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SYSTEMATIC REVISION OF THE SPOTTED ANTPITTA (GRALLARIIDAE: *HYLOPEZUS MACULARIUS*), WITH DESCRIPTION OF A CRYPTIC NEW SPECIES FROM BRAZILIAN AMAZONIA

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Abstract.—We present a systematic revision of the polytypic Spotted Antpitta (Grallariidae: *Hylopezus macularius*) based on morphometric, plumage, vocal, and molecular characters. Morphological and vocal analyses were based, respectively, on 97 specimens and 106 recordings. Molecular phylogenies were inferred on the basis of 1,352 base pairs of the mitochondrial DNA genes 16S, ND2, and cytochrome *b* from 30 specimens, including several outgroups. Our results revealed the existence of an undescribed taxon endemic to the Madeira–Xingu interfluvium, similar in morphology to *paraensis*, but vocally and genetically readily distinguished from the latter and any other taxon grouped under *H. macularius*. We also found that populations from the Negro River basin (currently treated in *paraensis*) and those from northern Peru and southern Venezuela (placed in *diversus*) should be treated as a single taxon, for which the name *dilutus* is available. Reconstructed phylogenies recovered, with overall strong support, the reciprocal monophyly among four main lineages of the Spotted Antpitta, three corresponding to already named taxa (*dilutus*, *macularius*, and *paraensis*), and one to the unnamed taxon, which we describe. We show that those four taxa are also mutually diagnosed by a combination of both vocal and morphological features, and we recommend treating them as separate species under alternative species concepts. *Received 18 July 2011, accepted 11 February 2012.*

Key words: *Hylopezus*, molecular systematics, song evolution, species limits, Spotted Antpitta, taxonomy, vocal characters.

Revisão Sistemática do torom-carijó *Hylopezus macularius* (Grallariidae), com a descrição de uma nova espécie críptica da Amazônia Brasileira

Resumo.—Uma revisão sistemática da espécie politípica *Hylopezus macularius* (Grallariidae), baseada em caracteres morfométricos, de plumagem, vocais e moleculares, é apresentada. As análises morfológicas e vocais foram baseadas, respectivamente, em 97 espécimes e 106 gravações. As filogenias moleculares basearam-se em 1.352 pares de bases de DNA dos genes mitocondriais 16S, ND2, e cyt *b* de 30 espécimes, incluindo diversos táxons como grupos externos. Nossos resultados revelaram a existência de um táxon não descrito, endêmico do interflúvio Xingu - Madeira, similar morfologicamente a *paraensis*, mas distinguível vocal e geneticamente do último e de todos os demais táxons agrupados sob *H. macularius*. Também verificamos que as populações da bacia do rio Negro (atualmente tratadas como *paraensis*) e aquelas no norte do Peru e sul da Venezuela (alocadas em *diversus*) devem ser tratadas dentro de um único táxon, para o qual o nome *dilutus* está disponível. As árvores moleculares obtidas recuperaram com um forte apoio o monofiletismo recíproco entre as quatro linhagens principais de *H. macularius*, três das quais correspondem a táxons já nomeados (*dilutus*, *macularius*, e *paraensis*), e uma ao táxon anônimo, que é descrito neste trabalho. Nós mostramos que estes quatro táxons são mutuamente diagnosticáveis através de uma combinação de caracteres vocais e morfológicos, portanto recomendamos tratá-los como espécies separadas com base em conceitos de espécie alternativos.

The genus *Hylopezus* was described by Ridgway (1909) and currently includes eight species distributed throughout most of the Neotropics (Honduras to northeastern Argentina; Krabbe and Schulenberg 2003, Remsen et al. 2012). The endemic Spotted Antpitta (*H. macularius*) inhabits both upland and seasonally flooded lowland humid forests of the Amazon Basin. Currently, the Spotted Antpitta is treated as a polytypic species with three recognized subspecies: *H. m. macularius*, *H. m. paraensis*, and

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H. m. diversus (Krabbe and Schulenberg 2003). This taxonomic treatment began with Snethlage (1907a), who described *paraensis* as a subspecies of *H. macularius* and was later consolidated by Zimmer (1934), who lumped *macularius*, *paraensis*, and the new taxon he described, *diversus*, into a single biological species because plumage differences separating them were very subtle, suggesting only subspecific differentiation. In addition to the subspecies above, a fourth taxon, *H. m. dilutus*, was described by Hellmayr (1910) but was later synonymized with *paraensis* by Cory and Hellmayr (1924).

Recent field work that we and others have conducted indicates that pronounced vocal variation exists among subspecies of *H. macularius* and that major vocal patterns conflict strongly with all proposed taxonomic treatments based on plumage characters (Snethlage 1910, Cory and Hellmayr 1924, Zimmer 1934, Krabbe and Schulenberg 2003). For instance, Maijer (1998) showed that *H. auricularis* (until then regarded as a subspecies of *H. macularius*) was vocally very distinct from any other taxa grouped under the Spotted Antpitta and, thus, deserved full species status, a recommendation that has been followed ever since (Krabbe and Schulenberg 2003, Remsen et al. 2012). Other similar examples of cryptic undescribed variation still persist in the polytypic *H. macularius* complex, suggesting that further splits are probably warranted (Krabbe and Schulenberg 2003, Remsen et al. 2012). Thus, a major multicharacter taxonomic revision is long due for the Spotted Antpitta complex to objectively base taxonomic decisions concerning the ranking of its taxa. Here, we use a combination of morphological, vocal, and molecular characters to review the taxonomy and interspecific limits in the Spotted Antpitta.

Methods

Genetic sampling.—Molecular analyses were based on 28 muscle tissue samples belonging to all currently recognized *H. macularius* subspecies (Krabbe and Schulenberg 2003), except *diversus*, and outgroups that included representatives of four other *Hylopezus* species (*H. auricularis*, *H. berlepschi*, *H. nattereri*, and *H. ochroleucus*) and another genus in Grallariidae (Thrush-like Antpitta [*Myrmothera campanisona*]). We also obtained samples from two study skins housed at the Museu Paraense Emílio Goeldi (MPEG; specimen numbers 42750 and 58982) through the removal of digital and metatarsal pads (Fig. 1; Appendix S1 in online supplementary materials [see Acknowledgments]).

Genetic samples obtained from skins were extracted from digital and metatarsal pads using the Qiagen (Valencia, California) DNeasy kit, following the manufacturer's protocol, whereas those obtained from muscle tissue were extracted following a phenol-chlorophorm method as described in Sambrook et al. (1989). Polymerase chain reaction (PCR) was used to amplify a segment of ~487 base pairs (bp) of the rRNA 16S mitochondrial gene (16s rRNA) with the following primers as described by Palumbi et al. (1991): (L-1987) and (H-2609). For the segment of ~477 bp of the cytochrome-*b* (cyt-*b*) gene, the following primers developed by Sorenson et al. (1999) were used: (L-15560) and (H-16064), whereas for the segment of ~388 bp of the NADH dehydrogenase subunit 2 (ND2), the following primers developed by Hackett (1996) were used: (L-5215) and (H-5578).

Amplification conditions for the segment of 16S rRNA gene consisted of initial denaturation at 94°C for 3 min, followed by 35 cycles of 0:30 s at 94°C, 1 min at 50°C, and 2 min at 72°C. Final extension was at 72°C for 7 min. Amplification of the cyt-*b* and ND2 segments had the following steps: 35 cycles of 30 s at 94°C, 1 min at 55°C, and 2 min at 72°C, followed by a final step of 7 min at 72°C. The PCR products were purified with ExoSap-It (Amersham Biosciences, Piscataway, New Jersey) and sequenced with Big Dye reagent Kit (Applied Biosystems, Foster City, California) following the manufacturer's protocols. Reagents not incorporated during the cycle sequencing reaction were eliminated by washing with isopropanol and products were run on an ABI Prism 3700 sequencer.

The sequences of each gene region were checked by eye, edited manually using the BIOEDIT software (Hall 1999), and aligned using the ClustalW application (Thompson et al. 1994). The following measures were taken to ensure that the DNA fragments sequenced were accurate and of mitochondrial origin (not pseudogenes): (1) both DNA strands were sequenced; (2) sequences were inspected using BIOEDIT (Hall 1999) for insertions, deletions, and stop codons that would result in a nonfunctional protein; and (3) possible saturation among ingroup sequences was examined by plotting the number of transition and transversion substitutions against *p*-distances for each pairwise comparison using the program DAMBE (Xia and Xie 2001).

