = 20; Fig. 3B), whereas the mean for highland and southern populations (highland *lepidonotus* and *griseiventris*) was 0.054 sec (range = 0.047–0.063, SD = 0.0051, n = 20; Fig. 3C). The difference was diagnosable under our criteria. However, when four examples for *gutturalis* were added to the highland and southern populations, the mean and variance were slightly larger 0.055 sec (range = 0.047–0.069, SD = 0.0066, n = 24), narrowly failing our statistical test.

Chirrs.—This call consisted of a short series (duration: $\bar{x}$ = 0.596 ± 0.189 sec, range = 0.248–1.020 sec, n = 52) of abrupt (5–9 millisec) notes, vertical on a spectrogram, repeated rapidly (~5

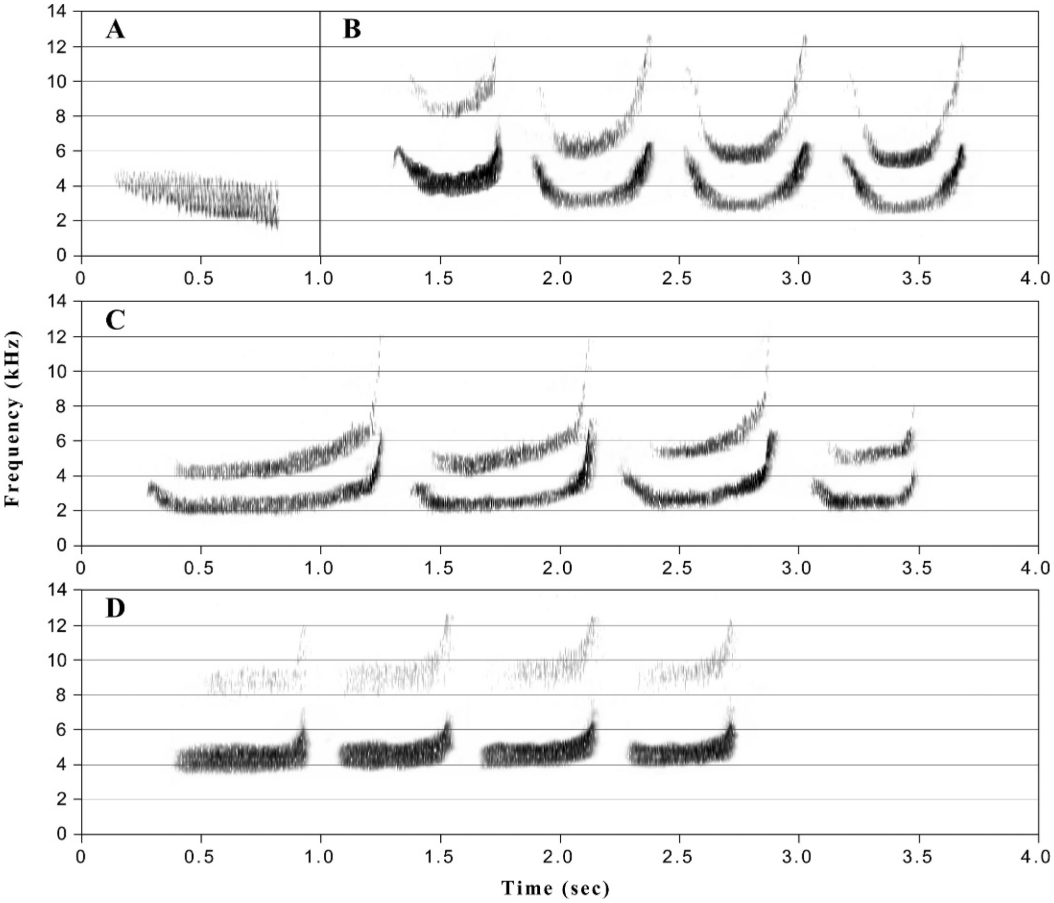

FIG. 4. Chirr and raspy calls of *Willisornis* populations. Nomenclature follows recommendations of this paper. Acronyms for recording archives in Appendix. (A) Chirr *W. p. griseiventris*, Humaitá, Amazonas, Brazil (ISL BMW 219:081). (B) Raspy call *W. p. poecilinotus*, Iwokrama Forest Reserve; Guyana (ISL BMW 158:003). (C) Raspy call *W. p. griseiventris*, right bank Rio Jiparaná opposite Palmeiras, Rondônia, Brazil (ISL BMW 208:020). (D) Raspy call *W. v. vidua*, Caxiuanã, Pará, Brazil (ISL BMW 180:048).

