# A NEW SUBSPECIES OF *SCLERURUS ALBIGULARIS* (GRAY-THROATED LEAFTOSSER) FROM NORTHEASTERN BOLIVIA, WITH NOTES ON GEOGRAPHIC VARIATION

Andrew W. Kratter \*

Museum of Natural Science and Department of Zoology and Physiology. Louisiana State University, Baton Rouge, LA 70803, U.S.A.

Resumen. Una nueva subespecie de Sclerurus albigularis (S. a. kempffi) es descrito. El tipo-localidad es La Serrania Huanchaca, de los bosques Amazońicos del noreste del departamento Santa Cruz, Bolivia. La subespecie, la cual es distinctamente pálida, se encuentra en elevaciones más bajas y bosques más secos que donded ocurren las otras subespecies de S. albigularis. También es más pequeña que los subespecies que son más cercas geograficamente: S. a. zamorae y S. a. albicollis. S. a. zamorae se encuentra al margen oriente de los Andes del Perú; S. a. albicollis se encuentra en el norte de Bolivia. Como especie, S. albigularis se conforma basicamente a la Ley Ecogeográfica de Gloger: las poblaciones de las regiones más húmedas son las más profundamente pigmentadas, y las poblaciones en las regiones más secas son las más pálidas. En S. albigularis, tamaño no coresponde a localidad geográfica.

Abstract. A new subspecies of Gray-throated Leaftosser (Sclerurus albigularis kempffi) is described from the Serrania Huanchaca, in lowland Amazonian forests in northeastern depto. Santa Cruz, Bolivia. This distinctly pale subspecies occurs at lower elevations and in drier forests than do other subspecies of S. albigularis. It is also smaller than the geographically nearest subspecies, which are found along the east slope of the Andes in Peru (S. a. zamorae) and northern Bolivia (S. a. albicollis). As a species, S. albigularis largely conforms to Gloger's Ecogeographic Rule: populations in the most humid regions are the most richly pigmented, and populations in driest areas are palest. Geographical trends in size are lacking in this species. Accepted 17 June 1996.

Key words: Sclerurus albigularis kempffi, new subspecies, conservation, natural history, geographic, variation, Bolivia.

## INTRODUCTION

The Serrania Huanchaca, straddling the Bolivian/Brazilian border in northeastern Santa Cruz, Bolivia, and western Mato Grosso, Brazil, is the westernmost upraised piece of the Brazilian shield. These highlands extend east to west across central Brazil and largely form the southern border of Amazonia. The Serrania, which rises to almost 2000 m elevation (in Brazil), is topped mostly by cerrado scrub vegetation (Bates et al. 1990). Lower elevations at the base of the escarpment are largely covered with humid tropical forest, although a few seasonally flooded grasslands (pampas) are interspersed (Bates et al. 1989, 1992; Kratter et al. 1993). The Bolivian portions of the Serrania and some adjacent lowlands form Parque Nacional Noel Kempff Mercado.

Personnel from the Museum of Natural Science at Louisiana State University (LSUMZ) and the Museo de Historia Natural "Noel Kempff Mercado" (MHNNKM) at the Universidad Autónoma "Gabriel Rene Moreno" in Santa Cruz, Bolivia, conducted avifaunal surveys of the Park from 1988–1990. Numerous records of interest have resulted from these surveys and have been published elsewhere (Bates et al. 1989, 1992; Kratter et al. 1993, Marantz & Remsen 1994). As mentioned previously (Kratter et al. 1993), specimens of Sclerurus albigularis (Graythroated Leaftosser), collected in tall humid forest along the southern base of the Serrania, appeared to represent a new form. With further evaluation and comparison with specimens from throughout this species' distribution, it is clear that these specimens are distinct and represent a new taxon, which may be known as:

#### Sclerurus albigularis kempffi, new subspecies

Holotype. Louisiana State University Museum of Natural Science (LSUMZ) # 153328; mist-netted by LSUMZ and MHNNKM personnel on 6 August 1990 in Parque Nacional Noel Kempff

Present address: Florida Museum of Natural History, University of Florida, Gainesville, FL 32601, U.S.A.

