

WHEN BLACK PLUS WHITE EQUALS GRAY: THE NATURE OF VARIATION IN THE VARIABLE SEEDEATER COMPLEX (EMBERIZINAE: *SPOROPHILA*)

F. Gary Stiles

Instituto de Ciencias Naturales, Universidad Nacional de Colombia,
 Apartado 7495, Bogotá D. C., Colombia.

Resumen. Las afinidades taxonómicas del Espiguero Variable (*Sporophila aurita*) y el Espiguero Alifajeadado (*S. americana*) han sido discutidos por más de 80 años. El descubrimiento de una zona de hibridación entre el primero y el Espiguero Gris (*S. intermedia*) — anteriormente no considerado como emparentado debido a que el plumaje definitivo del ♂ es gris, no blanco y negro — me estimuló a reexaminar esta cuestión. Mi hipótesis de trabajo era que existiera una relación estrecha entre todas estas formas. Esta hipótesis fue apoyada por la gran similitud morfológica y las distribuciones casi perfectamente complementarias de todas ellas, la identificación de otra zona de solapamiento y hibridación limitada, y por la existencia de variación previamente ignorada dentro de la especie *intermedia*. Concluyo que *S. intermedia* es un miembro integral del llamado “complejo del Espiguero Variable”, y que esto constituye un grupo monofilético reconocible al nivel de superespecie. Los patrones de distribución geográfica y divergencia morfológica me permiten reconocer los siguientes cuatro aloespecies: *S. corvina* (Espiguero Variable); *S. intermedia* (Espiguero Gris); *S. muraliae* (Espiguero del Caquetá); y *S. americana* (Espiguero Alifajeadado). Con base en un análisis cuantitativo de la variación dentro de *S. intermedia*, llego a la conclusión de que la subespecie *agustini* no es reconocible, como tampoco lo es *S. c. chocoana*, de acuerdo con otro estudio. Se propone una hipótesis tentativa para la historia zoogeográfica del grupo.

Abstract. The degree of relationship between the Variable (*Sporophila aurita*) and Wing-barred (*S. americana*) Seed eaters has been debated for over 80 years. The discovery of a zone of hybridization between the former and the Gray Seed eater (*S. intermedia*), not previously considered to be closely related because of its gray rather than black-and-white adult ♂ plumage, prompted me to reexamine this question. My working hypothesis of a close relationship between all of these forms was supported by their very similar morphology and almost perfectly complementary distributions, the recognition of another zone of limited overlap and hybridization, and by heretofore unappreciated variation within *S. intermedia* itself. I conclude that *S. intermedia* is in effect a member of an enlarged Variable Seed eater complex, a monophyletic unit best recognized at the superspecies level. Patterns of morphological differentiation and distribution lead me to propose the recognition of four allospecies: *S. corvina* (= “aurita”), Variable Seed eater; *S. intermedia*, Gray Seed eater; *S. muraliae*, Caquetá Seed eater; and *S. americana*, Wing-barred Seed eater. Quantitative analysis of the variation within *S. i. intermedia* indicates that the subspecies *agustini* is not recognizable; likewise, synonymization of *S. c. chocoana*, suggested in a previous study, is supported. A tentative hypothesis for the historical zoogeography of the group is proposed. Accepted 5 June 1996.

INTRODUCTION

The genus *Sporophila* includes some 30 species of small, bulbous-billed finches that inhabit mostly various sorts of nonforest habitats like savannas, open marshes, pastures, and second growth, and consume mainly grass seeds (Meyer de Schauensee 1952, Stiles 1983, Stiles & Skutch 1989,

Ridgely & Tudor 1989, Ouellet 1992). Although the genus occurs from southern Texas to central Argentina, the area of highest diversity is eastern South America south of the Amazon basin (Meyer de Schauensee 1952, Ouellet 1992). Males of *Sporophila* are mostly boldly patterned in combinations of black, white, gray, buff, and/or

chestnut; females and immatures are usually brownish, unpatterned, and often exceedingly difficult to identify when not accompanied by adult males. For these reasons, the taxonomy of *Sporophila* has been based almost exclusively on the definitive male plumages, with the characters of females and other aspects of morphology being used haphazardly if at all. Following Meyer de Schauensee (1952), the tendency has been to group the species according to male plumage patterns ("black-and-white", "gray", etc.), an arrangement recently further elaborated by Ridgely & Tudor (1989). However, what was originally devised for convenience has tended to become accepted as a taxonomic scheme, with the result that where ♂ plumages differ, two closely related species might be placed in different species groups and their relationship overlooked. Such a case is described in this paper.

Species limits in the *Sporophila aurita* — *S. americana* group, which might be called the "Variable Seedeater complex", have long been a source of debate (Chapman 1915, Hellmayr 1938, Meyer de Schauensee 1952, Olson 1981b, AOU 1983). At the present time, the major debate centers on whether two groups of races with black-and-white adult males and widely disjunct distributions, comprise a single species or two distinct species (or allospecies). The groups are *S. aurita*, with 4 or 5 subspecies in Middle and extreme western South America, and *S. americana*, with two disjunct forms (one possibly including two races) in South America east of the Andes. Treatment of all of these as races of a single species originated with Meyer de Schauensee (1952), and has been followed by many recent authors including Olson (1981b) and Ridgely & Tudor (1989). The AOU (1983) disagreed, preferring to treat the two groups as allospecies of a superspecies in view of differences in the pattern of the ♂ plumages, and the wide disjunction in their ranges. In either case, the debate has been limited to these two groups with black-and-white males.

That the solution to this problem might lie elsewhere occurred to me when I examined a series of *Sporophila* collected recently at several sites in the upper Río Sinú drainage S of Tierralta, departamento de Córdoba, NW Colombia (approx. 7°55'N, 76°20'W), by R. Jiménez and R. Tafur. Included in this collection were several putative hybrids between *S. aurita* and a species

not previously considered to be closely related, the Gray Seedeater *S. intermedia*. Once over my initial amazement, I decided to reevaluate the relationship between *S. americana* and *aurita* in the light of the possibility that *S. intermedia* might also be an integral member of the Variable Seedeater complex. The objective of this paper is therefore to present a detailed examination of the plumages, external morphology, and distribution of *S. intermedia* in relation to those of *S. americana* and *aurita*, in order to test my working hypothesis of a close relationship among all of these forms.

TAXONOMIC HISTORY

The first member of this complex to be described was *S. americana*, by Gmelin in 1789 from a plate by Daubenton in Buffon's "Histoire Naturelle d'Oiseaux". Originally the species was ascribed simply to "America", but the type locality was later restricted to Cayenne by Hellmayr (1938). Bonaparte described *aurita* in 1850, supposedly from Brazil, but the type was reexamined by Sclater (1871), who pronounced it typical of birds from C Panama, and the type locality was amended accordingly. Sclater had described *corvina* with its black male plumage from Oaxaca, Mexico in 1859, and two years later Cabanis described *hoffmannii* (with black-and-white males) from S Costa Rica.

Between 1863 and 1865 Lawrence named *semicolaris* and *fortipes* from Panama (later synonymized with *aurita*), *badiiventris* from E Nicaragua (a synonym of *corvina*), *collaris* from SW Panama (a synonym of *hoffmannii*), and *bicksii*, supposedly from C Panama but more likely from Buenaventura, Colombia: see Olson (1981b). This plethora of names was drastically pruned by Hellmayr (1938), who noted that *corvina* occurred along the Caribbean slope of Central America from Mexico to Panama, and ascribed the great variation among males from C Panama to hybridization between *corvina* and *aurita*. He accordingly recognized only one species in Middle America (*aurita*), with *corvina* as a subspecies.

In South America, *ophthalmica* was described from W Ecuador by Sclater in 1860, and considered a race of *aurita* by Chapman (1915, 1917). Chapman also (1915) described the subsequently controversial form *murallae* from "La

Muralla" (= Morelia), Caquetá, SE Colombia, as a cis-Andean race of *aurita*, comparing it with *ophthalmica* but suggesting that it might represent a "link" to *S. lineata* (= *americana*). Hellmayr (1938) strongly suggested that *murallae* might be closer to *americana* than to *aurita*. The next step was taken by Meyer de Schauensee (1952), who lumped *aurita* and its races into *americana*, considering *murallae* to represent the "perfect connecting link", and thereby setting the stage for the current debate. He also described the race *chocoana* in 1950, for the birds from the Pacific slope of Colombia S to Valle del Cauca, setting the N limit of *ophthalmica* in extreme SW Colombia.

The recent revision of this complex by Olson (1981b) clarified the confusion surrounding the name *aurita*. He showed that the notoriously variable population of C Panama is essentially a stable hybrid swarm between the Caribbean *corvina* and the Pacific *hicksii*. Since Bonaparte's original description of *aurita* was very vague and the type specimen had disappeared from the Paris Museum by 1935 (Hellmayr 1938), Olson argued that it is impossible to associate the name *aurita* with either parental population. This effectively invalidates this name, but to avoid confusion I will continue to use it, in quotes, until the concluding part of this paper. With better material than that available to previous authors, Olson also showed that *hoffmannii* was a valid race, but *chocoana* was a synonym of *hicksii*. However, he misinterpreted the statements of Meyer de Schauensee (1950, 1952) regarding the geographical limits of *ophthalmica* and *chocoana* (= *hicksii*).

In contrast to the confusion and debate surrounding the black-and-white portion of the Variable Seedeater complex, the taxonomic history of the Gray Seedeater has been relatively tranquil. The earliest name for the species, *grisea* Gmelin, was early shown to be unidentifiable and the name *intermedia* Cabanis 1851 (type locality Puerto Cabello, Venezuela) has been used nearly exclusively for over 75 years. The only taxonomic confusion has been with the Slate-colored Seedeater *S. schistacea*, which is similar in male plumage but quite distinct in morphology, as recognized by Meyer de Schauensee (1952). Three races have been split from nominate *intermedia* of N and E Colombia and N Venezuela: *insularis* Gilliard 1946 for the birds of Trinidad; *bogotensis* Gilliard 1946 for Colom-

bian populations W of the Eastern Andes and S of the Caribbean coastal plain; and *agustini* Meyer de Schauensee 1947 for the birds of the upper Magdalena valley of Colombia. Most recent debates have concerned the validity and geographic limits of these races (e.g., Olivares 1969). More problematical has been the "blackish race of the Gray Seedeater", *anchicayae*, described by Miller (1960) from the Anchicayá Valley of W Valle del Cauca, Colombia. This form was lumped into *bogotensis* by Hilty & Brown (1986) but ascribed to *americana* by Ridgely & Tudor (1989). In effect, both were half right: I consider "*anchicayae*" to represent hybrids between *S. i. bogotensis* and *S. "aurita" hicksii*, as discussed below. In spite of the problematic nature of "*anchicayae*", there had been no suggestion prior to the present study that *intermedia* was closely related to the Variable Seedeater complex, much less a member of it. Since the clue to the problem was provided by the Tierralta series mentioned above, the time has come to describe these specimens in detail and to demonstrate their connection with "*anchicayae*".

THE HYBRIDS: THE TIERRALTA SERIES AND "ANCHICAYAE"

The sample of *Sporophila* from the Tierralta area consists of 6 adult males, one ♂ molting from ♀-like (first basic?) to definitive plumage, and one ♀. All were collected between 6 June and 24 July 1991 in second-growth vegetation along various creeks and rivers (Río Verde, Quebrada Seferino, Quebrada Gaita, Quebrada Chibogadó) at elevations of 100–130 m, above the site for the Urrá hydroelectric project, as part of an environmental impact study. This general area was heavily forested through the 1970s, but colonization and deforestation have proceeded rapidly during recent years (R. Jiménez, pers. comm.).

The males of the Tierralta series include one apparently phenotypically "pure" *intermedia*, one apparently "pure" *hicksii*, and four that run the gamut between them (Fig. 1); the young molting ♂ also appears to be attaining an intermediate plumage, closer to *intermedia*. In most dimensions the *hicksii*-like birds tend to be smaller than the *intermedia*-like birds, but the correspondence is far from perfect (Fig. 2). The relation between plumage phenotype and bill color is also only approximate, with *intermedia*-

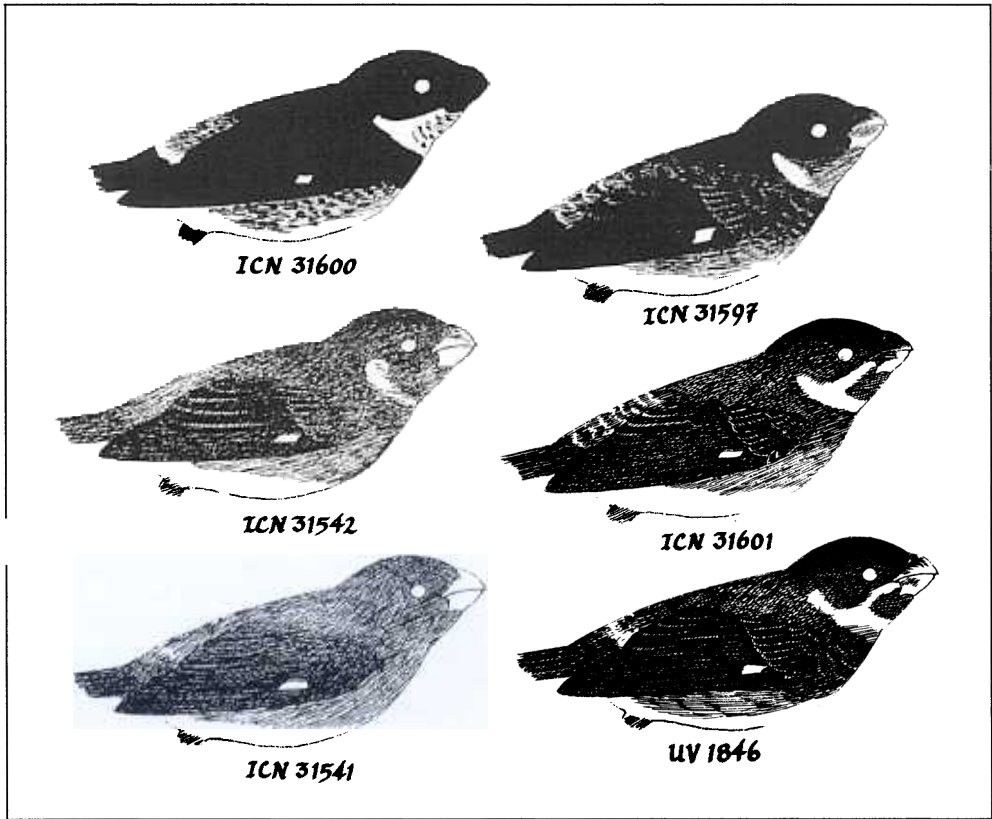


FIG. 1. Plumages of *Sporophila* males collected at Tierralta, and a specimen of "*anchicayae*" (UV 1846). ICN 31522 resembles ICN 31597 in plumage; ICN 31548 is acquiring a plumage like that of ICN 31542. Note resemblance between ICN 31601 and UV 1846. For abbreviations of museums see text.

like birds tending to have paler bills. The ♀ is small in most dimensions and might thus be closer to *hicksii* (see below), but is probably not safely assignable to either form.