Phylogenetic analysis.—Phylogenetic analyses were performed on the concatenated 16S–cyt *b*–ND2 data set, after a partition-homogeneity test implemented in PAUP*, version 4.0b10 (Swofford 2002), failed to detect significantly different phylogenetic signals among the three genes analyzed ($P > 0.05$). Genetic distances were also calculated in PAUP. We used PAUP to run a maximum-parsimony (MP) analysis on the concatenated data set using a heuristic search with tree bisection–reconnection (TBR) branch swapping and 100 random-addition replicates. Support for each node was assessed by 1,000 bootstrap replicates using a heuristic search, TBR branch swapping, and 10 random additions per replicate. Maximum-likelihood (ML) analyses were also carried out with PAUP under a general time-reversible (GTR) model of sequence evolution with invariable sites and gamma rate heterogeneity (GTR+Γ+I), which, according to JMODELTEST, version 0.1.1 (Posada 2008), was the best model of sequence evolution according to Akaike's information criterion (AIC). Nodal support in ML analyses was assessed by 100 bootstrap replicates with TBR branch swapping and one random addition per replicate. For Bayesian analyses (BA), we used JMODELTEST (Posada 2008) and MRMODELTEST, version 2.3 (Nylander 2004), to find the best model of evolution for each partitioning scheme and then tested different partitioning schemes with Bayes factor analysis (Kass and Raftery 1995) as follows: (1) all data combined, (2) three partitions (16S, cyt-*b*, and ND2), and (3) nine partitions (first, second, and third codon positions of the 16S, cyt-*b*, and ND2 genes). The Bayes factor analysis selected nine partitions as the best partitioning scheme. Each partition was assigned its own likelihood model on the basis of JMODELTEST and MRMODELTEST results. All parameters were unlinked between partitions (except for the topology and branch-length parameters) and were estimated as part of the analysis. Using MRBAYES, version 3.1.2 (Ronquist and Huelsenbeck 2003), two parallel runs were carried out, each with four Markov chains and for 10 million generations, sampling

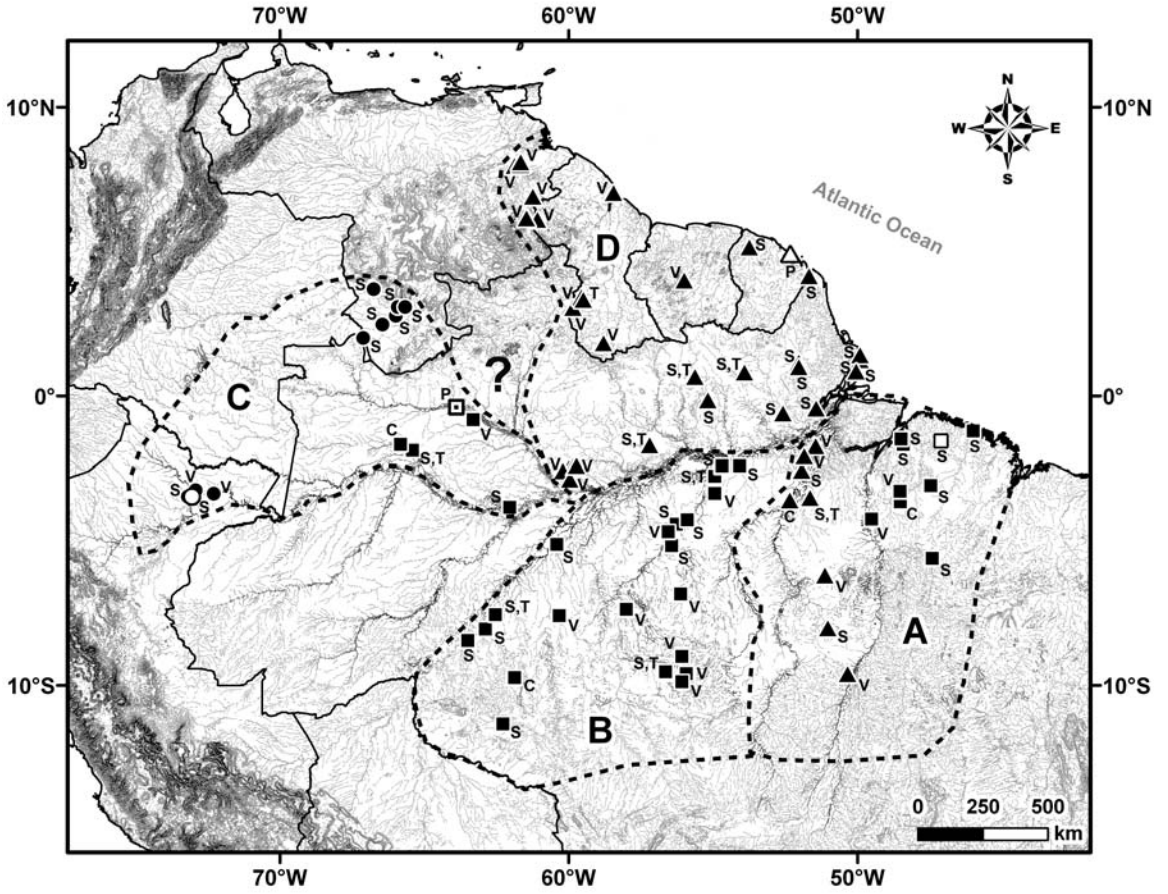

FIG. 1. Geographic distribution of specimens, vocalizations, and tissues of *Hylopezus macularius* taxa analyzed in the present study. We followed Krabbe and Schulenberg's (2003) subspecies definitions. Squares = *H. m. paraensis*, circles = *H. m. diversus*, and triangles = *H. m. macularius*. Type localities for each individual taxon are shown as white symbols. The lone white square with a small dot in the center indicates the type locality of *dilutus*, synonymized previously into *paraensis*, and thus not considered by Krabbe and Schulenberg (2003). Letters next to a symbol represent materials available for that given locality: P = photographs only; S = skins only; V = tape-recordings only; T = tissues only; S,V = skins and vocalizations only; S,T = skins and tissues only; and C = tape-recordings, skins, and tissues. Dashed lines delimit main lineages recovered by a molecular phylogeny and interpreted as natural populations as follows: A = *paraensis*, B = *whittakeri*, C = *dilutus*, and D = *macularius*. The question mark denotes an area between the Branco and Negro rivers where the presence and taxonomic identity of any H. *macularius* population are unknown. The conspicuous lack of any historical and modern records of H. *macularius* in southwestern Amazonia (Inambari area of endemism, sensu Da Silva et al. 2005) appear to reflect a true absence from this area (Krabbe and Schulenberg 2003, Whittaker et al. 2008).

the Markov chains every 1,000 generations. We used the resulting 10,000 parameter point-estimates minus the burn-in generations (1,000) to create a 50% majority-rule consensus tree and to calculate Bayesian posterior probabilities (PP) to assess nodal support. Using TRACER, version 1.5 (Drummond and Rambaut 2007), we determined that the chosen burn-in setting (10%) was sufficient for the log likelihood values of parallel runs to reach stationarity, with all parameters meeting benchmark effective sample-size values (>200).

Morphological analyses.—We examined 97 study skins, belonging to all taxa described so far and grouped under the polytypic *H. macularius* (*dilutus*, *diversus*, *macularius*, and *paraensis*), housed at various institutions (Appendix S2 in online supplementary materials; see Acknowledgments). In addition to those specimens, high-resolution digital pictures of *H. m. macularius* and *H. m. dilutus* type specimens were examined (see Fig. 1 and Appendix S2). To avoid discrepancies between researcher measurements, only data on the 65 specimens measured by L.S.C. were included in the statistical analyses. For the remaining 32 specimens examined only by A.A. at the American Museum of Natural History (AMNH), Carnegie Museum (CM), and Naturhistorisches Forschunginstitut, Museum für Naturkunde (ZMB), only information on plumage and color were incorporated into the study (Appendix S2).

Measurements of the following characters were taken to the nearest 0.1 mm with an electronic caliper: wing length, tail length, tarsus length, bill length from the distal points of the nostrils to the tip of the bill, bill depth and width at the distal point of the nostrils, average length of the whitish portion of the lower pectoral feathers, average width of the whitish portion of the lower pectoral feathers,

and average width of the blackish terminal area of the lower pectoral feathers. Averages for the three last characters were calculated on the basis of measurements of five individual feathers each. All morphological nomenclature follows Proctor and Lynch (1993). We used Smithe (1975, 1981) as a standard color reference when describing plumage tones. Groupings for statistical analysis of morphological data were based on the molecular phylogeny obtained (see below), which recognized four main lineages in *H. macularius* (Fig. 1). We assessed normality of morphometric data with Kolmogorov-Smirnov tests and used discriminant function analyses (DFA) to test for differences in the morphometric space among lineages. We combined both sexes in the analyses because there was no evidence of sexual dimorphism for any character. Missing morphometric values for some specimens were estimated using a missing value analysis, based on the linear regression of the observed variables. Missing values never represented >10% of the total measurements obtained for each character. All statistical analyses were performed with SYSTAT, version 12, for Windows (Systat Software, San Jose, California). In all tests, statistical significance was accepted at $P \leq 0.05$.

Vocal analyses.—We analyzed 106 different recordings, including >310 distinct songs, from 51 localities throughout the Amazon, belonging to all subspecies of *H. macularius* (*dilutus*, *diversus*, *macularius*, and *paraensis*); only one song or call per individual was used in the analyses (Fig. 1; Appendix S3 in online supplementary materials [see Acknowledgments]).