Mercado at the southern base of the Serrania Huanchaca, 86 km ESE from the village of Florida, prov. Velasco, depto. Santa Cruz, Bolivia (14°50'S, 60°25'W, c. 500 m elevation). The specimen, prepared by John P. O'Neill (# 7642), is an adult Q in nonbreeding condition (ovary 6 x 3 mm, ova and oviduct not enlarged), with a completely pneumaticized skull, little fat, and a body mass of 35 g.

Description. Capitalized color names are from Ridgway (1912). Crown and nape Olive-Brown, the forecrown feathers with dark edges, giving a scalloped appearance, and the hind crown and nape with light shaft streaks, imparting a somewhat streaked appearance. Back is Auburn, becoming somewhat richer in color towards the rump, which is Chestnut. Upper tail coverts are a contrasting Bay. Auriculars are Olive-Brown, but separated from crown by somewhat lighter supercilia. Chin and throat are white, blending to Pinkish-Buff malars. Lower throat is Olive-Gray. Upper breast is Sanford's Brown with light shaft streaks, becoming somewhat less rich dorsally. Lower breast and belly are Mummy Brown, becoming a somewhat richer Brussels Brown on flanks and undertail coverts. Upper wing coverts are Burnt Sienna. The Raw Umber remiges are edged Auburn on the outer webs. Tail is dark grayish-black. The soft part colors, recorded by O'Neill: iris brown; bill dusky black, base of mandible pinkish, feet and tarsi medium brown. Measurements: culmen (from base) 21.9 mm; wing chord 84.6 mm; tail 68.6 mm; and tarsus 21.6 mm.

Diagnosis. The general coloration of Sclerurus a. kempffi is paler overall than any other recognized subspecies of S. albigularis. This is the only subspecies to have deep bay or chestnut restricted to the upper tail coverts; in other subspecies this color generally extends anteriorally at least onto the rump. The nearest populations of this species (S. a. albicollis in western Bolivia and eastern Peru) are larger than S. a. kempffi, the upper breast is deeper rufous, the belly is slightly darker brown, the crown is less gray, and the back is a warmer, more rufescent brown. Andean populations from Ecuador to southern Peru (S. a. zamorae) differ from kempffi in their darker underparts, with a grayer chin and throat, a

deeper rufous upper breast, and a richer brown belly. The upperparts are also darker on zamorae, particularly the crown and nape, which barely contrast with the upper back. In plumage, the most similar populations to kempffi are within the nominate subspecies, which is found in the Andean foothills in central Colombia, in northern Venezuela, and on Trinidad and Tobago. The nominate subspecies differs from S. a. kempffi in having a somewhat more rufescent back and crown, and particularly extensive rufous on the uppertail coverts and rump; in addition the hind-crown and nape have less distinctive shaft streaks than kempffi. A limited sample (n=2) of S. a. kunanensis from the Perijá Mountains in Colombia and Venezuela was examined; these specimens, indistinguishable from S. a. albigularis, differed from kempffi in the same characters as the nominate subspecies. The subspecies S. a. propinguus from the Santa Marta Mountains in Colombia differs from kempffi in the more extensive rufous breast, the more rufescent upperparts, and the somewhat grayer throat. The richly plumaged subspecies S. a. canigularis from Costa Rica is much darker overall than kempffi, particularly on the crown, back, and belly.

*Distribution*. Humid forests at southern base of Serrania Huanchaca, depto. Santa Cruz, Bolivia. This species has not been found in humid forests along the west base of the Serrania Huanchaca (Bates *et al.* 1989, 1992, Kratter *et al.* 1993).

Paratypes. Seven other specimens were mist-netted by LSUMZ and MHNNKM personnel in 1990 at the same site as the holotype: LSUMZ 153331, or, 2 August, prepared by O'Neill; LSUMZ 153327, °, 4 August, prepared by R. T. Chesser; MDC 287 (in MHNNKM), or, 6 August, prepared by M. D. Carreño; LSUMZ 153330 (10 August) and LSUMZ 153329 (12 August) Q and O prepared by O'Neill; LSUMZ 153332, Q, 15 August, prepared by T. S. Sillett. The specimens agree with the holotype, except for the following: (1) LSUMZ 153327, gray on the lower throat is nearly absent and the back is somewhat more rufescent; (2) LSUMZ 153329, entire throat is washed pale gray (3) nape streaking more prominent and upper tail coverts concolor with rump; (4) LSUMZ 153331 and

ype	specimen no.	sex	date	Bill	Wing	Tail	Tarsus
		ç	ug.	21.9		68.6	21.6
		ď	ug.	23.1		56.6	21.0
		0"	ug.	23.2		58.6	20.8
		ç	ug.	22.9		64.6	19.9
		o	ug.	23.6		65.2	21.6
		ç	.ug.	23.6		59.0	21.8

TABLE 1. Measurements of holotype and paratypes. All dates from 1990.