Miller's (1960) original description of *anchicayae* included a detailed description of his two males, and a well-executed drawing of the type by G. Christman. This drawing portrays a bird whose plumage is virtually identical to that of the most intermediate (ICN 31601) of the Tierralta series (cf. Fig. 1); from the description, the other ♂ is very similar to the type. In addition, a specimen in the collection of the Universidad del Valle (UV 1846) has a plumage very like that of Miller's drawing and ICN 31601 (Fig. 1). It was taken by J. I. Borrero and G. Cataño at 340 m

along the Río Anchicayá, very close to Miller's type locality, on 22 February 1968. I have no doubt that this specimen is *anchicayae*, which in turn represents hybrids between *S. "aurita" hicksii* and *intermedia*, in this case of the race *bogotensis* (see below). Moreover, it seems likely that the *anchicayae*-ICN 31601 plumage, essentially exactly intermediate between the two putative parent species, represents the F1 phenotype, with the other Tierralta males resembling more one or the other parental species representing F2 phenotypes or backcrosses. It is noteworthy that none of the latter phenotypes have been taken in the Río Anchicayá region, a point I shall return to below. The fact that the Tierralta hybrids were taken at several sites within a radius of

approximately 20 km, and represent apparent backcrosses as well as a putative F1, presents much stronger evidence for a close relationship between *intermedia* and "aurita" than would a single isolated hybrid individual (cf. Cracraft 1989). This is an important consideration since occasional hybridization occurs rather widely in *Sporophila*, even with species of related genera (Sick 1963; see below).

Given the existence of two zones of limited overlap and hybridization between "aurita" and *intermedia*, I decided that a detailed examination of plumage, morphology, and distribution of these two species in Colombia and adjacent areas was warranted. In the process, I found that the degree of variation in plumage of the various

forms, while often mentioned, had never been precisely quantified, and that such an analysis could shed light on the taxonomic validity of several of the described subspecies as well as on the relationship between the Gray and Variable Seedeaters.

METHODS

For this study I examined a total of 297 specimens in the following museums (for each museum, I give in parentheses the number of specimens of each form in the following order: *intermedia/bogotensis/hicksii/ophthalmica/murallae/americana/hybrids*): Instituto de Ciencias Naturales, Universidad Nacional de Colombia (64/42/7/33/4/0/6); Museo de la Universidad

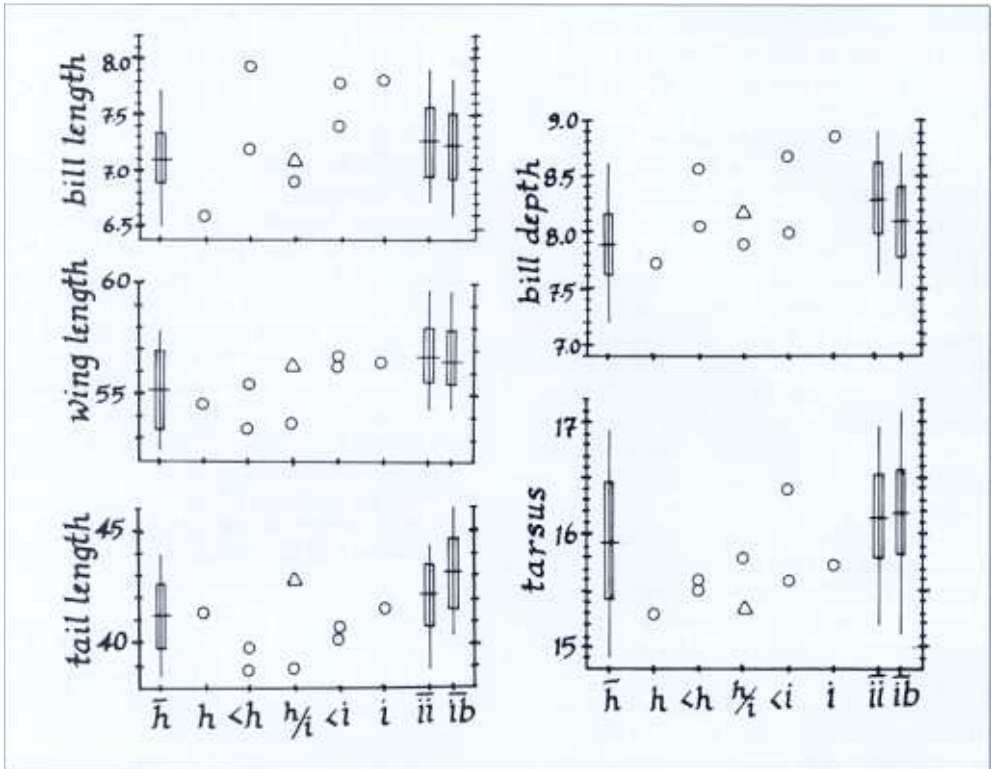


FIG. 2. Measurements (in mm) of *Sporophila* males collected at Tierralta (circles) and "anchicaya" (triangle) in relation to plumage type. Abbreviations: h = "pure" *hicksii* (ICN 31600 in Fig. 1); $<h$ = closer to *hicksii* (ICN 31522, 31597); h/i = intermediate between *hicksii* and *intermedia* (or *bogotensis*): ICN 31601, UV 1846; $<i$ = closer to *intermedia* (ICN 31522, 31548); "pure" *intermedia* (ICN 31541). \bar{h} , \bar{i} , $i\bar{b}$ means and standard deviations (see Table 7) for *hicksii*, *intermedia*, and *bogotensis*, respectively.

de La Salle, Bogotá (11/12/0/0/16/0/0); Unidad de Investigación "Federico Medem" (UNIFEM) of the Instituto de Recursos Naturales (Inderena), Bogotá (5/3/33/0/0/0/0); Universidad del Valle, Cali (0/17/27/0/0/0/1); and the Naturhistorisches Museum in Vienna, Austria (3/0/0/6/0/7/0). In addition, Miguel Lentino of the Colección Phelps in Caracas, Venezuela, and Manuel Marín A. of the Museum of Natural History of Louisiana State University in Baton Rouge measured 5 specimens of *americana* and 13 of *murallae* for me, giving a total sample of 315 specimens.

All measurements were taken to the nearest 0.1 mm using dial calipers, of: wing chord, tail length, depth of bill at nostril, bill length from nostril, and tarsus length (cf. Baldwin *et al.* 1931). I chose length from nostril as my measure of bill length because of the difficulty in obtaining accurate measurements of exposed or total culmens of such bulbous-billed birds; and bill length from nostril yielded a significantly lower coefficient of variation in most taxa than did either culmen measurement. Because the sample distributions did not deviate significantly from normality (χ^2 tests), and variances were homogeneous (F-tests), measurements were analyzed by one-way ANOVA; where significant differences were found among samples I used Tukey tests to determine which samples differed significantly (Zar 1984). I determined by Student's t-tests that males and females of all forms differed significantly in wing length but not in measurements of the bill, tail, or tarsus ($P > 0.10$ in all cases). I therefore combined measurements of males and females for analyzing the latter measurements, but analyzed wing length for each sex separately. I also compared the mean ratios between various measurements for all forms; a ratio falling outside the 95 % confidence interval for the given measurements was considered to differ significantly from the remaining samples (Zar 1984).

I analyzed colors of females and immature plumages, and the depth of gray in adult males of *intermedia*, with reference to the color guides of Smithe (1975, 1981), based on the Munsell system. For certain aspects of male patterns (e. g., size of wing speculum), I made comparisons using t-tests; for others (e. g., size and intensity of neck-patches and throat-bands) I devised subjec-

tive scoring systems and analyzed these using two-sample Kolmogorov-Smirnov tests (Sokal & Rohlf 1981). I also made drawings of several representative individuals of all taxa to better illustrate the degree of plumage variation among males.

Distributions of the different taxa in Colombia were plotted from collecting localities of specimens in the aforementioned collections, from localities given by Meyer de Schauensee (1948–1952, 1950, 1952), Nicéforo & Olivares (1975), Serna (1981, 1984), and Negret (1992), and from unpublished field data of T. McNish, L. Rosselli, P. Salaman, and my own field notes. For the overall distributions of all forms of the complex, I also used information from French 1973 (Trinidad and Tobago), Snyder 1966 (Guyana), Phelps & Phelps 1950 and 1963 (Venezuela), Pinto 1944 (Brazil), Meyer de Schauensee (1952), and Ridgely & Tudor (1989), supplemented by Venezuelan and Peruvian localities supplied by M. Lentino and M. Marín, respectively.

RESULTS

Because the descriptions of various forms in the Variable Seedeater complex have been based on one or a few characters, some of which have subsequently been shown to be invalid, I will first characterize in detail the plumages of each recognizable member of the complex, in the process attempting to evaluate variation both within and between subspecies and species. I will then proceed to a quantitative analysis of external morphology to complete the characterization of each form. This in turn will permit me to reexamine the distributions of all forms, correcting previous errors due to misidentifications. Finally, I will attempt a zoogeographic overview of the complex and present my taxonomic conclusions.

Colors, patterns, and plumage sequences. *Sporophila "aurita"*: Uncertainty regarding the distributional limits of the races *hicksii* (including *chococana*) and *ophthalmica* (Olson 1981b) reflect insufficient understanding of the range of population and individual variation in both forms. To illustrate this variation, I have drawn representative examples of the adult male plumages of three Colombian populations: *hicksii* from northern Chocó and northern Antioquia, and from southwestern Valle del Cauca (Fig. 3); and *ophthalmica*

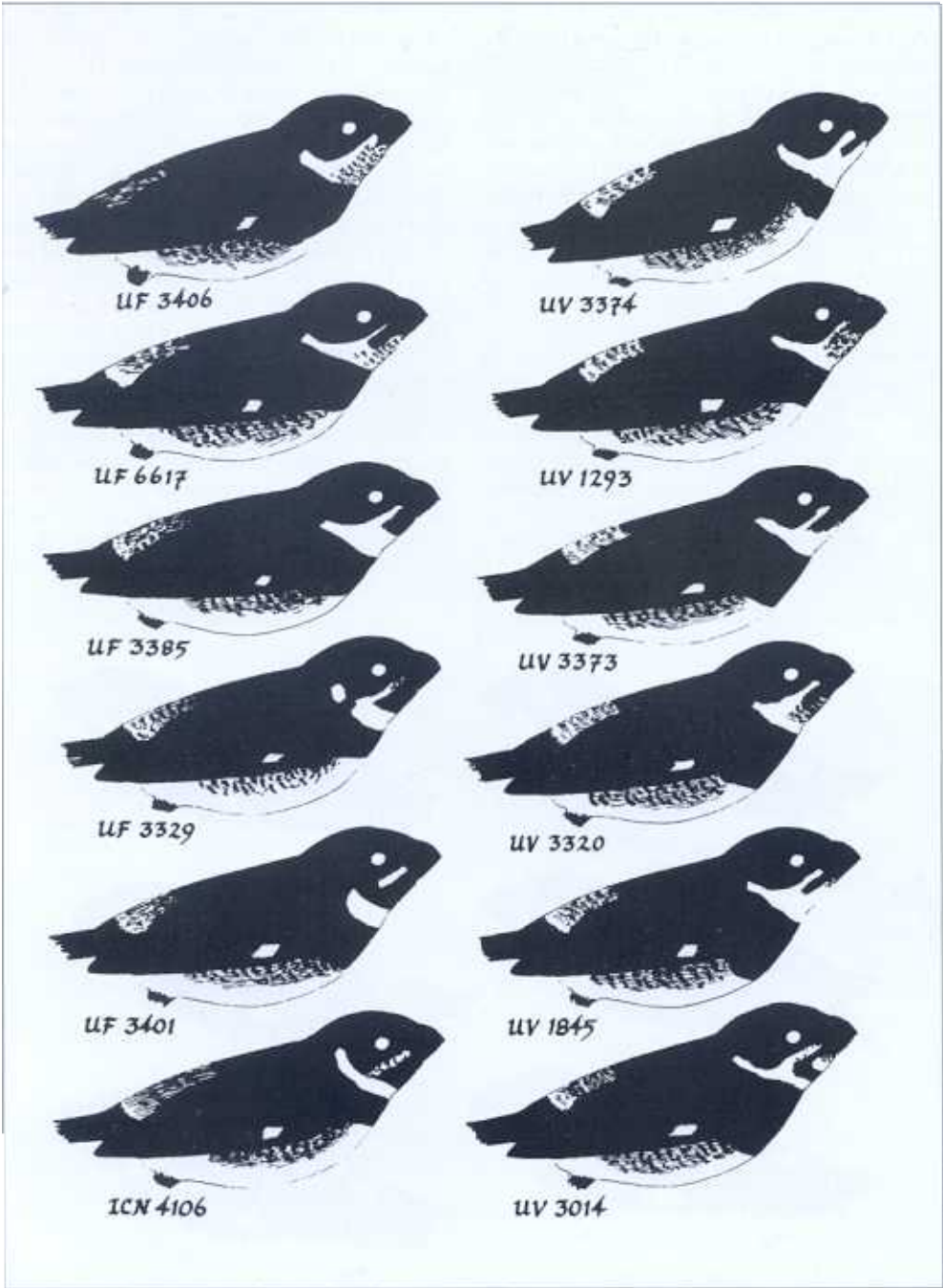


FIG. 3. Plumage variation in adult males of *S. "aurita" hicksii*. Left-hand column: N Choco — N Antioquia sample; right-hand column: W Valle del Cauca sample. Birds are arranged from palest-throated to darkest-throated, top to bottom.

from extreme southern Cauca and Nariño (Fig. 4). The latter two populations represent the closest known approach of the distributions of these two races (see below). These races were previously separated on the basis of the whiter throat and narrower pectoral band of *ophthalmica* relative to *hicksii* (cf. Olson 1981b), but from Figs. 3 and 4 this is evidently an oversimplification. A quantitative analysis of the variation in these and other features of the pattern of the adult ♂ plumage (Table 1) shows overlap in all characters, with the differences between the northern and Valle populations of *hicksii* being considerably less than the differences between the latter and *ophthalmica*. The two races differ significantly only in the width of the pectoral band, although the difference in the degree of dusky to blackish scaling and smudging on the sides and flanks also approaches significance. Two other characters are useful in distinguishing these subspecies. Most individuals of *ophthalmica*

(at least 17 of my sample of 22) show white on the lower eyelid, varying from one or two feathers to a conspicuous crescent (cf. Fig. 3); I have seen no *hicksii* ♂ with even a vestige of this mark ($\chi^2 = 20.25$, 1 d.f., $P < 0.001$). Also, the wing speculum of *ophthalmica* averages significantly longer than that of *hicksii* ($t = 6.64$, $P < 0.001$; cf. Table 2). Using a combination of characters, I can separate virtually all adult males of the two races examined to date. I should note here that Meyer de Schauensee (1950) distinguished *chocoana* of Colombia from *aurita* of Panama mainly on the basis of its whiter throat. From the present analysis and the data of Olson (1981b), I have no doubt that Olson was correct in considering *chocoana* a synonym of *hicksii*.

