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SPECIES LIMITS, DISTRIBUTION, AND BIOGEOGRAPHY OF SOME NEW WORLD GRAY-RUMPED SPINE-TAILED SWIFTS (*CHAETURA*, APODIDAE)

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Abstract. The New World swifts placed in the genus *Chaetura* (Apodidae) consist of two basic groups: the “gray-rumped” taxa and the “brown-rumped” taxa. Each basic group can be subdivided into three subgroups of taxa distinguishable by size: small, medium, and large. The “gray-rumped” subdivision consists of: the small *C. spinicauda*, the medium *C. martinica*, *C. cinereiventris*, and *C. fumosa*, and the large *C. egregia*. The “gray-rumped” group can be further subdivided in two additional subgroups: the “pale-rumped” and the “gray-rumped,” the former including *martinica*, *spinicauda*, *fumosa*, and *egregia*, and the latter the *cinereiventris* group. However, the *C. cinereiventris* group was not fully treated here, and it might not be as closely related to the others as has been suggested previously. Five subspecies, *Chaetura spinicauda fumosa*, *C. spinicauda aethalea*, *C. spinicauda latirostris*, *C. cinereiventris pachiteae*, and *C. cinereiventris egregia* might not be valid taxa. *Chaetura spinicauda fumosa* and *C. cinereiventris egregia*, presently considered to be subspecies, should be elevated to species rank. *Chaetura cinereiventris “pachiteae”* is a synonym of *C. cinereiventris egregia* which should be elevated to species rank, *C. egregia*. These two taxa are more closely related to *C. spinicauda* than to *C. cinereiventris*. In addition, *C. fumosa* and *C. egregia* are more closely related to each other than to *C. spinicauda*. The subspecies *C. spinicauda aethalea* and *C. spinicauda latirostris* should be included in the nominate subspecies. The “pale-rumped” group consists of four allopatric or parapatric species: *C. martinica*, *C. spinicauda*, *C. fumosa*, and *C. egregia*. These four species are closely interrelated, and they should be placed in a superspecies, to which the name “*martinica* superspecies complex” should be given. The geographic distribution of all four species in the “*martinica* superspecies complex” seems to be delimited by the natural terminus of humid vegetation. The geographic distribution of the species pair *C. spinicauda*–*C. egregia* in an area of uniform vegetation might be affected by interspecific competition. Accepted 6 September 1999.

Resumen. En los vencejos del Nuevo Mundo el genero *Chaetura* (Apodidae) esta compuesto de dos grupos básicos de taxones: los de “rabadilla gris” y los de “rabadilla café;” cada grupo puede ser subdividido en tres sub grupos de taxones que se pueden distinguir por el tamaño: pequeño, mediano y grande. La subdivisión de los taxones de “rabadilla gris” consiste en: la pequeña *C. spinicauda*, las medianas *C. martinica*, *C.*

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cinereiventris, y *C. fumosa*, y la grande *C. egregia*. Adicionalmente, los de “rabadilla gris” se subdividen en los de “rabadilla clara” que incluye *martinica*, *spinicauda*, *fumosa*, y *egregia* y en los de “rabadilla gris,” que incluye el grupo de *C. cinereiventris*. A pesar de que *C. cinereiventris* no fue incluida en su totalidad en este análisis, al parecer no esta tan relacionada a las otras como han sugerido varios autores. Cinco subspecies *Chaetura spinicanda fumosa*, *C. spinicanda aethalea*, *C. spinicanda latirostris*, *C. cinereiventris pachiteae*, and *C. cinereiventris egregia* pueden ser invalidas. *Chaetura spinicanda fumosa* y *C. cinereiventris egregia*, que ahora se consideran como subspecies, deben elevarse al nivel de especie. *Chaetura cinereiventris “pachiteae”* es un sinónimo de *C. cinereiventris egregia* que debería elevarse al nivel de especies, *C. egregia*. Estos dos últimos taxones están filogenéticamente mas cercanos a *C. spinicanda* que a *C. cinereiventris*. Además *C. fumosa* y *C. egregia* están filogenéticamente mas cercanas el uno al otro que a *C. spinicanda*. Dos subspecies *C. spinicanda aethalea* y *C. spinicanda latirostris* deberían unirse con la subespecie nominal. El grupo de taxones de “rabadilla clara” consiste de cuatro alopatricas o parapatricas especies: *C. martinica*, *C. spinicanda*, *C. fumosa*, y *C. egregia* las cuales están filogenéticamente muy cercanas en una superespecie, por la cual se sugiere el nombre de “complejo superespecie *martinica*.” La distribución geográfica de las cuatro especies del “complejo superespecie *martinica*” esta delimitada por el termino natural de la vegetación humeda. La distribución geográfica del par de especies *C. spinicanda*–*C. egregia* parece ser que es afectada por competencia interespecífica.

Key words: New World spine-tailed swifts, *Chaetura*, Apodidae, taxonomy, distribution, species limit, biogeography.

INTRODUCTION

Among swifts (Apodidae), the New World spine-tailed species placed in the genus (*Chaetura*) are the most widespread, as they occur throughout the New World, and are specially abundant in the tropics. Based on this report and a previous study of the New World spine-tailed swifts (Marín 1997), the *Chaetura* swifts consist of two basic groups: the “brown-rumped” and the “gray-rumped” swifts. The various species of *Chaetura* have very similar life histories, morphology, and spatial distribution. Furthermore, these species are phenotypically extremely similar, and have very few morphological or ecological characters that one can use as indices to their phylogenetic relationships. This great uniformity might be attributed to selection pressures from their aerial life style which does not leave much space for large structural changes. The genus *Chaetura* as a whole is characterized by the presence of cryptic species (*sensu* Mayr 1970). An understanding of the similarity within species in the group is made more complicated by a shortage of museum specimens for most species (many species and sub-

species were originally described from a single specimen), by the fact that the degree of intraspecific variation is poorly known, and because the timing of migration and breeding distribution are uncertain in some species.

