SPECIES STATUS OF THE WHITE-FRONTED MANAKIN, LEPIDOTHRIX SERENA (PIPRIDAE), WITH COMMENTS ON CONSERVATION BIOLOGY¹

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Abstract. The White-fronted Manakin, Lepidothrix serena (formerly in the genus Pipra), is currently recognized as a polytypic species that includes nominate serena, from the eastern Guianan region, and suavissima, from southern and eastern Venezuela and Guyana. Nominate serena and suavissima are significantly different in plumage, syringeal morphology, and vocalizations. The distribution of the two forms has not been completely documented, but no contact between the populations is known. Derived morphological and behavioral novelties indicate that the two forms are sister taxa, and that they constitute distinct phylogenetic and biological species. The recommended common name of the newly recognized Lepidothrix suavissima is the Tepui Manakin. Maintenance of the current biological species taxonomy may underestimate the diversity of species in the Neotropics and hamper the documentation of diversity in the Neotropics that is important to conservation biology.

Key words: Pipridae; Lepidothrix serena; Lepidothrix suavissima; species limits; syringeal morphology; vocalization; Neotropics; conservation biology.

INTRODUCTION

The current species limits of many Neotropical birds are based on taxonomic decisions made by ornithologists in the early and mid-twentieth century. Many polytypic species of Neotropical birds were established on the basis of plumage characters alone in complete absence of natural history information (e.g., Ridgway 1907, Hellmayr 1929, Meyer de Schauensee 1966). Most of these taxa are currently considered to be valid biological species, even though the species limits among the differentiated forms within them may never have received detailed consideration. Reevaluation of polytypic Neotropical taxa has revealed many highly distinct forms that are essentially hidden within wide-ranging polytypic species. For example, Robbins and Ridgely (1992) have shown that the isolated Chocó endemic Nyctiphrynus rosenbergi is highly differentiated in song, plumage, and mass from the Amazonian N. ocellatus, with which it was formerly combined in a "biological" species. Indeed, rosenbergi is probably not even as closely related to ocellatus as are the distinct Central American species vucatanicus and mcleodii (Robbins and Ridgely 1992). Analyses of molecular differentiation of Neotropical passerine birds demonstrate that many isolated populations that are recognized as subspecies, or not recognized as separate taxa at all, are much more genetically differentiated than many biological species of Nearctic passerines (Capparella 1988, 1991; Hackett and Rosenberg 1990; Hackett 1993). These studies strongly suggest that there are many more species of Neotropical birds than currently recognized. This underestimate of Neotropical diversity could lead to inaccuracies in analyses of regional endemism and the reconstruction of the biogeographic history of these regions that are critical to conservation biology. Reanalysis of variation in plumage, morphometrics, other aspects of morphology, molecular characters, and behavior of many Neotropical birds is required to re-evaluate the status of these wide-ranging, polytypic biological species.

Here, I address the species limits of two differentiated basal taxa of manakins (Pipridae). *Lepidothrix serena* is currently recognized as a polytypic species composed of two allopatrically or parapatrically isolated populations in northern South America. The nominate form of *serena* was originally described by Linnaeus (1766) from Cayenne material, and placed in the genus *Pipra*. A second taxon was subsequently described as *Pipra suavissima* by Salvin and Godman (1882) based on specimens from Roraima and the Me-

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rume Mountains in then British Guiana. The two forms were treated as separate species by Hellmayr (1906) and Chubb (1921), but they were combined as subspecies of *Pipra serena* without comment by Hellmayr (1910, 1929). No comments in the literature were made on the systematics of *serena* until Haffer (1970, 1974) and Snow (1975, 1979) proposed that the polytypic *serena* be included in a species-group with *coronata*, *nattereri*, *iris*, *vilasboasi*, *coeruleocapilla*, and *isidorei*. Prum (1988) proposed a phylogeny of the monophyletic *serena* species group based on plumage traits in which nominate *serena* and *suavissima* were hypothesized to be sister taxa.

In a phylogenetic analysis of the entire Pipridae, I uncovered no evidence of relationship between the serena species group and the rest of genus Pipra. Based on syringeal morphology, the serena species group is more closely related to a group including Manacus, Chiroxiphia, and Antilophia. Given evidence of the polyphyly of Pipra (sensu Hellmayr 1929, Snow 1979), I removed the serena species group from Pipra and placed it in its own genus, for which the name Lepidothrix Bonaparte was available (Prum 1992).