There is a definite difference in coloration of the adult females of the two forms as well, as noted by Meyer de Schauensee (1952). Females *hicksii* are duller, more olive-brown above (between 123, Raw Umber and 28, Olive

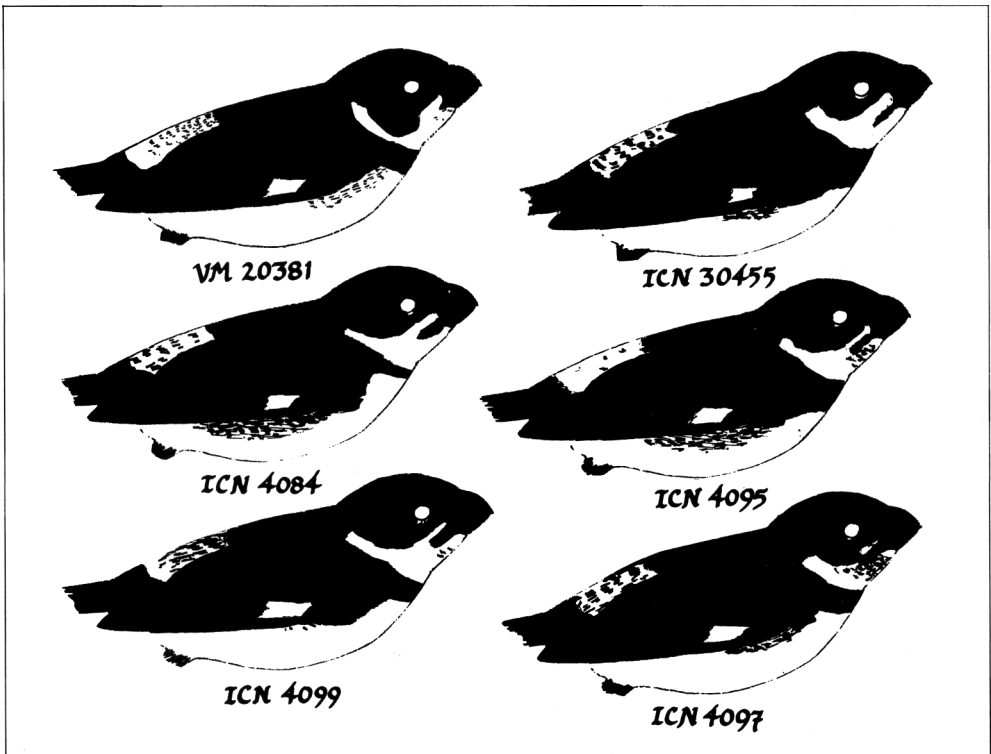


FIG. 4. Plumage variation in adult males of *S. "aurita" ophthalmica*; compare with *hicksii* (Fig. 3).

TABLE 1. Comparisons of different components of the definitive male plumage between three Colombian populations of *Sporophila aurita* by Kolmogorov-Smirnov two-sample tests. Populations are: NCA = N Chocó, N Antioquia (*hicksii*); WVC = W Valle del Cauca (*hicksii*); and SCN = S Cauca and Nariño (*ophthalmica*).

Populations and Plumage Areas	Plumage Scores				Σ	D_{max}^1	Definitions
	0	1	2	3			
A. Throat Pattern							
		4	8		15	.145 n.s.	0 = Entirely white
		6	9		17		1 = Chin < 1/4 black = small malar streak.
					22		.270 n.s. 2 = 1/4-1/2 of throat black, including 1/2 + of chin.
							3 = > 1/2 of entire throat black
B. Breast-Band							
		2	9	4	15	.045 n.s.	0 = Incomplete: center of chest gray or white.
		3	10	4	17		1 = Complete, v. narrow at center.
			8	0	22		.460* 2 = Complete, moderately broad, especially at sides.
							3 = Complete, broad.
C. Sides and Flanks							
					15	.152 n.s.	0 = Entirely white
					17		1 = Gray, < 1/4 with dark smudging.
		13	6	0	22		.374° 2 = 1/4-1/2 of area with dark smudging or scaling.
D. Rump							
NCA			11	2	15	.161 n.s.	0 = Clear white
MVC			10		17		1 = Some gray or dusky smudging.
SCN		10	10		22	.251 n.s.	2 = Gray or black \geq white.
							3 = Mostly dusky to blackish with some white.

Abbreviations for probabilities: n.s. = $P > 0.10$; ° = $0.10 > P > 0.05$; * = $P < 0.05$; ** = $P = < 0.01$.

Brown); the throat, chest, and sides are paler (near 123A, Cinnamon; center of chest approaching 26, Clay Color), shading to buffy-white (near 54, Cream) on the abdomen. Females *ophthalmica* are a richer, more ochraceous brown above (brighter than 123, Raw Umber), paler ochraceous-tawny (between 123A, Cinnamon and 123B, Clay Color) on the throat, breast, and sides, shading to pale ochraceous yellow (paler and brighter than 123C, Yellow Ocher) on the belly. Young females *hicksii* are brighter above and more yellowish below than adults,

whereas young females *ophthalmica* are duller than their respective adults, such that most immatures of the two forms are indistinguishable.

Sporophila intermedia: Gilliard (1946) separated *bogotensis* from nominate *intermedia* on the basis of its supposedly darker, more blackish head and upper back, and the presence of white "post-auricular" patches (absent in *intermedia*). Gilliard's type was from Lomitas, Valle del Cauca, and his series included birds from Valle, Cauca, Tolima,

TABLE 2. Size of wing speculum (greatest length of exposed white area from primary coverts to distal end of speculum) in various samples of the Variable Seedeater complex.

Taxon	Sample		$\bar{x} \pm SD$ (mm)	
<i>S. "aurita" hicksii</i>	NCA	15	4.55 \pm 0.54	2.2–5.3
	WVC	17	4.83 \pm 0.64	3.8–6.0
<i>S. "aurita" ophthalmica</i>	SCN	22	6.04 \pm 0.60	4.6–7.3
<i>S. americana americana</i>	CAP	5	3.48 \pm 0.96	2.2–4.5
<i>S. a. murallae</i>	CPA	11	2.66 \pm 0.90	1.6–4.5
<i>S. intermedia intermedia</i>	NCL	18	3.00 \pm 0.72	0.9–5.2
	LLN	16	3.09 \pm 0.83	1.4–5.1
<i>S. intermedia bogotensis</i>	VMG	19	4.08 \pm 0.62	2.6–6.0
	MCP	22	4.14 \pm 0.71	2.8–6.4

Samples: NCA = Northern Chocó-Northern Antioquia; WVC = Western Valle del Cauca; CAP = Cayenne-Pará, Brasil; CPA = Caquetá, Putumayo, Amazonas; NCL = Northern Caribbean lowlands; LLN = Llanos, Norte de Santander; VMG = Valle del Magdalena; MCP = Medellín area, Cauca Valley, Pacific slope.

Huila, and Antioquia. Meyer de Schauensee (1947) separated *agustini* from *bogotensis* on the basis of its paler gray upperparts with the crown not darker than the back, larger white spots on the sides of the neck, and a larger white area on the abdomen. He gave the range of *agustini* as the Magdalena Valley, north to N Tolima (Honda). Miller (1947, 1952) did not collect any form of *intermedia* in the upper Magdalena Valley, and later (1960) stated that specimens of *agustini* he had examined were not paler gray than *bogotensis*, but that *agustini* was "doubtless recognizable by the combination of characters ascribed to it". The problematic nature of this form was highlighted by Olivares (1969), who found that large series from the Magdalena Valley and adjacent slopes in N Huila, Tolima, and W Cundinamarca included birds showing the supposed diagnostic features of both *bogotensis* and *agustini*, as well as intermediates. He thus considered this entire area to represent a zone of intergradation, in effect leaving at best a small area in S Huila for "pure" *agustini*.

I examined quantitatively the variation in plumage of adult males of *S. intermedia* throughout Colombia in order to evaluate the validity of *agustini* and to verify the characteristics of *bogotensis* relative to those of *intermedia*. I found considerable variation in the darkness of the gray coloration in males throughout Colombia west

of the Andes (Table 3). Populations from the middle Magdalena Valley and from Valle del Cauca are statistically indistinguishable in the darkness of the gray coloration of the crown, back, rump, and breast (only in the latter does the difference even approach significance). I can also detect no difference between these populations in the size of the white neck spot or in the size of the white area on the abdomen, and the proportion of both populations showing the neck spot is similar (Table 4). Perhaps the proportion of dark birds with inconspicuous neck spots is slightly higher in Valle, but the range of variation in both populations is such that no clear-cut division into two races is possible. Thus I tentatively consider *agustini* to be a synonym of *bogotensis*, while acknowledging that the case will not be entirely closed until a good series from the type locality of *agustini* can be included in the analysis.

When *bogotensis* (including the Magdalena Valley birds) is compared with nominate *intermedia* (Fig. 5), a number of interesting facts emerge. First, I could detect no statistically significant difference between these forms in the depth of the gray coloration, or in the size of the white area on the abdomen (Table 3). The two races do differ strongly in several other characters, however. The white neck spot is significantly larger and is more frequently present in *bogo-*

TABLE 3. Comparisons of the depth of gray coloration of various plumage areas in two samples of *Sporophila intermedia bogotensis* and in *S. i. intermedia*, by Kolmogorov-Smirnov two-sample tests. The scale of depth of gray is that of Smithe (1971, 1975). For abbreviations for probabilities see table 1.

SAMPLES, PLUMAGES AREAS	DEPTH OF GRAY									Σ	Dmax
	darker						paler				
	82—	82	82+	83—	83	83+	84—	84	84+		
CROWN											
<i>bogotensis</i> :											
Valle del Cauca	2	5	6	2	0	0	0	0	0	15	} 0.095 n.s.
Magdalena Valley	6	13	15	9	1	0	0	0	0	44	
Total	8	18	21	11	1	0	0	0	0	59	} 0.208 n.s.
<i>intermedia</i>	0	7	5	7	1	0	0	0	0	30	
BACK											
<i>bogotensis</i> :											
Valle del Cauca	0	1	6	7	1	0	0	0	0	15	} 0.217 n.s.
Magdalena Valley	0	2	9	27	6	0	0	0	0	44	
Total	0	3	15	34	7	0	0	0	0	59	} 0.105 n.s.
<i>intermedia</i>	0	0	6	18	6	0	0	0	0	30	
RUMP											
<i>bogotensis</i> :											
Valle del Cauca	0	0	0	0	7	6	2	0	0	15	} 0.079 n.s.
Magdalena Valley	0	0	0	3	21	15	3	2	0	44	
Total	0	0	0	3	28	21	5	2	0	59	} 0.241 n.s.
<i>intermedia</i>	0	0	0	3	20	5	1	1	0	30	
BREAST											
<i>bogotensis</i> :											
Valle del Cauca	0	0	0	8	6	1	0	0	0	15	} 0.374°
Magdalena Valley	0	0	0	7	25	8	4	0	0	44	
Total	0	0	0	15	31	9	4	0	0	59	} 0.132 n.s.
<i>intermedia</i>	0	0	0	15	15	6	2	2	0	31	

tensis (Table 4). The size of the wing speculum averages significantly larger in *bogotensis* as well (Table 2; $t = 4.53$, $P < 0.001$). A previously overlooked but highly interesting aspect of the pattern of *bogotensis* is a band of paler gray across the lower throat, effectively connecting the white spots on the sides of the neck. This mark

is lacking altogether in 77% of my sample of *intermedia*, the remainder having but a faint trace of paler gray on the throat. By contrast, over 90% of *bogotensis* have at least a trace, and over half show a definite pale band crossing the throat, a highly significant difference (Table 4). As in the case of *hicksii* vs. *ophthalmica* discussed

TABLE 4. Comparison of aspects of plumage pattern in two samples of *S. i. bogotensis*, and in *S. i. intermedia*, by Kolmogorov-Smirnov two-sample tests. For abbreviations for probabilities see Table 1.