In the present study, the criterion for establishing species limits in *Chaetura* work is based on morphological and geographical data. Additional work, particularly molecular studies; might therefore modify my conclusions. In the New World spine-tailed swifts, I found (Marín 1997) that body size is often the best way to distinguish among closely related species.

The aim of this study was to investigate the taxonomic position and distribution of some members of the “gray-rumped” swifts using a phenetic approach. This paper adds new information on morphometrics and distribution on some species of New World spine-tailed swifts.

MATERIALS AND METHODS

The present analysis is based primarily on personal examination of 321 study skins from the “gray-rumped” group in museums (see

TABLE 1. Measurements in mm (mean \pm 1 SD) of some species and subspecies of *Chaetura*. Sample sizes are given in parentheses.

Wing ¹	Tail ²	Tail ³	Tail spines ⁴	Exposed	Tarsus	Wing	Mass (g)
			min	max	culmen	span	
<i>Chaetura martinica</i>							
111.2	38.1	34.7	2.0	5.0	4.3	9.3	n/d ⁵
± 2.22	± 1.46	± 1.38		± 0.24	± 0.32		± 0.75
(49)	(49)	(37)		(49)	(47)		(5)
<i>Chaetura "spinicauda" fumosa</i>							
113.0	40.3	35.0	2.0	7.0	4.8	10.5	275.0
± 2.36	± 1.86	± 1.47		± 0.24	± 0.81	± 5.14	± 1.31
(23)	(20)	(19)		(27)	(27)	(5)	(10)
<i>Chaetura spinicauda aetherodroma</i>							
104.6	39.3	34.4	3.0	10.0	4.6	10.2	255.7
± 1.77	± 1.97	± 1.63		± 0.26	± 0.41	± 16.42	± 0.82
(51)	(40)	(31)		(33)	(38)	(19)	(22)
<i>Chaetura spinicauda spinicauda</i>							
105.9	39.9	33.8	5.0	8.0	4.5	10.0	259.0
± 2.44	± 1.53	± 1.12		± 0.27	± 0.67		± 0.54
(38)	(40)	(8)		(35)	(37)	(1)	(7)
<i>Chaetura egregia</i>							
117.6	42.0	36.8	3.0	6.0	4.9	10.9	284.8
± 1.26	± 1.62	± 1.57		± 0.29	± 0.44	± 1.89	± 1.53
(15)	(16)	(13)		(15)	(16)	(3)	(12)

¹Wing flat.

²Tail spines included.

³Tail spines not included.

⁴Sample size, same as for the tail.

⁵No data.

Acknowledgments). Literature data were used with extreme caution because I have found many misidentified museum specimens and suspect that some literature records may be erroneous. Similarly, I have avoided most sight records because of the great difficulties in field identification of some *Chaetura* swifts.

Field work was carried out in Costa Rica,

1983–1986 (49 weeks), and 1995–1997 (40 weeks); Ecuador, 1987–1992 (52 weeks); and Bolivia, 1993 (6 weeks) and specimens collected in those trips were deposited in the Western Foundation of Vertebrate Zoology (WFVZ) and Museum of Natural Science at Louisiana State University (LSUMNS).

Data on latitude and longitude sometimes

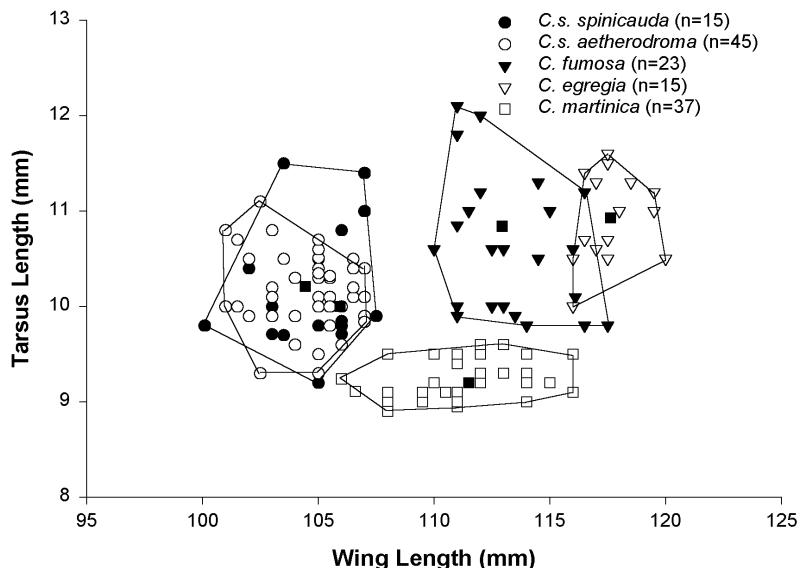


FIG. 1. Scatter plot of tarsus length versus wing length, showing the separation of three groups of species (small, medium, and large; see text). Solid squares are the species or subspecies means from Table 1.

are given to help define distributional ranges, type localities, and areas of possible intergradation. Latitudes and longitudes were taken from the gazetteers of USBGN [Costa Rica] (1956), Selander & Vaurie (1962), Fairchild & Handley (1966), Paynter (1982, 1992), Paynter & Traylor (1981, 1991), Vanzolini (1992), and National Imagery and Mapping Agency, NIMA GEO base (www.nima.mil).