The vocalizations were categorized as "loudsongs" and "calls" (sensu Willis 1967) through auditory and visual comparisons of spectrograms. The *H. macularius* loudsong usually consists of six clear whistled notes. We measured the duration of each of the six notes, the duration of each of the five intervals between notes, and the interval between loudsongs, thus yielding 15 different time-related characters for each individual song. However, because some individuals, especially those found between the Madeira and Xingu rivers ascribed by current taxonomy to *paraensis*, sometimes omitted one or two final notes from their loudsongs, only 10 time-related vocal characters present in the majority of vocalizations (94%) were included in statistical analyses. These measurements were made in the waveform; when necessary, background noise was removed through lowpass and highpass filtering.

Following the method proposed by Isler et al. (1998), we calculated the mean value and standard deviations for all quantitative vocal variables measured in three bouts of loudsong. Only one song or call recording per individual was used in the analyses. To evaluate the difference between any two populations in any of the 15 quantitative variables, we used the following criteria. First, we considered two continuous and normally distributed variables diagnostic only if their ranges did not overlap and if the means (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) met the requirement: $X_a + t_a\,SD_a \leq X_b - t_b\,SD_b$, where t_i is the t score at the 97.5 percentile of the t distribution for $n - 1$ df (Isler et al. 1998). In addition, we ran a DFA in SYSTAT to determine whether the taxa under study could be diagnosed in the multivariate song space (based on 10 variables; see Table 1). Again, to avoid pseudoreplication, only one song or call recording per individual was used in the analyses. The sample size of loudsongs obtained for *H. m. diversus* and *H. m. dilutus* was not sufficient for statistical analyses (Fig. 1 and Appendix S3), so they were analyzed only in a qualitative fashion.

Loudsong and call frequency measurements were made using audiospectrograms and refer to the fundamental harmonic, which in all vocalizations analyzed was also the dominant one. The "max frequency" measurement corresponded to the frequency at which the maximum power occurs within a given time interval (Charif et al. 2004). Thus, the values given are the dominant frequency measured while considering the entire duration of each note. The syntax and note structure (sensu Isler et al. 1998) were analyzed qualitatively through a blind inspection and grouping of printed sonograms, followed by an assessment of whether the groupings matched the populations under study. Audiospectrograms and all song and call measurements were carried out using RAVEN PRO, version 1.3 (Cornell Laboratory of Ornithology, Ithaca, New York), with all vocalizations digitized at a sample rate of 44.1 kHz and 16 bits in the mono pattern.

Results

Molecular phylogenetics.—We obtained 1,352 bp from segments of the 16S rRNA (487 bp), ND2 (388 bp), and cyt-*b* (477 bp) mitochondrial genes for 19 specimens of *H. macularius* and 11 outgroup taxa (Appendix S1). Of these, 309 bp (~22.8%) were phylogenetically informative. No stop codons were observed. Transition versus transversion plots do not indicate saturation among ingroup taxa. All phylogenetic trees obtained by MP, ML, and BA grouped all *H. macularius* samples in a strongly supported clade, but the node connecting it to its sister group (*H. ochroleucus*) was highly supported only in BA (Fig. 2). Nevertheless, MP, ML, and BA trees ruled out the possibility that *H. auricularis* (once regarded as a subspecies of *H. macularius*) is nested in the Spotted Antpitta clade (Fig. 2). Within *H. macularius*, four major reciprocally monophyletic clades were recovered with overall high statistical support (Figs. 1 and 2), indicating that two of the subspecies of *H. macularius* recognized by Krabbe and Schulenberg (2003) and sampled genetically in this study are paraphyletic with strong statistical support, because they include the non-sister clades A+D (*macularius*) and B+C (*paraensis*; Fig. 2). The phylogenetic position of the third subspecies (*diversus*) was not assessed because of the lack of tissues from nearby its type locality, but both morphological and vocal evidence suggests that this taxon is included in clade C (see below). Because the molecular phylogeny obtained contrasted strongly with currently recognized subspecies limits in *H. macularius* (Krabbe and Schulenberg 2003), clades or populations A–D (Figs. 1 and 2) will be referred to as natural evolutionary units for a taxonomic reassessment of the entire group based on morphological and bioacoustical characters.

Morphological characters.—A DFA analysis found significant differences among some populations of *H. macularius* in the morphometric space, with the first two canonical discriminant variables accounting for 89.6% of the total variation based mainly on the contributions of tarsus length, bill depth, bill width, and the extent of white on the pectoral spots (Wilks's lambda = 0.2339, $P = 0.0001$; Fig. 3 and Table 2). Population C is distinguished from the others by significantly shorter tarsi and greater bill depth and width values, whereas population B differs from populations A, C, and D by the highest bill-width values in the entire sampling (Table 3). Finally, populations A and D overlap broadly in the morphometric space (Fig. 3 and Tables 2 and 3).

TABLE 1. Mean (± SD) values of 15 continuous and 3 discrete loudsong and call characters evaluated in the present study (left) and results of the pairwise test of diagnosability in loudsong characters among four taxa of the *Hylopezus macularius* complex (right). The taxonomy follows that proposed for the *H. macularius* complex in the text.

	Taxon				Pairwise diagnosability test [a]					
Vocal variable	*paraensis* (*n* = 27)	*whittakeri* (*n* = 28)	*dilutus* (*n* = 4)	*macularius* (*n* = 45)	*paraensis vs. whittakeri*	*paraensis vs. dilutus*	*paraensis vs. macularius*	*whittakeri vs. dilutus*	*whittaker vs. macularius*	*dilutus vs. macularius*
Number of notes	5.96 ± 0.19	4.93 ± 0.19	6.00 ± 0.00	5.97 ± 0.26	*	N.D. 1st	N.D. 1st	*	*	N.D. 1st
Duration of the song [b] (s)	2.34 ± 0.13	2.66 ± 0.36	2.08 ± 0.15	2.36 ± 0.15	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 2nd	N.D. 1st	N.D. 1st
Pace (number of notes/ duration) [b]	2.55 ± 0.13	1.85 ± 0.15	2.88 ± 0.20	2.53 ± 0.17	*	N.D. 1st	N.D. 1st	*	*	N.D. 1st
Duration of first note(s)	0.24 ± 0.03	0.24 ± 0.03	0.25 ± 0.06	0.24 ± 0.03	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Duration of second note(s)	0.22 ± 0.02	0.25 ± 0.03	0.23 ± 0.01	0.21 ± 0.03	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Duration of third note(s)	0.23 ± 0.03	0.26 ± 0.03	0.21 ± 0.03	0.21 ± 0.04	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Duration of fourth note(s)	0.24 ± 0.03	0.26 ± 0.03	0.24 ± 0.02	0.21 ± 0.03	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Duration of fifth note(s)	0.22 ± 0.03	0.24 ± 0.07	0.21 ± 0.02	0.21 ± 0.03	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Duration of sixth note(s) [b]	0.22 ± 0.04	0.22 ± 0.06	0.21 ± 0.05	0.20 ± 0.03	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Duration of first interval(s)	0.16 ± 0.03	0.27 ± 0.05	0.13 ± 0.02	0.19 ± 0.04	N.D. 2nd	N.D. 1st	N.D. 1st	N.D. 2nd	N.D. 1st	N.D. 1st
Duration of second interval(s)	0.19 ± 0.04	0.41 ± 0.09	0.14 ± 0.03	0.21 ± 0.04	N.D. 2nd	N.D. 1st	N.D. 1st	*	N.D. 2nd	N.D. 1st
Duration of third interval(s)	0.20 ± 0.04	0.39 ± 0.06	0.13 ± 0.02	0.24 ± 0.04	N.D. 2nd	N.D. 2nd	N.D. 1st	*	N.D. 2nd	N.D. 2nd
Duration of fourth interval(s)	0.21 ± 0.04	0.40 ± 0.08	0.14 ± 0.02	0.21 ± 0.05	N.D. 2nd	N.D. 2nd	N.D. 1st	*	N.D. 2nd	N.D. 1st
Duration of fifth interval(s) [b]	0.22 ± 0.05	0.29 ± 0.13	0.16 ± 0.02	0.24 ± 0.05	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 2nd
Interval between loudsongs [b]	22.14 ± 11.93	12.43 ± 3.18	10.32 ± 8.16	17.64 ± 6.13	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st	N.D. 1st
Notes structure [c]	—	—	—	—	Yes	Yes	Yes	Yes	Yes	Yes
Syntax [c]	—	—	—	—	Yes	Yes	Yes	Yes	Yes	No
Total differences in loudsong characters	—	—	—	—	4	2	2	7	4	1
Calls [b,d]	*n* = 1 (7 calls)	*n* = 1 (5 calls)	[e]	*n* = 1 (3 calls)	—	—	—	—	—	—
Number of notes	8	5–6	—	10–12	—	—	—	—	—	—
Duration of the call (s)	0.97 ± 0.03	0.81 ± 0.06	—	1.01 ± 0.06	—	—	—	—	—	—
Pace (number of notes/ duration)	8.27 ± 0.27	7.11 ± 0.10	—	10.87 ± 0.39	—	—	—	—	—	—

[a] N.D. 1st = not diagnosable according to the first criterion (i.e., ranges do not overlap); N.D. 2nd = diagnosable according to the first criterion but not diagnosable according to the second criterion (i.e., means and standard deviations of the population with the smaller set of measurements [a] and the population with the larger set of measurements [b] meet the requirement: $X_a + t_a\,SD_a \leq X_b - t_b\,SD_b$ where t_i = the *t*-score at the 97.5 percentile of the *t*-distribution for $n - 1$ degrees of freedom; see text for details). Asterisk indicates normally distributed vocal character in which populations differ diagnostically according to both first and second criteria of diagnosability (see text for details).