SAMPLES, PATTERN	PLUMAGE SCORES					Σ	Dmax	DEFINITIONS
	0	1	2	3				
WHITE PATCH, SIDE OF NECK								
<i>bogotensis</i>								
Valle del Cauca	2		4	4	15	0.171 n.s.	0 = absent 1 = faint, gray 2 = small, distinct 3 = large, distinct	
Magdalena Valley		6	20	11	44			
Total	9	11	24	15	59	0.648**		
<i>intermedia</i>	24	3	3	0	0			
PALE BAND ACROSS THROAT								
<i>bogoten:</i>								
Valle del Cauca		5		2	15	0.101 n.s.	0 = absent 1 = faint, pale area 2 = faint band 3 = distinct band	
Magdalena Valley	4	15	16		44			
Total		20	21	11	59	0.647**		
<i>intermedia</i>	23		0		30			
SIZE OF WHITE AREA ON BELLY								
<i>bogotensis</i>								
Valle del Cauca			9	2	15	0.276 n.s.	0 = $< 1/4$ white 1 = $1/4 - 1/3$ white 2 = $1/3 - 1/2$ white 3 = $1/2$ white	
Magdalena Valley		6	19	18	44			
Total	2		28	20	59	0.061 n.s.		
<i>intermedia</i>	0	6	12	12	30			

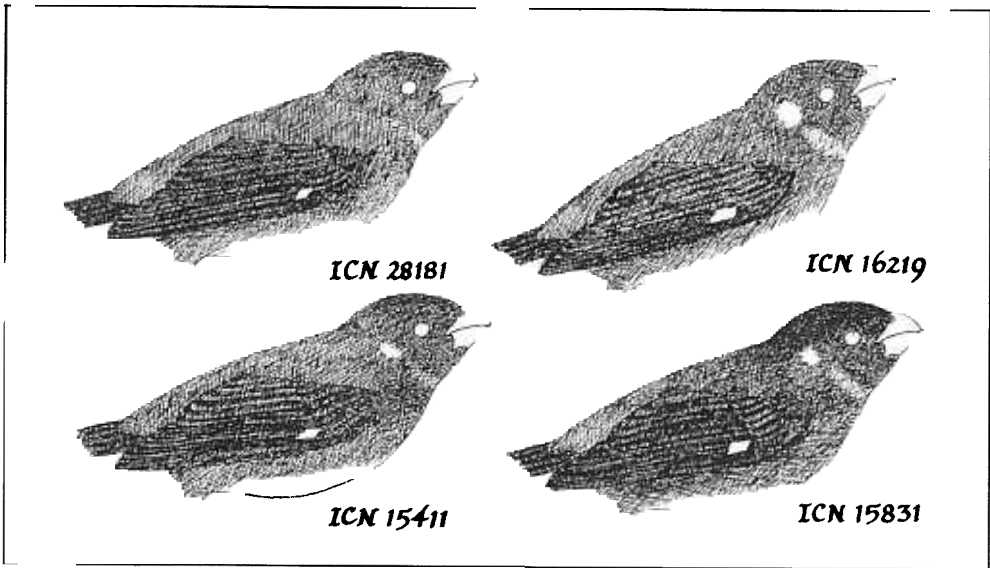


FIG. 5. Plumage variation in adult males of *S. intermedia*. Left: *S. i. intermedia*; upper bird is "typical" uniform gray with just a trace of pale on throat; lower bird is a more patterned individual from Norte de Santander (see text). Right: *S. i. bogotensis*. Upper bird is "agustini" phenotype, lower bird is darker "bogotensis" phenotype, according to Meyer de Schauensee (1947); both birds were collected at La Vega, Cundinamarca.

above, use of multiple characters permits the discrimination of over 90 % of the males of *bogotensis* from those of *intermedia*, and I consider *bogotensis* a valid race. Of particular interest is the fact that the pale neck-spots and throat-band of most *bogotensis* occupy precisely the same area as does the white band across the throat in "aurita": in fact, in *hicksii* this mark may rarely be broken into separate neck-spots and throat-band, much as in *bogotensis* (UF 3329 in Fig. 3).

A noteworthy aspect of the variation within *intermedia* itself is that the proportion of males with at least a trace of the neck spot and/or throat band is higher among specimens from Norte de Santander than among those from other areas (4 of 10 vs. 3 of 20 for neck spots, 3 of 10 vs. 3 of 20 for throat bands). As will be discussed below, Norte de Santander is also the only place where *bogotensis* has been reported from the east slope of the Andes-Sierra de Perijá; the stronger neck and throat pattern among the *intermedia* from this area could be the result of gene flow from *bogotensis*.

Adult females of the two races also differ. Those of *intermedia* are olive-brown on the head

and upperparts (near 29, Brownish Olive, but paler); the throat is paler, the malar area brighter and more ochraceous (near 123B, Clay Color), shading to between 123A (Raw Umber) and 39 (Cinnamon) on the breast and sides, and paler, near 54 (Cream) on the belly. Adult females of *bogotensis* are paler and grayer; the head and upperparts are a grayish brown (between 79, Glaucous, and 119B, Dark Drab), the breast and sides a buffier brown (between 223D, Tawny, and 39, Cinnamon), shading to a duller buffy-white on the abdomen. The amount of pale, horn color to yellow on the bill also may be greater in females of *bogotensis*: most have $\frac{1}{4}$ or more of the bill pale, and nearly $\frac{1}{3}$ show extensive pale areas on the maxilla, whereas nearly all *intermedia* skins examined had less than $\frac{1}{4}$ of the bill pale. However, because of possible postmortem changes in bill color the degree to which this difference may be evident in live birds remains to be determined.

Interestingly, as in the case of *ophthalmica* and *hicksii* above, immatures of both sexes are much more similar than are the adult females. In both races the first-year birds are olive-brown

tinged with ochraceous above (nearest 123, Raw Umber); the breast and sides are brighter, more ochraceous (nearest 123B, Clay Color), shading to a paler buffy yellowish (between 123D, Chamois and 54, Cream) on the abdomen. Females in this plumage average slightly more yellowish below than do males, and sex for sex immatures of *intermedia* may average slightly brighter overall than those of *bogotensis*, but most are indistinguishable. Also noteworthy is the great similarity of these immatures to those of *bicksii* and *ophthalmica* in the corresponding plumage: I cannot safely separate most immatures of any of these forms on the basis of plumage color.

Sporophila americana, including *murallae*: Of greatest interest here is the extent to which *murallae* represents the "perfect connecting link" between *americana* and "*aurita*". Unfortunately, I was able to examine only five males and two females of *americana* in detail, and hence the degree of individual variation in this form is probably underestimated in the following analyses. Compared to males of either race of "*aurita*", those of *americana* have much less heavily marked throats: 4 of 5 had white throats with at most a faint clouding of gray. The black pectoral band is usually incomplete in *americana*, the center of the breast being either white or clouded with gray. The sides and flanks of *americana*

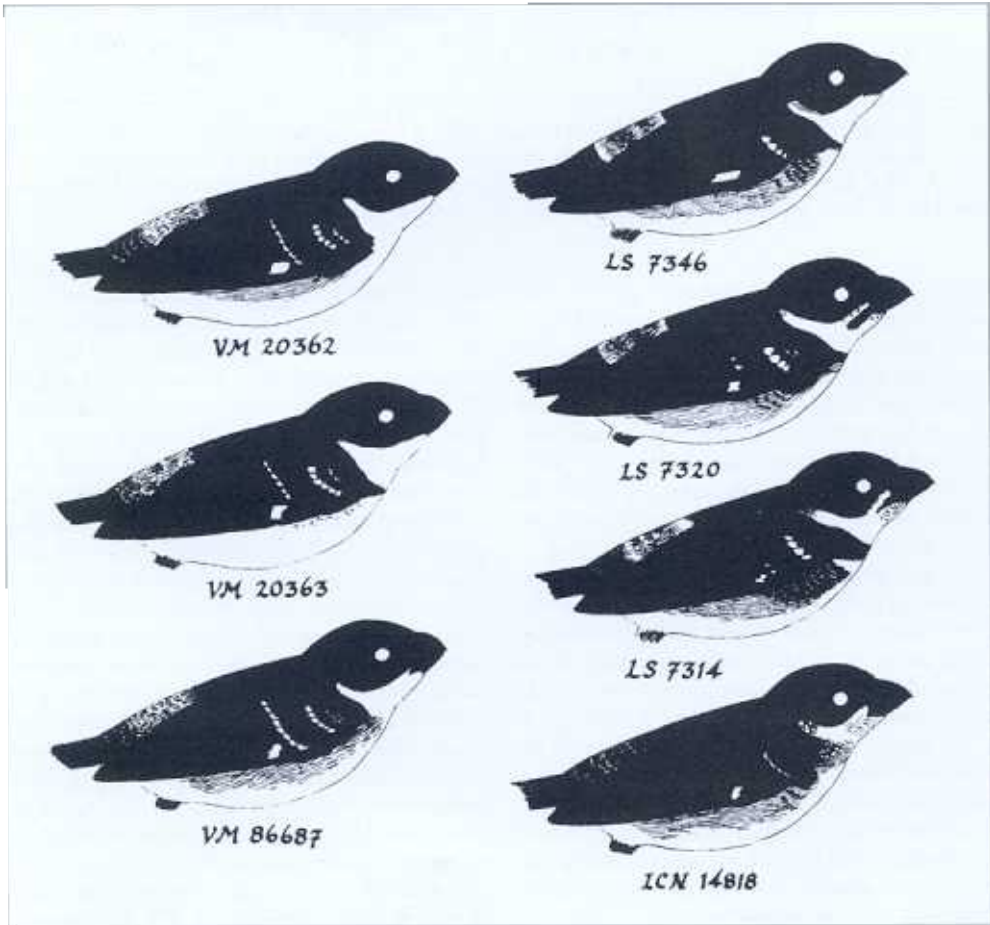


FIG. 6. Plumage variation in *S. americana* (three birds at left) and *murallae* (four birds at right). Compare with Figs. 3, 4.

show significantly less dark markings than *hicksii*, being more like *ophthalmica* in this respect; however, in *americana* these markings tend toward a uniform gray clouding rather than the dusky smudging of *ophthalmica* (and *hicksii*). The rump of *americana* is intermediate in color between that of *ophthalmica* (which has, on average, the whitest rump) and *hicksii*, in which the rump is darker, averaging more like the latter (Table 4). The wing speculum of *americana* averages smaller than that of *hicksii*, and much smaller than that of *ophthalmica* (Table 2; statistical tests not performed due to the small sample of *americana*). The most striking difference between *americana* and all forms of "*aurita*" is the presence of one to three well-developed wing-bars in the former; no specimen of "*aurita*" I have seen has even a vestige of such a mark (Fig. 6).

In most of these features, males of *murallae* resemble those of *americana* much more closely than those of "*aurita*" (Table 4). In both throat pattern and the completeness of the pectoral band, *murallae* differs significantly from both forms of "*aurita*" but not from *americana*, although in the second feature the two races of the former also differ significantly. The sides and flanks of *hicksii* are significantly more heavily marked with black or dusky than are those of the other forms, which do not differ among themselves; however, most of the sides and flanks of *murallae* show a uniform gray clouding like that of *americana* and unlike the dusky smudging of males of "*aurita*". The rump of *murallae* averages darker than that of any other form, but differs significantly in this respect only from that of *ophthalmica*. The wing speculum of *murallae* averages smaller than that of any other form, that of *americana* being closest. The only character by which *murallae* could be considered intermediate between *americana* and "*aurita*" is its less well-developed wing-bars; but even here, all males *murallae* I have seen possess at least one such bar, compared to none in "*aurita*" (Table 4). Thus, in this character as well *murallae* is actually much closer to *americana*.

Females of *murallae* are duller and browner overall than are those of any form of "*aurita*". The head and upperparts are dull olive-brown (closest to 28, Olive Brown); the throat, breast, and sides are paler, nearest to 26, Clay Color but

slightly duller, shading to dull buff (near 223D, Tawny) or pinkish-buff (121D). An immature ♂ is similar but the belly is buffy-white; in none of the specimens I have seen is there even a trace of yellow or ochraceous. Unfortunately, I was unable to compare the females of *americana* with the color standards of Smithe (1975, 1981). My notes describe them as very uniform brownish overall: plain dull olive-brown above, slightly paler buffy-brown below, shading to paler buff on the abdomen. Although a more detailed, standardized description of the ♀ plumage of *americana* is clearly desirable, it appears to be most similar to that of *murallae*. Females of both appear to show some resemblance to those of *hicksii*, but are very different from those of *ophthalmica*. In sum, the status of *murallae* as the link between *americana* and "*aurita*" rests almost entirely upon a single feature: its less well-developed wing-bars. In all other aspects of both ♂ and ♀ plumages, *murallae* is either much closer to *americana* or is more extreme than either *americana* or "*aurita*". I therefore conclude that lumping of these two groups based on the supposed intermediacy of *murallae* is not justified.

A more general conclusion from this analysis is that the uniting of *americana* and "*aurita*" at any taxonomic level while excluding *intermedia*, is likewise untenable. Evidence from hybridization and the similarity of immature plumages argues for a closer relationship between *intermedia* and "*aurita*" than between either of these and *americana*. The throat markings of *bogotensis* also provide a link between *hicksii* and nominate *intermedia*; in this respect *bogotensis* is a more convincing "connecting link" than is *murallae*!

This analysis clearly indicates that *americana* and *murallae* are each other's closest relatives, but the relationship could be less close than that between, say, *ophthalmica* and *hicksii*. The two populations of the latter two forms that are closest geographically are also the most similar in pattern (Table 3), but the same might not be true of *americana* and *murallae*. Closest geographically to *murallae* are the *americana* populations of the middle Amazon, although the gap is much greater (see below). The Amazonian populations were split from *americana* as the race *dispar* by Todd (1922) on the basis of supposedly larger size, larger wing speculum and whiter rump in

the males, and duller coloration of the females (brownish to grayish olive vs. rich brown above, dull buffy-white vs. strongly buff below). Pinto (1944) did not accept this split, considering that the differences were bridged by individual variation; but Meyer de Schauensee (1952) recognized *dispar* as being whiter below and on the rump, and with the black collar more prominent to complete. A quantitative analysis along the lines of those presented here could help settle the question, which in any case is beyond the scope of this paper. However, to the extent that Todd and Meyer de Schauensee are correct regarding at least the characters of the males, the Amazonian

birds may differ more from *murallae* in most features than do those from the Atlantic coastal districts. Because neither author attempted to define possible plumage changes with age, little can be concluded with respect to the females.

External morphology. For the analyses of variance of measurements, I was able to amass samples of at least 10 individuals of each sex for all forms except for females of *americana* ($n = 2$). Samples of *hicksii*, *bogotensis* and nominate *intermedia* were sufficiently large that I was able to divide them geographically, to evaluate possible within-subspecies variation in measurements as

TABLE 5. Comparisons of features of the definitive male plumages between four "black-and-white" members of the Variable Seedeater complex, by Kolmogorov-Smirnov two-sample tests. Definitions of plumage patterns and abbreviations for probabilities as in Table 1.