Wing measurements were taken from the flattened wing, because it gives the longest possible measurement of the wing and because it yields less individual variation, from person to person, than measuring the chord (pers. observ.); other measurements follow Baldwin *et al.* (1931). Wing length and tarsus length were used as indicators of body size for the morphometric analyses. Tail measurements were not used in this report because in *Chaetura* spine-tailed swifts they vary as much as 10 mm owing to the degree of tail wear (tail-spines) (Marin 1997 and

Table 1). I do, however, present tail measurements with and without tail spines (see Table 1). Body masses were analyzed only in some cases because sample sizes were small and available for some species only (Table 1).

Nomenclature, but not sequence of species and subspecies, follows primarily Peters (1940). English names, when used, follow Meyer de Schauensee (1982).

RESULTS AND DISCUSSION

Chaetura martinica. This species was described by Hermann in 1783 (*fide* Peters 1940) with Martinique Island as type locality and it was the first New World spine-tail swift to be reported. Its distribution is confined to the islands of Guadeloupe, Dominica, Martinique, St. Lucia, and St.Vincent (Bond 1973, AOU 1983).

I examined 50 specimens, including the

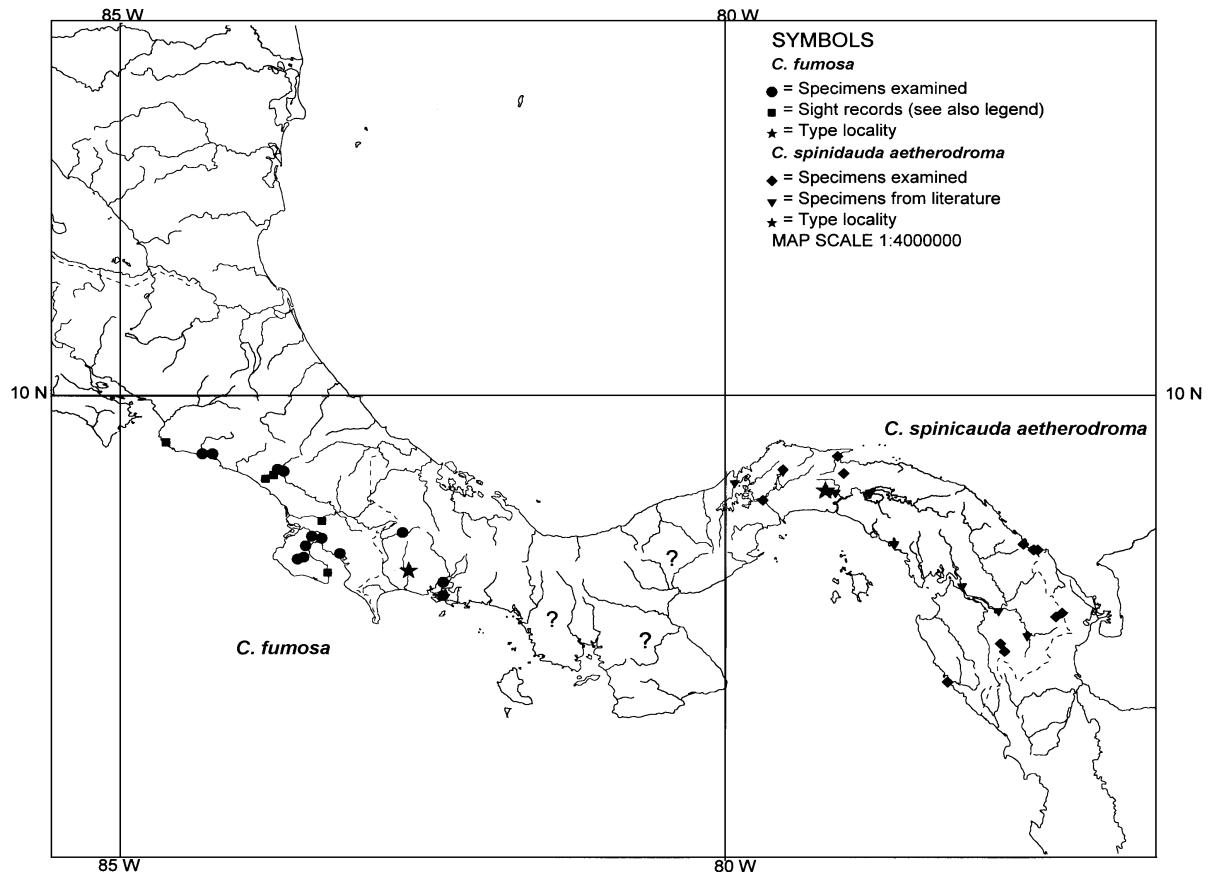


FIG. 2. Map of Costa Rica and Panama showing the known locality records for *Chaetura fumosa* and *Chaetura spinicauda aetherodroma*. Solid squares are primarily my own sight records or a single specimen not examined from (MVZ). For *Chaetura spinicauda aetherodroma*, solid triangles are specimens not seen by me, reported by Wetmore (1968). Stars are the type localities for *C. fumosa* in western Panama and *C. s. aetherodroma* in central Panama.

type of *Chaetura dominicana* (Lawrence 1877) (AMNH 55103), from these islands, except St.Vincent (AMNH, ANSP, BMNH, FMNH, and LSUMZ) and I found no phenotypical differences among the different insular populations. Nevertheless, I found a considerable intraspecific variation in wing size, larger than in any other species of *Chaetura* (see Fig. 1). However, this wing variation is not statistically significant between sexes (Mann-Whitney U-test, $U = 379, P = 0.796$) or among the different island populations (Kruskal-Wallis, $H = 1.63, P = 0.652$).