[b] Not included in multivariate analysis.

[c] Pairwise diagnosability assessed qualitatively for these qualitative loudsong characters.

[d] Not submitted to the pairwise diagnosability test.

[e] No call sample available for this taxon.

The four natural populations of *H. macularius* are also very similar in plumage, although population C is distinguished from the others by the following characteristics: (1) less olivaceous and more brownish (color no. 28) upperparts; (2) shaft-streaks on the mantle absent or obsolete; (3) deeper ochraceous subterminal band of pectoral feathers; (4) darker black terminal band of pectoral spots; and (4) wingbars extended only to the middle rather than the tips of the wing (Fig. 4). Population D, on average, has deeper buff flanks (color no. 123B) than all remaining populations and less conspicuous shaft-streaks on the mantle than populations A and B (Fig. 4). Populations A and B could not be mutually differentiated by any plumage character (Fig. 4).

Vocal characters.—The pairwise diagnosability tests showed diagnostic features in all (two) qualitative (syntax and notes structure) and 5 of the 15 quantitative loudsong traits analyzed (number of notes, pace, duration of second, third and fourth intervals; Tables 1 and 4). Moreover, vocal differences among the taxa are visually apparent on sonograms of representative loudsongs (Fig. 5).

A DFA based on the loudsong characters measured also showed a clear separation between population B and populations A and D, with the first two canonical discriminant variables accounting for 94.3% of the total variation (Wilks's lambda = 0.088, $P = 0.0001$; Fig. 6); the obtained DFA classified correctly most loudsong samples, including all those of population B (Table 5). Because of a lack of sufficient vocal samples, population C was not included in the DFA analysis, but loudsong structure in this population resembled closely those of population D (Tables 1 and 4 and Fig. 5). The duration of the second note and the duration of the second interval (between the second and third notes) were the most useful in discriminating populations A–D (Table 1). Furthermore, the number of loudsong notes was an important character setting apart birds of population B (in which >90.9% of the recordings sampled contained songs with five or four notes) from those

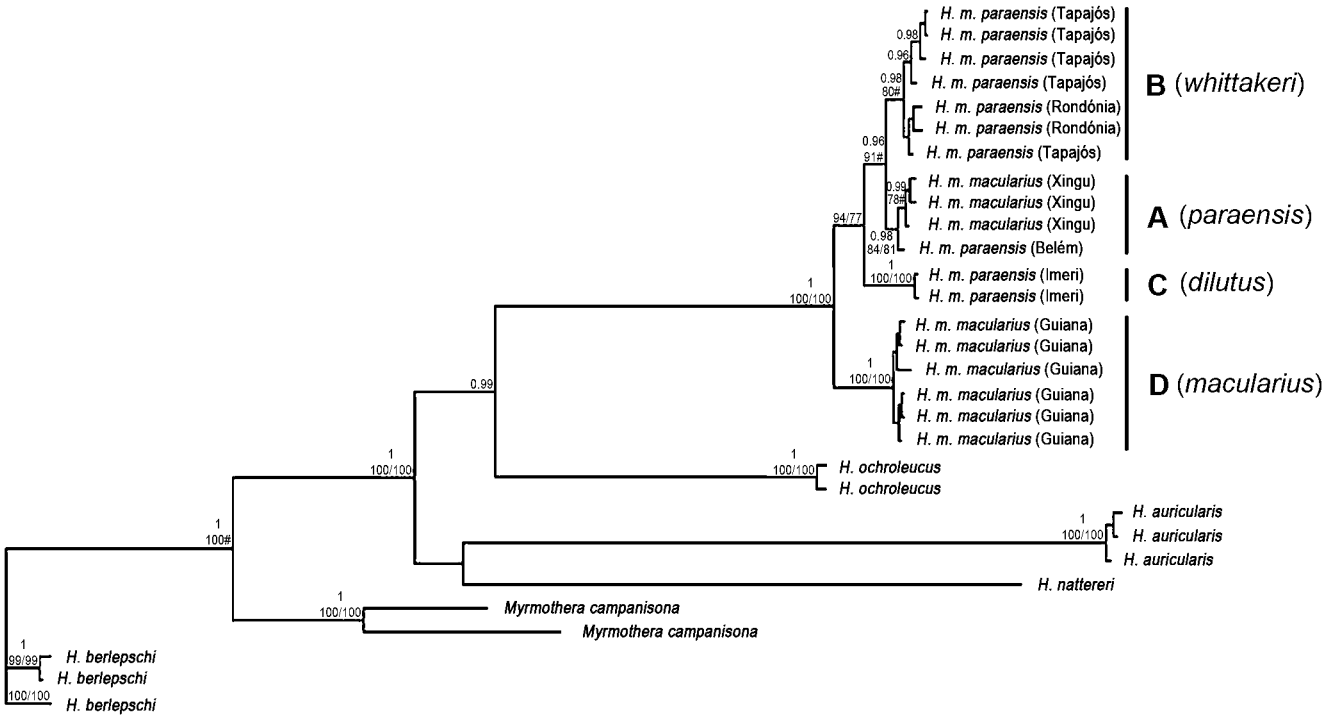

FIG. 2. Bayesian molecular phylogeny obtained for different taxa grouped under *Hylopezus macularius* (following Krabbe and Schulenberg 2003) and outgroups based on 1,352 bp of the 16S rRNA, ND2, and cytochrome-*b* mtDNA genes. Numbers above branches denote indices of Bayesian posterior probabilities (top), maximum parsimony (MP; before slash), and maximum likelihood (ML; after slash) nodal support. Values for poorly supported nodes, as indicated by bootstrap values <75% for (MP and ML) and <95% (Bayesian), are not shown. A pound sign (#) denotes nodes with bootstrap values ≥75% only for MP. Names in parentheses at the tips of branches of *H. macularius* taxa denote Amazonian areas of endemism as recognized by Da Silva et al. (2005). All four main lineages of the *H. macularius* complex are labeled A–D next to the taxon name with priority applicable to each clade, which we interpret as species-level taxa (see text for details).

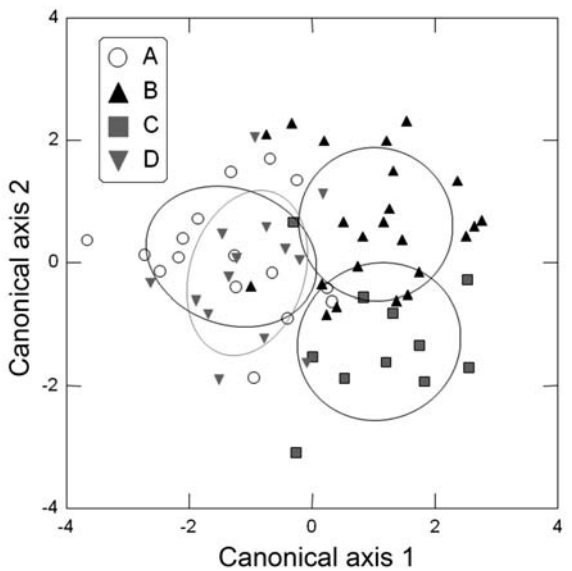

FIG. 3. Graphic representation of scores of the first two axes of a discriminant function analysis separating specimens belonging to natural populations A–D of *Hylopezus macularius* based on measurements of 9 morphometric characters (see Figs. 1 and 2 and text for details).

of populations A, C, and D (in which birds often uttered songs with six notes; Tables 1 and 4).

From a quali-quantitative perspective, the loudsong of population A (Fig. 5A) was characterized by notes of nearly identical shape and dominant frequency (861.30 Hz), although occasionally some notes (especially the fourth) exhibited a slightly lower frequency around 689.10 Hz. Unlike in the remaining populations, the third, fifth, and sixth notes showed a richer harmonic structure, with subharmonics present, which

TABLE 2. Summary of classification accuracy of specimens of *Hylopezus macularius* belonging to natural populations A–D (see Figs. 1 and 2) obtained through a discriminant function analysis based on measurements of 9 morphometric characters (see text for details). Numbers before and after slashes represent, respectively, values obtained without and with jackknife procedures. The number of specimens of each population included in the analysis is shown in parentheses.