153332, nape streaking nearly lacking. An additional individual (LSUMZ 153969,  $\sigma$ , 6 August, prepared by O'Neill) was collected at the type locality and prepared as a skeletal specimen. Measurements of the paratypes (except MHNNKM and skeletal specimens) and holotype are given in Table 1.

*Etymology.* This taxon is named *kempffi* in honor of Noel Kempff Mercado, the late Bolivian ornithologist. He was the first to study birds in the Serrania Huanchaca, and the national park now encompassing the Bolivian part of the Serrania, the type locality of *Sclerurus albigularis kempffi*, is named in his honor. The natural history museum in Santa Cruz, Bolivia, also shares his name.

## CONSERVATION

Sclerurus albigularis kempffi is definitely known only from the type locality, which lies in the buffer zone of Parque Nacional Noel Kempff Mercado. Humid forests here are restricted to a narrow band (c. 20 km wide) along the southern periphery of the Serrania (J. M. Bates, pers. comm.). The species has not been found in recently studied sites in humid forest to the north of the Serrania, along the western periphery of the Serrania, nor on several forest fragments on the Serrania's plateau (Bates et al. 1989, 1992). Humid forest is more extensive on the gently sloping, but as yet unexplored, eastern flank of the Serrania (T. J. Killeen, unpubl. data), but much of the adjacent forest on the Brazilian side of the border has been cleared. Selective logging was occurring at the type locality in 1990 and a dirt road had been hewn through the forest for extracting timber along the entire southern periphery of the Park.

Populations of terrestrial, insectivorous birds in interior forests, such as leaftossers, have been shown to be particularly susceptible to the effects of forest fragmentation (Karr 1982, Canaday 1991, Stouffer & Bierregaard 1995) or selective logging (Thiollay 1992). In Amazonian Brazil, all three Sclerurus species present (mexicanus, caudacutus, rufigularis) showed steep declines or disappeared from forest patches following fragmentation (Stouffer & Bierregaard 1995). Thiollay (1992) found steep declines in populations of these same three Sclerurus species following selective logging in French Guianan forests. All species in Sclerurus are similar in general habitat selection and behavior (Ridgely & Tudor 1994), and similar negative effects with logging may be expected with Sclerurus albigularis. Thus, increasing logging pressures in humid forests adjacent to the Serrania Huanchaca may threaten the only known population of this distinct subspecies.

## NATURAL HISTORY

All specimens were mist-netted in the undergrowth of tall humid forest. The terrain at the type locality, 5 km south of the Serrania's escarpment, was slightly rolling, with increasingly dissected streambeds closer to the mountains. Undergrowth was mostly open, but thickets of spiny bamboo (*Guadua* sp.) were found along streams. Scrubbier vegetation with thick viney understory occurred on rocky outcroppings, especially near the escarpment. Most emergent canopy trees in the forest were deciduous. The humid forest forms a narrow band (<25 km wide) along the southern and western bases of the Serrania, probably as a result of orographic precipitation. Drier deciduous forest is found just south and west of the site, away from the Serrania.