There is confusion in the literature concerning the taxonomic affinities of this species. *Chaetura martinica* was treated "tentatively" as being conspecific with *C. cinereiventris* by Lack (1956). *Chaetura martinica* and *C. cinereiventris* are treated as superspecies in AOU (1983). Sibley & Monroe (1990) considered that *C. martinica*, *C. cinereiventris* and *C. egredia* should be included in a superspecies, a treatment not followed by AOU (1998). Even though some authors have considered *C. cinereiventris* as being conspecific, or as part of a superspecies, with *C. martinica*, I think that *C. cinereiventris* might not be as closely related to the other four taxa in the gray-rumped swifts, namely *C. martinica*–*spinicauda*–*fumosa*–*egredia*, as others believe. My reasons for this conclusion are: a) the basic body color in *C. cinereiventris* is various tones of gray, whereas in members of the *C. martinica*–*spinicauda*–*fumosa*–*egredia* group the body is various tones of sooty brown, and b) the four taxa of the *martinica* group have white at the base of feathers in the loral areas, whereas this is not so in *C. cinereiventris*, where the loral feathers' base is velvet black. The only character the *martinica* and *cinereiventris* group have in common is the "grayish" pale rump. Because of these reasons I suspect that the pale rump in *martinica* and *cinereiventris* groups might be a case of a character convergence rather than a phylogenetic character.

Chaetura "spinicauda" fumosa. This taxon was originally described by O. Salvin (1870) as a new species *Chaetura fumosa*. The type specimen (BMNH # 1888.7.30.52) is from NW Panama: prov. Chiriquí, Bugaba (08°29'N, 82°37'W)[often misspelled as Bogaba, e.g., Peters (1940)]. The type and the type series were collected in the region of Veragua (not prov. of Veraguas) prior to the formation of Panama as a nation state. At present the region of Veragua encompasses at least three modern Panamanian provinces: Chiriquí, Bocas del Toro, and Veraguas. E. Arcé collected several specimens labeled "Veragua, Chiriquí" (e.g., BMNH # 90.2.18.47). These specimens were collected in the vicinity of the town of Chiriquí, prov. of Chiriquí [region of Veragua]. According to Salvin (1870), Arcé made many collections in the Chiriquí area around 1867 and his results were published in parts, several (?) by Salvin or Sclater, separately or together.

The taxonomic position of *Chaetura fumosa* has been controversial. Its rank has been switched from that of a species to that of a subspecies of one of two different species. For example, Bangs (1908) and Hellmayr (1908) independently treated *fumosa* as a subspecies of *Chaetura spinicauda*, whereas Ridgway (1911), Cory (1918), and Stone (1918) considered it a subspecies of *C. cinereiventris*. Chapman (1917), Griscom (1932) and Rogers (1939) noted a difference between the specimens of southern Costa Rica and southwestern Panama and those from central and eastern Panama, and western Colombia (see Fig. 2). But all of these authors treated this taxon differently. To distinguish *fumosa* versus *spinicauda*, Griscom (1932) assigned specimens from central and eastern Panama to nominate *C. s. spinicauda* and specimens from southern Costa Rica and southwestern Panama to *C. fumosa*. Rogers (1939) treated the populations from central and eastern Panama as nominate *C. s. spinicauda* and those from

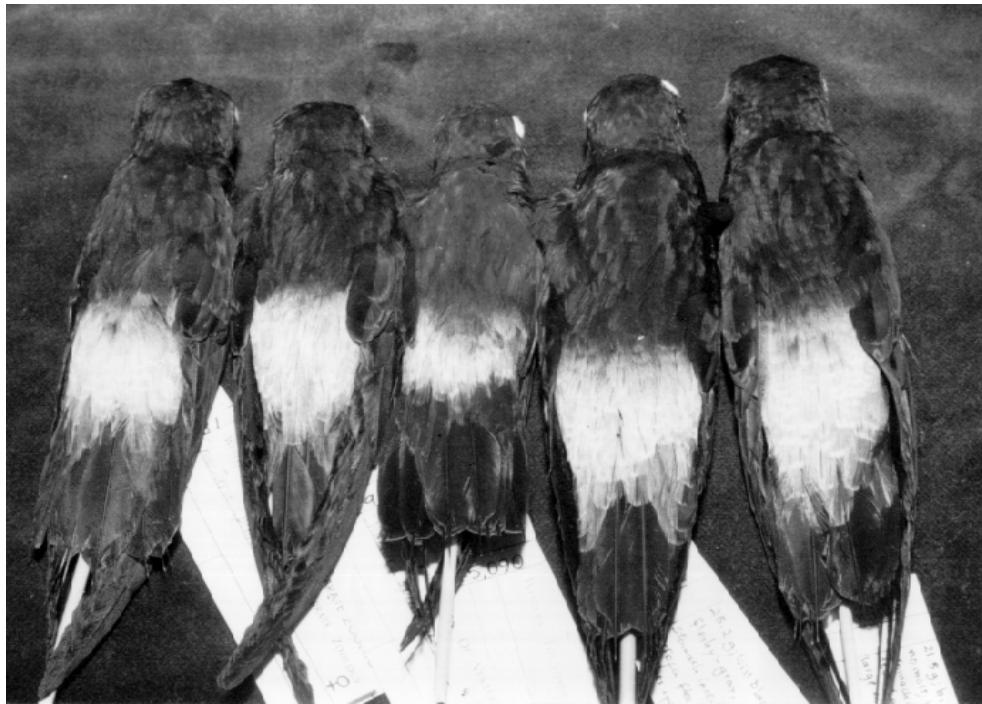


FIG. 3. Differences in rump pattern between three species of “gray-rumped” spine-tailed swifts; from left to right: The first and second specimens are *Chaetura fumosa*, third specimen *C. spinicauda*, and forth and fifth specimens *C. egregia*.