notes in 0.1 sec), and typically descending in pitch (e.g., apex of notes ~ 5 mHz descending to ~4 mHz) (Fig. 4A). Chirrs have been recorded for all populations. No diagnostic differences in chirrs were found among *Willisornis* populations, although the duration of chirrs of *nigrigula* and *vidua* overlapped only slightly. Average chirr duration in *nigrigula* recordings was 0.728 ± 0.209 sec, range = 0.420–1.020, n = 10), whereas that of *vidua* was 0.399 ± 0.053 sec, range = 0.322–0.444, n = 6). Difference in means met student's t-test at 99%. At times chirrs were combined with contact calls.

Raspy Series.—Notes in raspy series were typically repeated 2–4 times but were sometimes given individually or in longer series. Typical *poecilinotus* calls had ''U'' shaped notes (Fig. 4B); the series descending slightly in pitch, sounding like ''cheery, cheery, churry, churry.'' The call of *griseiventris* typically had the initial part of the note truncated, making it look like a ''J'' in a spectrogram, and the base of the notes typically rose slightly in frequency (Fig. 4C). Few calls were available for *duidae*, *lepidonotus*, and *gutturalis*, but they suggested intermediacy between *poecilinotus* and *griseiventris* and, consequently, differences among these five subspecies were not considered diagnostic. We suspect that analysis of larger samples may detect diagnostic differences in raspy series among these populations. Note shapes in raspy series of *vidua* and *nigrigula*, in contrast, differed consistently from those of other

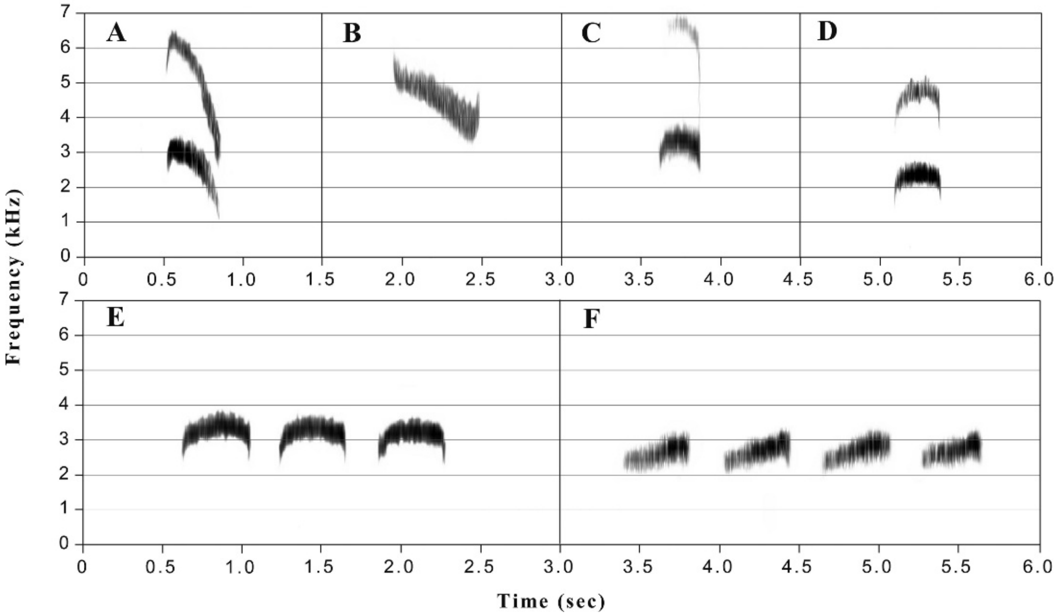

FIG. 5. Other calls of *Willisornis* populations. Nomenclature follows recommendations of this paper. Acronyms for recording archives in Appendix. (A–B) Down-slurred calls. (A) *W. p. griseiventris*, Rio Bararati, Amazonas, Brazil (ISL BMW 229:045). (B) *W. p. poecilinotus*, Iwokrama Forest Reserve, Guyana (ISL BMW 155:021). (C–E) Inverted U shaped calls. (C) *W. p. poecilinotus*, 25 km SE Maripa, Bolívar, Venezuela (ISL BMW 071:003). (D) *W. p. poecilinotus*, Iwokrama Forest Reserve, Guyana (ISL BMW 144:012). (E) *W. p. lepidonotus*, El Tigre, Loreto, Peru (ISL JA 01:050). (F) Upscale call *W. p. griseiventris*, Fazenda Rancho Grande, Rondônia, Brazil (ISL KJZ 016:034).

