

Quantifying Subspecies Analysis: A Case Study of Morphometric Variation and Subspecies in the Woodcreeper Genus *Dendrocolaptes*

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CHAPTER 11

QUANTIFYING SUBSPECIES ANALYSIS: A CASE STUDY OF MORPHOMETRIC VARIATION AND SUBSPECIES IN THE WOODCREEPER GENUS *DENDROCOLAPTES*

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ABSTRACT.—Many authors have criticized the use of subspecies, but most of this criticism has been directed at the inconsistent treatment of subspecies rather than the inutility of diagnosable populations. To assess the validity of a taxon, one must include in the analysis those characters used in the original diagnosis and remember that different character sets may lack geographic concordance. We examined morphometric variation using 3,027 specimens representing all five species and 30 subspecies in the woodcreeper genus *Dendrocolaptes* (Dendrocolaptinae). Most subspecies in the genus differ in plumage patterns and coloration, but a few taxa were described using characters of size and structure. We sought to assess quantitatively, on the basis of the *D*-statistic (Patten and Unitt 2002), those subspecies described using mensural characters, to quantify morphological variation, and to examine the influence of ecological correlates in the genus. Males average slightly larger than females but have a less massive bill. *Dendrocolaptes certhia* has a wider bill than *D. sanctithomae*, and *D. picummus puncticollis* has a slimmer bill than other *D. picummus*. Although previously considered a subspecies-group within *D. certhia*, *D. sanctithomae* has a shorter and slimmer bill that appears to reflect a greater dependence on foraging over army ants; these species also differ vocally and in plumage. Bill length in Middle American populations of *D. sanctithomae* varies as a smooth cline and, when combined with weak and potentially clinal variation in plumage and bill coloration documented in an earlier study of plumage variation, our data failed to support the recognition of *D. s. nigrirostris* and *D. s. colombianus*. Amazonian, montane, and Chaco representatives of *D. picummus* differ structurally, but subspecies differ little morphometrically within each region. *Dendrocolaptes hoffmannsi* broadly overlaps Amazonian *D. picummus* morphometrically, but its plumage patterns are distinctive. The only subspecies in this complex described exclusively on the basis of mensural characters, *D. p. casaresi*, appears to be slightly larger than *D. p. pallescens*, but we had too few specimens to assess diagnosability. We conclude that reanalysis of described subspecies using quantitative, statistical methods will provide a clearer starting point for studies of biogeography, migration, and other aspects of evolutionary biology than will subspecies based solely on qualitative judgment.

Key words: *Dendrocolaptes*, *D*-statistic, ecological correlates, morphometrics, quantitative analysis, subspecies diagnosis, woodcreepers.

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Cuantificación en los Análisis de Subespecies: un Estudio de Caso de la Variación Morfométrica y las Subespecies en el Género *Dendrocolaptes*

RESUMEN.—Muchos autores han criticado el uso de subespecies, pero la mayor parte de esas críticas se ha dirigido más al tratamiento poco consistente de las subespecies que a la inutilidad de las poblaciones diagnosticables. Para determinar la validez de un taxón, uno debe incluir en el análisis aquellos caracteres utilizados en el diagnóstico original y recordar que diferentes conjuntos de caracteres pueden carecer de concordancia geográfica. Examinamos la variación morfométrica en 3027 especímenes representativos de las cinco especies y 30 subespecies del género *Dendrocolaptes* (Dendrocolaptinae). La mayoría de las subespecies difieren en sus patrones de plumaje y coloración, aunque unos pocos taxones fueron descritos utilizando caracteres de tamaño y estructura. Nuestros objetivos fueron evaluar cuantitativamente usando el estadístico *D* (Patten y Unitt 2002) a aquellas subespecies que fueron descritas usando caracteres mensurativos, cuantificar la variación morfológica y examinar la influencia de correlatos ecológicos en el género. Los machos fueron en promedio ligeramente más grandes que las hembras, pero presentaron picos más pequeños. *Dendrocolaptes certhia* tiene un pico más ancho que *D. sanctithomae* y *D. picummus puncticolis* tiene un pico más delgado que el de otras formas de *D. picummus*. A pesar de que anteriormente se consideraba un grupo de subespecies dentro de *D. certhia*, *D. sanctithomae* tiene un pico más corto y delgado que parece reflejar su gran dependencia en seguir ejércitos de hormigas para forrajear. Estas especies también se diferencian en sus vocalizaciones y plumaje. La longitud del pico en las poblaciones mesoamericanas de *D. sanctithomae* varía como una clina suave. Combinando esa variación con la variación débil y posiblemente clinal del plumaje y la coloración del pico documentada en un estudio anterior, nuestros datos no apoyan el reconocimiento de las subespecies *D. s. nigrirostris* y *D. s. colombianus*. Los representantes de *D. picummus* de las regiones amazónicas, montañas y del Chaco difieren estructuralmente pero las subespecies de una misma región difieren poco morfométricamente. La única subespecie en este complejo que fue descrita exclusivamente con base en caracteres mensurativos, *D. p. casareti*, parece ser levemente más grande que *D. p. pallescens*, pero contamos con muy pocos especímenes como para hacer un diagnóstico. Concluimos que el re-análisis de las subespecies descritas usando métodos estadísticos cuantitativos brindará puntos de partida más claros para los estudios de biogeografía, migración y otros aspectos de biología evolutiva que las subespecies basadas sólo en juicios cualitativos.

A SUBSPECIES IS a collection of one or more populations that occupy a distinct breeding range and that are diagnosable from other such populations (Mayr and Ashlock 1991). Well-defined subspecies play a key role in studies of geographic variation, and they are useful for studying migration, adaptation, and speciation. Indeed, in evolutionary studies it is important to distinguish primary differentiation from secondary contact with hybridization, something that may be best accomplished using a biological species concept with subspecies (Johnson et al. 1999). Still, the use of subspecies has been criticized by many authors (e.g., Wilson and Brown 1953, Selander 1971, McKittrick and Zink 1988, Zink 2004). Most such criticism appears to stem from the uneven application of the concept, which has led to the recognition of many invalid taxa, rather than from the potential importance of well-defined and readily diagnosable subspecies (Parkes 1982; Patten and Unitt 2002; Patten, this volume; Remsen, this volume). Moreover, many critics of subspecies fail to

acknowledge that most such taxa were described before the advent of modern statistics and have never been examined using the numerous sophisticated techniques now applied in studies of geographic variation (Remsen 2005, this volume). Patten and Unitt (2002) emphasized that the diagnosability of populations, as opposed to mean differences between them, is the key to effectively defining subspecies. The key to diagnosability is the degree of overlap allowed between populations and not the statistical difference between the means of populations that may overlap extensively (Patten and Unitt 2002; Patten, this volume; Remsen, this volume), although authors have varied on the percentage of individuals in a given population that must differ from those in all other such populations (usually varying in the range of 75–100%; Amadon 1949, Marshall 1967, Mayr 1969, Amadon and Short 1992).

There is some disagreement about the degree of concordance expected among multiple character sets at various taxonomic levels. Wilson and

Brown (1953) argued that empirical studies contradicted the assumption of a coadapted system in which multiple character sets vary geographically in a coordinated manner within species, and they went on to say that populations that show a high degree of geographic concordance in multiple character sets are probably specifically distinct. More recently, however, Avise and Ball (1990) stressed that subspecies should be recognized only when there are concordant patterns of geographic variation in multiple, independent, genetically based characters. Even these authors noted, however, that natural selection can result in some character sets showing geographic patterns contrary to the main phylogenetic signal. In either case, the only logical place to begin the assessment of a subspecies is to examine characters originally used to describe the taxon in question, because even though new character sets may support the recognition of a particular taxon, one cannot discount taxa without examining the characters used in their original diagnosis.

Many avian subspecies have been described on the basis of plumage characters; however, there are also many taxa based on size or shape differences that are best assessed using mensural characters. Plumage coloration and patterns used to define subspecies may have arisen from adaptations for crypsis or from sexual selection; however, morphometric characters likely reflect adaptations for locomotion or foraging (Bock 1966, Karr and James 1975, Fitzpatrick 1985, Leisler and Winkler 1985) or they result from adaptations of body size to climatic variation (James 1970). Although the results of morphometric studies may be dominated by relationships of size, with the first principal component (PC1) of such analyses sometimes treated as a general size factor (see Zink and Remsen 1986, Rising and Somers 1989), shape differences are likely to provide better clues to differences in locomotory ability or foraging behavior (Karr and James 1975, Fitzpatrick 1985, Leisler and Winkler 1985). In birds, wing structure is adapted primarily for flight and the legs for walking or perching. The tail seems to be somewhat less tied to flight than the wings, and in some species this has allowed some modifications of the tail through sexual selection in addition to, or even instead of, adaptation for various forms of locomotion. Bill shape, among the most variable of structural features in birds, reflects adaptation to foraging and consuming a variety of food items (Bock

1966, Fitzpatrick 1985). One may therefore expect closely related species that differ in locomotory behavior (including migration) or foraging behavior to have concomitant differences in body size and shape.