southwestern Panama as *C. spinicauda fumosa*. Although Chapman (1917) assigned Costa Rican and Colombian specimens as *C. s. fumosa*, he indicated that “possibly the Colombian bird deserves [taxonomic] separation.” Wetmore (1951) using size differences between the Costarican and southwestern Panama versus the central and southeastern Panamanian populations to describe the southernmost taxon as a new subspecies, *C. spinicauda aetherodroma*. He gave its range as extending from central Panama eastward and southward to western Colombia (see below). Subsequent authors have treated *C. fumosa* as subspecies of *C. spinicauda*. Probably because of lack of specimens, few authors mentioned differences besides size between *C. “s.” fumosa* and *C. spinicauda aetherodroma*.

Phenotypically, *C. “s.” fumosa* differs from *C. s. aetherodroma* by its darker ventral plumage, increasing in darkness toward the lower belly, and by its noticeably broader pale rump that extends to the upper tail coverts, with gray feathers tipped white extending to the gray feathers of the upper tail coverts (see Fig. 3). *C. “s.” fumosa* is significantly larger than *C. s. aetherodroma* in wing length (wl) t-test $t_{wl} = 17.4$, $P < 0.001$, df = 72; tarsus length $t_d = 4.5$, $P = 0.00002$, df = 54, culmen length $t_d = 3.4$, $P = 0.001$, df = 54, and body mass $t_{bm} = 8.5$, $P < 0.001$, df = 30; (see also Fig. 1 and Table 1.).

Both *C. “s.” fumosa* and *C. s. aetherodroma* are phenotypically very different from each other (see Fig. 3) and seem to be completely allopatric (Fig. 2). There are year-round speci-

TABLE 2. Current and proposed scientific and English names for some species of the “gray-rumped” New World spine-tailed swifts *Chaetura* spp.

Current	Proposed	Old or proposed English name
<i>Chaetura spinicauda spinicauda</i>	No change	Band-rumped Swift
<i>Chaetura s. latirostris</i>	<i>Chaetura s. spinicauda</i>	“
<i>Chaetura s. athalea</i>	“	“
<i>Chaetura s. aetherodroma</i>	No change	“
<i>Chaetura spinicauda fumosa</i>	<i>Chaetura fumosa</i>	Costa Rican Swift
<i>Chaetura “cinereiventris” egregia</i>	<i>Chaetura egregia</i>	Pale-rumped Swift
<i>Chaetura cinereiventris pachiteae</i>	“	“
<i>Chaetura martinica</i>	No change	Antilles Swift

mens showing a non migratory pattern for both *C. “s.” fumosa* and *C. s. aetherodroma* from within their respective ranges (see below). In addition, none of the specimens I examined showed any intermediary sign of potential gene flow.

Besides the size differences between *C. spinicauda aetherodroma* and *C. “spinicauda” fumosa*, from the examination of 78 study skins of both taxa, I found that the phenotypic differences are greater than the differences between *C. pelagica* and *C. vauxi* (see Marín 1997). To be consistent in delimiting species in the New World *Chaetura*, I therefore recommend that *C. “s.” fumosa* be considered a full species. For an English name I suggest Costa Rican Swift (see Table 2).

The present distribution of *C. fumosa*, based primarily on specimens, is in southern Costa Rica from near Jacó (09°36'N, 84°37'W), east along the coast and coastal cordillera. *Chaetura fumosa* is also present at the northern end of the inland valley of the El General, where I have recorded up to 1000 m. It extends east to the Panama province of Chiriquí. Because specimens are lacking I am not certain how far east it extends, but it is possible that it reaches as far as to Veraguas province. Both the northwestern and south-

eastern limits of *C. fumosa*'s range coincide with the limits of humid tropical forest and the beginning of fairly dry seasonal forest. The boundaries lie in the northwest with the Guanacaste area in Costa Rica and in the southeast with the Azuero Peninsula in western Panama near the border of Veraguas and Herrera provinces. Chantler & Driessens (1995) give a large range overlap between *C. fumosa* and *C. s. aetherodroma*. My data indicate that there is no such overlap. Furthermore, the distributional range of *C. fumosa* given by these authors erroneously as western Costa Rica, western Panama, and southward to northern Colombia.

Chaetura spinicauda aetherodroma. The type locality is Panama: prov. Panamá, Chepo (09°10'N, 79°06'W). Wetmore (1951) expected intergradation between *C. “s.” fumosa* and *C. s. aetherodroma* in the western part of the province of Panamá or eastern Chiriquí province, but there are no records of these birds from that area, and I doubt that either *C. fumosa* or *C. spinicauda aetherodroma* crosses the fairly dry area of the Azuero Peninsula (see Fig. 2). Wetmore (1951) did not mention or compare *C. s. aetherodroma* with nominate *C. spinicauda*, even though several