Within the polytypic species Lepidothrix serena, I discovered a tremendous difference in syringeal structure between the two subspecies that is greater than that found between many families of oscine birds (Prum 1990a, 1992). As a result, I have analyzed the variation in the distribution, plumage, size, syringeal morphology, and song of nominate serena and suavissima to re-evaluate the status of the two taxa.

METHODS

Study skins and spirit specimens were observed from the collections of the American Museum of Natural History (AMNH), the British Museum (Natural History) (BM), the University of Kansas Museum of Natural History (KU), the Royal Ontario Museum of Natural History (ROM), and the United States National Museum of Natural History (USNM). Distributions of *serena* and *suavissima* were plotted from published records and from localities on museum specimens. Plumage was described from museum study skins and compared to a standard color reference (Smithe 1975). Tarsus, flat wing, and tail were measured on 60 specimens of *serena* and *suavissima*. Twelve cleared-and-stained, and iodine-stained syringeal specimens of both species were observed and illustrated using a Wild M5 stereo dissection microscope (serena: ROM 127643, USNM 515106, 515108, 515109, 515113, 515114; suavissima: AMNH 9366, 9368, 10376, 10377, 816768, BM-A-1968-46-19). Tape recordings of vocalizations were collected from my own field recordings, recordings by Tom Davis, and from recordings by Paul Schwartz, Theodore A. Parker III, and Mario Cohn-Haft deposited at the Cornell Laboratory of Natural Sounds (LNS). Analyses of vocalizations were done using Canary 1.1 computer software produced by the Cornell Laboratory of Natural Sounds. Sonogram figures were prepared using Kay Elemetrics Vibralyzer 7030-A.

RESULTS

DISTRIBUTION

The nominate form of serena is distributed from the Acary Mountains (in disputed territory along the southern border between Guyana and Suriname), to the interior of Suriname and French Guiana, south to near Manaus, Brazil and southern Amapá near the mouth of the Amazon River (Fig. 1). Snow (1979) overlooked the Acary Mountain record (Blake 1950), and several Brazilian localities (Willis 1977, Novaes 1978) in his description of the range of nominate serena. Several other localities have been published subsequently that further established the range of serena in northern Amazonian Brazil (Willis and Oniki 1988, Stotz and Bierregaard 1989, Bierregaard 1990). Large portions of the presumed range of serena have not yet been documented. Based on current information, serena likely occurs in portions of western and southern Suriname, and northern Pará, Brazil between Manaus and Amapá. In Suriname, serena occurs in primary forest above 200 m in altitude, and is not found in coastal forest (Haverschmidt 1968, Prum 1985).

Populations of *suavissima* have been recorded throughout the tepui highlands of southern Venezuela (just reaching into Brazil at the southern tip of Venezuela), in northeastern Venezuela, and in western, central, and eastern Guyana (Fig. 1). There are no records of *suavissima* from the southern third of Guyana or the entire Rio Branco drainage, Brazil. This lack of records may reflect the actual distribution. Moskovits et al. (1985) did record *suavissima* at the Ecological



FIGURE 1. Map of the distribution of nominate serena and suavissima. Circles are serena localities. Squares are suavissima localities.

Station of Maracá on the Uraricoera River, Roraima, Brazil (03°25'N, 61°40'W). However, Stotz (1993) recorded a hybrid between suavissima and Lepidothrix coronata in northern Roraima, Brazil (04°29'N, 61°09'W) about 50 km from the closest known locality at Pauri-tepui in southern Venezuela. The distribution of suavissima may extend a little further into Roraima, Brazil than is currently known, but it is probably not generally distributed south of current localities in the Rio Branco drainage or to the Rio Negro. In Venezuela, suavissima has been recorded between 500-1,800 m (Meyer de Schauensee and Phelps 1978), and would appear to be restricted to tepuis, but old collections in central Guyana indicate that suavissima may range down to near sea level.