TAXA AND PLUMAGE AREAS	PLUMAGE SCORES				Σ	Dmax values
	1	2	3			
A. THROAT PATTERN						
<i>hicksii</i>	0	10	17	4	32	h vs. o = .339°
<i>ophthalmica</i>	3	12	7	0	22	h vs. m = .656*
<i>murallae</i>	7	4	0	0	11	o vs. m = .500*
<i>americana</i>	4	1	0	0	5	m vs. a = .160 n.s.
B. BREAST-BAND						
<i>hicksii</i>	0	5	19	8	32	h vs. o = .480**
<i>ophthalmica</i>	1	13	8	0	22	h vs. m = .844**
<i>murallae</i>	6	5	0	0	11	o vs. m = .501*
<i>americana</i>	3	2	0	0	5	m vs. a = .054 n.s.
C. SIDES AND FLANKS						
<i>hicksii</i>	0	9	19	4	32	h vs. o = .446*
<i>ophthalmica</i>	3	13	6	0	22	h vs. m = .446°
<i>murallae</i>	0	8	3	0	11	o vs. m = .136 n.s.
<i>americana</i>	1	3	1	0	5	m vs. a = .200 n.s.
D. RUMP						
<i>hicksii</i>		6	21	4	32	h vs. o = .326°
<i>ophthalmica</i>	2	10	10	0	22	h vs. m = .239 n.s.
<i>murallae</i>	0		4	0	5	m vs. a = .545*
<i>americana</i>	0		4	0	5	m vs. a = .364 n.s.

TABLE 6. Relative development of wingbars in *Sporophila americana* and *murallae*. 0 = none; 1 = trace (spots, faint scaling); 2 = continuous, narrow; 3 = continuous, broad. Dmax = from Kolmogorov-Smirnov two-sample tests. For abbreviations see Table 1.

TAXA	SCORES				Σ	Dmax
	0	2	3			
LESSER COVERTS						
<i>americana</i>	1	3	1	0	5	} .52
<i>murallae</i>	8	3	0	0	11	
MIDDLE COVERTS						
<i>americana</i>	0	0	0	5	5	} .73*
<i>murallae</i>	0	3	5	3	11	
GREATER COVERTS						
<i>americana</i>	0	1	2	2	5	} .80*
<i>murallae</i>	6	5	0	0	11	

well. The two samples of *intermedia* were cis-Andean (the Llanos, Norte de Santander) and trans-Andean (the Caribbean coastal lowlands); those of *bogotensis* were from the Magdalena Valley (the supposed range of “*agustini*”) and the Medellin area, Cauca Valley, and Pacific slope; and those of *hicksii* were from N Choco-N Antioquia, and SW Valle del Cauca. Thus, including the single samples of *ophthalmica*, *murallae*, and *americana*, a total of nine samples were analyzed (Table 5).

Highly significant variation among these samples in bill length, bill depth, wing length (the sexes tested separately), and tail length, and significant variation in tarsus length, were detected by these analyses (Table 6). The results of each analysis will now be considered in detail.

Bill length from nostril: most striking was the highly significant separation of *murallae* from all the other forms on the basis of its long bill. Next longest was the bill of *americana*, which was significantly longer than that of *hicksii* but not of the other taxa. No significant differences in bill length were found between any of the forms of “*aurita*” and *intermedia* (Table 6).

Bill depth: the thickest-billed form was *americana*, but its bill was not significantly deeper than those of most samples of *intermedia*. At the opposite extreme was *murallae*, whose bill was

not significantly thinner than most samples of “*aurita*”; the latter differed significantly from *intermedia*, but not *bogotensis*, in bill depth. One of the supposed characters of *agustini*, a less massive bill than that of *intermedia*, is not supported by this analysis: the Magdalena Valley population of *bogotensis* does not differ from *intermedia* in this respect, whereas the more western sample does so (Table 6). With the exception of *murallae*, bill depth decreases from east to west over all samples (Table 5).

Tail length: variation in this measurement showed no clear pattern with respect to geography or taxa (Tables 5,6). The shortest-tailed were the two samples of *hicksii*; the longest-tailed forms were the western sample of *bogotensis*, *murallae*, and *americana*. Within both *intermedia* and *bogotensis*, the two samples differed considerably (though not significantly) in tail length.

Tarsus length: within several taxa (*bogotensis*, *intermedia*, *murallae* vs. *americana*) tarsi of the more eastern sample averaged longer than those of the more western birds; in *hicksii*, birds of the northern sample had longer tarsi than those of the southern sample. In general, however, variation in tarsus length was less than in any other dimension examined (Tables 5 and 6).

Wing length, males: the longest-winged form was *murallae*, which differed significantly from all

TABLE 7. Measurements (mean, standard deviation, sample size) of nine samples of the Variable Seedeater complex. Measurements of males and females combined except for wing length.

SAMPLE	Bill length from nostril	Bill depth	Wing length (♂)	Wing length (♀)	Tail length	Tarsus length
<i>intermedia</i> (northern)	7.25±0.26 n=31	8.27±0.31 n=23	56.82±1.24 n=20	54.88±1.42 n=11	41.92±1.27 n=29	16.12±0.39 n=30
<i>intermedia</i> (cisandean)	7.21±0.25 n=45	8.28±0.28 n=43	57.14±1.37 n=23	55.49±1.21 n=22	42.27±1.45 n=44	16.15±0.40 n=45
<i>bogotensis</i> (Magdalena)	7.17±0.27 n=37	8.16±0.30 n=35	56.23±1.08 n=20	54.50±1.74 n=17	42.66±1.33 n=36	16.21±0.37 n=36
<i>bogotensis</i> (western)	7.17±0.28 n=39	8.02±0.34 n=38	56.38±1.14 n=25	54.61±1.41 n=14	43.31±1.43 n=37	15.97±0.50 n=39
<i>hicksii</i> (northern)	7.10±0.24 n=41	7.96±0.30 n=36	54.86±1.52 n=22	53.86±1.24 n=17	40.79±1.26 n=40	16.14±0.58 n=40
<i>hicksii</i> (Valle del Cauca)	7.06±0.25 n=30	7.93±0.31 n=26	54.26±0.89 n=18	53.12±1.19 n=11	41.59±1.32 n=23	15.86±0.56 n=29
<i>ophthalmica</i>	7.19±0.24 n=39	7.94±0.28 n=39	54.42±0.92 n=26	53.09±0.99 n=13	42.18±1.33 n=38	16.03±0.31 n=39
<i>murallae</i>	8.16±0.39 n=33	7.89±0.38 n=33	58.26±1.44 n=21	56.97±1.13 n=12	43.21±1.98 n=32	16.11±0.72 n=33
	7.41±0.31 n=11	8.44±0.20 n=10	56.82±0.97 n=10	54.75 n=2	43.18±1.71 n=11	16.56±0.48 n=11

others except the cisandean sample of *intermedia*. Nearly as long-winged as the latter was *americana*; the shortest-winged were the two races of "aurita". Among linear dimensions, wing length is usually considered the best indicator of overall size among closely related forms that do not differ in migratory behavior. On this basis, the members of the Variable Seedeater complex tend to increase in size from west to east, the main exception to this trend being the large size of *murallae*.

Wing length, females: the order of the samples was almost exactly the same as for males, with only two adjacent samples (the southern sample of *hicksii* and *ophthalmica*) changing places; *murallae* was separated even more clearly from the remaining forms by its long wing (Table 6).

The morphological differences detected in the preceding analysis can be placed in clearer perspective by considering the ratios between mean measurements (Table 7). The ratio of bill depth to bill length is especially notable as it separates *murallae* completely from all the other

forms, even at the individual level (Fig. 7). This is the only form with a bill as long or longer than it is deep; all others have thick, stubby bills, and the deepest bill relative to its length is precisely that of *americana*. Considering bill depth in relation to wing length, again *murallae* (shallowest) and *americana* (deepest) are at the opposite extremes of the distribution, with only the value for *murallae* outside the 95 % confidence interval of the mean (Table 7). The ratio of bill length to wing length again separates *murallae* from the remaining forms. Ratios of tail length to wing length and tarsus length to wing length yield patterns less easy to interpret. Relative to wing length, *ophthalmica* had the longest tail and tarsus; both samples of *intermedia* averaged short-tailed whereas *bogotensis* (especially the western sample) was long-tailed relative to the overall mean ratio. The northern sample of *hicksii* averaged short-tailed, the southern sample, long-tailed (and thus approached *ophthalmica* in this respect). By contrast, both samples of *hicksii* had relatively long tarsi, whereas all samples of

intermedia and *bogotensis* had tarsi of relatively short to moderate length. In both of these ratios, *murallae* and *americana* differed rather strongly: the tail and tarsus of the former were short relative to the wing, while those of the latter were long, relative to the overall mean. However, in neither of these ratios did any form differ from the rest as strongly as did *murallae* in bill shape (Table 7).

The overall conclusion to emerge from this analysis is that *americana*, *intermedia*, and "*aurita*" are quite similar in overall proportions, especially bill shape, and differ mainly in size (see above). Tail length was the only dimension in which variation appeared to be of a more irregular, perhaps mosaic nature. The one form that does not fit the general pattern, especially in bill shape, is *murallae*: in 4 of the 5 cases this form is at one extreme of the distribution of ratios, differing significantly from the rest in bill and wing length (and in both ratios involving bill length). Of particular interest is the fact that

the form most different from *murallae* in most morphological ratios is *americana*, precisely the most similar in plumage. This strongly supports the idea that these two are much less closely related than are the other pairs (*hicksii-ophthalmica*, *intermedia-bogotensis*) under consideration, as was suggested above by possible patterns of plumage variation within *americana* itself.

Patterns of distribution and areas of overlap. I have plotted all Colombian collecting localities and reliable sight records available to me in Figs. 8 and 9, while Fig. 10 gives the overall ranges of all members of the Variable Seedeater complex. In the following paragraphs I will attempt to clear up previous misunderstandings due to misidentifications.

S. "aurita" hicksii: this form occurs from the Golfo de Urabá region (E to extreme W Córdoba) and the Panama border south in the Pacific lowlands and foothills to S Valle del Cauca; the

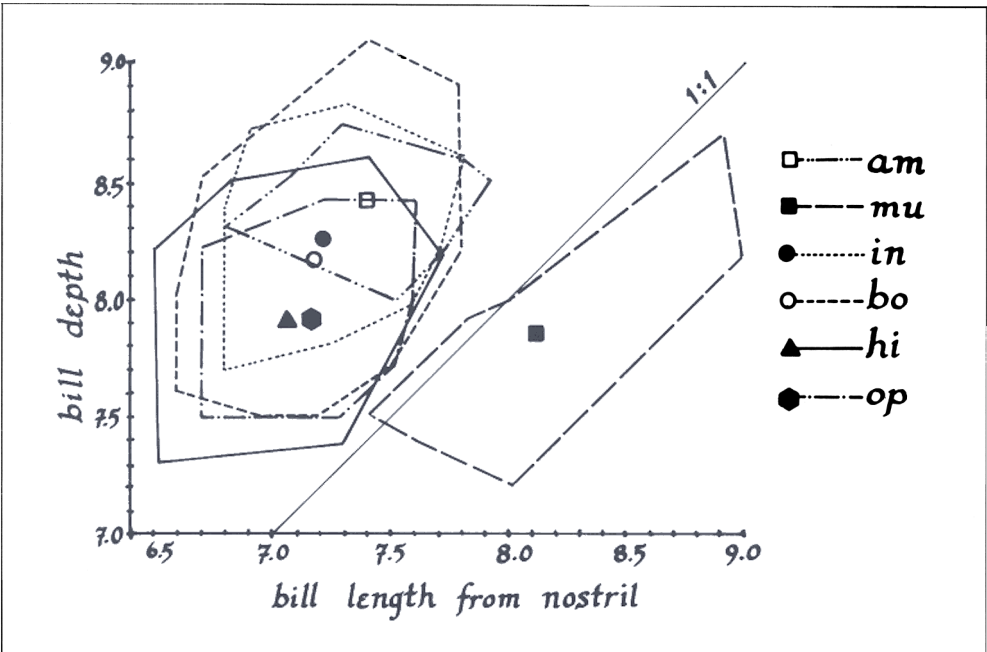


FIG. 7. Means and polygons enclosing all individuals measured for bill length vs. bill depth, for six taxa of the Variable Seedeater complex. Taxa are: am = *americana*; mu = *murallae*; in = *intermedia*; bo = *bogotensis*; hi = *hicksii*; op = *ophthalmica*.

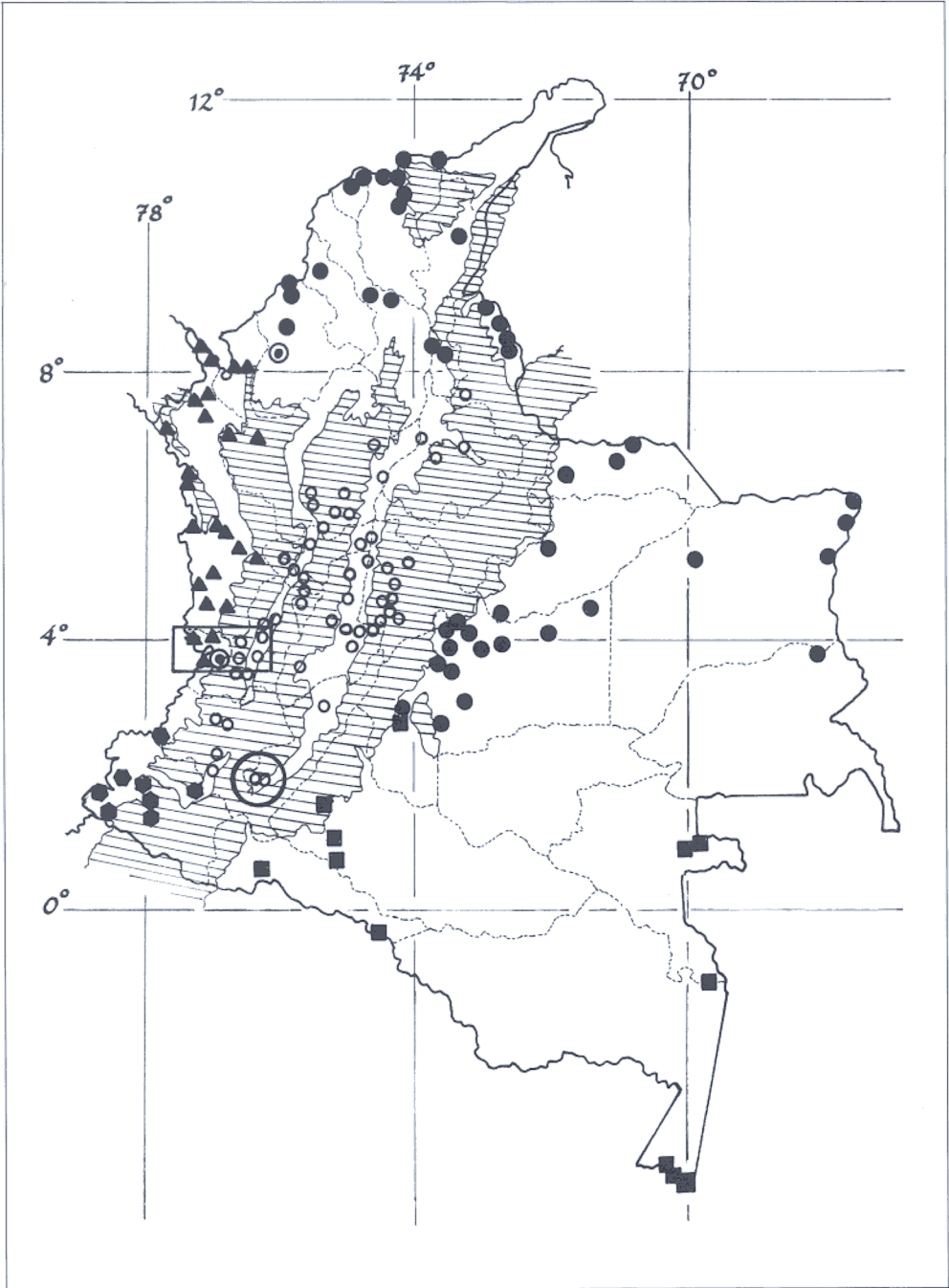


FIG. 8. Distributions of members of the Variable Seed-eater complex in Colombia. Solid circles = *intermedia*; open circles = *bogotensis*; triangles = *bicksii*; hexagons = *ophthalmica*; squares = *murallae*; circle and dot = contact-hybridization zones. Type locality of "agustini" is circled; area of rectangle (Valle del Cauca) is enlarged in Fig. 9.