populations. Notes delivered by *nigrigula* and *vidua* (Fig. 4D) lacked the down-pitched beginning of the note and had a flat or sometimes ascending, vibrant base of wider frequency range than notes of the other populations.

Other Calls.—Calls other than contact calls, chirrs, and raspy series were relatively rarely recorded and, in most instances, the recordist did not clearly attribute the call to a *Willisornis* population. Four differently shaped calls have been recorded, including down-slurred, inverted U shaped, and upslurred notes. The most common type was down-slurred, ~0.2–0.4 sec in duration, and descending generally in the range of 4.0 to 1.5 mHz (Fig. 5A). Calls of this type were found in recordings of *griseiventris*, *nigrigula*, *vidua*, and *lepidonotus* above 800 m. A longer (0.45–0.6 sec), higher pitched, down-slurred (6 to 4 mHz) *''pseer''* (Fig. 5B) has been recorded twice for *poecilinotus*. Short (~0.25 sec), inverted U shaped notes sounding like an abrupt *''wheet''* were recorded for *poecilinotus* in the 2.6–3.4 mHz frequency range (Fig. 5C) and in the 1.9–2.3 mHz frequency range (Fig. 5D) for *gutturalis* in which the notes were doubled, for *lepidonotus* below 800 m in a short series (Fig. 5E), and for an uncertain population near the contact zone between *gutturalis* and *griseiventris*. An abrupt upscale note given in series was recorded for *griseiventris* (Fig. 5F) and for *lepidonotus* below 800 m. The meager data suggest differences in other calls between northern and southern populations may be identified with a larger number of recordings.

Little is known of the functions of vocalizations in the *Willisornis* complex. K. J. Zimmer observed and tape-recorded a display by a male *nigrigula* in the presence of a female-plumaged individual in August 1991 near the Rio Cristalino, Mato Grosso, Brazil. Perched on a slender diagonal branch ~0.7 m above the ground, the male drooped his wings, stretched his neck up vertically, and extended his head up and down rapidly on a vertical axis, calling continuously all the while. The calls included raspy series and chirrs, and other calls, and are the only indication we had of the behavioral role of these vocalizations.

Biogeography of Parapatric Populations

Biogeographic analysis indicated numerous instances of apparent parapatry between morphologically distinct neighbors. Populations separated by the Amazon River (*poecilinotus* with *griseiventris*, *nigrigula*, and *vidua*; *duidae* with *gutturalis* and *griseiventris*; and *lepidonotus* with *gutturalis*) were considered to be allopatric rather than parapatric as gene flow between them is highly unlikely. We provide brief summaries of morphological distinctions and consider biogeographic relationships between neighboring pairs of parapatric subspecies starting with *poecilinotus* and *duidae* in the north and proceeding counterclockwise around the Amazon Basin (localities provided in Fig. 1).