The closest localities in the known distributions of the two taxa come along the lower Courantyne River, which forms a portion of the border between Guyana and Suriname. In eastern Guyana, suavissima is known from Tiger Creek, a small west or left bank tributary of the Courantyne (Chubb 1921, Stephens and Traylor 1985). Nominate serena is known from several localities in central and eastern Suriname, but no records are available from western Suriname along the lower Courantyne. However, serena is known from the Acary Mountains which are between the left bank of the upper Courantyne, and the east or right bank of the New River. The known distributions of serena and suavissima are allopatric. It is possible that serena and suavissima come into parapatric contact somewhere on the

Species Sex	Tarsus			Flat Wing			Tail		
	n	Mean	SD	n	Mean	SD	n	Mean	SD
serena									
Male	12	16.2	0.47	13	52.2	0.83	12	26.9	2.18
Female	12	15.5	0.72	11	54.2	1.74	11	27.6	1.38
Significance (t-test)	P = 0.015			P = 0.0055			P = 0.34		
suavissima									
Male	22	15.2	0.48	21	57.9	1.07	22	28.3	1.07
Female	13	15.1	0.41	13	58.6	1.04	13	29.8	1.01
Significance (t-test)	P = 0.41			P = 0.048			P = 0.0002		

TABLE 1. Sexual dimorphism in tarsus, flat wing, and tail in nominate serena and suavissima. See text for details.

lower Courantyne or New Rivers. However, nominate serena and suavissima both prefer humid forests above 200 m in altitude, and their ranges may be separated from one another along the lower Courantyne by inappropriate white sand savannah-woodland or humid forests below 200 m.

PLUMAGE

The plumage of serena and suavissima are similar, but both sexes of each form have distinctive, fixed differences in plumage coloration. (Capitalized color names refer to Smithe [1975]). Males of serena and suavissima are velvety black on the head, back, wings, tail, and upper breast, and have a white forecrown, a blue rump (Venetian Blue), and a yellow belly. In male serena, the belly is Spectrum Yellow, and a small patch on the upper breast is Orange Yellow; the forecrown is white with a slight Sky Blue tinge in very few specimens (illustrated in Haverschmidt 1968). In male suavissima, the belly is Orange Yellow, the upper breast is entirely black, and the trailing edge of the forecrown is Sky Blue (illustrated in Meyer de Schauensee and Phelps 1978). No intermediates in male plumage were observed, and none has been described.

Female serena and suavissima are both largely grass green above. Female serena are light sulfur yellow below. Female suavissima are brighter yellow below, and have a distinct blue tinge on the forecrown.

Both sexes of both forms have black legs, black bills, and brown irises. The iris of *serena* was erroneously illustrated as white by P. Barruel in Haverschmidt (1968); the artist apparently matched the iris color to the white of *Pipra aureola* and *Pipra erythrocephala*. This error was repeated in an illustration of *suavissima* by G. Tudor in Meyer de Schauensee and Phelps (1978), and by Prum (1988) in a phylogenetic analysis of the *serena* species group. Data from recent specimens with soft part colors described (USNM), and photographs from Suriname (R. O. Prum, VIREO) and near Manaus (VIREO) document that the iris color of all populations is brown.

SIZE

Both serena and suavissima exhibit significant sexual dimorphism in size (Table 1). In serena, males were significantly smaller than females in wing length (t-test, $P \le 0.0055$), but significantly larger in tarsus length (t-test, $P \le 0.015$). Males and females were not different in mean tail length (t-test, $P \le 0.34$). In suavissima, males were significantly smaller than females in wing (t-test, $P \le 0.048$) and tail (t-test, $P \le 0.0002$) lengths, but were similar in tarsus length.

In general, *serena* is slightly smaller than *sua-vissima*, and males are smaller than females. The exception is in tarsus length in *serena* which is bigger in males. Although many of these differences are statistically significant, they are not great enough to make individuals of each taxon diagnosably different in size.