The woodcreepers are a monophyletic group of ~50 species (Marantz et al. 2003) presently recognized as a subfamily within a large Neotropical radiation of the Furnariidae (Irestedt et al. 2002, Remsen et al. 2009). Woodcreepers represent a remarkably cohesive group with respect to both morphology and behavior, but the species differ conspicuously in size, bill shape, and foraging behavior (Marantz et al. 2003). Although most woodcreepers forage by gleaning and probing, some species, especially those that take prey primarily in association with swarms of army ants, forage more by sallying than by probing (Willis 1972, 1982, 1992; Marantz et al. 2003). The five members of the genus *Dendrocolaptes* are relatively large, slim woodcreepers with short bills that are dorsoventrally compressed to varying degrees (Marantz 1992, Marantz et al. 2003). Observations of foraging by these birds have further revealed the importance of sallying, and this is especially true of those species that forage primarily in association with army ants (especially *Eciton burchelli*; Willis 1982, 1992).

Species in the genus *Dendrocolaptes* are best treated as representatives of two groups defined on the basis of plumage patterns (see Marantz 1997). Taxa in the *D. certhia* complex (including *D. sanctithomae*) have the head and body barred extensively (the barred woodcreepers), but those in the *D. picumnus* complex (including *D. platyrostris* and *D. hoffmannsi*) have the head, neck, and breast streaked to a varying degree (the streaked birds). All *Dendrocolaptes* show some indication of barring on the belly. Two poorly marked forms were assigned to their respective groups on the basis of faint barring on the head and body (*D. certhia concolor*) or fine streaking on the breast (*D. hoffmannsi*). Within *D. picumnus*, subspecies-groups were recognized on the basis of geography (Amazonian, Chaco, and montane), and the montane taxa were further subdivided on the basis of plumage similarity. Montane subspecies that occur in the central portion of the range (group A) have the underparts less extensively streaked on a weakly barred background, but peripheral populations (group B) have more extensive streaks on an essentially unmarked background (see Marantz 1997).

Our study had two primary goals. First, using a sample combining the holdings of most museums in the New World that house large numbers of woodcreeper skins, we sought to assess the validity of taxa that were described on the basis of morphometric characters. Although most taxa in this complex were defined on the basis of plumage characters (see Marantz 1997), a few subspecies in the genus were described largely or exclusively on the basis of mensural characters. In particular, two Middle American subspecies of *D. sanctithomae* (*D. s. nigrirostris* and *D. s. colombianus*) were defined primarily on the basis of differences in bill length (Todd 1950). One additional subspecies in *Dendrocolaptes* was described exclusively on the basis of mensural differences: *D. picumnus casaresi* (Steullet and Deautier 1950), but sample sizes were small. Taken together with an earlier study of plumage variation in this complex (Marantz 1997), our morphometric analysis provides an assessment of all taxa presently recognized in this genus. Our secondary goal was to examine overall patterns of morphometric variation in all five species in the genus *Dendrocolaptes* and to determine whether differences in foraging behavior noted by Willis (1982, 1992) correspond to discrete structural differences, particularly those in bill shape. We set out to demonstrate that quantitative analysis of patterns of geographic variation provides a sounder baseline for studies of biogeography, migration, and other aspects of evolutionary biology than will studies based on qualitative fractionation of that variation.

METHODS

MORPHOMETRIC DATA

Marantz measured 3,027 specimens of the five species in the genus *Dendrocolaptes* (Table 1 and Fig. 1; see Acknowledgments). Our sample included specimens representing all 30 subspecies either listed in Peters (1951) or described since that publication, and all 23 subspecies recognized by Marantz et al. (2003). Species-level taxonomy follows Marantz et al. (2003).

Using either dial or digital calipers, we measured, to the nearest 0.1 mm, nine characters on each specimen. In addition to standard measurements of wing chord, tail length, and tarsus (tarsometatarsus) length (Baldwin et al. 1931), we

TABLE 1. Species of *Dendrocolaptes* used in the present study and, for each, the plumage group, sample size used in morphometric analyses, and tendency to forage in association with army ants (the latter based on Willis 1982, 1992). *Dendrocolaptes picumnus* was further divided into four subspecies-groups on the basis of geography and plumage patterns.

Species	Plumage group	<i>n</i>	Foraging behavior
<i>D. sanctithomae</i>	Barred	463	Army ants
<i>D. certhia</i>	Barred	755	Generalized
<i>D. picumnus</i> ^a	Streaked	560	Army ants ^b
<i>D. hoffmannsi</i>	Finely streaked	26	Army ants
<i>D. platyrostris</i>	Streaked	738	Generalized

^a*D. picumnus* subspecies-groups (and their sample sizes) are as follows. Amazonian (*n* = 207): *D. p. picumnus*, *D. p. validus*, *D. p. transfasciatus*. Chaco (*n* = 73): *D. p. pallescens*, *D. p. extimus*, *D. p. casaresi*. Montane (group A; *n* = 168): *D. p. costaricensis*, *D. p. veraguensis*, *D. p. multistrigatus*. Montane (group B; *n* = 122): *D. p. puncticollis*, *D. p. seilerni*, *D. p. olivaceus*.

^bAmazonian *D. picumnus* rely extensively on foraging in association with army ants, but it is likely that army ants are less important to montane and Chaco populations, which occur at elevations or in a region, respectively, in which army ants are probably an unreliable resource.

obtained six bill measurements. Visual inspection from above revealed that the bills of most woodcreeper species are compressed laterally, and therefore are quite narrow, whereas those of *Dendrocolaptes* are generally broad and bowed outward along their edges. To quantify this expansion, we measured three sets of bill characters. The width and depth of the bill were measured both at the anterior edge of the nares (bill width and depth at the nares) and at the anterior feathering along the culmen (bill width and depth at the base). Bill length was measured both from the anterior edge of the nares (bill length) and from the insertion point at the skull (total culmen). Body mass was recorded when reported on the label, and we noted molt, wear, or damage that could have affected our measurements.

MEASUREMENT ERROR

The variability among repeated measures of the same character on a given individual should be considered whenever mensural characters are studied, because measurement error can affect subsequent morphometric analyses (Francis

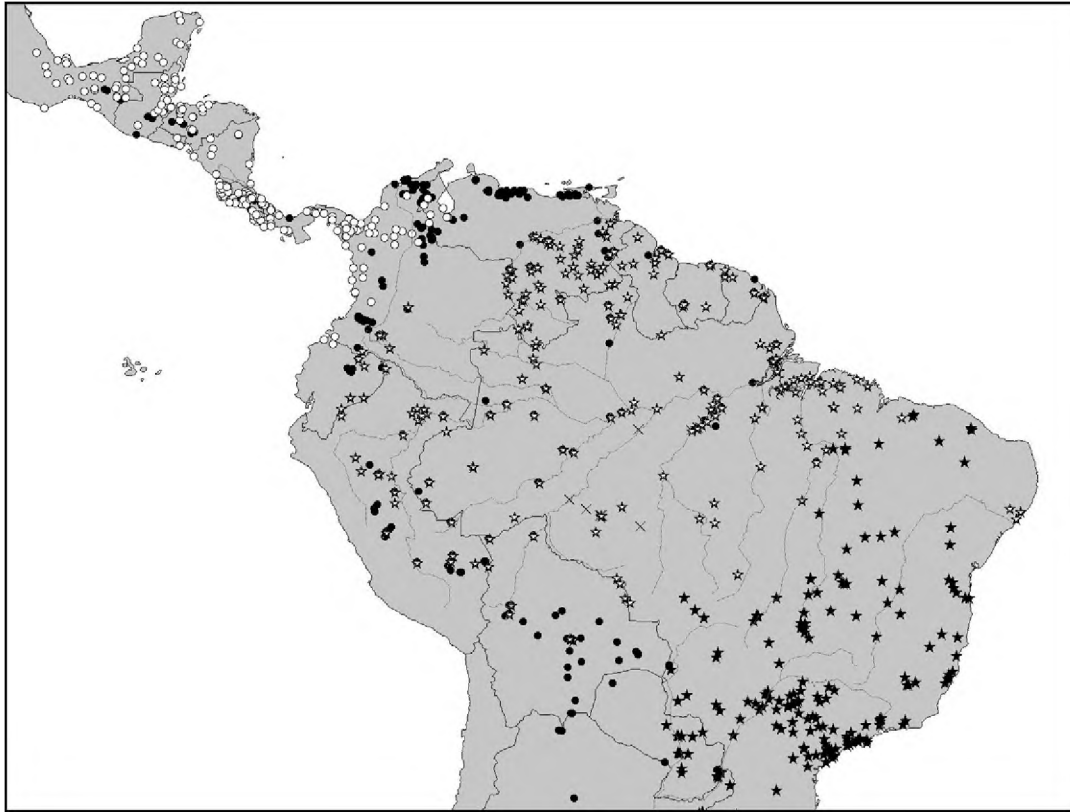


FIG. 1. Geographic sampling of *Dendrocolaptes* specimens used in this study (white circles are *D. sanctithomae*, $n = 553$; black circles are *D. picumnus*, $n = 714$; open stars are *D. certhia*, $n = 881$; black stars are *D. platyrostris*, $n = 851$; multiplication symbols [×] are *D. hoffmannsi*, $n = 28$).

and Mattlin 1986, Lougheed et al. 1991). Accordingly, the extent of measurement error associated with each morphometric character under study ought to be assessed and reported. If measurement error is too high for a particular character, that character should be excluded from subsequent analyses. We used repeated measurements and a model II analysis of variance (ANOVA) to estimate measurement error for a subset of our sample (see Bailey and Byrnes 1990). Most specimens were measured only once, but to assess the extent of measurement error, we took three sets of measurements from 25 individuals each from eight taxa (*D. sanctithomae sanctithomae*, *D. certhia radiolatus*, *D. c. concolor*, *D. hoffmannsi*, *D. picumnus validus*, *D. p. puncticollis*, *D. platyrostris platyrostris*, and *D. p. intermedius*). All specimens measured for this analysis were males, with the exception of 8 female *D. hoffmannsi* that were included because too few males were available.