Contact Between W. p. poecilinotus and W. p. duidae.—Females are distinguished by gray underparts in *poecilinotus* (brown in *duidae*) and buffy ''scales'' on the lower back of *poecilinotus* (white in *duidae*). Males differ only by a smaller interscapular patch in *poecilinotus*. Geographic ranges of *poecilinotus* and *duidae* are only partially delimited by rivers. The Río Orinoco may separate the subspecies at the northernmost end of their contact zone. The most proximate specimen locations are from Caño Usate (COP, *poecilinotus*) and Campamento Manaka (COP, *duidae*), Amazonas, Venezuela, ~90 km apart. The Rio Orinoco lies between these locations as well as between Caño Usate and Colombian specimens from Vichada (Instituto Humboldt). Ranges of *poecilinotus* and *duidae* at the southern end of their contact zone in Amazonas, Brazil, extend to the left and right banks of the lower Rio Negro, respectively. Extensive fieldwork did not find either taxon on the many islands (Anavilhanas Archipelago) in this broad river (Cintra et al. 2007), although *duidae* occupies some islands in the upper Rio Negro near São Gabriel da Cachoeira. No barrier appears to prevent antbirds from coming into contact in the region between the upper Orinoco and the right bank of the Rio Branco; *poecilinotus* alone appears to occupy the area below the Rio Branco south to the Amazon. Apparent hybrids have been collected in the Valle de los Monos on the southern slope of Mt. Duida, Amazonas, Venezuela, where *poecilinotus* has been collected on the southeastern slope and *duidae* on the western slope. As described by Zimmer (1934) and corroborated by reexamination of the pertinent specimens by MLI, one (AMNH 273015) of five females collected closely resembles *duidae*, one (AMNH 273017) is indistinguishable from *poecilinotus*, and the remaining three (AMNH 273015, 273018, 273686) have a mixture of ventral and back scale coloration of the two populations. The most proximate locations to the southeast of Mt. Duida in Venezuela are Río Putaco (COP, *poecilinotus*) and Ocamo (AMNH, *duidae*), ~100 km distant. Further southeast in Brazil, an even greater distance, ~280 km, separates specimens from the Rio Dimiti in Amazonas and the vicinity of Caracaraí, Roraima, although the intervening region is poorly studied ornithologically. No hybrids other than those from Mt. Duida are known.

Contact Between W. p. duidae and W. p. lepidonotus.—Chapman (1923) described the *duidae* male as paler gray below, the female as more reddish and brighter throughout compared to *lepidonotus*. In addition, the interscapular patch was found to be smaller in *duidae* (Zimmer 1934). Chapman's original description and Zimmer's (1934) analysis were based on specimens from near the extremes of their ranges: Venezuela and northwestern Brazil for *duidae* and Peru and Ecuador for *lepidonotus*. Later Colombian specimens from along the base of the Andes in Meta were identified as *duidae* and those from western Caquetá and Putumayo as *lepidonotus* (Meyer de Schauensee 1964). Most recently, the population in the Sierra de Chiribiquete, Caquetá, Colombia, was identified as *duidae* (Stiles et al. 1995) which, along with the population in Tonantins, Amazonas, Brazil (CM), closes the gap between their ranges. However, a sufficient series of specimens from the intermediate region in Colombia has not yet been procured to examine possible clinality in morphological characters.

Contact Between W. p. lepidonotus and W. p. griseiventris.—Females are distinguished by brown underparts in *lepidonotus* (gray in *griseiventris*) and white ''scales'' on the lower back of *lepidonotus* (absent in *griseiventris*). Males do not differ diagnosably. The Río Ucayali separates the ranges of *lepidonotus* and *griseiventris* in central Peru. However, further south towards the headwaters of the Río Ucayali, no river appears to perform this function. The closest confirmed locations are Kiteni; Cuzco (LSUMZ) for *lepidonotus* and the east slope of Cordillera de Pantiacolla, Madre de Dios (FMNH), for *griseiventris*. These locations are ~190 km apart and are separated by mountainous terrain with elevations >2,000 m. There are more proximate locations to the north in intervening terrain of lower elevation cited in the literature with unidentified subspecies.

Contact Between W. p. gutturalis and W. p. griseiventris.—Females are distinguished by brown underparts in *gutturalis* (gray in *griseiventris*) and white ''scales'' on the lower back of *gutturalis* (absent in *griseiventris*). Females of *gutturalis* also typically have crown redder than back (concolor in other populations). Males of *gutturalis* have black throat patches (absent in *griseiventris*). The geographic range of *gutturalis* is the smallest of any subspecies, restricted in Peru and Brazil to the region immediately south of the Amazon and east of the lower Río Ucayali (Fig. 1). The extent of its range to the east and south is unclear. The likelihood that the Rio Juruá provides a barrier in a section of their contact zone is supported by specimens of female *gutturalis* from Eirunepé (formerly João Pessôa) on the left bank of the Juruá and by male *griseiventris* from Santa Cruz on the Rio Eiru, a right bank tributary (Pinto 1942, 1978; specimens examined at MZUSP). However, sight records from both banks of the Rio Juruá at the Reserva Uakarai were identified as *griseiventris* (Andrew Whittaker, pers. comm.). To the southwest, in the Juruá–Ucayali interfluvium, *griseiventris* has been found at Divisor, Loreto, Peru, and at two other locations west of the Sierra del Divisor (Vriesendorp et al. 2006:195). Consequently, known ranges of *gutturalis* and *griseiventris* are separated by ~280 km of probably suitable habitat in this region with no river barriers.