SYRINGEAL MORPHOLOGY

Prum (1992) described the syringeal morphology of *serena* and *suavissima* in detail; however, a larger sample including five more syringeal specimens of *serena* was examined for this analysis. Syringeal terminology and variation in the syringeal morphology of manakins is described in Prum (1992). The syrinx of *suavissima* is similar to other species of *Lepidothrix* except that it is slightly larger in diameter, has an extended series of dorsally cartilaginous tracheal A elements, and a few double, medially cartilaginous, complete A elements (Figs. 2A, B). The syrinx of serena has all of the features of suavissima with an additional suite of derived features that are unique among all manakins (Figs. 2C, D). All of the unique features of the syrinx of serena are related to its increase in size. The diameter of the syrinx of serena is 3.8 mm at A1 (n = 7; SD = 0.11), and 2.8 mm at A10 (n = 7; SD = 0.13). The diameter of the syrinx of suavissima is 2.6 mm at A1 (n = 6; SD = 0.13), and 1.6 at A10 (n = 1, 2, 3, 3)6; SD = 0.05). The mean diameters of A1 and A6 of nominate serena and suavissima differ by more than nine standard deviations, and are significantly different at the P < 0.01 level. Associated with the widening of the syrinx, the trachea in serena is twisted and distorted in shape into an oval, in cross section. The bronchi are also expanded in size, and the B elements are further distorted in shape. Further, the slight medial, cartilaginous connections among the bronchial A elements in suavissima are expanded in serena into a large cartilaginous plate that is connected to the dorsal and ventral ends of four or five bronchial A elements, and forms a cartilaginous plate that is the medial surface of the bronchi (Fig. 2C). Because of the distortion of the bronchial diameter, this cartilaginous plate is frequently buckled or depressed into the bronchial lumen. In serena, the series of dorsally cartilaginous tracheal A elements extends at least to A15 but can continue to A19. All species of Lepidothrix lack intrinsic syringeal muscles, and the M. tracheolateralis of serena inserts on A1 as in other species of the genus.

SONG

Recordings of *serena* come from the Brownsberg Nature Park, Suriname (04°55'N, 55°12'W) [tape recordings by R. O. Prum, and T. Davis], and near Manaus, Brazil (02°40'S, 60°00'W) [LNS 48743]. The available recordings of *suavissima* were made in Rio Grande, eastern Venezuela (07°58'N, 61°53'W) [P. Schwartz recordings, housed at LNS], and on La Escalera, in southeastern Venezuela (06°00'N, 61°10'W) [LNS 30446].

I described the song of *serena* in Suriname as a soft, throaty, rolling "*whree*" (Fig. 3A), with the quality of a toy police-whistle (Prum 1985). The *whree* notes are given in a long series by territorial males and are occasionally interspersed with low, throaty, whistled "boop" notes (Fig. 3B). During display, males also give a soft, descending "puurr" note (Fig. 3C). The whree and boop calls are essentially the same on tape recordings from near Manaus.

The vocalizations of *suavissima* have been previously described as a "squeak" by Meyer de Schauensee and Phelps (1978). Based on recordings, the main vocalization given by territorial males is a sharp, nasal, slightly rising "*aank*" (Fig. 3D). Males also give a rapid, emphatic, piping series of 7 or 8 notes which rise and fall in pitch and emphasis: "*whee-pee-pee-...-pee*" (Fig. 3E). This piping call was recorded following playback of the *aank* call and during counter-singing among males.

The territorial calls of serena and suavissima are similar in note structure and behavioral context. These calls are apparently homologs that have diverged since common ancestry between the two taxa. Sonograms of these vocalizations reveal that the *whree* calls are almost twice as long as *aank* calls (Figs. 3A, D; *whree*: n = 13. X = 253 msec, SD = 27; *aank*: n = 12, X = 136msec, SD = 22), and that this difference is statistically significant (t-test, P < 0.01). The two vocalizations also differ in frequency and frequency modulation. The whree call of serena has a primary frequency band between 1.5 and 2.2 kHz. Recordings of the call sometimes show other weaker harmonic bands near 4 and 6 kHz (Prum 1985), but under other conditions no identifiable harmonics are recorded. The whree call either rises slightly in pitch, from 1.5-1.8 kHz to 2.0-2.2 kHz, or it remains centered on a single band of frequencies. All whree calls show distinctive, rapid oscillations between the maximum and minimum frequencies over very short time intervals. These frequency modulations give the call its throaty, rolling quality.

In contrast, the *aank* call of *suavissima* is composed of a main frequency band that begins near 1.5–1.6 kHz and rises rapidly over a few msec to form a wide band between 2.2 and 2.4 kHz for the last two thirds of the note (Fig. 3D). Many recordings show weaker harmonic bands at 1.2, 3.6, 4.8, and 6.0 kHz. The *aank* call shows none of the rapid frequency modulations found in the *whree* call.

The other vocalizations of *serena* and *suavissima* are apparently unique to each taxon, and not homologous to any vocalizations in the oth-



FIGURE 2. Syringeal morphology of nominate serena and suavissima. (A) Dorsal and (B) ventral views of the syrinx of suavissima (AMNH 816768, 9366 respectively); (C) Dorsal and (D) ventral views of the syrinx of nominate serena (ROM 127643). See text for descriptions. A1 indicates the A1 syringeal supporting element.