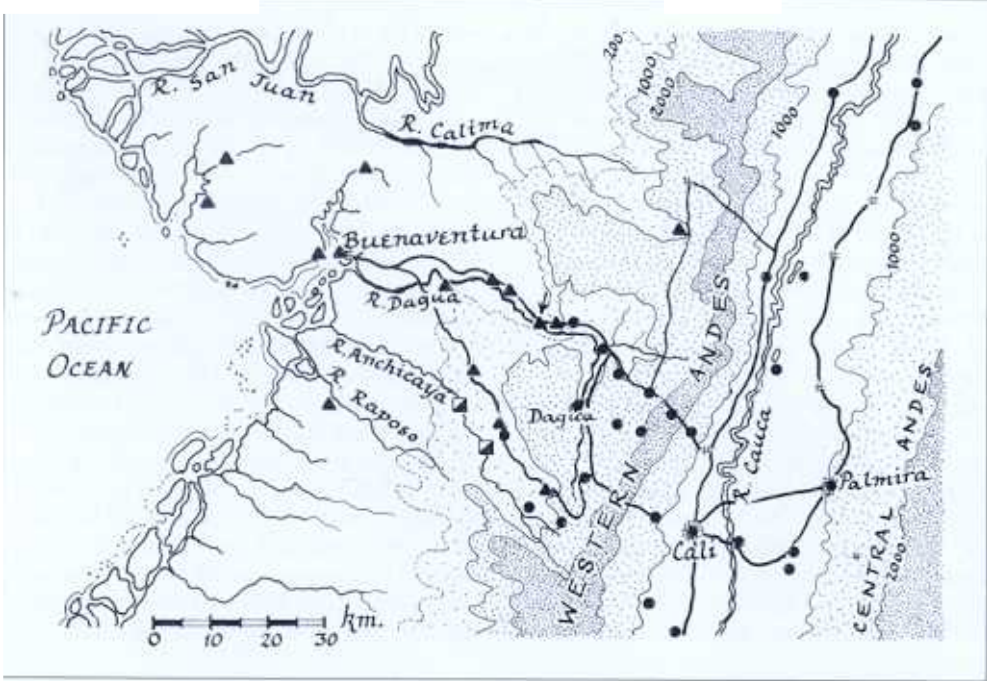


FIG. 9. Locality records for *S. "aurita" hicksii* and *S. intermedia bogotensis* in Valle del Cauca, Colombia; symbols as in Fig. 8. An arrow indicates Cisneros (see text).

southernmost recorded locality is Río Raposo, ca. 30 km S of Buenaventura. Meyer de Schauensee (1950, 1952) gave the Río Dagua area (just south of the latitude of Buenaventura) as the southern limit of this form, but Olson (1981b) misinterpreted this to mean that the Dagua region formed "the boundary between *chocoana* (= *hicksii*) and *ophthalmica*". Olson assigned specimens from Cisneros, on the N side of the Río Dagua, to *ophthalmica*, apparently on the basis of their white throats (which, by itself, is not a reliable character — see Table 1) Also, Chapman (1917) had placed birds from Cisneros in *ophthalmica*, but this was before any other "aurita" had been taken on this slope; Meyer de Schauensee himself (1952) included the Cisneros birds in *chocoana* (= *hicksii*). I have examined 12 other specimens taken within a few km of Cisneros: all are *hicksii*.

S. "aurita" ophthalmica: This form has been recorded from the Pacific lowlands and foothills from extreme SW Cauca (Guapi) S through

Nariño and W Ecuador to extreme NW Peru. When citing the Río Dagua region as the southern limit of *chocoana*, Meyer de Schauensee (1952) actually placed the northern limit of *ophthalmica* in the Río Patía region in Nariño, well S of Guapi. Between the closest recorded localities of the two forms (Río Raposo and Guapi) there is a gap of ca. 150 km; whether this is due to an absence of birds or simply a lack of collecting remains to be determined.

S. i. intermedia: The most wide-ranging member of the complex, this form occurs in the northern lowlands of Colombia (from W Córdoba eastward), Venezuela, and probably extreme W Guyana; west of the Andes it extends south to the lower Magdalena valley; eastwards it occupies an extensive range in the Maracaibo Basin and the Llanos of Colombia and Venezuela. The southern limits of *intermedia* are approximately the Sierra de la Macarena and the Río Guaviare (Puerto Inírida) in Colombia; this form extends locally to ca. 100 km S of the Río Orinoco in

Venezuela (Phelps & Phelps 1950, 1963). In addition, there are recent records of *intermedia* from the Territory of Roraima in N Brazil, near the S edge of the Guyana Shield (Silva & Willis 1986, Silva & Oren 1990). This apparently isolated, possibly relict population (see below) is the only one presently known in Brazilian territory. The population of Norte de Santander in the W end of the Maracaibo Basin shows the greatest resemblance in pattern to *bogotensis*, as noted above; the latter has been taken at Las Ventanas near Ocaña on the E slope of the Sierra de Perijá (Meyer de Schauensee 1952), and contact between the two races in this area is not unlikely. It is also highly likely that these races are in contact over a broad zone in NW Antioquia and E Santander, given the extensive deforestation in the lower and middle Magdalena valley over the last 40–50 years. I know of no recent collections from this region, however. This race is also resident on Trinidad (this population is sometimes separated as the race *insularis* Gilliard, although most recent treatments do not

recognize this split), where it formerly occurred widely but is now rare due to cage-bird trapping (French 1973), and on the dry islands off the N coast of Venezuela (Phelps & Phelps 1950, 1963). *S. i. bogotensis*: this race is basically confined to the middle and upper Cauca and Magdalena valleys, extending across the N end of the Cordillera Central in the deeply incised, warm valleys of the Medellín region. It occurs regularly to 1800 m or more on the adjacent slopes, especially in drier, more open areas; this has doubtlessly permitted it to cross to the E side of the Sierra de Perijá via the low (ca. 1500m) passes near Ocaña, and to reach the Pacific slope of the Cordillera Occidental in the dry upper valleys of the Dagua and Patía rivers of SW Colombia. In these valleys, *bogotensis* extends locally down to below 400 m, and it is at this lower extreme that the hybrids with *bicksii* ("*anchicayaë*") have been taken. Two specimens from beyond this range assigned to *bogotensis* by Meyer de Schauensee (1948–1952), from Malagueta near the mouth of the Río San Juan N of Buenaventura, and

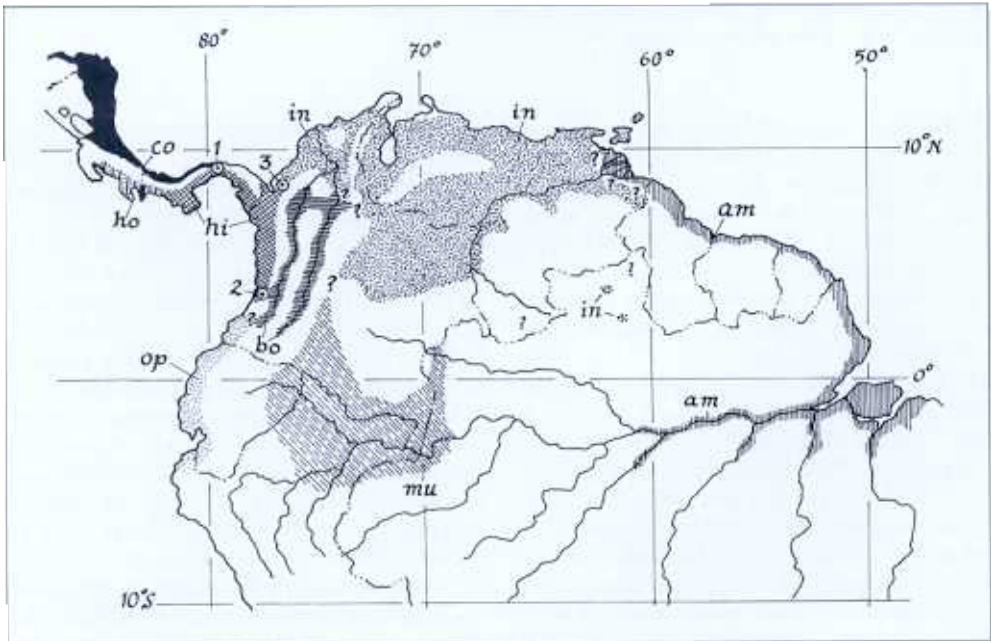


FIG. 10. Overall distributions of members of the Variable Seedeater complex in Central and South America; abbreviations for taxa as in Fig. 7. 1 = "*aurita*" hybrid swarm, C Panama; 2 = area of "*anchicayaë*"; 3 = Tierralta. ? = uncertain, possible zone of contact.

TABLE 8. Results of analyses of variance of measurements of samples¹ of members of the variable Seedeater complex, with results of Tukey a posteriori tests².

Measurement	F, p		Tukey test: means ordered from largest to smallest
Bill length from nostril	49.12, $P < 0.001$	306	MU AM IN IC BM BW OP HN HV _//_/_____
Bill depth	9.10, $P < 0.001$	276	AM IC IN BM BW HN OP HV MU _____
Tail length	11.10, $P < 0.001$	290	BW MU AM BM IC OP IN HV HN _____
Tail length	2.83, $P < 0.05$	302	AM BM IC HN IN MU OP BW HV _____
Wing length, males	26.44, $P < 0.001$	185	MU IC AM IN BW BM HN OP HV _____//_____
Wing length, females ³	12.25, $P < 0.001$	117	MU IC (AM) IN BW BM HN HV OP _____

1 = Samples are: HN = *hicksii*, northern sample; HV = *hicksii*, Valle del Cauca sample; OP = *ophthalmica*; BW = *bogotensis*, western sample; BM = *bogotensis*, Magdalena Valley sample; IN = *intermedia*, northern Caribbean lowlands sample; IC = *intermedia*, Cisandean sample; AM = *americana*, MU = *murallae*.

2 = Lines join samples not significantly different. Number of dashes indicates degree of significance separating samples: /// = $P < .001$; // = $P < .01$; no dash = $P < .05$.

3 = *americana* not included in analysis; position of mean in parenthesis.

Quimarí in the mountains on the border of Córdoba and Antioquia (NW of Tierralta), were later reidentified as *S. schistacea* (Meyer de Schauensee 1952). In addition, there is an immature ♀ (ICN 23891) collected at Buenaventura by C. J. Marinkelle that is labeled *S. i. bogotensis*, but from plumage and measurements it is at least as likely to be *hicksii* (recall that immatures of these two are very similar). Unfortunately, the specimen is missing most of the tail, and tail length is the most useful measurement for distinguishing these forms (cf. Tables 7 and 8). If, as I suspect, this specimen is indeed *hicksii*, then there is no record of *bogotensis* lower than ca.

350 m on the Pacific slope (where I observed it at El Cauchal, Valle in May 1993).

S. a (?) murallae: this form occurs in the upper Amazon region in SE Colombia, E Ecuador, NE Peru, and adjacent extreme W Brazil. A sight record from "Caño Duda" (= Río Duda?) on the W side of the Sierra de la Macarena (cited in Hilty & Brown 1986) is unconfirmed; however, the riverine scrub along the Río Duda apparently constitutes a corridor for migrations of several species of *Sporophila* (M. Alvarez, pers. comm.). So far as is known, *murallae* is strictly a lowland bird of riverine scrub, not entering the Andean foothills at any point. A supposed record of this

form from Soatá, far to the north in the mountains of Boyacá (Niccéforo & Olivares 1975), is erroneous: I have examined this specimen, which is *S. luctuosa*.

S. americana: this form inhabits the narrow strip of coastal lowlands and the adjacent lower river valleys of NE South America, from the Orinoco delta of extreme E Venezuela to the mouth of the Amazon in Pará, Brazil; and along both banks of the Amazon, including the lower parts of several major tributaries, E as far as the area of Manaus. The Amazonian populations might be separable as the race *dispar*, although this point remains controversial (Pinto 1944, Meyer de Schauensee 1952) in the absence of a quantitative analysis. At least in Venezuela, *americana* is restricted to forest edge and second growth adjacent to mangrove swamps (Meyer de Schauensee & Phelps 1979). The species is also resident on Tobago, occurring in a greater variety of open habitats (French 1973), as is also the case in Guyana (Snyder 1966). There are two old records, apparently of strays, from the N coast of Trinidad (Sclater 1871). A gap of ca. 500 km separates the westernmost populations of *americana* near Manaus from the nearest populations of *murallae* of extreme W Brazil and NE Peru.