Contact Between W. p. griseiventris and W. p. nigrigula.—The extension of the gray of the underparts to the sides of the head (ear coverts and lores) distinguishes female *nigrigula* from *griseiventris*. Males of *nigrigula* have a black throat, while throats of male *griseiventris* are plain gray. The Rio Canumã and, continuing further upstream, the Rio Sucunduri, separates their ranges (regions of locations 22 and 24; Fig. 1). However, the range of *griseiventris* passes the headwaters of the Rio Sucunduri to reach the Rio Tapajós above Jacareacanga, where it overlaps *nigrigula* and may hybridize with it locally (BMW observations and recordings of both taxa). Beyond this point, to the south, only *griseiventris* has been found on the left (west) bank of the Rio Tapajós and its major tributary, the Rio Teles Pires, whereas *nigrigula* occurs on the right (east) bank of these rivers.

Contact Between W. p. nigrigula and W. p. vidua.—Males of *nigrigula* have discreet black throat patches which are absent in *vidua*, the throat of which tends to be more whitish than its gray underparts. Females of *vidua* differ from *nigrigula* by having flanks suffused reddish-yellow-brown (slightly tinged in *nigrigula*) and wing edgings grayish-brown (reddish-yellow-brown in *nigrigula*). Interscapular patches are larger in *nigrigula* (15–20 mm) than in *vidua* (0–10 mm). The known geographic ranges of *nigrigula* and *vidua* with one exception are separated by a wide geographic gap west of the Rio Xingu (Fig. 1), although much of the region between the known ranges of these populations is unexplored ornithologically. The only known convergence of *nigrigula* and *vidua* is based on sight records by BMW in September 1994 of males within ~1 km of each other at Riozinho, Area Indigena Kayapó, Pará; it cannot be considered definitive, but does serve to suggest the possibility of parapatry of these forms in this poorly studied region.

DISCUSSION

Diagnostic differences in loudsongs, raspy series, and contact calls were documented between two groups of taxa that were also distinct in plumage: *nigrigula* and *vidua* of southeast Amazonia, and the remaining populations. However, compared to other widespread Amazonian thamnophilid complexes studied by the authors (e.g., Isler et al. 2007a, b), relatively few vocal differences meeting our guidelines for species status were found among other populations in the *Willisornis* complex. Consequently, we recommend the complex be considered to consist of two species and seven subspecies:

Willisornis poecilinotus (Cabanis)—Common Scale-backed Antbird

W. p. poecilinotus (Cabanis)
W. p. duidae (Chapman)
W. p. lepidonotus (Sclater and Salvin)
W. p. griseiventris (von Pelzeln)
W. p. gutturalis (Todd)

Willisornis vidua (Hellmayr)—Xingu Scale-backed Antbird

W. v. nigrigula (Snethlage)
W. v. vidua (Hellmayr)

The proposed English name of *W. vidua* is taken from the major river that flows through the center of its geographic range.

Within each of these two groups, differences in plumage characters, such as the presence/absence of a black throat patch, served to distinguish almost all subspecies at the 100% level. The single exception was *duidae* and *lepidonotus*, whose differences in coloration (redder female, paler male in *duidae*) may or may not prove to be clinal when additional specimens are obtained in Colombia. The clear differences in plumage characters led us to concentrate our analysis on the biogeographic relationships between members of pairs of parapatric populations. Considering *duidae* and *lepidonotus* as a single taxon (*lepidonotus* has priority), locality data indicated that geographic ranges of five pairs of taxa (*poecilinotus/lepidonotus*, *lepidonotus/griseiventris*, *gutturalis/griseiventris*, *griseiventris/nigrigula*, and *nigrigula/vidua*) were not separated, or only partially separated, by wide river barriers. Large geographic gaps in our knowledge of the taxa occupying these potential contact zones currently prevents us from ascertaining whether: (1) some or all of these plumage-defined populations are evolving independently and deserve species status under the BSC; (2) there is widespread intergradation between neighbors; or (3) secondary contact of populations is only incipient, and the evolutionary dynamic in regions of overlap is yet to unfold. Consequently, we reserve judgment on the possible species status of the taxa listed as subspecies. Field work in potential contact zones is needed not only to obtain morphological data and material for genetic analysis, but also to record vocalizations. Differences in vocal characters between these populations did not meet our conservative requirements to be diagnosable, but recordings from contact zones may provide a different perspective. Geographically fine-grained recording of loudsongs can provide a test of whether vocalizations converge or diverge in contact zones, and it is possible that calls rarely recorded for the complex may differ diagnosably.