Because tarsus length had extremely high measurement error (Table 2)—that is, it was not repeated with high precision—we excluded it from all analyses. Measurements of bill length, width, and depth taken at the nares and at the base were highly correlated. Of these, length measurements were the most highly correlated ($r = 0.87$, $n = 2,928$; Sokal and Rohlf 1995), but corresponding measurements of bill width and depth also had a strong overall correlation (width: $r = 0.74$, $n = 3,013$; depth: $r = 0.74$, $n = 3,005$). Because length, width, and depth measurements taken at the base of the bill had higher measurement error than comparable measurements taken at the nares (Table 2), we discarded from multivariate analyses (described below) all three measurements taken at the base of the bill. The remaining five characters—wing chord, tail length, and bill length, depth, and width measured at the anterior edge of the nares—had relatively low measurement error (<5%).

TABLE 2. Measurement error (% ME), estimated from a model II ANOVA (Bailey and Byrnes 1990) of nine mensural characters of *Dendrocolaptes*.

Character	MS _{total}	MS _{among}	MS _{within}	s ² among	s ² within	% ME
Bill length at nares	3.58	10.62	0.075	0.075	3.52	2.09
Total culmen	4.44	13.00	0.178	0.178	4.27	3.99
Bill width at nares	0.50	1.47	0.013	0.013	0.49	2.65
Bill width at base	0.81	2.24	0.097	0.097	0.71	12.00
Bill depth at nares	0.30	0.88	0.016	0.016	0.29	5.22
Bill depth at base	0.56	1.61	0.042	0.042	0.52	7.52
Tarsus length	1.12	2.64	0.362	0.362	0.76	32.35
Wing chord	38.99	116.89	0.139	0.139	38.92	0.36
Tail length	29.98	88.71	0.684	0.684	29.34	2.28

STATISTICAL ANALYSES

Depending on the analysis performed, males and females were either pooled or examined separately (the male bill averaged ~1.5% longer, but ~4% narrower and ~1.5% shallower; male wing chord and tail length averaged 1–1.5% longer). To reduce the effects of age-related variation (see Marantz et al. 2003), we excluded birds in juvenal plumage and those in which bill dimensions had not yet reached full size. We included in multivariate analyses only those individuals for which all characters could be measured.

We conducted canonical discriminant analysis, by sex, to determine whether morphology alone could distinguish among the five *Dendrocolaptes* spp., and we examined concordance between mensural differences among species and subspecies-groups and expectations based on ecomorphology. Prior probabilities were set equal among groups (i.e., any given specimen had a one-in-five chance of being classified as a particular species). We conducted similar analyses for subspecies within species. Because discriminant analysis may result in inflated Type I error rates, especially when variation is clinal in nature (Skalski et al. 2008), we used this method in a heuristic manner as a first attempt to determine whether subspecies and subspecies-groups are separable. Classification to a group was considered correct only if the posterior probability of assignment to that group was ≥ 0.90 . We also used discriminant analysis to generate synthetic multivariate scores to be used in subsequent pairwise analyses. All such statistics were performed using SAS, version 9.1.3 (SAS, Cary, North Carolina). We used the *D*-statistic (Patten and Unitt 2002) to test diagnosability for all pairwise comparisons among

taxa for which there was a mensural component in the original diagnosis.

RESULTS

Our bill measurements attempted to quantify lateral and dorsoventral compression of the bill. Of the three sets of bill characters, only the two width measurements differed conspicuously among species: the bill was consistently wider at the nares in relation to the base in *D. certhia* than in *D. sanctithomae* (Fig. 2) and markedly narrower at the nares in relation to the base in *D. p. puncticollis* than in all other *D. picummus* (not shown). All remaining discussion of the bill characters (length, width, and depth) reflects exclusively those sets of measurements taken from the anterior edge of the nares.

Canonical discriminant analysis distinguished *Dendrocolaptes* spp. on the basis of mensural characters (Fig. 3). Although *D. certhia* and *D. sanctithomae* were treated as conspecific for many years, *D. certhia* differed markedly in structure from all other species as a result of its generally larger bill (Fig. 3 and Table 3), and *D. certhia* and *D. sanctithomae* were seldom misclassified as one another (Table 4). Still, *D. sanctithomae*, especially, and *D. picummus* exhibit considerable morphometric variation, so specimens of these species were misclassified more frequently than those of other taxa (Table 4). Belying appearances in two-dimensional space (Fig. 3), *D. hoffmannsi* differs structurally from other species (Table 4), but our small sample size for this species did not allow for its finer discrimination.

When the barred and streaked groups were examined separately, discrimination improved. Discriminant analysis of the two barred woodcreepers

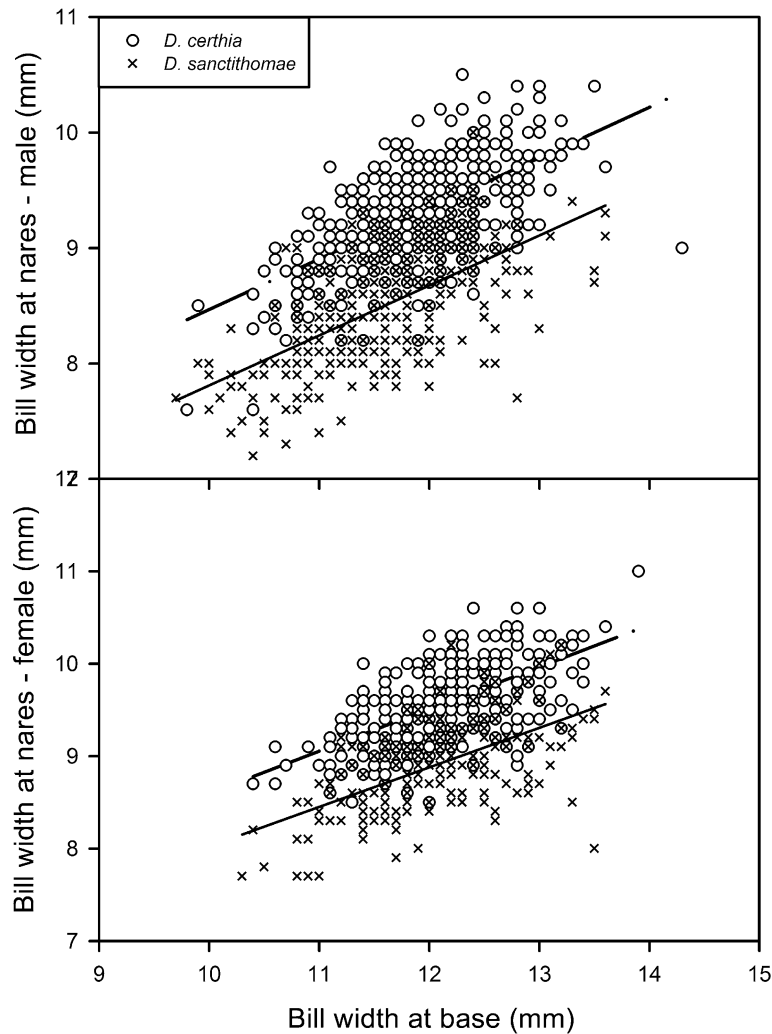


FIG. 2. Larger values for bill width at the nares in relation to those at the base in *Dendrocolaptes certhia* reflect greater lateral expansion of the bill than in *D. sanctithomae* (above males, below females).

resulted in the correct classification of ~85% of individuals for both species (Fig. 4; 85.3% for *D. certhia*, $n = 755$; 84.3% for *D. sanctithomae*, $n = 463$). Bivariate plots further revealed that the longer and wider bill of *D. certhia* separated most males and many females from *D. sanctithomae* (Fig. 5). Similar analyses of the streaked taxa (*D. picumnus*, *D. platyrostris*, and the weakly streaked *D. hoffmannsi*) resulted in effective discrimination of the three species in this complex and of biogeographically defined subspecies-groups within *D. picumnus* (Table 5 and Fig. 6); however, two groups of montane subspecies in this complex

that differ in plumage patterns were not separated morphometrically.