Aside from these records and the specimens from Rondônia mentioned below, most records of this species have been in much more humid forests in montane areas. In Central America, S. a. canigularis has been found in wet montane forests in Costa Rica from 600-1500 m (Slud 1964, Stiles & Skutch 1989) and from 1000–1800 m in similar forests in western Panama (Chiriquí: Wetmore 1972, Ridgely 1976). In northern South America, the species occurs in wet forests from 900 to 2200 m in the Santa Marta Mountains of Colombia (S. a. propinguus; Todd & Carriker 1922, Fjeldså & Krabbe 1990), and at 500–2200 m in the Perijá Mountains on the Venezuelan-Colombian border (S. a. kunanensis, USNM specimens; Alvedo & Gines 1950). The nominate subspecies is found from 900 to 1700 m along the humid north slope of the Venezuelan Andes from Carabobo east to the Paria Peninsula (Meyer de Schauensee & Phelps 1978) and in montane areas of Trinidad and Tobago (AMNH and ANSP specimens). Two populations of the nominate subspecies are found in humid montane forests in central Colombia. These populations, which may be isolated from other populations of this subspecies, occur at 1200 m on the east slope of the eastern Andes (AMNH specimens) and at 1800 m in the nearby Cordillera Macarena (Hilty & Brown 1986). Sclerurus a. zamorae is found on the humid east slope of the Andes (750-1700 m) from central Ecuador (prov. Morono-Santiago) south to southern Peru (depto. Puno). In the southeastern part of its range, S. albigularis occurs at somewhat lower elevations. Sclerurus a. albicollis is found in the Andean foothills of Bolivia (380-1100 m, LSUMZ and CM specimens from deptos. La Paz, Beni, and western Santa Cruz) and also about 250 km east of the Andes at 600 m in hilly lowland forests at Balta, depto. Ucayali, Peru (O'Neill 1974). In Rondônia, Brazil, this species (subspecies unknown) was collected at only 100 m in lowland forest (D. Stotz, in litt.). In lowland southwestern Amazonia, this species may be restricted to humid sites that receive locally heavy precipitation, such as near serranias. These lowland populations therefore are probably isolated from one another.

Given that eight specimens were netted in 23 days of field work at the type locale of S. a. kempffi, this taxon is probably fairly common here, although other populations of this species are usually considered local, rare, or uncommon (e.g., Todd & Carriker 1922, Ridgely 1976, Hilty & Brown 1986, Stiles & Skutch 1989, Ridgely & Tudor 1994), except the nominate subspecies in Trinidad, which is considered common (ffrench 1991). In spite of its relative commonness near the Serrania Huanchaca, the only observation was of a individual foraging on the ground, tossing leaf litter aside with its bill in viney undergrowth with dense Heliconia close to a stream. This foraging behavior is typical of the genus (Hilty & Brown 1986, Ridgely & Tudor 1994). The song of S. a. kempffi, tape-recorded at the type locale by the author (1 August 1990), is typical of the species (e.g., from Trinidad, Library Natural Sounds # 07022; T. A. Parker, pers. comm.). In addition, the foraging individual mentioned above gave a sharp "check" call when flushed.

# GEOGRAPHIC VARIATION

As a species, S. albigularis largely conforms to Gloger's Ecogeographic Rule: populations in the most humid regions are the most richly pigmented, and populations in driest areas are palest (see recent discussion in Zink & Remsen 1986). The greatest annual precipitation within the distribution of a S. albigularis is on the east slope of the Cordillera Central in Costa Rica (4000-6000 mm/year, Coen 1983) and on the east slope of the Andes in southern Peru (4000–7000 mm year; Unzueta 1975, Hoffman 1975). These two areas also have the darkest subspecies: S. a. canigularis in Costa Rica is the darkest race, and the next darkest is S. a. zamorae on the lower east slopes of the Andes in Peru and Ecuador (Hellmayr 1925, pers. obs.). Annual precipitation in the area of the palest form, S. a. kempffi in eastern Bolivia, is less than 1800 mm/year (Unzueta 1975, Hoffman 1975). With few exceptions, the races between these extremes in pigmentation occur in areas with intermediate levels of precipitation. For example, annual precipitation within the range of the relatively pale nominate subspecies is generally 2000-2500 mm/year, except in central Colombia, where

annual precipitation may exceed 4000 mm/year (Serrania Macarena; Schwerdtfeger 1976). The specimens here, however, are somewhat darker than from other parts of the subspecies' distribution (Hellmayr 1925). Annual rainfall in the distribution of S. a. albicollis (northern Bolivia and depto. Ucayali, Peru, probably western Brazil - see below), another relatively pale subspecies, is from 2000-4000 mm/year. This subspecies generally occurs at lower elevations than the more-richly pigmented S. a. zamorae in the very wet Andes of southern Peru nearby (see above). Interestingly, the highest elevation specimen examined of S. a. albicollis (LSUMZ 102308, from 1100 m in the isolated Serrania Pilon in western depto. Beni, Bolivia) is also the most richly pigmented, and tends toward zamorae in plumage color.