Collections of specimens and vocal recordings are needed from the Andean foothills (>800 m) population of *lepidonotus* given the suggestion in vocalizations and preliminary molecular studies that it may be distinct from lowland populations. The two available examples of the contact call of *lepidonotus* >800 m were short in duration and therefore similar to that of *griseiventris*.

Genetic analysis now underway at FMNH (J. M. Bates, pers. comm.) should provide relevant insights into the phylogenetic relationships of these taxa including whether members of parapatric pairs are closest relatives. Early results showed 6.8% divergence in two mitochondrial genes between *nigrigula* and *griseiventris* across the Rio Teles Pires near the confluence of the Rio Cristalino; 0.6% divergence of *griseiventris* between left bank Teles Pires and right bank Rio Jiparaná; 0.5% divergence between *nigrigula* on right bank Teles Pires and two sites (Serra dos Carajás and 52 km S Altamira) of *vidua* (Bates et al. 2004). In addition, a study of speciation in the region of the upper Rio Negro in northwestern Brazil found 10.8% genetic divergence between *poecilinotus* and *duidae* (Naka 2010). Differences in duration of contact call notes of *Willisornis* populations north and south of the Amazon suggest an early divergence that should be relevant to evolutionary studies as well as systematics.

Current knowledge provides only the ‘‘tip of the iceberg,’’ and valuable insights relevant to systematics, conservation, and broader studies of evolution await further investigation of the *Willisornis* complex.

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APPENDIX

Recordings Examined.—The following list identifies recordings used in the study by taxon, country, state or department, recording location, and recordist. Numbers following the recordist name identify the number of cuts per recordist per location. Acronyms for recording archives: BSA = Banco de Sonidos Animales, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá. FSM = Florida State Museum Sound Archive. ML = Macaulay Library, Cornell Laboratory of Ornithology, Ithaca; ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by Morton and Phyllis Isler. Many of these unarchived recordings either are in the process of being archived or will eventually be archived by the recordists. Nomenclature reflects recommended taxonomic position.

Willisornis p. poecilinotus: (53 recordings; 24 locations). Brazil: Amapá: Porto Grande (Zimmer 3 ISL); Amazonas: Rio Apuaú (Cohn-Haft 1 ISL), 60–90 km N Manaus (Bierregaard 1 ML, Stouffer 1 ML, Whitney 1 ISL, Whittaker 1 ISL), Reserva Ducke (Whitney 1 ISL). Guyana: Acarai Mountains (Robbins 1 ML), Baramita (Brumfield 1 ISL), Iwokrama Forest Reserve (Whitney 5 ISL), Kaieteur Fall (Milensky 1 ISL), Kako River (Robbins 2 ML), Kopinang (O'Shea 1 ML), Kuyuwini River (Finch 2 ML), Marshall Falls (Finch 1 ML), Nappi Village (Parker 1 ML), Sipu River (Milensky 1 ISL), Waruma River (O'Shea 1 ML). Suriname: Brownsberg Nature Reserve (Davis 2 ML, Whitney 2 ISL), Kraka-Zenderij Road (Whitney 1 ISL), Raleigh Vallen (Whitney 1 ISL), Voltzberg (Davis 1 ML, M. Isler 1 ML, Whitney 1 ISL). Venezuela: Amazonas: Junglaven Camp (Zimmer 1 ISL); Bolívar: El Palmar (Parker 2 ML, Schwartz 3 ML), La Escalera (Behrstock 1 ISL, M. Isler 1 ML, Macaulay 1 ML, Schwartz 1 ML, Whitney 1 ISL, Zimmer 2 ISL), 20–30 km SE Maripa (Stejskal 1 ISL, Whitney 2 ISL), Sierra de Lema (Behrstock 1 ISL, Zimmer 1 ISL).