Contrary to the effective separation of species, most subspecies were not readily diagnosed on the basis of mensural characters. With one exception (*D. c. polyzonus*), diagnosability was low (<50% correct classification) among subspecies of *D. certhia*, none of which were described on the basis of morphometric differences. Despite a small sample size ($n = 9$), *D. c. polyzonus* of Bolivia was the most distinct subspecies: 77.8% (7 of 9) were classified correctly because of the taxon's shallower bill and longer wings and tail

TABLE 3. Loadings (correlations between raw variables and synthetic variates) for canonical discriminant analyses of morphometric data for *Dendrocolaptes*. Males and females were analyzed separately. The first two axes are shown, except in the analysis for the *D. certhia* complex, for which the two species were separated along a single axis.

Character	All taxa combined				<i>D. certhia</i> complex		<i>D. picumnus</i> complex			
	Male (<i>n</i> = 1,523)		Female (<i>n</i> = 1,008)		Male (<i>n</i> = 740)	Female (<i>n</i> = 478)	Male (<i>n</i> = 792)		Female (<i>n</i> = 532)	
	DFI	DFII	DFI	DFII	DFI	DFI	DFI	DFII	DFI	DFII
Bill length	0.283	0.338	0.129	0.439	0.455	0.511	0.341	0.198	0.255	0.231
Bill width	0.415	0.257	0.449	0.104	0.876	0.849	0.261	0.732	0.151	0.803
Bill depth	0.570	0.042	0.522	0.243	-0.097	-0.146	0.169	0.936	0.033	0.944
Wing chord	0.111	0.352	0.260	0.508	0.079	0.162	0.992	0.057	0.988	0.107
Tail length	-0.032	0.213	0.354	0.290	0.499	0.556	0.750	0.045	0.734	0.133

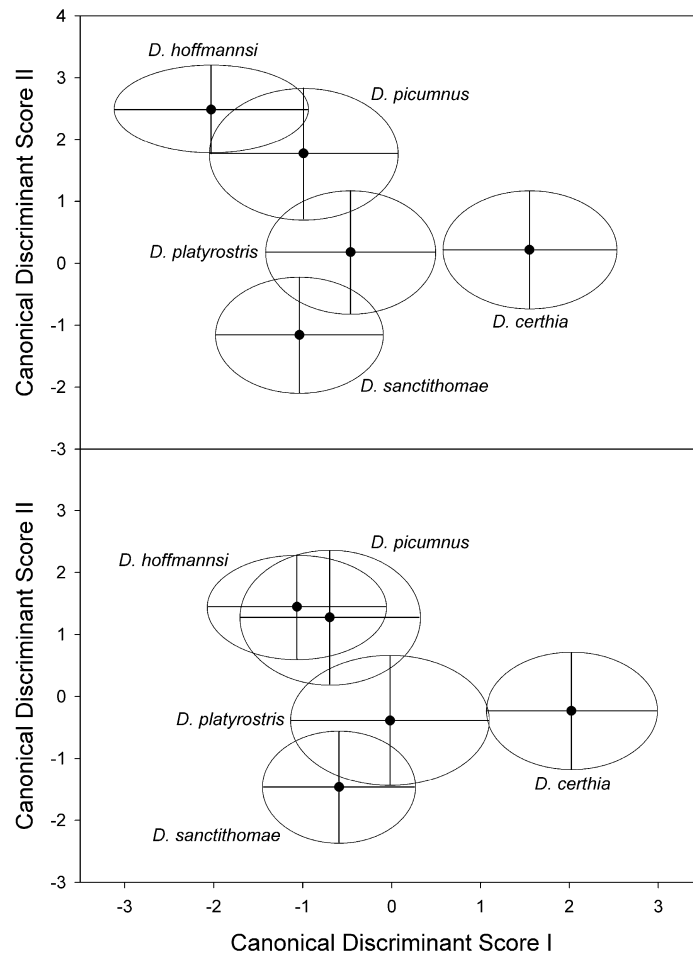


FIG. 3. Mean scores (ellipses = SD) on the first two canonical axes of discriminant analyses of *Dendrocolaptes* spp. using morphometric data (male top, female bottom). The first axis represents primarily bill depth and width in both sexes, and less so tail length in females; the second axis has its highest correlations with wing chord and bill length in both sexes (Table 3).

TABLE 4. Classification matrix from a canonical discriminant analysis of morphometric data from 2,542 adults representing all species of *Dendrocolaptes*. Classification percentages were averaged across the results from each sex ($n = 1,532$ males, $n = 1,010$ females).

Species	Percent classified as species					<i>n</i>
	<i>sanctithomae</i>	<i>certhia</i>	<i>hoffmannsi</i>	<i>picumnus</i>	<i>platyrostris</i>	
<i>D. sanctithomae</i>	42.1	14.3	4.5	13.4	25.7	463
<i>D. certhia</i>	12.1	82.8	0.3	2.1	2.8	755
<i>D. hoffmannsi</i>	3.9	0.0	80.8	15.4	0.0	26
<i>D. picumnus</i>	11.7	3.3	21.4	60.0	3.7	560
<i>D. platyrostris</i>	16.5	3.3	0.7	2.0	77.5	738

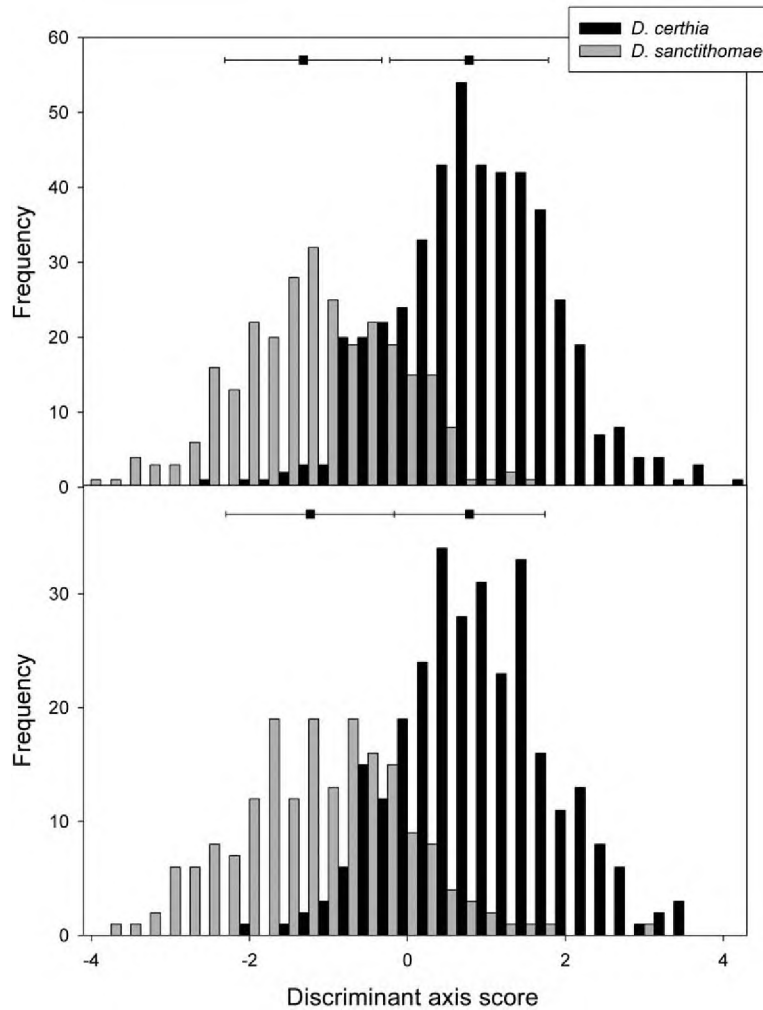


FIG. 4. Histograms of canonical discriminant scores from a morphometric analysis of *Dendrocolaptes certhia* and *D. sanctithomae* (male top, female bottom).

TABLE 5. Classification matrix from a canonical discriminant analysis of morphometric data from the streaked species of *Dendrocolaptes* and, within *D. picumnus*, subspecies-groups (see Table 1). Classification percentages were averaged across the results from each sex ($n = 792$ males, $n = 532$ females).