Populations	A	B	C	D	Correctness (%)
A (*n* = 16)	11 / 8	2 / 5	0 / 0	3 / 3	68.7 / 50
B (*n* = 23)	8 / 3	21 / 18	0 / 0	1 / 2	91.3 / 78
C (*n* = 11)	0 / 1	0 / 6	11 / 4	0 / 0	100 / 36
D (*n* = 14)	0 / 2	1 / 3	0 / 0	13 / 9	92.8 / 64
Total (*n* = 64)	12 / 14	24 / 32	11 / 4	17 / 14	86 / 61

Table 3. Standard measurements of selected morphometric characters and weight data of natural populations A–D of the *Hylopezus macularius* complex (Figs. 1 and 2). Values are in millimeters and represent means, with ranges in parentheses where appropriate.

Population	Sex	Sample size	Wing	Tail	Tarsus	Bill length	Bill width	Bill depth	Body mass (g) [a]
	Male	4	83.6 (81.1–86.8)	38.5 (34.1–39.2)	35.4 (34.3–37.2)	13.6 (12.2–14.0)	5.5 (5.0–6.0)	5.3 (5.1–5.8)	43 (42–44)
A	Female	3	81.4 (80.8–87.0)	38.8 (34.9–40.8)	35.2 (33.8–38.5)	12.3 (12.3–14.2)	5.2 (5.2–6.4)	5.6 (5.1–5.9)	45.20 (42–48.4)
	Unknown	9	83.9 (81.1–87,0)	36.3(34.1–38.6	35.6 (36.2–38.5)	15.4 (12.6–14.2)	5.6 (5.4–5.9)	5.8 (5.7–6.0)	—
	Total	16	83.4	37.4	35.5	14.6	5.5	5.7	44.1
	Male	10	86.1 (82.5–90.5)	40.1 (37.4–42.7)	35.0 (32.4–36.4)	13.2 (12.5–13.9)	5.8 (5.3–6.3)	5.8 (5.5–5.9)	44.1 (40–47)
B	Female	3	85.2 (83.9–86.9)	40.8 (36.6–44.6)	34.4 (33.8–34.7)	13.0 (12.1–14.0)	5.9 (5.7–6.1)	5.8 (5.7–5.9)	42.4
	Unknown	10	86.1 (83.1–90.1)	37.0 (33.9–39.6)	35.2 (33.7–37.6)	13.4 (12.7–14.0)	5.9 (5.1–7.7)	6.2(5.6–6.7)	—
	Total	23	86.0	38.9	35.0	13.3	5.9	6.0	43.2
	Male	3	84.2 (83.8–84.8)	36.8 (36.4–37.0)	32.8 (30.9–34.3)	12.7 (12.2–13.3)	6.2 (6.1–6.4)	5.8 (5.8–5.9)	42.8 (39–45.5)
C	Female	4	82.8 (79.9–85.4)	37.0 (35.0–39.2)	33.6 (31.8–35.6)	12.9 (12.2–12.9)	6.0 (5.8–6.1)	6.0 (5.9–6.2)	—
	Unknown	4	82.6 (79.0–84.3)	34.0 (31.0–35.6)	34.5 (34.0–35.2)	13.3 (13.0–13.8)	6.3 (5.7–6.9)	5.9 (5.7–6.1)	—
	Total	11	83.1	35.8	33.7	13.0	6.2	5.9	42.8
	Male	5	84.6 (82.9–88.9)	39.7 (38.2–41.4)	36.2 (34.8–38.6)	12.7 (11.5–13.6)	5.7 (5.2–6.1)	5.8 (5.5–6.3)	42 (41–43)
D	Female	2	80.6 (78.2–83.0)	38.0 (35.0–41.1)	33.9 (32.2–35.6)	12.6 (11.7–13.6)	5.8 (5.7–5.9)	6.0 (5.8–6,2)	39.5
	Unknown	7	82.8 (78.8–87.9)	35.4 (33.9–36.6)	35.6 (33.7–36.9)	13.0 (11.9–13.9)	5.9 (5.6–6.8)	5.4 (5.1–5.6)	39
	Total	14	83.1	37.3	35.5	12.8	5.8	5.6	40.1

[a] Body mass information not available for some specimens.

gave them a distinct raspy quality (Fig. 5A). In population A, multisyllabic calls (Table 1 and Fig. 7A) differed from those of populations B and D by the number of notes (8); its duration is slightly longer than in population B and nearly the same as in population D.

In population B, two characters readily distinguished its loudsong from those of the remaining populations: (1) number of notes, which in 90.9% of the samples consisted of only four or (more often) five, and less often (9.1% of the samples) six notes, as in the remaining populations; and (2) pace, which was shorter than in any other population (mean ± SD = 1.85 ± 0.15 s; Table 1 and Fig. 5B). The interval between the second and third notes was longer than in any other population and longer than those between the other notes of the song (0.41 ± 0.09 s; Table 1 and Fig. 5B). Calls differed most conspicuously from those of populations A and D by the smaller number of notes (five or six) and shorter duration (Table 1 and Fig. 7B).

In population C, loudsongs were readily distinguished from those of the other populations by the shorter duration of all note intervals (ranging, on average, from 0.13 to 0.16 s), thus also yielding an overall shorter loudsong (2.08 ± 0.15 s; Table 1 and Fig. 5C) than in any other population. Furthermore, the syntax of the loudsong in this population differed markedly from that of populations A and B by having two different types of notes, following the pattern A A B A B B, which was found also in population D; the notes of type A were flatter in frequency, whereas notes of type B showed a strongly ascending–descending pattern of frequency modulation (Fig. 5C, D). Unfortunately, only 12 loudsongs belonging to 4 recordings obtained at 4 different localities were analyzed, and no calls for population C were available.

Finally, population D's loudsong followed the same pattern observed in population C, in which the first, second, and fourth notes and the third, fifth, and sixth notes formed two groups of notes very similar in shape (Fig. 5D). Calls (Fig. 7C and Table 1) differed from those in populations A and B by the larger number of notes (10–12), which were longer in duration than those of population B but nearly equal in duration to those of population A.

Taxonomy.—Our results indicated that each natural population of H. *macularius* recognized in the present study (A–D) can be mutually diagnosed through a combination of vocal, molecular, and morphological features and, thus, can be interpreted as basal taxa deserving formal taxonomic recognition (Figs. 2, 4, and 6; Table 4). As discussed in detail in Appendix S4 (in online supplementary materials; see Acknowledgments), already existing names are applicable to populations A (*paraensis*), C (*dilutus*), and D (*macularius*), but no available name exists for population B, which is formally described below. We also discuss below the evidence supporting the treatment of all four natural populations of H. *macularius* as species-level taxa.

Discussion

Species limits and loudsong evolution in the H. macularius *complex.*—Despite the sampling limitations of our study, we have demonstrated that the current taxonomy of the Spotted Antpitta complex contrasts strongly with its evolutionary history (Figs. 1 and 2). When interpreted together, these findings allow a redefinition of species limits in the *H. macularius* complex, whose taxa have been historically treated as subspecies (Cory and Hellmayr 1924, Peters 1951, Krabbe and Schulenberg 2003).

The statistically well-supported reciprocal monophyly recovered for the four lineages of the Spotted Antpitta identified here (Fig. 2), added to their vocal diagnoses (Fig. 4), which remain constant within each clade, are indicative of species-level status under the phylogenetic species concept (PSC) and the biological species concept (BSC). Under the PSC, their reciprocal combined

Fig. 4. Dorsal (top) and ventral (bottom) views of some of the few plumage characters that distinguish natural populations A (MPEG 55691), B (MPEG 56066), C (MPEG 42750), and D (MPEG 66340) of *Hylopezus macularius*. Scale bar = 30 mm. See text for details.

molecular, vocal, and morphological diagnoses provide the basis for considering populations A–D of the Spotted Antpitta as separate species, whereas under the BSC the congruent evolution between genetic and vocal characters, added to the absence of genetic paraphyly and vocally intermediate individuals in our sampling, are also indicative of species-level status for these lineages, even though such congruence does not guarantee reproductive isolation. For instance, it is possible that our relatively sparse genetic sampling could simply have missed introgressed individuals, particularly in areas where the ranges of parapatric taxa abut, such as the Negro–Branco interfluve (where the presence and identity of the local Spotted Antpitta taxon remain unknown; Fig. 1) and headwaters of the Xingu River.

Furthermore, the absence of nuclear markers in our molecular phylogenetics analysis represents another source of difficulty in properly detecting introgressed individuals in our sampling. Even though only a new study, with much denser sampling in terms of molecular markers and individuals throughout Amazonia, could document the presence and contribution of introgressed individuals to the genetic make-up of the four main mitochondrial lineages of the Spotted Antpitta identified in our study, the following two lines of evidence suggest that they nevertheless represent biological species. First, our genetic sampling of 19 individuals came from 13 localities (all three Paranaíta localities—see Appendix S1—were lumped together in Fig. 1 and count as a single locality) scattered across all areas of endemism inhabited by the Spotted Antpitta (Krabbe and Schulenberg 2003; Fig. 1) and, thus, can be regarded as representative at least over a broad geographic scale. The strong statistical support obtained for the mitochondrial DNA (mtDNA) reciprocal monophyly of all four main lineages of the Spotted Antpitta (Fig. 2) offer unequivocal evidence that, even if present, introgression between lineages is not

TABLE 4. Summary of loudsong characters that distinguish pairs of populations of the *Hylopezus macularius* complex treated as species in the present study. The total number of vocal variables distinguishing each pair is shown in parentheses.