To study geographical variation in morphometrics, four mensural variables (length of culmen, wing chord, tail, and tarsus) were measured on 80 study skins from throughout the range of *S. albigularis* (see Appendix). Differences between sexes were slight. In the three subspecies with adequate samples (n=21, n=20,and n=12 for *S. a. zamorae, albicollis*, and mainland *albigularis*, respectively), the only significant difference between sexes was for wing in *zamorae* (t=2.3, *P*=0.033), about what would be expected from Type 1 error with twelve comparisons. Therefore, sexes were combined in the following analyses.

All four mensural variables showed significant variation among subspecies in ANOVAs (Table 2). In post-ANOVA contrasts (Scheffe's tests), the subspecies described herein (S. a. kempffi) averaged significantly shorter in culmen and wing than the two geographically nearest subspecies (albicollis and zamorae). These two latter subspecies accounted for most other significant post-ANOVA contrasts. Both albicollis and zamorae were significantly larger than the island populations of albigularis in bill, wing, and tarsus. The southerly albicollis was significantly larger in wing than canigularis of Costa Rica and propinguus of the Santa Marta Mountains. Both albicollis and zamorae were significantly larger in tarsus than kunanensis from the Perijá Mountains. Interestingly, S. a. kunanensis also significantly differed from propinguus from the nearby Santa Marta Mountains in tarsus, although only a limited sample of kunanensis (n=2) was examined.

Principal Component Analysis (PCA) was used to investigate multivariate trends within S. albigularis. The correlation matrix was used to produce individual PCA loadings for the 74 specimens examined. All four mensural variables had high positive loadings on the first PCA axis, indicating that this axis reflected overall size

TABLE 2. Geographic variation in measurements of *Sclerurus albigularis* subspecies. Sample sizes (n), means and standard deviations ( $x\pm SD$ ), and standard errors (SE) are given for each character. F-test and associated *P*-value are for the single-factor ANOVA of the character. The *albigularis* subspecies is split into mainland populations from Colombia and Venezuela and populations from the islands of Trinidad and Tobago (see text).

c 1 ·	Bill (F=5.46, <i>P</i> <0.0001) n x+SD SE		Wing (F=14.22, <i>P</i> <0.0001) n		Tail (F=3.19, <i>P</i> =0.0055) n			Tarsus (F=9.50, <i>P</i> <0.0001) n				
Subspecies												
	n	X±3D	3E	п	X±3D	3E	n	XI3D	3E	n	x±3D	эe
kempffi	6	$23.05{\pm}0.63$	0.26	6	$83.87 \pm 2.22$	0.91	6	$62.10{\pm}4.69$	1.92	6	$21.12 \pm 0.71$	0.29
albicollis	18	$24.88{\pm}0.73$	0.17	20	90.53±2.59	0.58	20	69.41±5.56	1.24	20	22.75±0.69	0.15
zamorae	20	$24.90 \pm 0.83$	0.18	21	90.23±2.88	0.63	19	69.57±5.34	1.23	21	22.81±1.24	0.27
propinquus	8	24.44±0.74	0.26	8	84.42±2.86	1.01	8	68.51±4.43	1.56	8	$22.52 \pm 1.55$	0.55
kunanensis	2	23.88±0.10	0.07	2	84.96±1.81	1.28	2	67.02±5.59	3.95	2	19.07±1.06	0.75
<i>albigularis</i> (islands)	5	23.14±0.86	0.39	6	82.58±1.46	0.60	6	63.29±2.63	1.07	6	19.95±0.46	0.19
<i>albigularis</i> (mainland)	12	24.24±1.19	0.34	12	87.16±2.46	0.71	11	70.73±2.48	0.75	12	21.60±1.02	0.29
canigularis	5	$24.25 \pm 1.12$	0.50	5	85.51±2.55	1.14	5	67.20±5.06	2.26	5	21.90±1.47	0.66