Group	Percent classified as group						<i>n</i>
	Amazonian	Chaco	Montane A	Montane B	<i>hoffmannsi</i>	<i>platyrostris</i>	
<i>D. picumnus</i>							
Amazonian	65.3	6.3	2.8	3.6	18.8	3.1	207
Chaco	8.4	58.7	8.3	9.5	5.5	9.5	73
Montane (A)	7.9	23.0	49.0	10.6	8.2	1.2	168
Montane (B)	4.6	8.8	6.2	76.6	0.8	2.8	112
<i>D. hoffmannsi</i>	11.4	11.1	2.9	5.6	69.0	0.0	26
<i>D. platyrostris</i>	1.1	10.0	0.6	2.4	0.4	85.5	738

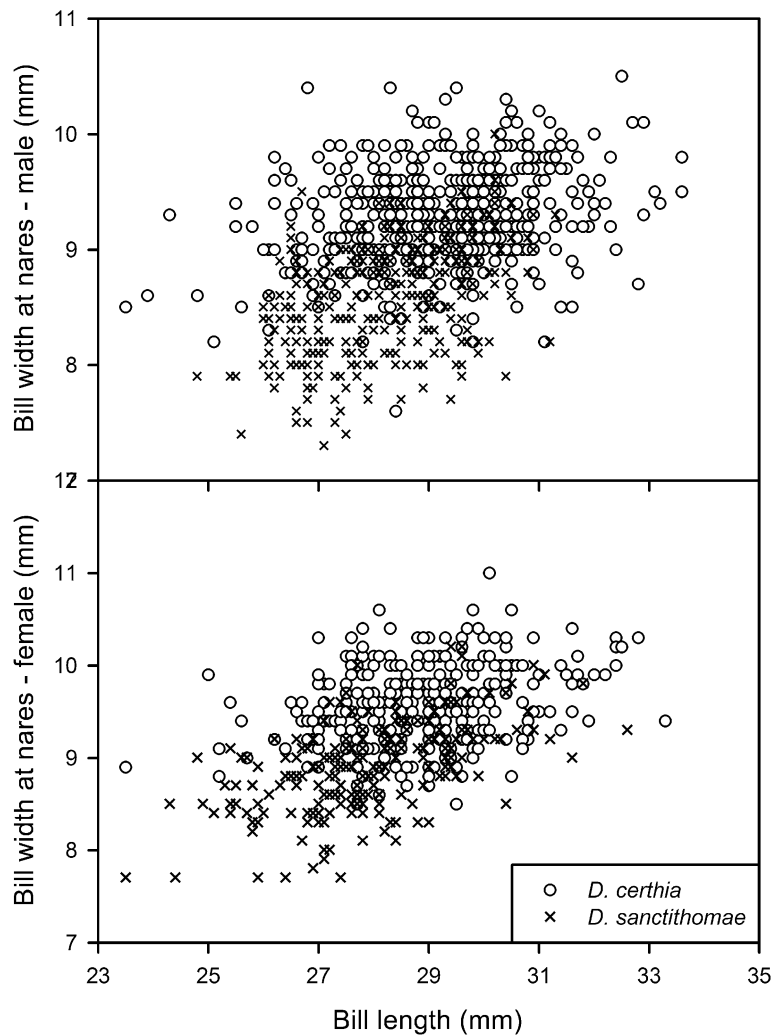


FIG. 5. Bill length vs. bill width of *Dendrocolaptes certhia* and *D. sanctithomae* (male top, female bottom).

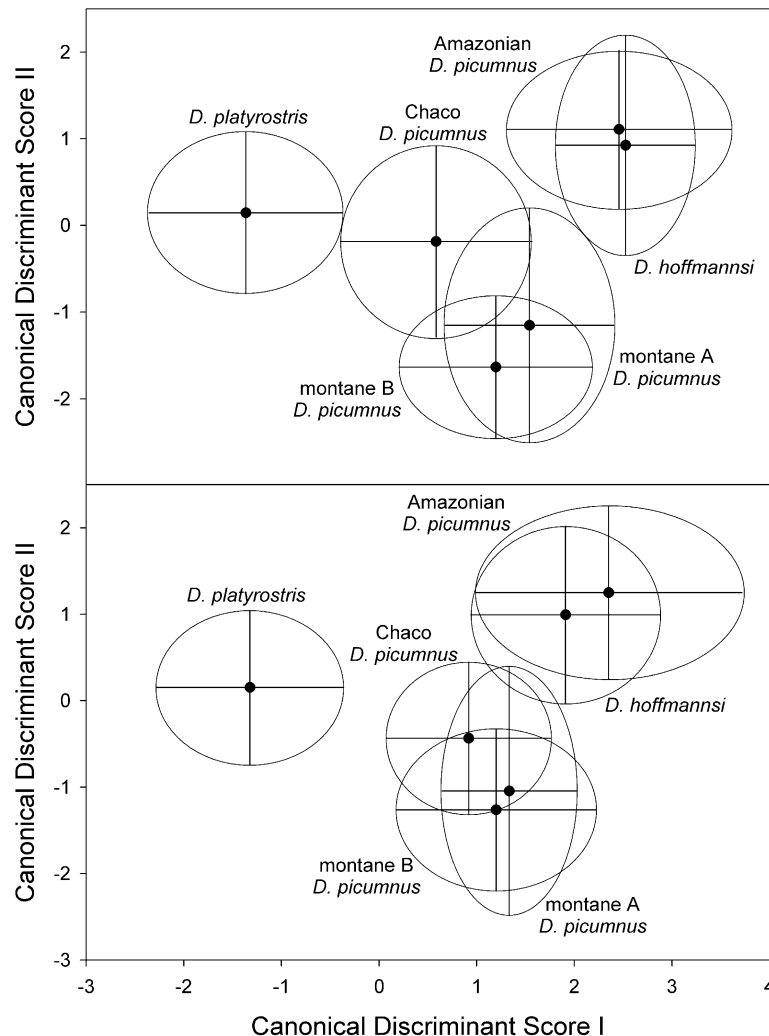


FIG. 6. Mean scores (ellipses = SD) on the first two canonical axes of discriminant analyses using morphometric data for species and subspecies in the *Dendrocolaptes picumnus* complex (Table 6). In both sexes (male top, female bottom), the first axis reflects size, with high positive scores for wing chord and tail length, and the second reflects bill mass, with high positive scores for both width and depth (Table 3).

(not shown). Despite weighing less on average (Marantz et al. 2003), *D. c. concolor* differed little in structure from other subspecies of *D. certhia* (not shown).

Subspecies of *D. sanctithomae* likewise could not be diagnosed with high confidence. Sample sizes were small (<10 specimens) for four of the eight described subspecies, but for those with adequate sample sizes, only nominate *D. s. sanctithomae sensu stricto* could be diagnosed at >50%. Subspecies described from Middle America and

northwestern South America (*D. s. nigrirostris* and *D. s. colombianus*), in part on the basis of bill length, were particularly problematic because bill length appeared to vary in a smooth cline from southern Mexico south to northern Colombia (Fig. 7).

Only one subspecies of *D. picumnus* was described solely on the basis of mensural differences; even so, diagnosability on the basis of morphometrics was somewhat higher among subspecies of *D. picumnus* (Table 6) than in *D. certhia*. Diagnosability

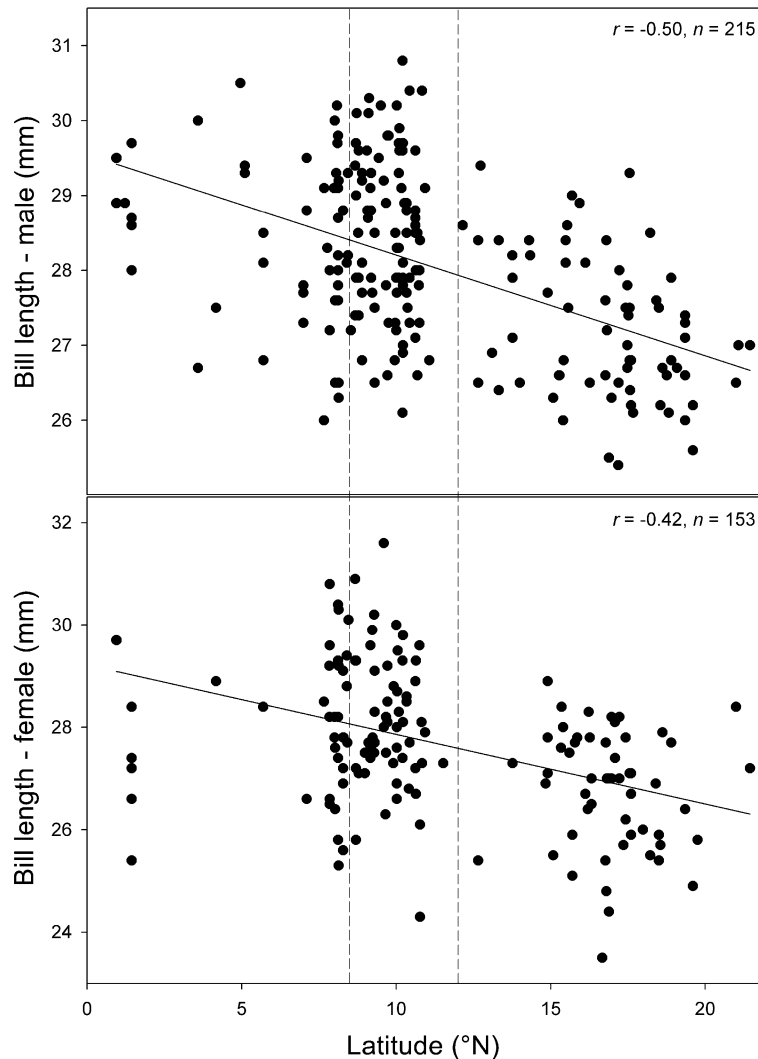


FIG. 7. Variation in bill length of *Dendrocolaptes sanctithomae* across latitude from western Ecuador to southern Mexico represents a smooth cline (adult male top, adult female bottom). Vertical lines mark geographic breaks between named subspecies: from south to north, *D. s. colombianus*, *D. s. nigristrois*, and *D. s. sanctithomae*.