The most revealing contact zones are those where a race of *intermedia* occurs with one of the forms with black-and-white males. *S. i. bogotensis* meets *hicksii* along the Río Anchicayá (and perhaps elsewhere) in SW Valle del Cauca, Colombia, where at least three hybrids have been taken between 340 and 450 m. That ten years elapsed between Miller's collecting of "*anchicayae*" and the Borrero-Cataño specimen suggests either that sporadic hybridization occurred over a period of years, or that a stable but very localized hybrid population exists. The uniformity of these hybrids in plumage, particularly compared to the Tierralta series, suggests that all are F1 hybrids: there is no suggestion of backcrossing. Also, during two weeks in this general region in May 1993, I saw only apparently "pure" *hicksii* and *bogotensis*. I therefore believe that hybridization between these forms is at best rare at present. However, the *hicksii*-like throat pattern shown by most *bogotensis* (but not *intermedia*) might indicate a period of frequent hybridization and introgression in the past, following which isolating mechanisms have been nearly

perfected. The very narrow zone of overlap may indicate different ecological preferences (wetter areas for *hicksii*, drier and more open areas for *bogotensis*). These differences might be further reinforced by ecological incompatibility as reflected in their extremely similar bills (and presumably, seed preferences).

To judge from the range of phenotypes present (Fig. 1), hybridization — including backcrossing — is much more frequent between *hicksii* and nominate *intermedia* in the Tierralta region. The two forms have probably come into contact in this area only very recently (see above), and in effect we might be seeing a recreation of the initial contact between *hicksii* and *bogotensis* in Valle. That apparently "pure" parental phenotypes occur in the Tierralta contact zone suggests that hybridization is not totally free, however. More information from this area, especially a quantitative study of ♂ phenotypes and song, would be highly interesting; unfortunately, the area is at present very dangerous due to guerrilla activity.

By contrast, there is no evidence for hybridization between *intermedia* and either *murallae* or *americana*. Although both *murallae* and *intermedia* have been reported from the Río Duda W of the Sierra de la Macarena, it is unlikely that either breeds there, at least regularly (see above), and no other possible contact has been found (or seems likely, given their apparently different ecological preferences). On present knowledge, a gap of ca. 200 km separates the isolated (?) population of *intermedia* in N-C Brazil from the *americana* populations along the Amazon. The intervening area of Brazil has been poorly collected, however. Although *americana* and *intermedia* appear to overlap in extreme E Venezuela and adjacent Guyana, the two have never been taken at precisely the same localities (M. Lentino, in litt.) and in fact may not occur sympatrically, at least for breeding. Although *intermedia* has been found in a variety of open and second-growth habitats in Venezuela, it seems not to occur in the specific habitat of *americana* (Phelps & Phelps 1963, Meyer de Schauensee & Phelps 1979). Of particular interest is the complete replacement between the two on Trinidad and Tobago, suggestive of competitive exclusion: their extremely similar overall morphology,

especially their bills, might preclude coexistence — especially on islands (cf. Grant 1968). From the scanty data available, it appears that *americana* and *intermedia* might be acting as parapatric species; clearly ecological studies comparing the situation on Trinidad and Tobago with that in eastern Venezuela would be very valuable. Whether these species have ever hybridized is also moot: it is perhaps suggestive that the supposed distinguishing characteristic of *insularis*, the regular possession of a white neck-patch, recalls the situation in *bogotensis*. Again, a quantitative analysis of plumage characteristics might prove helpful.

The overall conclusion from this analysis of distribution is that the Variable Seedeater complex does indeed appear to represent a group of very closely related forms. There is almost perfect complementarity of distributions; the very narrow zones of overlap are characterized by hybridization (perhaps more frequent where contact has been more recent) or, possibly, parapatry in the case of *americana* and *intermedia*. The most isolated member of the complex, in distribution as well as morphology, is *murallae*.

BIOGEOGRAPHY OF THE VARIABLE SEEDEATER COMPLEX

Viewing the overall distributions of all forms of the Variable Seedeater complex as a unit (Fig. 10), an interesting pattern emerges. In the central part of this distribution occur the two forms with gray male plumages (*intermedia* and *bogotensis*), while all of the forms with black-and-white ♂ plumage ("*aurita*", *murallae*, and *americana*) occupy peripheral positions. Moreover, all of the areas occupied by the latter forms are wetter (annual rainfall 2500–3000 mm or more) than those inhabited by the forms with gray males, as might be expected from Gloger's Rule. Another point of interest is that no member of the complex occupies the Guyana Shield, geologically the oldest region of northeastern South America. The area to the north of the Shield, on the coastal slope, is occupied by *americana*, which continues around its southern periphery along the Amazon. Even the isolated population of *intermedia* in Roraima, Brazil is at best on the very edge of the Shield (Silva & Oren 1990).

Also, *murallae* has been recorded to the W and S of the Sierra de Chiribiquete of SE Colombia, which geologically pertains to the same formation as the Venezuelan tepuis (Estrada & Fuertes 1993), but not in the Chiribiquete region itself (Stiles *et al.* 1995). The areas occupied by *americana* along the northeastern coast, and by "*aurita*" along the Pacific coast, are also among the geologically youngest regions of the continent.

Several lines of evidence, including turnover of fossil avifaunas (Brodkorb 1971, Vuilleumier 1984), molecular data (Sibley & Ahlquist 1990), and present distribution patterns (Haffer 1967, 1974, 1985) indicate that most extant species of birds, especially oscine passerines, originated during the Pleistocene. Therefore, an understanding of the Quaternary historical geography of northern South America is essential for developing a hypothesis for the evolution of the Variable Seedeater complex.

By the end of the Pliocene, the major patterns of topographic relief of northern South America were essentially modern: the Andes and related ranges had nearly or quite attained their present elevations, and a land connection with Central America had been established. For lowland taxa, faunal exchange between the Amazon-Orinoco basins and the Pacific slope or with Central America was now possible only via the lowlands north of the Andes or, to a lesser degree, via the Porculla Pass (presently over 2000 m) in N Peru (Haffer 1967, 1979). During most of the Pliocene, much of the Amazon basin was covered by a large lake or epicontinental sea but by the Pleistocene, deposition of huge amounts of sediments derived from the nascent Andes had transformed this area into an alluvial plain dissected by large rivers, and possibly with extensive wetlands (cf. Simpson 1979, Haffer 1979, Fjeldså 1985).

The alternating glacial and interglacial periods of the Pleistocene undoubtedly had a decisive influence upon dispersal and speciation in the Variable Seedeater complex. During glacial periods, cooler and drier conditions probably prevailed over most of South America; lowered sea levels increased the lowland areas along the coasts. During the warmer, wetter interglacials, higher sea levels resulted in the submergence of most of the Amazon valley, forming a long gulf that extended west nearly to the Andes (Simpson

1979, Fjeldsa 1985). Paleoclimatic data from the last glacial maximum (LGM) of ca. 18,000 years ago show that arid conditions prevailed in some parts of the Amazon basin, but that the currently arid lowlands of N Colombia and N Venezuela had a more mesic climate (Schubert 1988, Kronberg *et al.* 1991). The cooler climates of the LGM lowered vegetation zones by 1200–1500 m and temperatures by 6–7°C (van der Hammen 1974). Whether or not one accepts in detail the scheme of forest refugia of Haffer (1974, 1985), it seems inevitable that during glacial periods savannas and other open vegetation types expanded at the expense of closed evergreen forest, with the reverse occurring during the interglacials. Thus, for nonforest lowland birds like *Sporophila*, glacial periods probably facilitated dispersal through the lowlands but restricted crossing of mountain barriers. The interglacials probably tended to fragment distributions of savanna taxa, and to the extent that mountain slopes became forested, may not have facilitated dispersal of such taxa across mountain passes. Thus, it seems likely that most or all dispersal occurred through the lowlands during glacial periods, throughout the Pleistocene among members of the Variable Seedeater complex.

Based upon present-day patterns of species diversity (see Meyer de Schauensee 1952, Ouellet 1992), the origin and early radiation of the genus *Sporophila* probably occurred on and around the

Brazilian Shield. The present-day species of this region most similar in plumage and morphology to the members of the Variable Seedeater complex is *S. collaris*, a widespread, common, and variable inhabitant of grassy marshes and wet savannas (Ridgely & Tudor 1989). This species was considered to be “allied to” *S. americana* by Hellmayr (1938). Differentiation of the Variable Seedeater complex probably began when a thick-billed sporophiline related or ancestral to *collaris* moved northward from the Brazilian Shield and colonized the marshes or riverine habitats of the Amazon basin during an early glacial period of the Pleistocene. During the subsequent interglacial, when the Amazon became a deep bay or gulf, this population became adapted to shoreline habitats, possibly associated with mangrove as is *americana* today; the expansion of forests to the south isolated this population from the proto-*collaris* of the shield. During this period, this proto-*americana* population probably occupied appropriate habitat all around the gulf, though its expansion northward along the Atlantic coast might not have occurred until later, as the coastal savannas of NE South America occur on Pleistocene sediments (Sarmiento 1983).

Part of this population may have continued to occupy wet savannas, particularly on the north side of the Amazon gulf. With the next (last?) glacial cycle and the expansion of these savannas this population spread northward

TABLE 9. Ratios of mean measurements of members of the Variable Seedeater complex. Abbreviations for samples as in Table 8.

RATIOS	IN	IC	BM	BW	HN	HV	OP	MU	AM	X	95 % Confidence Interval
Bill depth/ bill length	1.14	.15	14	1.12	12	1.12	10	0.97	19	12	0.98 —1.26
Bill length/ wing length	0.128	0.126	0.127	0.127	0.129	0.130	0.132	0.140	0.130	0.120	0.120—0.139
Bill depth/ wing length	0.146	0.145	0.145	0.142	0.145	0.146	0.146	0.135	0.148	0.144	0.136—0.153
Tail length/ wing length	0.738	0.740	0.759	0.768	0.743	0.767	0.775	0.742	0.760	0.755	0.722—0.787
Tarsus length/ wing length	0.284	0.283	0.288	0.283	0.294	0.292	0.295	0.276	0.291	0.287	0.273—0.301

through the present-day Llanos and onto the northern coastal plain, and thence into the Magdalena and Cauca Valleys and Central America, and down the Pacific slope of South America. With the lowered sea levels, both the land connection to Central America and the coastal plains were much broader than at present, facilitating this expansion. That this expansion could have been quite rapid, in geological terms, is suggested by the rapid range expansions of various open-country birds in recent years as man has removed forest barriers (cf. Kiff 1975, Stiles & Skutch 1989 for examples). It is also probable that the range of *intermedia* on the N side of the Amazon was once more extensive than at present; the population of N-C Brazil, apparently isolated from other populations of the species by 300 km or more, may represent a relict of a once continuous distribution.

The increasing humidity and expanding forests of the next (present?) interglacial fragmented this population, first isolating the Central American and Pacific coast birds from those of the rest of South America. That segment occupying the Llanos and the Caribbean coast of present-day Colombia and Venezuela, exposed to a drier and/or more seasonal climate, evolved grey male plumage to become the current species *intermedia*. In Central America, the populations of the Pacific slope became isolated from those of the more humid Caribbean slope. Increasing humidity selected for more black pigmentation in the latter population, producing *corvina*; on drier Pacific slope, the black-and-white male plumage was retained. Still later in this interglacial, forest barriers further fragmented the Pacific populations, giving rise to the currently recognized subspecies *hoffmannii*, *hicksii*, and *ophthalmica*. Gene flow between the Magdalena-Cauca and Caribbean slope populations of *intermedia* was probably interrupted at least intermittently as well; the former developed more patterned gray plumage, resulting in *bogotensis*. In any case, it seems likely that isolation between *intermedia* and *bogotensis* was never as complete as between either of them and the Central American-Pacific slope populations. Gene flow between the *intermedia* and *bogotensis* might have occurred for a comparatively long time in the broad expanse of the lower Magdalena Valley

or via the low passes near Ocaña in Norte de Santander.

The final stage of this process would then have been the establishment of secondary contact between *corvina* and *hicksii* in central Panama, perhaps reflecting deforestation in precolombian or colonial times; the hybrid swarm in this area apparently has been stable for well over a century (Olson 1981b), and there are some historical indications that when the Spaniards arrived, the Indians maintained extensive savannas in this area by burning (Bennett 1968). Secondary contact between *hicksii* and *bogotensis* is possibly more recent, the spread of the latter onto the Pacific slope having been facilitated by low passes in the Cordillera Occidental and dry, rain-shadow valleys. It is possible that a period of more extensive hybridization and introgression occurred in the past (which might help to account for the more patterned plumage of *bogotensis* relative to *intermedia*), following which isolating mechanisms between these two forms have been nearly perfected. The most recent contact zone is that between *intermedia* and *hicksii* around Tierralta, probably dating from no more than 20 years ago; continued monitoring of the interactions of the two forms in this zone will be critical to documenting future trends, and will help to clarify their status.

The origin of *murallae* was almost certainly quite independent of that of the *intermedia*-*aurita* clade. The most likely sequence of events was for a part of the original *protoamericana* population occurring around the head of the Amazon gulf during an early interglacial period, to have become isolated as the sea level dropped during the following glacial period. This population may well have occupied a humid region just east of the Andes during this glacial period, when it became adapted to wet riverine scrub. Certainly the present-day distribution of *murallae* corresponds closely to that of a species presumed to have differentiated in the Napo refugium of Haffer (1974, 1985). However, given the degree of morphological differentiation of *murallae*, I suspect that it has remained isolated in approximately its present distribution for considerably longer than the interval since the last glacial maximum. The only way in which *murallae* could form a connecting link between *americana* and *aurita* would be via

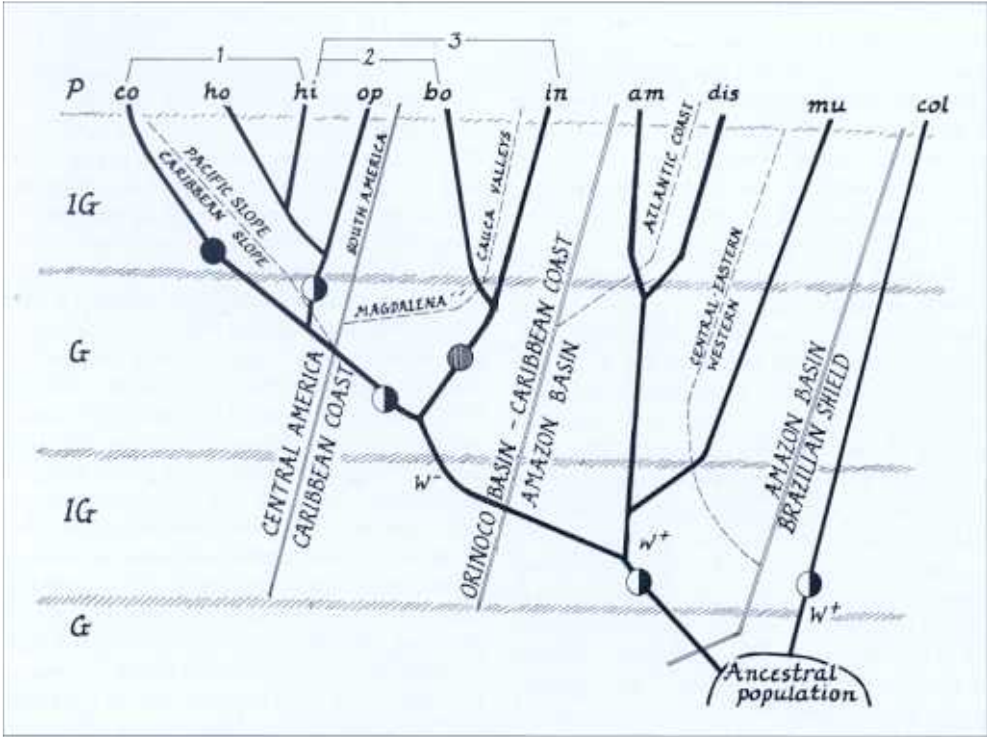


FIG. 11. A graphical hypothesis regarding the historical biogeography and evolution of the Variable Seedeater complex. G = glacial periods; IG = interglacial periods; P = present. Abbreviations of taxa: col = *collaris*, dis = *dispar*, others as in Fig. 7. Black, black-and-white, and hatched circles represent male plumage color; w+ = wingbars, w- = no wingbars. Numbers and brackets connecting some taxa represent current hybridization as in Fig. 10.

dispersal of a proto-*murallae* stock to the Pacific slope via the North Peruvian Low (Porculla Pass) and subsequent expansion northward on the Pacific slope. However, neither a detailed examination of plumage and morphology nor the present-day ecology of *murallae* support this alternative. In fact, had such a dispersal event occurred, one could make at least as strong a case for the end result being the Thick-billed Seedeater, *S. peruviana*, rather than "*aurita*".