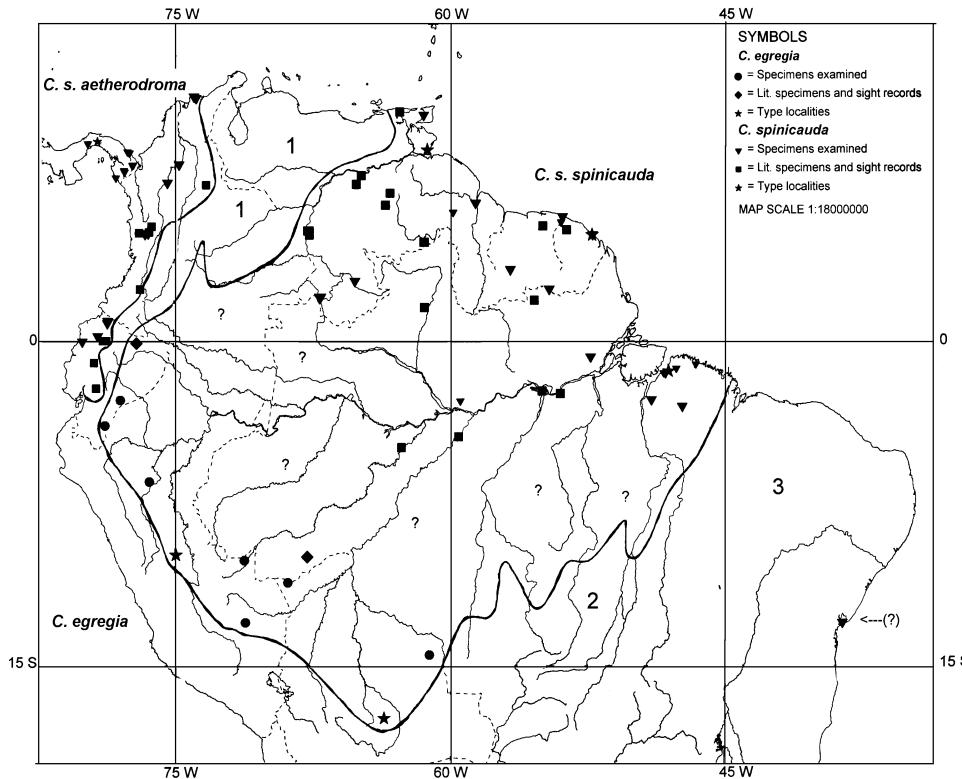


FIG. 4. Distribution of *Chaetura spinicauda aetherodroma* (Northwestern South America) and *C. s. spinicauda* (Northeastern South America). Squares represent reliable specimens reported in literature from: Berlepsch & Hartert (1902), Gyldenstolpe (1950), Phelps & Phelps (1958), Schifter (1992), or specimens not seen by me but deposited at USNM, and INC, or some of my own sight records. Stars represent type specimens from any relevant taxon mentioned on the text. Distribution of *Chaetura egregia* (upper Amazonia); Solid diamonds represent specimens reported by Pinto & Camargo (1954) and Meise (1964), but not seen by me, or my own sight records. Numbers represent dry or semi-dry habitats: 1 = Los llanos; 2 = cerrados region; 3 = caatinga region, and they seem to be uninhabited by *C. spinicauda*. Question marks represent gaps as to what taxon might be present in the area or in one case two specimens from Bahia. A line is given around the approximate forest-covered area around the Amazon basin.

authors included the Panamanian population in nominate *C. spinicauda* (see above). In addition, Wetmore (1951) did not mention that some authors, e.g., Stone (1918), considered the Panamanian form of *C. spinicauda* as a subspecies of *C. cinereiventris* (see above).

Phenotypically, *C. s. aetherodroma* is very similar to nominate *C. spinicauda*. These two

taxa which are disjunctly distributed, nevertheless show some morphometric differences (see Table 1, Fig. 3). Wing length (wl) and body mass (bm) differ significantly (t-test $t_w = 3.12$, $P = 0.0025$, $df = 75$; $t_{bm} = 3.72$, $P < 0.001$, $df = 27$). However, I found no significant difference in tarsus length (tl) and culmen length (cl) (t-test $t_{tl} = 1.45$, $P = 0.15$; $t_{cl} =$

1.13, $P = 0.259$; both $df = 73$). Therefore, it seems that size and geography provide a basis to keep *C. s. aetherodroma* as a separate subspecies.

Chaetura spinicauda aetherodroma ranges from central, and eastern Panama, and western Colombia to southwestern Ecuador, reaching up to 1500 m in Panama (Wetmore 1968) and in western Ecuador (Marín 1993) (see Figs 2 and 4). The arid-semiarid and savanna habitats (see below) seem to be a general barrier to the distribution of this species. Toward the south, its distribution seems to be limited by the arid Tumbezian region (Ecuador-Peru), to the east by the Andes, to the northeast by the arid Guajira Peninsula, and in the llanos region, and to the northwest by the fairly dry area of the Azuero Peninsula, Panama.

Chaetura spinicauda "aethalea". This taxon was described by Todd (1937) and diagnosed as having a darker general coloration and different "the gloss of the back" when compared with a "good" series of the nominate form. Glossiness is related to the freshness of the feathers (Marín 1997 and references therein) and thus is not a useful taxonomic character. Todd considered *aethalea* closest to *C. "spinicauda" fumosa* from "Central America." Although that area was not specified, but probably Costa Rica. Todd restricted the distribution of *Chaetura spinicauda "aethalea"* to south of the Amazon River and west at least to the Tapajós River. The type locality for this taxon is Benevides, Para, Brazil ($01^{\circ}03'S$, $44^{\circ}46'W$) collected by S. M. Klages on 18 September 1918. I examined a paratype (FMNH # 302446), collected by S. M. Klages, on the same site, and date as the type, as well as several specimens from the vicinity (deposited at the AMNH, BMNH, and LACM). I compared these skins to specimens of the nominate form, which is the closest in distribution. I found no difference in visible char-

acters nor size difference in wing length (wl), tarsus length (tl), or culmen length (cl) between *Chaetura spinicauda "aethalea"* and *Chaetura spinicauda spinicauda* (t-test $t_{wl} = 1.82$, $P = 0.076$, $df = 36$; $t_{tl} = 0.469$, $P = 0.641$, $df = 35$; $t_{cl} = 1.75$, $P = 0.089$, $df = 33$) (see also Table 1, Fig. 1). Therefore, I consider *Chaetura spinicauda "aethalea"* indistinguishable from *Chaetura spinicauda spinicauda* and recommend to treat it as a synonym of *spinicauda*.