was especially high for *D. p. puncticollis*, which has an unusually long and narrow bill, but morphometric diagnosability of *D. p. extimus*, *D. p. picumnus*, *D. p. transfasciatus*, and *D. p. veraguensis* was also reasonably high (>70%; Table 6). The only subspecies described on the basis of morphometrics is *D. p. casaresi*, particularly in relation to *D. p. pallescens*. Diagnosis on bill length was perhaps possible (Fig. 8), but other characters overlap considerably. Additional specimens of *D. p. casaresi* are needed to clarify its taxonomic status.

Separation on the basis of morphometric data of the two subspecies of *D. platyrostris* was relatively high along a single axis that contrasted bill size and wing length. Averaged across sex, 77.5% of *D. p. intermedius* and 74.0% of *D. p. platyrostris* specimens were classified correctly as a result of the relatively larger bill yet shorter wing of the former.

Among those taxa for which either the original description or subsequent analyses found a morphometric component, only two (*D. p.*

TABLE 6. Classification results for subspecies of *Dendrocolaptes picumnus* from a canonical discriminant analysis using morphometric data for adults. Classification percentages were averaged across the results from each sex.

Group/subspecies	Percent classified correctly	<i>n</i>
Amazonian		
<i>D. p. picumnus</i>	75.3	85
<i>D. p. validus</i>	38.9	108
<i>D. p. transfasciatus</i>	71.4	14
Chaco		
<i>D. p. pallescens</i>	40.3	62
<i>D. p. extimus</i>	80.0	5
<i>D. p. casaresi</i>	66.7	6
Montane (A)		
<i>D. p. costaricensis</i>	57.1	21
<i>D. p. veraguensis</i>	80.0	5
<i>D. p. multistrigatus</i>	46.5	86
Montane (B)		
<i>D. p. puncticollis</i>	95.0	60
<i>D. p. seilerni</i>	18.2	88
<i>D. p. olivaceus</i>	40.0	20

multistrigatus and *D. p. puncticollis*) were statistically diagnosable on the basis of mensural characters (Table 7). Two additional taxa may be diagnosable (*D. s. sheffleri* and *D. p. casaresi*), but our sample sizes were too small.

DISCUSSION

MEASUREMENT ERROR

Most characters were measured with an error of <5%, but measurement error accounted for >30% of the variation in tarsus length and ~12% in measurements of bill width at its base. Using a similar method, Loughheed et al. (1991) found error to be minimal in wing chord, high in tarsus length, and intermediate in a measure of tail length for the American Coot (*Fulica americana*), but they did not include external measurements comparable to our bill characters. In most birds, both wing chord and tail length are large values that can be measured with minimal error, so measurement error is expected to be small. That the tips of woodcreeper rectrices represent the feather shafts further results in a low error compared with corresponding measurements in other passerines, in which worn feather tips become frayed and difficult to measure. That is, although the tail tip wears over time, resulting in seasonal variation, repeated measurements of the same specimen can be made with a high degree of accuracy. Tarsus length is challenging to measure repeatedly because it is often difficult to determine the last undivided scute. This character is therefore measured either with high precision, if the correct scute is chosen, or with large error (1–2 mm) if the incorrect scute is chosen. We suspect that the “glaring error” noted

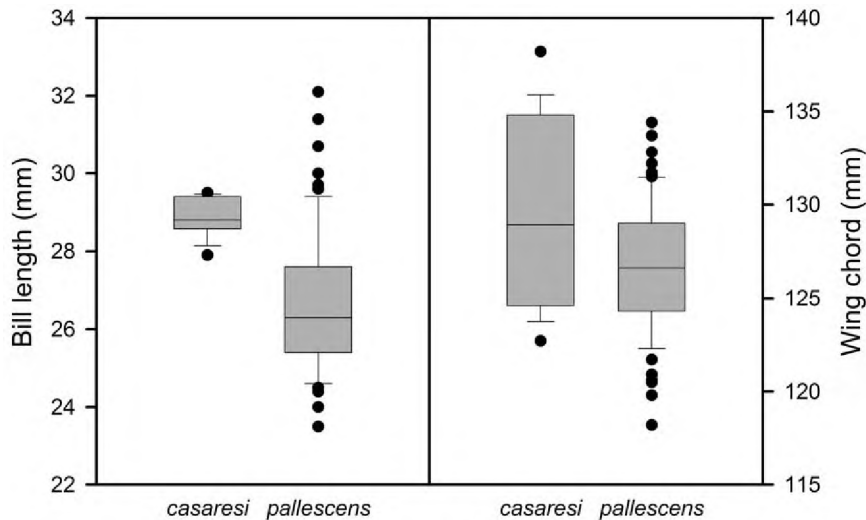


FIG. 8. Box plots of bill length and wing chord in *Dendrocolaptes picumnus casaresi* ($n = 9$ for bill length, $n = 12$ for wing chord) vs. *D. p. pallescens* ($n = 70$ for both characters). Sexes were combined for this analysis.

TABLE 7. Summary of primary characters used in the original description (or mentioned by Cory and Hellmayr [1925] for older taxa) for all recently recognized (Peters 1951, Marantz et al. 2003) subspecies in the genus *Dendrocolaptes*. Our assessment of morphometric diagnosability and our recommendations for subspecies validity are based on plumage and morphometrics; for invalid subspecies, we list the subspecies name that should be considered the senior synonym. Pairwise comparisons were made between taxa with a mensural component in their diagnosis or those we found to be relatively diagnosable using discriminant analysis. The sexes were combined for all comparisons except that between *D. p. multistrigatus* and *D. p. picummus*, for which we averaged values for the two sexes because of apparent sexual differences.

Subspecies	Characters used in description	Morphometrically diagnosable?	Taxonomic status
<i>D. sanctithomae</i>			
<i>D. s. sheffleri</i>	Plumage, bill color, size	Unclear ^a	Valid
<i>D. s. legtersi</i>	Plumage	No	<i>D. s. sanctithomae</i>
<i>D. s. nigrirostris</i>	Plumage, bill length	No ^b	<i>D. s. sanctithomae</i>
<i>D. s. columbianus</i>	Plumage, bill length	No ^b	<i>D. s. sanctithomae</i>
<i>D. s. hesperius</i>	Plumage	No	Valid
<i>D. s. hyleorus</i>	Plumage, bill shape	No ^b	<i>D. s. punctipectus</i>
<i>D. s. punctipectus</i>	Plumage	No	Valid
<i>D. certhia</i>			
<i>D. c. radiolatus</i>	Plumage	No	Valid
<i>D. c. juruanus</i>	Plumage	No	Valid
<i>D. c. polyzonus</i>	Plumage, size	No ^b	Valid
<i>D. c. concolor</i>	Plumage	No	Valid
<i>D. c. ridgwayi^c</i>	Plumage	No	<i>D. c. concolor</i>
<i>D. c. medius</i>	Plumage	No	Valid
<i>D. picummus</i>			
<i>D. p. validus</i>	Plumage, bill color	No	Valid
<i>D. p. transfasciatus</i>	Plumage	No ^b	Valid
<i>D. p. pallescens</i>	Plumage	No	Valid
<i>D. p. extimus</i>	Plumage	No ^b	<i>D. p. pallescens</i>
<i>D. p. casaresi</i>	Morphometric	Unclear ^d	Insufficient data
<i>D. p. costaricensis</i>	Plumage	No	Valid
<i>D. p. veraguensis</i>	Plumage	No ^b	<i>D. p. costaricensis</i>
<i>D. p. multistrigatus</i>	Plumage, bill shape	Yes ^b	Valid
<i>D. p. puncticollis</i>	Plumage, bill shape	Yes ^b	Valid
<i>D. p. seilerni</i>	Plumage, size, bill shape	No ^b	Valid
<i>D. p. olivaceus</i>	Plumage	No	Valid
<i>D. platyrostris</i>			
<i>D. p. intermedius</i>	Plumage	No ^b	Valid

^aSample size for *D. s. sheffleri* was too small to make a morphometric comparison, but its plumage and bill coloration differ strikingly from those of other subspecies.