	H. paraensis	*H. whittakeri*	*H. dilutus*
H. whittakeri	(4) Number of notes Song pace Notes structure Syntax	—	—
H. dilutus	(2) Notes structure Syntax	(7) Number of notes Song pace Interval lengths (2^{nd}, 3^{rd}, 4^{th}) Notes structure Syntax	—
H. macularius	(2) Notes structure Syntax	(4) Number of notes Song pace Notes structure Syntax	(1) Notes structure

widespread enough to promote extensive admixture and merging of their mtDNA haplotypes; more importantly, the acquisition and maintenance of reciprocal monophyly between parapatric sister lineages typically indicate the final stages of the speciation process and that reproductive isolation has been reached (de Queiroz 2005, Patten 2010). Second, mtDNA reciprocal monophyly among lineages is mirrored by significant differences in vocal characters, for which our sampling is more extensive (51 localities; Fig. 1). The importance of vocal characters as a premating isolating mechanism in Grallariidae was recently underscored by a study showing that loudsong variation appears to have a strong genetic basis in this family (Cadena et al. 2007), which agrees with the pattern documented here for the Spotted Antpitta. Furthermore, pairwise tests of diagnosability contrasting the loudsongs of the unnamed population B birds (see description below) with those of the other Spotted Antpitta populations always found more than three characters distinguishing them (Table 4), which is the minimum number found to distinguish syntopic and allopatric pairs of sister biological species of antbirds (Thamnophilidae), a family closely related to the Grallariidae (Isler et al. 1998, 2005, 2007; Braun et al. 2005; Isler and Whitney 2011). On the other hand, diagnosability tests contrasting the loudsongs of *dilutus*, *macularius*, and *paraensis* involved a smaller number of diagnostic characters: two between *macularius* and *paraensis* and between *dilutus* and *paraensis*, and only one between *dilutus* and *macularius* (Table 4).

Interestingly, using the same diagnosability tests employed in our study, Chaves et al. (2010) showed that only two diagnosable vocal characters can distinguish three reciprocally monophyletic populations of the Dull-mantled Antbird (*Myrmeciza laemosticta*) complex (Thamnophilidae) separated by large genetic distances, prompting those authors to suggest that only two diagnostic characters may be necessary for two populations to be considered distinct species in this complex. In agreement with their study, our data further indicate that, in fact, only one loudsong character passing the diagnosability tests of Isler et al. (1998) can distinguish

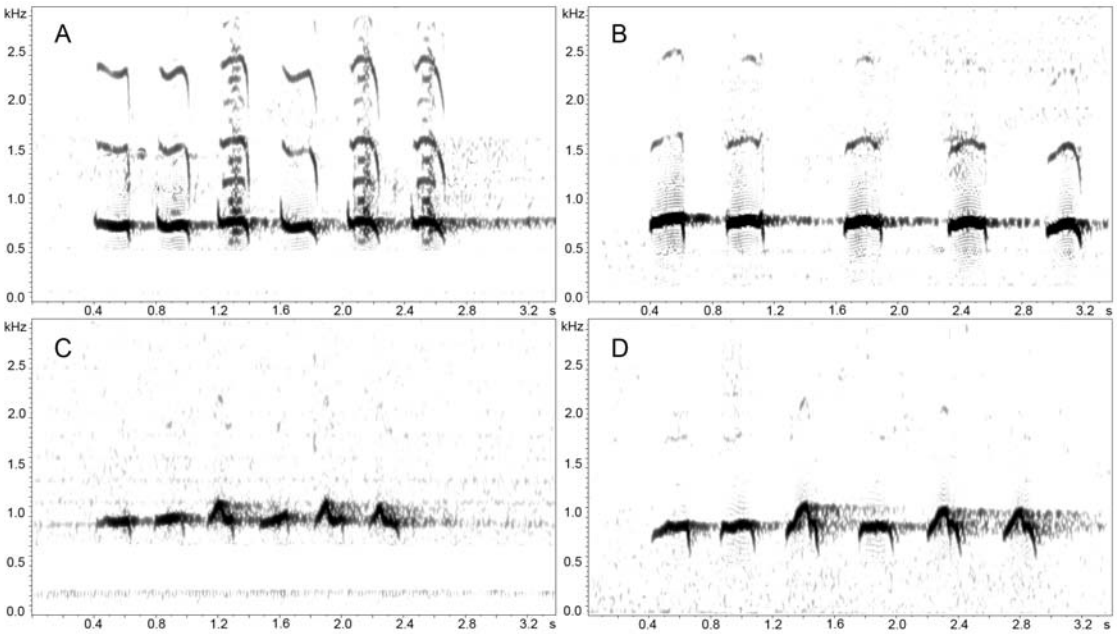

FIG. 5. Representative loudsong audiospectrograms of populations A–D of *Hylopezus macularius* (window type Hamming, window size 1,300 samples, time grid 90% overlap, and DFT size 16,384 samples). (A) Population A (*H. paraensis*), Caxiuanã, Pará, Brazil (C. A. Marantz, MLS 127444). (B) Population B (*H. whittakeri*), Alta Floresta, Mato Grosso, Brazil (P. R. Isler, MLS 48068). (C) Population C (*H. dilutus*), Maraã, Lago Cumapi, Amazonas, Brazil (A.A., 1 PAC). (D) Population D (*H. macularius*), Rupununi, Guyana (T. A. Parker III, MLS 73054).

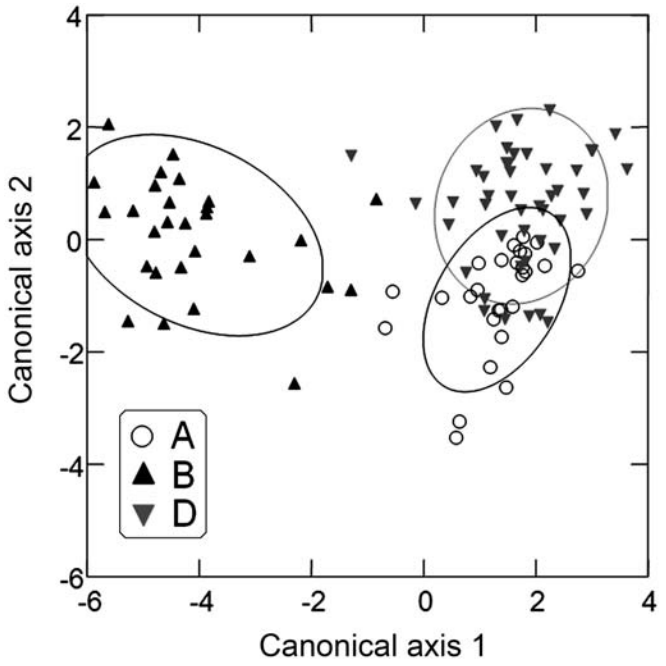

Fig. 6. Graphic representation of scores of the first two axes of a discriminant function analysis based on measurements of 10 characters related to the duration of individual notes and intervals between notes distinguishing loudsongs of *Hylopezus macularius* natural populations A (*H. paraensis*), B (*H. whittakeri*), and D (*H. macularius*; see Figs. 1 and 2 and text for details). Population C (*H. dilutus*) was not included in the analysis because of a very small sample size.

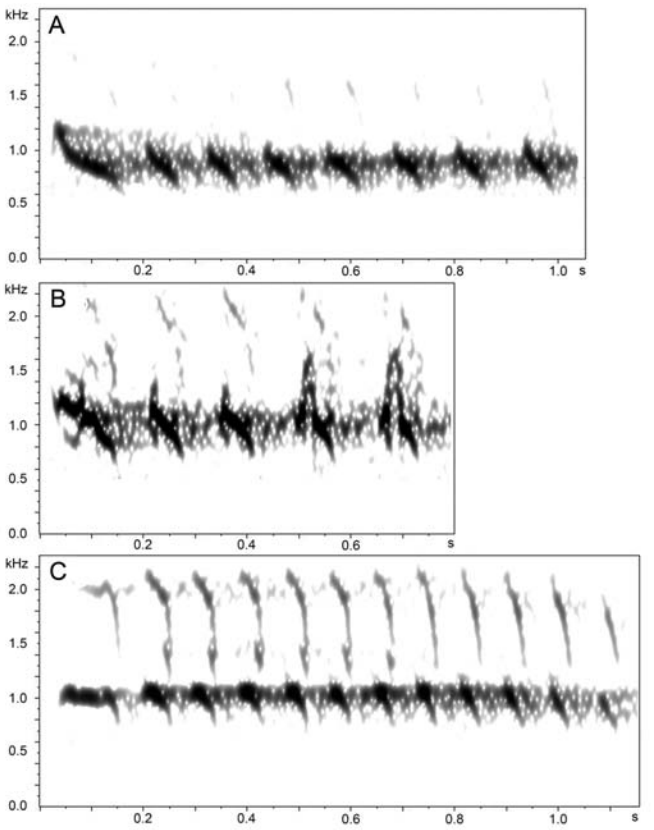

Fig. 7. Representative call audiospectrograms of populations A, B, and D of *Hylopezus macularius* (window type Hamming, window size 800 samples, time grid 90% overlap, and DFT size 16,384 samples). (A) Population A, Caxiuanã, Pará, Brazil (A. Whittaker, 1 PAC). (B) Population B, Parque Nacional da Amazônia, Pará, Brazil (A. Whittaker, 1 PAC). (C) Population D, Bolívar, Venezuela (T. A. Parker III, MLS 34472).