Two odd specimens attributed to *Chaetura spinicauda "aethalea"* are from the vicinity of Bahia ($12^{\circ}59'S$; $38^{\circ}31'W$), Brazil. One was collected on 13 December 1905 (BMNH 1906.12.21.235) and the second is unsexed and has no date (NMW 42.551), and the locality seems to be uncertain (Schifter 1992). I do not know of any other specimens from eastern Brazil. Whether this reflects a lack of collecting in the Atlantic forest of eastern Brazil, a confusion of existing specimens with *C. cinereiventris*, or a very small unnoticed Atlantic population, cannot be determined at this time. These two specimens might represent an isolated population and a potential new subspecies (see Fig. 4); the nearest specimen records are c.1600 km farther north. Furthermore, the caatinga and cerrado regions are arid and semiarid areas that may be a barrier in gene flow for the Amazonian and eastern Brazilian populations (see Fig. 4, above and below).

Chaetura spinicauda "latirostris". Zimmer & Phelps (1952) described this subspecies on the basis of 17 specimens and gave as type locality Jobure, Territorio Delta Amacuro, Venezuela ($08^{\circ}45'N$, $60^{\circ}50'W$). These authors justified subspecies rank for *latirostris* on the basis that this population differed from other *C. spinicauda* populations by "larger (broader) bill, with a less sharply decurved culmen." No measurements were given, however, to document this difference quantitatively. Culmen morphology in swift skins is a poor taxo-

nomic character unless specimens are fresh. Furthermore, *aetherodroma* was described as nearly the same time as *aethalea* (see above) by Zimmer & Phelps (1952). They compared size and color differences with a mixed series of specimens from Costa Rica, Panama, and Colombia, all labeled as *C. "s." fumosa*. Among the color differences they mentioned was less bluish back in *latirostris*, but this color varies with the amount of plumage wear. I examined two specimens attributed to this subspecies (including the type at the AMNH) which I found it to be phenotypically indistinguishable from *Chaetura spinicanda spinicanda* or the "southern" *Chaetura spinicanda "aethalea"*. My measurements of the type specimen (wing length was 104 mm, tail 38 mm, exposed culmen 4.5 mm, tarsus 9.2 mm) are within the range of the nominate form (see Table 1 and Fig. 1). I conclude from this comparisons that there is no justification for recognizing *latirostris* and *aethalea* be merged with *Chaetura spinicanda spinicanda*.

Chaetura spinicanda spinicanda. Nominate form was originally described from Cayenne, French Guyana (04°56'N; 52°20'W) by Temminck (1839) according to Peters (1940). Based on specimens and reliable accounts, *Chaetura s. spinicanda* has a widespread distribution throughout the Guianas and the lower Amazon basin (Fig. 4). *Chaetura spinicanda* is found wherever there is tropical rain forest (*sensu lato*) in this region except in southern Amazonia which might be a sampling factor. Its distributional limits seem to be the open plains of the llanos to the northwest, and the caatinga and cerrado regions to the south, and to the west *Chaetura spinicanda* is replaced by *C. egregia*. In this respect the distribution of *Chaetura spinicanda* parallels that of *C. spinicanda aetherodroma* in being either limited by dry areas or replaced by other larger *Chaetura* species (see above and Figs 2 and 4).

Chantler & Driessens (1995) give a misleading distributional map for *C. spinicanda* as if were at least four allopatric populations, my data indicate that there are only two allopatric populations. Furthermore, the distributional range of *C. spinicanda* given by these authors erroneously as the southern part of the Amazon basin and the caatinga region. My data indicate that there is no data for the southern part of the Amazon basin, and that *C. spinicanda* does not inhabit the caatinga region (see also above).

Chaetura "cinereiventris" egregia. Its description, Todd (1916), was based on a single specimen, from the Río Surutú, depto., Santa Cruz, Bolivia (17°27'S, 63°40'W). Since its description, it has been placed under *C. cinereiventris* *egregia* by several authors, e.g., Peters (1940) and Bond & Meyer de Schauensee (1943). It is treated by some authors as a separate species e.g., Pinto & Camargo (1954) and Chantler & Driessens (1995).

O'Neill (1969) was the first to find this taxon sympatric with *cinereiventris*, but he did not make any comments on the status of the taxon. Afterward, Davis (1986) collected a specimen in northern Peru, depto. de San Martin, where he found it in a mixed species flock with *C. brachyura* and an unidentified *Chaetura* "possibly" *cinereiventris*. Subsequently, Parker & Remsen (1987) found *cinereiventris* and *egregia* sympatric in Bolivia and questioned whether *egregia* should be treated as a subspecies of *cinereiventris*.