^b D_{ij} values are from the pairwise index of Patten and Unitt (2002); $D_{ij} > 0$ indicates that the taxon is diagnosable morphometrically, whereas $D_{ij} < 0$ indicates that it is not. Comparisons and the sample sizes for each are as follows: *D. s. nigrirostris* ($n = 215$) vs. *D. s. sanctithomae* ($n = 156$) (bill length: $D_{ms} = -2.4$, $D_{sn} = -2.1$); *D. s. columbianus* ($n = 82$) vs. *D. s. nigrirostris* ($n = 215$) (bill length: $D_{cn} = -4.0$, $D_{nc} = -3.7$); *D. s. hyleorus* ($n = 14$) vs. *D. s. punctipectus* ($n = 13$) (bill depth: $D_{hp} = -0.9$, $D_{ph} = -0.6$); *D. c. polyzonus* ($n = 11$) vs. *D. c. juruanus* ($n = 69$) (wing chord: $D_{pj} = -10.3$, $D_{jp} = -15.6$); *D. p. transfasciatus* ($n = 14$) vs. *D. p. picummus* ($n = 88$) (discriminant function scores of all characters: $D_{ep} = -1.73$, $D_{pe} = -0.93$); *D. p. casaresi* ($n = 9$) vs. *D. p. pallescens* ($n = 70$) (bill length: $D_{cp} = -2.4$, $D_{pc} = -0.5$); *D. p. veraguensis* ($n = 5$) vs. *D. p. costaricensis* ($n = 25$) (discriminant function scores of all characters: $D_{vc} = -2.4$, $D_{cv} = -1.7$); *D. p. multistrigatus* ($n = 91$) vs. *D. p. picummus* ($n = 90$) (discriminant function scores of bill characters averaged across the sexes: $D_{mp} = 0.58$, $D_{pm} = 0.78$); *D. p. puncticollis* ($n = 73$) vs. all other subspecies of *D. picummus* ($n = 546$) (discriminant function scores of bill characters: $D_{po} = 0.9$, $D_{op} = 1.0$); *D. p. seilerni* ($n = 119$) vs. *D. p. multistrigatus* ($n = 91$) (bill length: $D_{sm} = -4.8$, $D_{ms} = -4.1$); *D. platyrostris intermedius* ($n = 286$) vs. *D. p. platyrostris* ($n = 486$) (discriminant function scores of all characters: $D_{ip} = -1.7$, $D_{pi} = -1.9$).

^cPrevious analysis of plumage variation suggested that *D. c. ridgwayi* was described on the basis of a population showing characters of hybridization between *D. c. medius* and *D. c. concolor* (Marantz 1997).

^dWe did not find our small sample of *D. c. casaresi* to be diagnosable.

by Loughheed et al. (1991) was one such error. Bill characters are usually measured with high precision, but the total value for width and depth measurements is small, so even a small error is large in relation to the total. Measurements of bill characters are more repeatable from the anterior edge of the nares than from the anterior feathering along the culmen because precise determination of the latter is more difficult (see also Winker 1998). Similarly, bill depth measurements are less repeatable than those for width, probably because to take these measurements one often needs to compress the partially open bill on a study skin.

SEXUAL DIMORPHISM

Woodcreepers are not sexually dimorphic in plumage pattern or coloration, but the sexes of some species differ in size or shape. Size dimorphism, as measured by wing length, is marked in both species of *Deconychura* (Bierregaard 1988) and, to a lesser degree, in two species of *Dendrocincla* (Willis 1972, 1979), with males slightly larger than females in both cases. In *D. picummus*, *D. certhia*, and *D. sanctithomae*, males have slightly longer wings than females, yet in small samples of birds with body-mass data, females weighed slightly more (Willis 1982, 1992); in all three species, differences in both characters were small. Willis (1992) did not find sexual differences in bill length. Using a larger number of measurements in a sample that included many of the same birds examined by Willis, we found that males averaged slightly (1–1.5%) larger than females in all length characters (bill length, wing chord, and tail length). Although behavioral observations suggest that female *Dendrocolaptes* are dominant over their mates (Willis 1982, 1992), the contradiction between the slightly larger size of males suggested by our mensural data and the apparently greater body mass of females found by Willis (1982, 1992) supports Winker's (1998) caution regarding the comparison of body mass in males and females taken during the breeding season.

In spite of their greater length, the bills of male *Dendrocolaptes* were both narrower and shallower than those of females, which hints at the possibility of differences in prey taken or in the methods used to obtain prey. Extensive foraging observations by Willis (1982, 1992) apparently did not reveal any sexual differences in foraging behavior; however, such determination would be challenging given the difficulty of sexing birds in the field.

Apparent differences in head plumage, with birds appearing to have either "ruffed" (*sensu* Willis 1982:272, Willis and Oniki 2001:232) or smooth heads (representing, respectively, either males or females), may be the best way to sex *Dendrocolaptes* in the field (Willis 1982, 1992; Willis and Oniki 2001), but such differences were not easily assessed from museum skins.

MORPHOMETRIC VARIATION AND ECOMORPHOLOGY IN *DENDROCOLAPTES*

Woodcreeper species differ most conspicuously in their overall size and bill shape (Marantz et al. 2003), and in large part these two characters define the genera. Bills in members of the genus *Dendrocolaptes* differ from those of most other woodcreepers in being relatively short and compressed dorsoventrally rather than laterally, yielding a relatively wide but shallow bill that resembles those of many flycatchers (Tyrannidae); *Dendrocolaptes* also have relatively long tails (Marantz 1992, Marantz et al. 2003). Within the genus, two groups of species are distinguished on the basis of plumage patterns. Two species are barred throughout the body (*D. sanctithomae* and *D. certhia*), and two other species are streaked boldly on the head, neck, and breast (*D. picummus* and *D. platyrostris*); two taxa (*D. hoffmannsi* and *D. c. concolor*) are weakly marked and thus difficult to assign to a group on this basis alone (Marantz 1997). Morphologically and behaviorally, *D. concolor* is a weakly marked, southern Amazonian representative of *D. certhia* (Willis 1992, Marantz 1997), with which it was merged recently (Marantz et al. 2003). *Dendrocolaptes hoffmannsi* is more difficult to place, having been treated in the past as a member of either the barred group or the streaked group (see Willis 1982, Raikow 1994, Marantz 1997). Vocal and behavioral data suggest that it is best recognized as a plain member of the *D. picummus* complex (Marantz et al. 2003), and Willis (1982) even suggested that it may represent a subspecies of *D. picummus*, a treatment that makes sense both biogeographically and morphometrically (Figs. 1 and 6).

We found a moderate degree of separation among the five presently recognized species of *Dendrocolaptes*; however, the barred and streaked groups were not supported by structural characters. Because discriminant analysis using mensural characters tends to superimpose the two groups atop one another, we also examined structural

patterns of each group on its own. Morphometric analysis of the barred species resulted in separation of most *D. sanctithomae* and *D. certhia*, primarily on the basis of the longer and consistently wider bill of *D. certhia*. Willis (1992) documented marked differences in foraging behavior between *D. sanctithomae* and *D. certhia*. *Dendrocolaptes sanctithomae* foraged almost exclusively in association with swarming army ants (primarily *Eciton burchelli*), whereas *D. certhia* foraged extensively away from army ants and often with mixed-species flocks. *Dendrocolaptes sanctithomae* was observed foraging closer to the ground on average, by dropping down to take prey flushed by the ants, but *D. certhia* took prey primarily at higher levels by sallying, often to the undersides of leaves. It would therefore seem that *D. certhia* uses a foraging technique similar to that of an "upward-striker" (*sensu* Fitzpatrick 1980:45), a guild that Fitzpatrick (1985: table 1) found to possess a relatively long, wide bill in Tyrannidae. By contrast, *D. sanctithomae*, observed by Willis (1992) to more often drop down onto prey over ant swarms, which presumably requires less specialization (see Fitzpatrick 1985), possesses a bill structure more typical of other *Dendrocolaptes*. The recent split of *D. sanctithomae* from *D. certhia* is supported not only by our morphometric data and by foraging behavior, but also by vocalizations and well-defined differences in plumage (Marantz 1992, 1997; Willis 1992; American Ornithologists' Union 1998; Marantz et al. 2003).

Morphometric patterns among the streaked *Dendrocolaptes* appear to be dominated by size, with *D. platyrostris* small and the Amazonian *D. picumnus* and *D. hoffmannsi* large. In fact, we found less distinction morphometrically between *D. hoffmannsi* and Amazonian *D. picumnus* than between the other subspecies-groups of *D. picumnus*, thus providing some support for Willis's (1982) suggestion that these two may be conspecific. The songs of these two species are also remarkably similar (Ridgely and Tudor 1994, Marantz et al. 2003, C. A. Marantz field recordings), and its geographic distribution is almost identical to that of the equally poorly marked *D. c. concolor* discussed above (Peters 1951, Marantz et al. 2003). The peripheral populations of *D. picumnus* of the dry Chaco and humid montane regions are intermediate in size. The Amazonian taxa forage primarily over swarming army ants, where they are subordinate only to the even larger woodcreepers in the genus *Hylexetastes* (Willis 1982). Their larger size compared with syntopic *D. certhia* is presumably advantageous in these encounters. Willis

(1992) suggested that aggression from the larger woodcreepers may shape foraging behavior in *D. certhia*, but it remains unclear to what degree the small size of peripheral populations of streaked *Dendrocolaptes* in the Atlantic Forest, Chaco, and montane regions reflects an absence of *D. certhia* (i.e., character release). The less massive bill of the montane subspecies of *D. picumnus* presumably reflects a tendency toward more gleaning and probing by birds that occur at elevations at which Willis and Oniki (1978) indicated that army ants are an unreliable source of flushed prey. It is also possible that they take smaller prey.