FIGURE 3. Sonograms of vocalizations of nominate *serena*: (A) two examples of the *whree* call, (B) the *boop* call, and (C) the *puurr* call. Sonograms of vocalizations of *suavissima*: (D) two examples of the *aank* call, and (E) the piping call. See text for descriptions.

er's repertoire. The soft *boop* call of *serena* is a short note (~100 msec) that rises slightly from 0.8 to 1.0 kHz (Fig. 3B). The soft, descending *puurr* that is given during display appears as a series of 10 to 12 short notes that begin near 1.5 kHz and descend to near 1 kHz over 250-300 msec (Fig. 3C).

The agonistic, piping trill given by suavissima is a series of seven or eight notes (Fig. 3E). Each note rises rapidly in frequency over 50–55 msec and then drops back to the initial frequency in ~15 msec. The first and last notes in the series have initial and maximum frequency ranges of 2.3–3.5 kHz. Each note in the series increases in frequency range until the middle notes, which vary from 2.6–4.3 kHz, and then tapers off to resemble the values of the initial notes. In some recordings, these calls show related harmonic bands at 6–8 kHz and above 10 kHz. Interestingly, in all three available recordings, male suavissima alternated strictly between seven and eight note trills.

DISCUSSION

Nominate serena and suavissima differ significantly in many aspects of plumage, syringeal morphology, and song. The plumage differences between the two forms are found in both males and females, and are fixed among populations. The syringeal morphology of the two taxa is tremendously different. The syrinx of nominate serena has a suite of unique, derived syringeal features which constitute a major change in syringeal organization. This degree of syringeal differentiation is unknown previously among any avian congeners, and certainly not among conspecifics (Prum 1992). Consequently, the two taxa differ significantly in the acoustic structure of their vocalizations. Despite striking differences in syringeal morphology, the main territorial calls of the two taxa are apparently homologous, and differ in length and frequency and frequency modulation. Each taxon has additional vocalizations that have no apparent homolog in the other's

vocal repertoire. Since most vocalizations of suboscine passerines are considered to be innate and not learned (Kroodsma 1984), the vocal differences between the two forms also constitute evidence of genetic differentiation rather than merely of cultural divergence. The two taxa also differ slightly in size.

These data support the conclusion that *serena* and *suavissima* are distinct, basal, diagnosable lineages (Cracraft 1983, McKitrick and Zink 1988) with independent evolutionary histories and fates (Wiley 1978, Frost and Hillis 1990). On this basis, I would recommend that the two taxa be recognized as separate phylogenetic, or evolutionary species (Wiley 1978, Cracraft 1983, McKitrick and Zink 1988, Frost and Hillis 1990).

These data also support the conclusion that these taxa are distinct biological species. In applying the biological species concept to these allopatric or parapatric taxa, the degree of differentiation between serena and suavissima must be gauged as an indication of the likelihood of extensive interbreeding were they to come in contact with one another. One way to address this issue is to compare the degree of differentiation to other currently recognized biological species of manakins and other suboscines. The degree of plumage differentiation between serena and suavissima is similar to species of the Pipra erythrocephala clade, the Pipra aureola clade, and Chiroxiphia (Prum 1992). Unfortunately, variations in the application of the biological species concept among authors make other comparisons unclear. Although the highly differentiated species of Manacus hybridize along certain limited areas of secondary contact (Haffer 1970, 1974; Parsons et al. 1993), they have been considered by various authors to be a single biological species (Haffer 1970, 1974; Snow 1975, 1979) or a group of distinct biological species (American Ornithologist's Union 1983; Hilty and Brown 1986; Stiles and Skutch 1989; Ridgley and Gwynne 1989; Prum 1990b, 1992; Parsons et al. 1993). There is little agreement on how much morphological integration or interbreeding is required to constitute grounds for combining differentiated taxa into a polytypic species. Comparing other characteristics, the amount of syringeal differentiation between serena and suavissima is more extensive than among other manakin congeners (Prum 1992). The consequent differences in vocalizations are extensive, and at least as divergent as other biological spe-

cies of manakins (R. O. Prum, pers. observ.). Vocal differentiation has been used as evidence of species differences in tyrant flycatchers (Tyrannidae) in which songs are innate (e.g., Lanyon 1978, Johnston 1980). Since territorial vocalizations and male plumage are used in mate attraction displays in manakins, it is likely that differentiation in these traits is directly related to mate preferences that would be maintained in secondary contact. In conclusion, differentiation in plumage, size, syringeal morphology, and vocalizations between serena and suavissima are significant, comparable or in excess of the level found in other recognized biological species of manakins and tyrant flycatchers, and likely to result in reproductive isolation if these taxa were in secondary contact. For these reasons, I recommend that serena and suavissima be recognized as separate biological species.