Table 5. Summary of classification accuracy of loudsong types of *Hylopezus macularius* belonging to natural populations A, B, and D (see Figs. 1 and 2) obtained through a discriminant function analysis based on measurements of 10 characters related to the duration of individual notes and intervals between notes. Numbers before and after slashes represent respectively values obtained without and with jackknife procedures. The number of tape-recordings included in the analysis is shown in parentheses. Population C was not included in the analysis because of a very small sample size. See text for details.

Populations	A	B	D	Correctness (%)
A (*n* = 28)	26 / 15	0 / 1	2 / 12	92.8 / 54
B (*n* = 27)	0 / 0	27 / 27	0 / 0	100 / 100
D (*n* = 45)	4 / 6	1 / 3	40 / 36	88.8 / 80
Total (*n* = 100)	30 / 21	28 / 31	42 / 48	93 / 78

reciprocally monophyletic mtDNA lineages separated by comparatively high (i.e., 3.5%) uncorrected genetic *p*-distances, which are also known to differ in morphometrics and, to some extent, in plumage as well (i.e., *dilutus* and *macularius*; Figs. 3 and 4). However, given our poor sampling of *dilutus*, it seems premature to infer reproductive isolation between *dilutus* and *macularius*, given the results of the loudsong diagnosability tests (Table 4) and the uncertain phylogenetic affinities of the former, whose recovered sister relationship to *paraensis* and the unnamed population B lacked significant statistical support, thus not allowing the rejection of a putative monophyly involving *macularius* and *dilutus* (Fig. 2).

Therefore, we interpret our combined results as evidence supporting the recognition of four phylogenetic (populations A–D) and three biological (populations A, B, and C+D) species in the Spotted Antpitta complex. It should be mentioned, though, that the biological species recognized here would likely not pass the phenotypic diagnosability test described by Tobias et al. (2010) for assigning species rank based on the BSC because of their high degree of plumage and morphometric conservatism (Fig. 4 and Table 2). Tobias et al. (2010) advocated a test whereby it is impossible for any pair of taxa to reach a minimum fixed threshold (defined as seven character points) to be classified as separate biological species, if they have experienced heterogeneous rates of evolution in phenotypic traits, such as that observed between morphological and vocal characters in the Spotted Antpitta complex. Hence, this test does not seem appropriate to define interspecific limits in the Spotted Antpitta complex because it devalues the contribution of bioacoustical characters by comparatively overestimating the degree of morphological differentiation necessary for reproductive isolation in a dense-forest-interior lineage known to use vocal characters as a premating isolating mechanism (Cadena

et al. 2007). Furthermore, species-rank diagnosability tests such as those put forward by Tobias et al. (2010) and Patten and Unitt (2002) do not incorporate genetic data in their calculations and, thus, are not entirely suited to fully integrated multicharacter data sets such as the one discussed here. On the other hand, populations A–D of the Spotted Antpitta all meet the requirements for biological species ranking in the context of parapatry according to the British Ornithologists' Union (Helbig et al. 2002), given that they (1) are diagnosable and (2) do not appear to hybridize. However, as explained above, our poor sampling of population C makes it still premature to infer that it is reproductively isolated from the parapatric population D.

Taxonomic recommendations.—On the basis of the combined character analyses presented and discussed above, we recommend the splitting of the *H. macularius* complex into four phylogenetic (populations A–D) and three biological species (populations A, B, and C+D), one of which (population B) has yet to be named and is here described as

Hylopezus whittakeri, sp. nov.

Alta Floresta Antpitta
Torom-de-alta floresta (Portuguese)

Grallaria macularia (Temminck, 1823): Snethlage 1907b: 288 (part: specimen from Cussary at ZMB examined).

Grallaria maculata diluta Hellmayr, 1910: 370 (part: specimen from Calama at AMNH examined).

Grallaria macularia paraensis Snethlage, 1910: Snethlage 1914: 317 (part: specimen from Cachoeira do Cahy at ZMB examined); Zimmer 1934: 21 (specimen from Limoal at AMNH examined); Cory and Hellmayr 1924: 356 (part: specimens from Calama and Cachoeira do Cahy); Gyldenstolpe 1941: 8 (specimens from Aveiro, Caxiricatuba, Marai, and Patinga at the Naturhistoriska Riksmuseet, Stockholm, Sweden, not examined); Peters 1951: 271 (part: specimens from the Madeira, Tapajoz, and the Jamauchim).

Hylopezus macularius paraensis (Snethlage, 1910): Krabbe and Schulenberg 2003: 709 (part: specimens from south of the Amazon, between the Madeira and Xingu rivers).

Hylopezus sp. nov.: Whittaker 2009: 28.

Holotype.—MPEG 56099. Skin, adult male, skull 100% ossified, testes 4 × 2 mm, collected in the understory of upland (*terra firme*) forest on 23 July 2002 by D. Davison, W. Figueiredo, and L. W. Figueiredo in Belterra, Floresta Nacional do Tapajós, Sucupira base, Km 117 of the BR-163 highway, state of Pará, Brazil (03°21′22″S, 54°56′57″W). Tissue samples deposited at the Laboratório de Genética e Biologia Molecular, Campus Universitário de Bragança, Universidade Federal do Pará (LGBM) under accession number WN 350. Mitochondrial 16S rRNA, ND2, and cyt-*b* gene sequences deposited in GenBank (JQ775791, JQ775820, JQ775850).

Paratypes.—MN 21895: skin, collected at Jamary, state of Rondônia, Brazil. MPEG 34420: skin, adult female, skull 100% ossified, collected in the understory of *terra firme* forest by G. P. Silva on 12 September 1974 at Rio Aripuanã, Humboldt, Cachoeira Dardanelos, state of Mato Grosso, Brazil (10°10′S, 58°37′W). MPEG 38808: skin, adult male, skull 100% ossified, testes 7 × 4 mm, collected in the understory of *terra firme* forest by M. S. Brígida on 23 November 1986 at Alvorada d'Oeste, Linha 64, Br 429 Km 87, state of Rondônia, Brazil (11°24′S, 62°24′W). MPEG 39819: skin, adult male, skull 100% ossified, testes 6 × 3 mm, collected in the understory of *terra firme* forest by T. Schulenberg on 15 October 1986 at Cachoeira Nazaré, west bank Rio Ji-paraná, state of Rondônia, Brazil (9°44′S, 61°53′W). MPEG 39820: skin, adult male, skull 100% ossified, testes 7 × 4 mm, collected in the understory of *terra firme* forest by A. T. Peterson on 14 October 1986 at Cachoeira Nazaré. MPEG 39821: skin, female, skull 40% ossified, ovarium 8 × 4 mm, collected in the understory of *terra firme* forest by A. T. Peterson on 26 October 1986 at Cachoeira Nazaré. Tissue samples deposited at the Field Museum of Natural History (FMNH) under accession number 389869. Mitochondrial 16S rRNA, ND2, and cyt-*b* gene sequences deposited in GenBank (JQ775785, JQ775814, JQ775844). MPEG 58757: skin, adult male, skull 100% ossified, testes 7 × 5 mm, collected in the understory of *terra firme* forest by M. P. D. Santos and G. C. Silva on 4 April 2005 at Humaitá, Terra Indígena Parintintin, Aldeia Traíra-Chororó, state of Amazonas, Brazil (7°33′S, 62°33′W); prepared by M. Santa-Brígida under field number MPDS 719. Tissue samples deposited at MPEG. Mitochondrial 16S rRNA, ND2, and cyt-*b* gene sequences deposited in GenBank (JQ775790, JQ775815, JQ775845). MZUSP 58838: skin, male, collected at Fordlândia, state of Pará, Brazil.

Diagnosis.—Phenotypically, the new species can be unambiguously assigned to the genus *Hylopezus* (Grallariidae) on the basis of its relatively small size, tarsi without scutellations and inner edge convolutions, absence of rictal bristles, basal portion of primaries buffy forming a contrasting wing bar, underparts predominantly white with the chest more or less streaked with black, and tail less than half as long as the wing (Lowery and O´Neill 1969). Within *Hylopezus*, measurements and plumage coloration similar to those of other taxa in the *H. macularius* complex, being closest to population A (to which the name *paraensis* applies; Appendix S4), from which it is separable only through vocal and genetic characters (see below). Distinguishable from population C (to which the name *dilutus* applies; Appendix S4) by more conspicuous mantle shaft-streaks, more olivaceous upperparts, much paler ochraceous subterminal bands of pectoral spots, and wingbars occupying the entire length of the wing (Fig. 4). From population D (to which the name *macularius* is applicable; Appendix S4), the new taxon is distinguished by much paler flanks and more conspicuous mantle shaft-streaks (Fig. 4).