This hypothesis for the evolution of the Variable Seedeater complex is summarized graphically in Fig. 11. It seems plausible in that it accounts for the results of analyses of plumage, morphology, and distribution. However, there are numerous points of uncertainty and doubtless alternative scenarios could be devised.

Although the general sequence of events may be correct, the timing is obviously tentative; a longer time span, involving more glacial-interglacial cycles and perhaps extending back into the Pliocene, might apply. However, studies that suggest such a time frame (e.g., Capparella 1988, Bates & Zink 1994) deal mainly with suboscine taxa rather than with the possibly more recent radiation of the nine-primaried oscines.

In conclusion, evidence from hybridization, morphology, and distribution are compatible with the hypothesis that the enlarged Variable Seedeater complex represents a monophyletic unit; this conclusion is in turn compatible with a plausible historical biogeographic hypothesis. Genetic information will probably be required

to test these hypotheses and perhaps to provide more satisfactory alternatives. Further analyses will also be required to determine the relationships of this complex to such taxa as *peruviana* of Pacific South America and several Brazilian forms, especially *collaris*, as well as *torqueola* of N Central America.

Perhaps the most likely candidate for inclusion in the Variable Seedeater (s. l.) clade is the similarly heavy-billed White-collared Seedeater, *S. torqueola*. Given that the currently arid Caribbean littoral of Colombia and Venezuela apparently had a more mesic climate during at least the last glacial maximum (Schubert 1988), it is possible that *americana* once occurred more widely here, and might even have reached Central America prior to the arrival of the "aurita" group. Because *torqueola* has wing-bars, its direct ancestry might lie with *americana* rather than with "aurita". Until very recently *torqueola* was confined to Mexico and N Central America; it occurs in sympatry with *corvina* in E Mexico and with *hoffmannii* in W Costa Rica. Within the last 20 years *torqueola* has expanded its range to both slopes of W Panama, greatly increasing the area of sympatry with "aurita", but to my knowledge no hybrids between these forms have ever been recorded. Subsequently, *intermedia* might have replaced (or displaced) *americana* on the N Caribbean littoral as this area became increasingly arid. The only change required in the above scheme to accommodate *torqueola* would be to place the arrival of *americana* on the N coast of South America somewhat earlier, with subsequent fragmentation of its range by forest expansion in S Central America and arid conditions on the Caribbean littoral. Molecular genetic data, as well as a thorough study of its plumage and morphology, will be required to clarify the affinities of *torqueola*.

TAXONOMIC CONCLUSIONS

The major conclusions from the above analyses may be summarized as follows: a) the Variable Seedeater complex may be regarded as a monophyletic group comprising two clades: *americana* (including *dispar*) and *murallae*; and *intermedia*, *bogotensis*, *corvina*, *hicksii*, *ophthalmica*, and *hoffmannii*; b) *agustini* and *chocoana* are synonyms of *bogotensis* and *hicksii*, respectively; c) the

species *intermedia* (including *bogotensis*) and "aurita" are more closely related to each other than either is to *americana* or *murallae*; the latter does not constitute the "connecting link" between *americana* and "aurita"; and d) the relationship between *americana* and *murallae* is less close than either that between *intermedia* and *bogotensis*, or that between the four races of "aurita". It is possible that *torqueola* is also a member of the *americana* clade, but further study is required on this point; for lack of data, I do not include it here.

I feel that the most appropriate level at which to recognize the Variable Seedeater complex as a taxonomic unit is the superspecies. Because of the limited, sporadic nature of the hybridization between *bogotensis* and *hicksii*, and the very localized zone of hybridization between the latter and *intermedia*, in which parental phenotypes apparently occur in appreciable frequencies (cf. Short 1969), *intermedia* and "aurita" are appropriately considered allospecies. The apparent parapatry between *americana* and *intermedia* also suggests that they could be considered allospecies (Haffer 1992). I also conclude that the morphological distinctness and isolated distribution of *murallae* indicate that this form merits consideration as an allospecies rather than as simply a subspecies of *americana*. I thus consider the Variable Seedeater complex to represent a single (*americana*) superspecies comprising the allospecies *americana* (Wing-barred Seedeater), *intermedia* (Gray Seedeater), "aurita" (Variable Seedeater), and *murallae*.

Two questions of nomenclature remain: the correct species name for "aurita", and an appropriate English vernacular name for *murallae*. I accept the arguments of Olson (1981b) regarding the invalidity of the name *aurita*; unfortunately, he effectively sidestepped the question of what to call "aurita" should this taxon be accorded (allo)species rank. The next oldest name for a member of this group, and the oldest that applies unequivocally to a recognizable taxon, is *corvina* Sclater 1859. The Variable Seedeater in the strict sense should therefore be called *Sporophila corvina*, which would include the subspecies *corvina*, *hoffmannii*, *hicksii*, and *ophthalmica*. I support Olson's (1981b) recommendation that the name *aurita* be retained solely as an informal designation for the hybrid swarm of central Panama.

In the past, *murallae* has been called "La Muralla Seed-eater" (Chapman 1915) or "La Murelia Seed-eater" (Hellmayr 1938), both of which are garbled versions of the name of the type locality of Morelia in the Department of Caquetá, SE Colombia. Because *murallae* has been considered a subspecies of *americana* in all recent treatments, no more appropriate species-level name has been proposed. Rather than simply correcting these old names, I propose a more inclusive toponym, Caquetá Seed-eater. Morelia is a rather obscure locality in any case, and historically the name "Caquetá" referred to most of SE Colombia, the wide area drained by the Río Caquetá.

The taxonomy and nomenclature proposed here may be summarized as follows:

Sporophila americana Superspecies

Sporophila murallae Chapman 1915. Caquetá Seed-eater.

Sporophila americana (Gmelin 1789). Wing-barred Seed-eater. Included subspecies: *americana*, *dispar* Todd 1922 (possibly a synonym of *americana*)

Sporophila intermedia Cabanis 1851. Gray Seed-eater. Included subspecies: *intermedia* (synonym: *insularis* Gilliard 1946), *bogotensis* Gilliard 1946 (synonym: *agustini* Meyer de Schauensee 1947).

Sporophila corvina (Sclater 1859). Variable Seed-eater. Included subspecies: *corvina* (synonym: *badiventris* Lawrence 1865), *ophthalmica* Sclater 1860, *hoffmannii* Cabanis 1861 (synonym: *collaris* Lawrence 1865), *hicksii* Lawrence 1865 (synonym: *chocoana* Meyer de Schauensee 1950).

Sporophila "aurita" (Bonaparte 1850) to be used for individuals with phenotypes intermediate between *S. c. corvina* and *S. c. hicksii* from C Panama. Synonyms: *semicollaris* Lawrence 1863 and *fortipes* (Lawrence 1865).

I emphasize that, as with the biogeographical scenario above, this classification is presented as a hypothesis, which it would be most desirable to test using molecular genetic information. As noted above, several other taxa also should be investigated as possible relatives or even members of the Variable Seed-eater complex, especially *torqueola*, which could easily be accommodated in

the above classification should the evidence so warrant.

DISCUSSION

The process of hybridization in the Variable Seed-eater complex. This study was stimulated by the recognition of hybridization between the species *corvina* and *intermedia*. It is worth exploring how hybridization could occur between two species whose adult male plumages are so different (at least at first sight) that their close relationship had previously gone unsuspected. Potential isolating mechanisms include size (*intermedia* being slightly larger), adult ♂ plumages and song (given that the females probably play the decisive role in mate choice, the lesser differences in adult ♀ plumages are probably less significant in this regard). The song of *intermedia* is a rather deliberate, melodious caroling of slurred whistles, trills, and chatters; that of *hicksii* is a more hurried, jumbled medley of whistles, trills, and sputters (pers. obs.; see also French 1973, Ridgely 1981, and Hilty & Brown 1986). On the other hand, such song differences might in themselves be ineffective isolating mechanisms in species like emberizine finches in which song learning undoubtedly occurs. Moreover, the two species are very similar in overall morphology, especially bill shape, and their immature plumages are virtually indistinguishable. This might be especially significant as males (and presumably females) *Sporophila* are known to breed in this plumage (cf. Stiles & Skutch 1989). It does not seem implausible that a young male could become imprinted on the "wrong" song in a contact zone, then sing and attract a hetero-specific mate before attaining the definitive plumage.

Members of the Variable Seed-eater complex often coexist with up to 5 other species of *Sporophila* plus species of *Tiaris*, *Volatinia*, and/or *Oryzoborus*, at least at some times of year (Meyer de Schauensee & Phelps 1979, Ridgely 1981, Hilty & Brown 1986, Stiles 1983, Stiles & Skutch 1989, Ouellet 1992). They nearly always have the thickest and/or most bulbous bills of these assemblages. Bill shape could therefore be important in species recognition and mate choice, much as apparently occurs in the related Galápagos finches *Geospiza* (Ratcliffe & Grant 1983). Thus, the very similar bills of *corvina* and *inter-*

media could lend themselves to errors of identification, especially among young males in which the distinct color differences of adults have not yet become manifest. Similarity in bill shape might also indicate similar seed preferences; depending upon the abundance of the most preferred seeds, this could facilitate cooccurrence or competitive exclusion. In new pastures and second growth on recently deforested ground, high residual soil fertility often results in very high grass seed abundance for a time; this could promote coexistence and hybridization following forest removal, as at Tierralta. Were bill shape demonstrated to be important in mate choice, this would constitute another argument in favor of according (allo)species status to *murallae*. It would be most interesting to conduct experiments on mate preferences among members of the Variable Seedeater complex, similar to those performed with Galápagos Finches by Ratcliffe & Grant (1983).

Beyond the Variable Seedeater complex. Numerous taxonomic problems remain in the genus *Sporophila*, as reviewed in varying detail by Meyer de Schauensee (1952), Ridgely & Tudor (1989), and Ouellet (1992). Many of these include questions of the status of allopatric, highly localized, and/or poorly known forms or possible hybrids, much as in the Variable Seedeater complex. Many of these problems stem from the fact that the taxonomy of the genus is still based almost exclusively upon the adult ♂ plumages (and all too often upon rather superficial examinations thereof). Detailed studies of morphology, and of the plumages of both sexes, have not yet been undertaken for most of the problematical forms. Hopefully, this paper will help to stimulate and orient such studies, which can perhaps most appropriately be carried out by workers resident in the Neotropics and able to engage in judicious collecting. In addition, molecular and genetic studies will surely shed further light upon difficult problems, or cases where morphological and plumage data appear to be somewhat at variance (as in the case of *murallae* vs. *americana*).

Most or all species of *Sporophila* are associated with open habitats and feed largely upon grass seeds, their breeding seasons being largely timed to seeding episodes (Skutch 1950, Stiles & Skutch

1989). Hence, their distributions have undoubtedly been affected by Pleistocene climatic fluctuations, probably inversely to those of humid forest birds. To date, most zoogeographic analyses of Neotropical birds have focused upon the latter, leading to concepts such as the forest refugia of Haffer (1974, 1985) and others, and the importance of riverine barriers (Capparella 1988). No comparably broad and detailed analysis of the nonforest avifauna has yet appeared, and until data from morphology, genetics, palynology and geology can be applied to such a synthesis, our understanding of the historical zoogeography of groups like *Sporophila* will remain speculative. Complicating factors in such an analysis for *Sporophila* in particular include the migratory behavior of many forms (briefly reviewed by Ridgely & Tudor 1989; see also Silva 1995), nomadic movements of others in response to sporadic seeding events of grasses or bamboos (e.g., *S. schistacea* in Costa Rica: Stiles & Skutch 1989), and recent changes as a result of forest clearance. The latter may bring into contact forms isolated since (presumably) the last glacial period (e.g., *hicksii* and *intermedia*), and the resulting interactions might clarify their status. In any case, the genus *Sporophila* would seem to represent a singularly appropriate group for further taxonomic and biosystematic analysis.

A final point worth comment here is the proposal of Olson (1981a) to unite the genera *Oryzoborus* and *Sporophila*. He stated that the ranges in bill proportions of the two genera are comparable, and that hybrids between the two genera had been reported from Brazil. His Fig. 1 purportedly demonstrated a continuum in bill shape between the two genera. However, I believe he overlooked a significant difference in patterns of bill allometry between the two groups. The thickness of the bill is directly proportional to the curvature of the culmen in *Sporophila* but not in *Oryzoborus*, in which culmens are at most slightly curved. Thus, the species of *Sporophila* most like *Oryzoborus* in bill thickness are the most different in bill shape. I therefore favor continued recognition of two genera, but agree with Olson (1981a) and Sick (1963) that they are closely related, as evidenced by their nests, eggs, plumage sequences, and songs (Stiles & Skutch 1989); they should be placed contiguously in any linear sequence.

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