MORPHOMETRIC DIAGNOSIS OF SUBSPECIES

Most woodcreeper subspecies have been described on the basis of plumage patterns, including those in *Dendrocolaptes* (Marantz 1997). Within presently recognized species in this group, taxa are similar structurally, yet they have subtly different plumage coloration and patterns that are usually manifest in the degree of richness in the coloration and in the width and definition of the streaking or barring. Given that few taxa in this complex were described largely or exclusively on the basis of morphometric characters, it was not surprising that morphometric analyses found few taxa to be diagnosable (Table 7).

Dendrocolaptes sanctithomae.—Three subspecies of *D. sanctithomae* from Middle America and northwestern South America (*D. s. sanctithomae*, *D. s. nigrirostris*, and *D. s. colombianus*) were distinguished primarily on the basis of subtle differences in plumage, bill length, and the extent of pale coloration at the base of the lower mandible (Todd 1950). Shortly after Todd (1950) described *D. s. nigrirostris* and *D. s. colombianus*, Binford (1965) questioned the validity of the former, indicating that he could not detect any differences in plumage between it and *D. s. sanctithomae*, and that subtle differences between these forms in bill size and coloration were insufficient to merit recognition. Marantz (1997) likewise found variation in plumage and the extent of pale coloration at the base of the bill to be subtle, inconstant, and potentially clinal in nature. Our morphometric analyses further revealed that bill length varies as a smooth cline, with shorter-billed birds in the north and longer-billed birds in the south (Fig. 7), thus supporting the recommendations by Binford (1965) and Marantz (1997) that all three populations be recognized under the name *D. s. sanctithomae*. Our sample of two *D. s. sheffleri*, apparently the only

two specimens of this taxon in existence, was too small to analyze morphometrically. Samples were larger for *D. s. hesperius*, yet we were unable to differentiate it morphometrically, again supporting Binford's (1965) finding on the basis of a smaller sample. Still, the conspicuously narrower barring and more grayish-brown cast to its underparts compared with *D. s. sanctithomae* supports its recognition (Binford 1965, Marantz 1997).

Dendrocolaptes certhia.—No taxa within *D. certhia* were described on the basis of mensural characters, so it was not surprising that our analyses were unable to distinguish subspecies. The longer wings and tail of *D. c. polyzonus* suggest that this southernmost form is larger than other taxa, but a larger sample than we had available would be necessary to examine the possible influence of Bergmann's Rule.

Dendrocolaptes picumnus.—We examined morphometric variation in the *D. picumnus* complex by looking at variation among species and subspecies-groups as a whole as well as among the subspecies of *D. picumnus* alone. Discrimination by subspecies was generally poor for *D. picumnus*, even when the function was based exclusively on this species. Although subspecies in *D. picumnus* were not strongly separated morphometrically, with few taxa distinguished at >75% confidence, biogeographically defined subspecies-groups are relatively well defined. Amazonian taxa are not only larger than the other subspecies (Fig. 6), they also have a relatively more massive bill that may facilitate capture of large prey available in association with swarming army ants. By contrast, as a potential result of their occurring at elevations above those in which army ants occur reliably (see Willis and Oniki 1978), the smaller taxa in montane regions have slimmer and more shallow bills that are probably better adapted for gleaning and probing and, perhaps, for taking smaller prey. Despite some variation in plumage patterns among montane subspecies of *D. picumnus* (see Marantz 1997), with one exception the montane subspecies were found to be similar structurally. Only *D. p. puncticollis* stands out from other taxa as a result of its particularly long, slim bill. This northernmost population of *D. picumnus* is restricted to highlands from southern Mexico to western Honduras (Morales-Pérez et al. 2000, Marantz et al. 2003), occurring at elevations largely above those frequented by army ants. Its long, slim bill, unusual in *Dendrocolaptes*, suggests that it forages more by gleaning and probing like a *Xiphorhynchus* than by sallying like other *Dendrocolaptes*.

The only subspecies in this complex described on the basis of mensural characters is *D. p. casaresi*. Our data suggest that *D. p. casaresi* may indeed have a longer bill and possibly longer wings than the similarly plumaged *D. p. pallescens*, but our sample was too small even to determine with confidence that birds from northwestern Argentina are larger than those from Bolivia and Paraguay, much less to show that there is no overlap between measurements of these taxa (Table 7 and Fig. 8) or to dismiss the possibility that such variation is clinal in nature. A definitive answer regarding this subspecies must await examination of specimens of *D. p. casaresi* housed in Argentine collections.

Dendrocolaptes platyrostris.—We found moderate separation between *D. p. platyrostris* and *D. p. intermedius* (not shown), largely reflecting the smaller size and relatively larger bill of the latter, which is most easily distinguished on the basis of its duller crown and overall paler coloration (Cory and Hellmayr 1925, Marantz 1997). We did not find an obvious relationship between plumage and morphometric intermediacy in the apparent contact zone for these forms in central Paraguay and São Paulo, Brazil (see Marantz 1997, Willis and Oniki 2001), but the complex geographic nature of this zone may complicate such a determination.

In sum, only three subspecies in the genus *Dendrocolaptes* were described largely or exclusively on the basis of morphometric characters. Two of these taxa, *D. s. nigrirostris* and *D. s. colombianus*, appear to refer to arbitrary breaks in clinal variation compounded by a transcription error (see Binford 1965) and should thus be synonymized with the nominate form. The third subspecies, *D. p. casaresi*, may be valid, but our sample was too small to support its recognition unequivocally.

THE UTILITY OF SUBSPECIES IN *DENDROCOLAPTES*

We began by suggesting that most criticism of the use of subspecies stems not from the importance of well-defined populations but instead from uneven application of the subspecies concept (see also Patten, this volume; Remsen, this volume). Only subspecies that are readily diagnosable using repeatable techniques will be useful in studies of geographic variation and other aspects of evolutionary biology. We therefore sought to assess taxa in the woodcreeper genus *Dendrocolaptes* using a large sample that represented all presently recognized taxa. The present morphometric

analysis, together with an earlier study of plumage patterns (Marantz 1997), examined the suite of characters originally used to diagnose these taxa. Our combined data set supports the synonymy of 7 of the 30 taxa that have been described in this complex, with the diagnosis of an eighth taxon uncertain, given our sample. A more superficial review of woodcreeper subspecies during the preparation of accounts for Marantz et al. (2003) suggested that a similar percentage of taxa should be synonymized across the family.

Biogeographic patterns are clarified by the reduced subset of diagnosable taxa in *Dendrocolaptes*. The continuous nature of lowland forest along the Caribbean Slope of Central America is more conducive to the clinal variation we documented, as opposed to the steps that were suggested by the past recognition of *D. s. colombianus* and *D. s. nigrirostris*. Similarly, the tiny geographic ranges of both *D. s. legetersi* and *D. p. extimus* (both known essentially from their type localities) were not supported biogeographically, given that both of these taxa were described from geographic regions that are relatively homogeneous (the eastern Yucatan Peninsula and the Paraguayan Chaco, respectively). *Dendrocolaptes s. hyleorus* and *D. p. veraguensis* likewise have geographically small ranges, but at least these taxa were described from somewhat more heterogeneous regions in which differentiation may be more likely (lowland valleys in northern Colombia and the mountains of central Panama, respectively). Only *D. c. ridgwayi* occupies a large, geographically bounded region (in southern Amazonia between the Rio Tapajós and the Rio Tocantins), but in this case, phenotypic heterogeneity and apparent clinal variation suggest that this population represents a hybrid swarm (Marantz 1997). With the synonymy of these taxa, the remaining subspecies occur in larger and geographically better-defined regions that better match the areas of endemism outlined by Haffer (1985) and Cracraft (1985).

We agree with Patten (this volume) and Remsen (this volume) that, rather than discarding the subspecies concept, the reanalysis of previously described taxa using quantitative methods and stressing diagnosability rather than mean differences will provide a robust starting point for studies of biogeography, migration, and other aspects of evolutionary biology. Our work provides an example in which the quantitative analysis of plumage and morphometric characters supported the synonymy of numerous poorly

defined subspecies, many with small and biogeographically unsupported ranges, thus resulting in a set of well-defined taxa whose distributions are concordant with recognized biogeographic characteristics.

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