An appropriate common name for the newly recognized species *Lepidothrix suavissima* is the Tepui Manakin, based on its distribution in this distinctive Neotropical land formation. The monotypic *Lepidothrix serena* should continue to be called the White-fronted Manakin.

Further field research in western Suriname, eastern Guyana, and the Rio Branco and Rio Jauaperi drainages, Brazil, could further elucidate the limits of the distributions of *Lepidothrix* serena and *L. suavissima*. At present the lower Courantyne River and the New River appear to delineate the northern border of the distribution of the two forms. The limits of their distribution in Brazil are even less well known. It is probable, however, that the range of *suavissima* does not extend much further into Brazil than currently documented, and that the lack of records of either form in Amazonia west of Manaus reflects the actual distribution of the two species.

The relationship between species limits and conservation biology has been outlined elsewhere (e.g., Eldredge 1992, Zink 1993). In general, the degree of precision of diversity estimates and consequent, taxon-oriented conservation efforts are limited by the precision of the taxonomy employed. Efforts to survey and catalogue avian diversity in the Neotropics using the currently recognized species limits will not recover the contribution to patterns of endemism made by highly differentiated taxa that are combined in wide-ranging polytypic species, such as the formerly polytypic *Lepidothrix serena*. There are dozens of other legitimate examples of differentiated allopatric taxa that are currently recognized as subspecies in the Neotropical suboscines alone (e.g., Chloropipo holochlora litae, Corapipo leucorrhoa altera, Laniisoma elegans buckleyi, Machaeropteru regulus striolatus, Pyroderus scutatus occidentalis, Rupicola peruviana sanguinolenta; sensu Snow 1979).

Unfortunately, subspecies are viewed by many ornithologists as an inconsequential category of diversity, or as too narrowly differentiated to be identified without specimens, special experience, or extra effort. Use of subspecific names is actively discouraged by many ornithological institutions. Contributors to this and other major American ornithological journals are instructed, "Do not give subspecific identification unless it is pertinent and has been critically determined" (Anon. 1992). Since ornithologists frequently do not view subspecies as pertinent to their research and generally believe that "critical" determination requires voucher specimens that are infrequently collected, much of what we could know about Neotropical birds has been obscured.

As an example, several publications in the last two decades have documented new localities of the polytypic White-fronted Manakin, Lepidothrix serena, in Brazil, near Manaus (Willis 1977, Willis and Oniki 1988, Stotz and Bierregaard 1989, Bierregaard 1990). These records represented a range extension of over 500 km from the nearest previously known locality (Blake 1950). In none of the publications was the subspecies of serena established. None mentioned whether voucher specimens of serena had been collected or deposited in any museum. To determine whether nominate serena or suavissima extended its range from the Guianas to the Manaus region. I had to rely on photographs deposited at Visual Resources for Ornithology (VIREO, Academy of Natural Sciences of Philadelphia), and undocumented memories of researchers who had been to the area.

This lack of appropriate documentation of avian diversity in the Neotropics has resulted in part from reliance by professional ornithologists on inadequate, current species taxa. Current species names are insufficient to characterize many of the units of diversity in the Neotropical avifauna, and they constitute a significant burden to the documentation and analysis of avian biogeographic patterns that are critical to establishing diversity estimates and conservation priorities. In many cases, amateur and professional ornithologists would identify and record well-differentiated taxa that are currently recognized as subspecies if these forms were given species status, or if subspecific identifications were actively encouraged.

Conservation efforts require that ornithological publications encourage the use of the most specific identification possible given the methods of observation or investigation. Although many subspecies are difficult to identify even with voucher specimens, ornithological publications should encourage, rather than discourage, their use. These identifications should be accompanied by documentation of how the determination was made. Additional research on species limits in polytypic Neotropical taxa is also essential to furthering our understanding of patterns of endemism. Although the needs of conservation biology cannot be considered a primary justification for recognizing phylogenetic or more finely differentiated biological species, it should be recognized that maintaining the taxonomic status quo could constitute a significant cost to conservation efforts in the Neotropics.

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