(Johnston & Selander 1971). However, S. albigularis lacked any overall geographical trends in size (Fig. 1). Two isolated populations, S. a. kempffi in eastern Bolivia and individuals from Trinidad and Tobago (part of the widespread nominate subspecies), were smaller than other populations and were more or less isolated on PCA1. The subspecies described herein, S. a. kempffi, and its geographically closest neighbor (S. a. albicollis) showed no overlap on PCA1 (Fig. 1). Differences in size between small-sized populations of S. a. albigularis on Trinidad and Tobago and large-sized populations on the mainland (as indicated by PCA1) were noted previously by Hellmayr (1925); however, he did not consider these differences large enough for taxonomic distinction and found no differences in plumage. The small sample of S. a. kunanensis examined (n=2) precluded firm conclusions, but this isolated race in the Perijá mountains on the Venezuelan-Colombian border appears to be somewhat smaller than the nearby S. a. propinguus in the Santa Marta Mountains of Colombia and the nominate subspecies in the Andes of Colombia and Venezuela (Fig. 1). This is particularly true for the tarsus (Table 2), although Alvedo & Gines (1950) did not find this difference in a sample of three *kunanensis* from Venezuela. PCA2 failed to isolated any subspecies or populations and did not show any general patterns (Fig. 1).

Sclerurus albigularis extends into western Brazil, but I was unable to examine the specimens. A specimen (Museu Emilio Goeldi 38745), collected in Rondônia (Alvorada do Oeste, Linha 64, Br. 429 km 97), was compared (by D. Lane) against all recognized subspecies (ANSP specimens) and the type series of *kempffi*. The Rondônia specimen appeared closest to the subspecies *albicollis* in plumage (D. Lane, in litt.). Another specimen of *albigularis* has been collected on the Rio Ji Paraná, Rondônia (elevation 100 m; D. Stotz., pers. comm.), but was unavailable for comparison. Interestingly, although

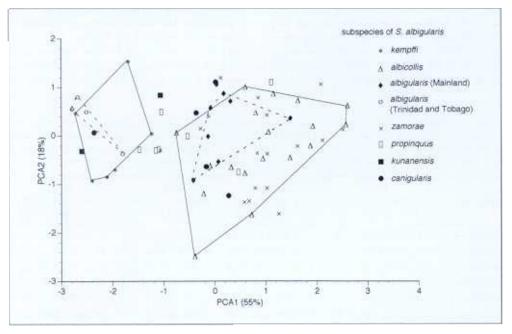


FIG. 1. Principal Component Analysis of the four morphometric variables. Percent of variation explained by each axis follows axis label. Subspecies of interest are outlined: *S. a. kempffi*, described herein, and its nearest geographical neighbor, *S. a. albicollis*, are outlined with solid lines; populations of *S. a. albigularis* on mainland and on Trinidad and Tobago are outlined with dashed lines.

the Amazonian avifauna at the Serrania Huanchaca shows a close affinity with the Rondônian area of endemism (Bates *et al.* 1989; see Cracraft 1985), these areas appear to support different subspecies of *Sclerurus albigularis*.

## ACKNOWLEDGMENTS

The Louisiana State University Museum of Natural Science's (LSUMZ) expedition to Parque Nacional Noel Kempff Mercado was funded by John S. McIlhenny. My expedition colleagues, John P. O'Neill, Terry Chesser, Scott Sillett, Maria Dolores Carreño, Armando Yépez, and Juan Surubí, are gratefully acknowledged for their help and companionship. Ing. Nestor Ruíz, director of the Parque Nacional Noel Kempff Mercado, supported our expedition in countless ways, as did Abel Castillo and Hermes Justiniano of the Fundación Amigos de Naturaleza in Santa Cruz. I am grateful to Lic. Arturo Moscoso who granted permission to work and collect in Bolivia. Lic. María Teresa de Centurion, Director, and Marcelo Zalles of the Museo de Historia Natural "Noel Kempff Mercado" helped with the permitting process in Santa Cruz and provided a valuable link between the MHNNKM and the LSUMZ. The following Museums kindly loaned their specimens: Museo de Historia Natural "Noel Kempff Mercado" (MHNNKM), Carnegie Museum (CM), American Museum of Natural History (AMNH), United States National Museum, Smithsonian Institution (USNM), Museo de Universidad San Marcos (MUSM) in Lima, Peru, the Academy of Natural Sciences in Philadelphia (ANSP), and the Museu Emilio Goeldi, Belem, Brazil. Tape recordings were provided by the Library of Natural Sounds, Cornell University. Doug Stotz and Mario Cohn-Haft gave me information on Rondônia specimens, and Dan Lane compared one of these with a sample from other areas. Amanda Stronza helped translate the abstract. Van Remsen, John Bates, and an anonymous reviewer gratefully shared information and commented on this manuscript.