Willisornis p. duidae: (29 recordings; 9 locations). Brazil: Amazonas: P. N. do Jaú (Pacheco 1 ISL, Whitney 1 ISL, Whittaker 1 ISL), Manacapuru (Whitney 1 ISL), São Gabriel da Cachoeira, island in Rio Negro (Whitney 2 ISL), São Gabriel da Cachoeira. L bank Rio Negro (Whittaker 1 ISL, Whitney 3 ISL, Zimmer 2 ISL), São Gabriel da Cachoeira. R bank Rio Negro (Cohn-Haft 1 ISL, Whitney 1 ISL, Zimmer 1 ISL). Colombia: P. N. N. Chiribiquete (M. Alvarez 10 BSA), Vaupés: Mitú (Hilty 2 ISL). Venezuela: Amazonas: Frente Isla Cigarrón (Schwartz 1 ML), Picua (Coons 1 ISL).

Willisornis p. duidae or *lepidonotus*: (4 recordings; 1 location). Colombia: Amazonas: Parque Nacional Natural Amaca-yacú (P. Isler 1 ISL, Whitney 3 ISL).

Willisornis p. lepidonotus below 800 m: (37 recordings; 18 locations). Ecuador: Morona-Santiago: Miazal (Whitney 1 ISL), Santiago (Robbins 1 ISL); Napo: La Selva Lodge (Behrstock 1 ISL, Coopmans 2 ML, Donahue 1 ML, Wolf 2 ISL), km 37 Maxus Road (Krabbe 3 ISL), Tiputini Biodiversity Station (Behrstock 1 ISL, Zimmer 2 ISL); Pastaza: Kapawi Lodge (Whitney 1 ISL, Wolf 1 ISL); Sucumbíos: Cuyubeno (Whitney 1 ML). Peru: Loreto: Colonia Angamos (Lane 1 ISL), 79 km WNW Contamana (Lane 3 ISL), El Dorado (Whitney 3 ISL), El Tigre (J, Alvarez 3 ISL), Explorama Lodge (Whitney 1 ISL), Intuto (Whitney 1 ISL), Quebrada Orán (Whitney 2 ISL), Quebrada Sucusari (P. Isler 1 ML), Sachacocha (J. Alvarez 1 ISL), Yanamono (Budney 2 ML, Whitney 1 ISL); San Martín: Tarapoto- Yurimaguas Road (Lane 1 ISL).

Willisornis p. lepidonotus above 800 m: (16 recordings; 8 locations). Ecuador: Napo: 15 to 80 km W of Loreto by road (J. Rowlett 1 ISL, R. Rowlett 1 ISL, Whitney 2 ISL, 1 ML, Wolf 1 ISL), Volcán Sumaco (R. Rowlett 1 ISL); Zamora-Chinchipe: Parque Nacional Podacarpus (Wolf 1 ISL). Peru: Cajamarca: Cordillera del Cóndor, (Schulenberg 1 ISL), Puesta Vigilancia (Schulenberg 1 ML); Loreto: 77 km WNW Contamana (Lane 3 ISL), ~90 km SE Juanjui (Lane 2 ISL); San Martín: Jirillo, 15 km NE (Schulenberg 1 ML).

Willisornis p. gutturalis: (12 recordings; 3 locations). Brazil: Amazonas: Benjamin Constant (Whitney 4 ISL), R. N. Palmarí (Whitney 5 ISL, Zimmer 1 ISL). Peru: Loreto: Tahuayo Lodge (Hornbuckle 2 ISL).