Vocally, the new taxon is uniquely distinguished from all those in the *H. macularius* complex by a loudsong normally composed of five (rarely four or six) notes with identical shapes, in which the second and third notes are separated by an unusually longer time interval (Figs. 5 and 6 and Table 4). Even though no tape-recordings that could be unambiguously assigned to the holotype were obtained, the characteristic loudsong of an individual of this new taxon was tape-recorded at the exact same locality where the holotype was collected on 17 September 1999 by C. A. Marantz (MLS 115081; Appendix S3). Samples of loudsongs of the new taxon can be found in Isler and Whitney (2002) and Marantz and Zimmer (2006).

Description of holotype.—Crown and nape blackish neutral gray (82); lores buff–yellow (53); broad eye ring yellow-ocher (123c) bordered by a continuous narrow blackish line; auricular region with distinct black and buff streaks; malar region crossed by a conspicuous black streak, contrasting with the whitish throat and center of chin. Upperparts olive (30) with conspicuous pale shaft-lines on the central portions of mantle feathers. Breast strongly marked with mixed black and buff-yellow (53) spots, with the black usually restricted to the v-shaped tips feathers. Flanks conspicuously buff (24); belly white; wing-coverts tipped yellow-ocher (123c), faint

cinnamon (123a) wing bars occupying the entire length of wing; primary coverts blackish, contrasting with a well-defined tawny (38) patch at the base of primaries; remainder of the primaries olive-brown (28).

Measurements of holotype.—Bill width at anterior end of nostrils 5.4 mm; bill depth at anterior end of nostrils 6.7 mm; bill length from anterior end of nostril to tip 13.7 mm; wing length 83.1 mm; tail length 39.6 mm; tarsus length 33.8 mm; body mass 40.0 g.

Variation in the type series.—The type series includes eight specimens: five males, two females, and one of unknown sex. No sexual dimorphism was detected in any of the measurements taken (Table 3) or characters studied. Two specimens (MPEG 39820 and 39821) present more visible yellowish mantle shaft-streaks on the back than the holotype. Other specimens (MZUSP 58838 and MPEG 38808) lack the discrete black line that subdivides the wing bar as present in the holotype and other specimens in the type series. Back color varies in several specimens, going from black olive (29) (MZUSP 58838) to olive-brown (28) (MN 21895); similarly, underwing coverts vary from clay color (123b) (MN 21895) to cinnamon (39) (MZUSP 58838).

Distribution.—The new taxon corresponds to natural population B of the *Hylopezus macularius* complex, whose distribution is restricted to the Madeira–Xingu interfluve in Brazilian south-central Amazonia (Fig. 1). So far, no Bolivian records belonging to any taxon of the *H. macularius* are known (Remsen et al. 2012), even though a paratype of the new taxon from Alvorada d'Oeste in Rondônia (MPEG 38808) represents the southernmost and closest record to the Bolivian border available to date (~150 km; Fig. 1).

Etymology.—We are pleased to name this new taxon after our colleague Andrew ("Andy") Whittaker, whose contributions to Amazonian ornithology over the past 20 years resulted in the description and rediscovery of several species, new country records, and many noteworthy range extensions. The common names Alta Floresta Antpitta (English) and *torom-de-alta floresta* (Portuguese) refer to a popular birding destination in Brazil where the new species is regularly found.

Habitat.—The new taxon is found on or very close to the ground in dense undergrowth of humid lowland forest (sea level to ~500 m), with an apparent preference for wet or flooded areas in upland *terra firme* forest, but also in drier transitional forest on the southern limit of its range in northern Mato Grosso (Lees et al. 2008). It also seems to be more commonly found around treefall gaps and streams, but rarely in more open and disturbed areas. In common with most Grallariidae, the new species seems very sensitive to the effects of habitat loss, fragmentation, and perturbation, given that it was found in only 25% of a sample of 31 variably sized (1.2–100,000 ha) forest patches in the Alta Floresta region, northern Mato Grosso, where the smallest occupied patch was 19 ha (Lees and Peres 2010, A. Lees pers. comm.).

We also recommend the treatment of the other natural populations of the Spotted Antpitta recognized in the present study as species-level taxa according to either the BSC or the PSC, as follows.

*Spotted Antpitta (*Hylopezus macularius*, Temminck [1830])*.—Distributed on the Guianan shield from the eastern bank of the Negro and Branco rivers in Brazil eastward through eastern Venezuela (Bolívar), Guyana, French Guiana, and the state of Amapá in Brazil (Fig. 1; see also Hilty 2003, Restall et al. 2006, Naka 2011). Statistical support for the reciprocal monophyly of *macularius* with respect to all other Spotted Antpitta lineages is very high according to all phylogenetic criteria employed (Fig. 2). Average pairwise uncorrected *p*-distances between *macularius* and other lineages are as follows: 3.5% (*dilutus*), 2.8% (*whittakeri*), and 2.7% (*paraensis*). On the other hand, pairwise *p*-distances within *macularius* range from 0 to 0.38% (average 0.17%). As shown earlier, there are two and four diagnostic loudsong features distinguishing *macularius* from *paraensis* and *whittakeri*, respectively, but only one separating it from *dilutus*, the reason that both should still be treated as subspecies under the BSC but as separate species under the PSC (Figs. 5 and 7; Tables 1 and 4; and see above). Morphologically, only minor differences in flank color and the intensity of pale shaft streaking on the back distinguish *H. macularius* from the other taxa.

*Zimmer's Antpitta (*Hylopezus dilutus*, Hellmayr, [1910])*.—Distributed north of the Amazon from the western banks of the Negro and Branco rivers in the Brazilian state of Amazonas through southern Venezuela (Amazonas), southern Colombia (Amazonas), eastern Ecuador, and northern Peru west of the Ucayali River (Fig. 1; Hilty and Brown 1986, Ridgely and Greenfield 2001, Schulenberg et al. 2007). Statistical support for the reciprocal monophyly of *dilutus* with respect to other Spotted Antpitta lineages is very high according to all phylogenetic criteria employed, but consistently poor when considering its sister relationship with the *paraensis*–*whittakeri* clade (Fig. 2). Therefore, the possibility that *dilutus* is actually sister to *macularius* cannot be entirely ruled out, even though this relationship was never recovered by any of the phylogeny estimates obtained in our study; furthermore, the highest pairwise genetic distances in the Spotted Antpitta complex involve *dilutus* and *macularius*, indicating an advanced degree of evolutionary independence even if they were sister taxa. Average pairwise uncorrected *p*-distances between *dilutus* and other lineages were as follows: 3.5% (*macularius*), 2.3% (*whittakeri*), and 2.3% (*paraensis*), whereas no genetic divergence was detected between the only two individuals of *H. dilutus* sequenced. Vocally, *dilutus* is distinguished from all other lineages by a significantly shorter loudsong lasting ~2 s (in other lineages, loudsong usually lasts 2.3–2.6 s; Tables 1 and 4 and Fig. 5), whereas morphologically birds from this group can be considered the most distinct among all Spotted Antpitta lineages, given their significantly shorter tarsi, greater bill depth and width values, and a brownish rather than greenish-olivaceous back with little or no pale shaft streaking (Table 2 and Figs. 3 and 4). All things considered, we recommend recognizing *dilutus* as a phylogenetic species or as a subspecies of *macularius* until new data provide a more accurate picture of its phylogenetic position and reciprocal vocal diagnosis within the Spotted Antpitta complex. The common name proposed here honors J. T. Zimmer's early contribution to the taxonomy of the *H. macularius* complex (Zimmer 1934).

*Snethlage's Antpitta (*Hylopezus paraensis*, Snethlage [1910])*.—Distributed south of the Amazon in Brazil from the Xingu River eastward in the state of Pará to the western part of the state of Maranhão, and southward to southern Pará (Snethlage 1914, Pacheco et al. 2007). Statistical support for the reciprocal monophyly of *paraensis* with respect to all other Spotted Antpittas is high according to all phylogenetic criteria employed (Fig. 2). Average pairwise uncorrected *p* genetic distances between *paraensis* and other lineages were as follows: 2.7% (*macularius*), 2.3% (*dilutus*), and 0.77% (*whittakeri*), whereas within *paraensis* it reached only 0.3% (average 0.1%). There are two diagnostic loudsong features distinguishing *paraensis* from each *dilutus* and *macularius* and four distinguishing it from *whittakeri* (Fig. 5 and

Table 4), the reason that it should be treated as a separate species under both the BSC and PSC. Morphologically, *paraensis* is hardly distinguished from *whittakeri* and *macularius* by slight differences in flank color and bill measurements, respectively. The common name proposed here honors E. Snethlage´s early contributions to the taxonomy of the *H. macularius* complex (Snethlage 1907a, 1910).

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