#### REFERENCES

Alvedo H., R., & R. H. Gines, 1950. Descripción de cuatro aves nuevas de Venezuela. Memorias. Sociedad de Ciencias Naturales (La Salle) 26: 59–71.

- Bates, J. M., Garvin, M. C., Schmitt, D. C., & C. G. Schmitt. 1989. Notes on bird distribution in northeastern Dpto. Santa Cruz, Bolivia, with 15 species new to Bolivia. Bull. Brit. Orn. Cl. 109: 236–244.
- Bates, J. M., Parker, T. A., III, Capparella, A. P., & T. J. Davis. 1992. Observations on the *campo, cerra*do and forest avifaunas of eastern Dpto. Santa Cruz, Bolivia, including 21 species new to the country. Bull. Brit. Orn. Cl. 112: 86–98.
- Canaday, C. 1991. Effects of encroachment by industry and agriculture on Amazonian forest birds in the Cuyabeno Reserve, Ecuador. Unpubl. Master's Thesis. Univ. of Florida, Gainesville, Florida.
- Coen, E. 1983. Climate. Pp. 35-46 in Janzen, D. H. (ed.). Costa Rican natural history. Chicago.
- Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Pp. 49–84 *in* Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, R., & F. C. Buckley (eds.). Neotropical Ornithology. Ornith. Monogr. No. 36. Washington, D. C.
- ffrench, R. 1991. A guide to the birds of Trinidad and Tobago, 2nd edition. Cornell.
- Fjeldså, J., & N. Krabbe. 1990. Birds of the high Andes: A manual to the birds of the temperate zone of the Andes and Patagonia. Zool. Museum, Copenhagen.
- Hellmayr, C. E. 1925. Catalogue of birds of the Americas. Part 4: Furnariidae-Dendrocolaptidae. Field Mus.. Nat. Hist 13: 1–390.
- Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton.
- Hoffman, J. A. J. 1975. Climatic atlas of South America. Geneva.
- Johnston, R. F., & R. K. Selander. 1971. Evolution of the House Sparrow. II. Adaptive differentiation in North American populations. Evolution 25: 1–28.
- Karr, J. R. 1982. Avian extinction on Barro Colorado Island, Panama, a reassessment. Amer. Naturalist 119: 220-239.
- Kratter, A. W., Carreño, M. D., Chesser, R. T., O'Neill, J. P., & T. S. Sillett. 1992. Further notes on bird distribution in northeastern Bolivia, with two species new to Bolivia. Bull. Brit. Orn. Cl. 112: 143–50.
- Marantz, C. A., & J. V. Remsen, Jr. 1994. First records of *Tangara cyanicollis melanogaster* from Bolivia. Bull Brit. Orn. Cl. 114: 230–1.
- Meyer de Schauensee, R., & W. H. Phelps, Jr. 1978. A guide to the birds of Venezuela. Princeton.
- O'Neill, J. P. 1974. The birds of Balta, a Peruvian dry tropical forest locality, with an analysis of their origins and ecological relationships. Ph. D. dissertation. Louisiana State Univ., Baton Rouge.
- Paynter, R. A., Jr. 1982. Ornithological gazetteer of Venezuela. Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.

- Paynter, R. A., Jr. 1992. Ornithological gazetteer of Bolivia. Second edition. Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.
- Paynter, R. A., Jr. 1993. Ornithological gazetteer of Ecuador. Second edition. Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.
- Paynter, R. A., Jr., & M. A. Traylor, Jr. 1981. Ornithological gazetteer of Colombia. Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.

Ridgely, R. S. 1976. Birds of Panama. Princeton.