Willisornis p. griseiventris: W of Madeira: (40 recordings; 23 locations). Bolivia: La Paz: Campamento Nuano (Tello 1 ISL), Chalalán (Whitney 1 ISL), Cadena Pilón (Parker 1 ISL), Puerto Linares (Wiedenfeld 1 ML), Serranía Tequeje (Hennessey 1 ML); Pando: Río Abuña, (Parker 1 ISL), Camino Mucden (Parker 3 ML), 12–20 km SW Cobija (Parker 1 ISL), San Juan de Nuevo Mundo (Parker 1 ISL). Brazil: Acre: Boca de Tejo (Whittaker 2 ISL); Amazonas: Amazon Lodge (Zimmer 2 ISL), Humaitá (Whitney 3 ISL), Lábrea (Whitney 1 ISL, Zimmer 1 ISL), Igarapé Santa Maria (Whitney 1 ISL), Tefé (Pacheco 1 ISL), Fazenda Toshiba (Marantz 1 ML), Tupana Lodge (Zimmer 4 ISL), Uará (Whittaker 1 ISL). Peru: Madre de Dios: Cuzco Amazonica Lodge (Marantz 1 ML), Explorer's Inn (Donahue 1 ML, M. Isler 1 ML, Kibler 3 ML, Parker 2 ML), Cordillera del Pantiacolla (Fitzpatrick 2 ML); Puno: Campamento Topo Tres (Schulenberg 1 ISL); Ucayali: Cerro Tahuayo (Meyer 1 ISL).

Willisornis p. griseiventris: E of Madeira: (74 recordings; 25 locations). Bolivia: Santa Cruz: Flor de Oro (Whitney 1 ISL), Los Fierros (Whitney 2 ISL), Perseverancia (Fisher 1 ISL, Parker 1 ISL, 1 ML). Brazil: Amazonas: Rio Atininga (Whitney 1 ISL), Rio Bararati (Whitney 5 ISL), Barra de São Manuel (Whitney 4 ISL), Borba (Whitney 1 ISL, Whittaker 1 ISL), Nova Olinda (Rio Aripuanã) (Whitney 1 ISL), Rio Ipixuna (Whitney 1 ISL), Puxurizal (Marantz 1 ML, Whitney 1 ISL), mouth of Rio Palomitas (Whitney 4 ISL), Pousada Jurumé (Whitney 2 ISL), Pousada Rio Roosevelt (Whittaker 2 ISL, Zimmer 1 ISL), Prainha Nova (Whitney 1 ISL), L bank Rio Sucunduri near BR 230 (Whitney 5 ISL); Mato Grosso: Alta Floresta (M. Isler 2 ISL, P. Isler 1 ISL, Parker 2 ISL, Whitney 3 ISL, Zimmer 5 ISL), R bank Rio Juruena opposite mouth Rio Bararati (Whitney 1 ISL), mouth of Rio São Benedito (Whittaker 1 ISL), mouth of Rio São Tome (Whitney 2 ISL); Rondônia: Rio Caracol (Whitney 1 ISL), R bank Rio Jiparaná opposite Palmeiras (Whitney 3 ISL), Serra dos Pacaás Novos (Whittaker 3 ISL), Palmeiras (Whitney 4 ISL), Porto Velho (Whitney 6 ISL), Fazenda Rancho Grande (Zimmer 3 ISL).

Willisornis vidua nigrigula: (47 recordings; 15 locations). Brazil: Amazonas: Igarapé Pedral (Whitney 4 ISL), Igarapé do Seringal (Whitney 2 ISL), 52 km W Jacareacanga (Whitney 1 ISL), R bank Rio Sucunduri near BR 230 (Whitney 3 ISL); Mato Grosso: Rio Cristalino (Michael 1 ML, Whitney 2 ISL, Zimmer 8 ISL); Pará: Parque Nacional de Amazonia (Whittaker 5 ISL), Aveiro (Whitney 3 ISL), Boim (Whitney 1 ISL), Cachimbo (Whittaker 1 ISL), Capelinha Trail (Parker 1 ML), km 209 S of Itaituba (Whitney 3 ISL), Jacareacanga (Whitney 3 ISL), Miritituba (Whitney 3 ISL, Willis 3 FSM), Porto do Meio (Whitney 1 ISL), Riosinho (Whitney 1 ISL), Rurópolis (P. Isler 1 ML).

Willisornis v. vidua: (39 recordings; 6 locations). Brazil: Pará: Serra dos Carajás (Whitney 3 ISL, Zimmer 2 ISL), Caxiuanã (Marantz 1 ML, Whitney 6 ISL, Whittaker 1 ISL, Zimmer 13 ISL), Reserva Indígena Kayapó (Whitney 1 ISL), Paragominas (Whitney 5 ISL), Fazenda Rio Capím (Zimmer 6 ISL); Tocantins: Babaçulândia (Pacheco 1 ISL).