In eastern Ecuador, near the northern end of the range, Marín *et al.* (1992) found *C. egregia* in a similar situation as those found near the southern end of its range by Parker & Remsen (1987). Thus, adding a further proof that *C. cinereiventris* and *C. egregia* occur sympatric throughout the latter's range and therefore they should be heterospecific. I have seen *C. egregia* in northeastern Ecuador near the Colombian border. Although I do

TABLE 3. The two basic groups of the New World spine-tail swifts of the genus *Chaetura*. The “brown-rumped” and “gray-rumped” swifts.

Brown-rumped	Gray-rumped
<i>C. pelagica</i>	<i>C. martinica</i>
<i>C. vauxi</i>	<i>C. spinicauda</i>
<i>C. chapmani</i>	<i>C. fumosa</i>
<i>C. viridipennis</i>	<i>C. egregia</i>
<i>C. meridionalis</i>	<i>C. cinereiventris</i>
<i>C. brachyura</i>	

not have specimens from the area, but I have no doubts that it may also occur in southern Colombia. However, the distribution of this species is still uncertain in some areas, such as in western Brazil. The only records for this species from Brazil, are three specimens from Rio Iquiri, Acre (09°58'N, 67°48'W) (Pinto & Camargo 1954). Although I have not seen the specimens, by size and description they fit this taxon. *Chaetura egregia* reaches up to 1000 m in its elevational range in eastern Ecuador (Marín 1993) and eastern Peru (Davis 1986).

The taxon that occurs sympatrically with *C. egregia* is *C. cinereiventris sclateri*. Phenotypically the former differs from the latter by its darker sooty brown versus dark gray coloration in the ventral plumage, and by having a broad pale-grayish rump versus a dark gray rump (see also Fig. 3). Morphometrically, *egregia* is larger than *cinereiventris*, and there is a statistically significant difference in wing length (wl), Mann-Whitney U-test, $U = 689$, $P < 0.001$, and body mass (t-test; $t_{bm} = 9.23$, $df = 36$, $P < 0.001$).

Phenotypically *C. egregia* is very different from *C. cinereiventris*, e.g., sooty brown body versus bluish-gray, but it has a close affinity with *C. fumosa* and a closer association with *C. spinicauda* than with *C. cinereiventris* (see above and Fig. 3).

Chaetura egregia has a close association with

C. fumosa, however, they are largely disjunctly distributed, but they are very similar in body and rump coloration and pattern, but also the former is larger (see Table 1 and Fig. 1). *Chaetura egregia* has also a close association with *C. spinicauda* but the former has a darker ventral plumage, increasing in darkness toward the lower belly, has a much larger and broader rump that extends to the upper tail coverts, with the gray feathers tipped white, and is considerable larger (Table 1 and Figs 1 and 3).

Chaetura “cinereiventris pachiteae”. Prior to all the Peruvian and Bolivian records of *C. egregia*, Meise (1964) described *Chaetura cinereiventris pachiteae* from Puerto Victoria, Ucayali region, eastern Peru (c. 09°53'S; 74°56'W). Although I have not examined the type, nor the specimens mentioned by Meise, but judging by photos of the specimens in the article, measurements, and mass of the specimens, without doubt they are *C. egregia* (see also above).

GENERAL CONCLUSIONS

Derived from this study and a previous taxonomic survey of the New World spine-tail swifts (Marin 1997), I found that the genus *Chaetura* can be divided in two basic groups, the “gray-rumped” and the “brown-rumped” spine-tailed swifts (Table 3). The former can be further subdivided into the “pale-rumped” and the “gray-rumped” groups. The pale-rumped consists of four species: *C. martinica*, *C. spinicauda*, *C. egregia*, and *C. fumosa*; and the gray-rumped consists of the *C. cinereiventris* group. Although *C. cinereiventris* was not fully treated here, it might comprise more than one species. The “pale-rumped” swifts’ basic body color is various tones of sooty-brown while that of the “gray-rumped” is various tones of bluish-gray. A further separation between these two groups is the color at the base of the feathers in the loral area, which is

white in the former and velvet black in the latter. Within the “pale-rumped” group, there are two subgroups of very closely related species pairs: *C. martinica/spinicauda* and *C. fumosa/egregia*. However, both of these subgroups, are more closely related within and between themselves than to *C. cinereiventris*, as some authors (e.g., Lack 1956, AOU 1983, 1988; Sibley & Monroe 1990) have suggested (see above). Nevertheless, the species *C. martinica*, *C. spinicauda*, *C. fumosa*, and *C. egregia* are closely associated and constitute a superspecies. For the English names of these species see Table 2. If this is accepted, they constitute the *martinica* superspecies, because *C. martinica* was the first one of the group to be described. I do not consider *C. cinereiventris* to be part of the *martinica* superspecies complex (see above), and at best it might be placed as the sister taxon to the *martinica* superspecies. This is pending, however, a full review of the *cinereiventris* group (Marín in prep.).

Swifts in general are regarded as very mobile birds, but it is surprising to see that some *Chaetura* swifts respect certain “barriers” in their distribution, like mountains and breaks in vegetation formations. All species in the *martinica* superspecies complex seem to be forest dependent. Different modes of speciation have contributed to the divergence within the gray-rumped group. The geographic distribution of *C. spinicauda* and *C. fumosa* seems to be delimited by the arid-semiarid habitat which seems to be a general barrier for the distribution of these taxa. The geographical replacement and distribution of the species pair *egregia–spinicauda* in a rather uniform vegetation zone might be attributed to competition parapatry *sensu* Haffer (1992) (see above and Fig. 4). The distribution of the *martinica* superspecies complex coincides with the distribution pattern of tropical rain forest (*sensu lato*), except that might be lacking (see above and Fig. 4) in the southeast Brazilian coastal rain forest region.

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