- Ridgely, R. S., & G. Tudor. 1994. The birds of South America. Vol. 2.: the suboscine passerines. Austin.
- Ridgway, R. 1912. Color standards and color nomenclature. Published by the author. Washington, D. C.
- Schwerdtfeger, W. 1976. The climate of Central and South America. World survey of climatology, vol. 12. Amsterdam.
- Slud, P. 1964. The birds of Costa Rica: distribution and ecology. Bull. Amer. Mus. Nat. Hist. 128: 1-430.
- Stephens, L., & M. A. Traylor, Jr. 1983. Ornithological gazetteer of Peru. Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.
- Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Ithaca.
- Stouffer, P. C., & R. O. Bierregaard, Jr. 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76: 2429-2445.
- Thiollay, J.-M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. Conserv. Biol. 6: 47–63.
- Todd, W. E. C., & M. A. Carriker, Jr. 1922. The birds of the Santa Marta Region of Colombia: a study in altitudinal distribution. Annals of the Carnegie Museum 14: 1–611.
- Unzueta Q., O. 1975. Mapa ecologia de Bolivia. Ministerio de Asuntas Campensinos y Agropecuarios, La Paz, Bolivia.
- Wetmore, A. 1972. The birds of the Republic of Panamá. Part 3. — Passeriformes: Dendrocolaptidae (Woodcreepers) to Oxyruncidae (Sharpbills). Washington, D. C.
- Zink, R. M., & J. V. Remsen, Jr. 1986. Evolutionary processes and patterns of geographic variation in birds. Pp. 1–69 in Johnston, R. F. (ed.). Current Ornithology, Vol. 4. New York.

APPENDIX. Specimens examined. Where appropriate, place-names follow Slud (1964), Paynter & Traylor (1981), Stephens & Traylor (1983), and Paynter (1992, 1993). See acknowledgments for museum codes. S. a. canigularis

Costa Rica (n=4): Bonilla (AMNH 390499), Cariblanco (AMNH 524499), Cerro Santa Maria (ANSP 128934), Guayabo (AMNH 390497)

Panama (n=1): Chiriquí: Boquela (AMNH 524500)

#### S. a. propinquus

Colombia (n=9): depto. Magdalena: Cincinati (AMNH 72828), Las Nubes (AMNH 71161, 71163, 72831), Las Vegas (ANSP 11927, LSUMZ 127433), Hacienda Vista Nieve (USNM 387233-34); depto. La Guajira: El Pueblito (ANSP 63097)

## S. a. albigularis

Colombia (n=2): depto. Meta: Buenavista (AMNH 122062, AMNH 122065)

Venezuela (n=9): estado Carabobo: Cumbre de Valencia (AMNH 524489-90); estado Aragua: Rancho Grande (USNM 351920, 595887) estado Sucre: Cristobal Colon (AMNH 120735-36, 120738, 120740)

Trinidad (n=5): St. George (AMNH 786059); Princestown (AMNH 59307); Mt. Tabor (ANSP 104985); Valencia (AMNH 524493); no locale (AMNH 60606) Tobago (n=1): Jarret Hall? (AMNH 524494)

## S. a. kunanensis

Colombia (n=2): depto. La Guajira: Monte Elías (USNM 369132), Tierra Nueva (USNM 369131)

#### S. a. zamorae

Ecuador (n=4): depto. Morono-Santiago (ANSP 176828);, prov. Loja: Zamora: (AMNH 129817, AMNH 167371);? Abanico, Oriente (USNM 371255)

Peru (n=17): depto. Amazonas: La Peca Nueva (LSUMZ 87914-15); depto. Cajamarca: Huarandosa (AMNH 182069-70), Paylon (LSUMZ 87911), San Ignacio (ANSP 117706-7), Puerto Tamborapa (ANSP 117705); depto. San Martin: Tarapoto (LSUMZ 116821-25); depto. Huánuco, Huachipa (CM 138564); depto. Pasco: Puellas (LSUMZ 105984); depto. Junín: Chanchamayo (AMNH 408593); depto. Puno: Río Tavara (MUSM 16200);

## S. a. albicollis

Peru (n=3): depto. Ucayali: Balta (LSUMZ 34174-75, 51959)

Bolivia (n=17): depto Santa Cruz: Cerro Hosane (CM 79303, CM 79352, CM 79398), Santa Ana (ANSP 120562), Río Yapacani (CM 50860, CM 50869), Río Surutú (CM 43868, CM 79850, CM 80627, CM 80641, CM 125091-92, LSUMZ 37661), Buena Vista (CM 119925), Mataracú (LSUMZ 36063), depto. Beni: Serrania Pilón (LSUMZ 124095); depto. La Paz: Puerto Linares (LSUMZ 102038).

## S. a. kempffi

Bolivia (n=6): depto. Santa Cruz: Parque Nacional Noel Kempff Mercado (LSUMZ 153327-32)