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A FAUNAL SURVEY OF STREBLID FLIES (DIPTERA: STREBLIDAE) ASSOCIATED WITH BATS IN PARAGUAY

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ABSTRACT: An extensive survey of the ectoparasites infesting bats in Paraguay provides information regarding the taxonomy and host distribution of streblid bat flies at a geographic interface between subtropical and temperate habitats. Five families of bats representing 45 species, including Molossidae (5 genera and 15 species), Natalidae (1 genus and 1 species), Phyllostomidae (11 genera and 15 species), Noctilionidae (1 genus and 2 species), and Vespertilionidae (4 genera and 12 species) were collected from 24 localities across Paraguay and sampled for ectoparasites. In total, 2,467 bat flies were collected, representing 11 genera and 31 nominal species of Streblidae, of which 6 genera and 24 species are new records for Paraguay. No streblids were collected from vespertilionid bats; 23 species infested phyllostomids, 6 species noctilionids, 1 species a natalid, and 1 species molossids. Streblid bat flies were highly specific to certain host groups and individual host species, and their geographic distributions closely followed those of their host bats. Of 31 streblid species surveyed, 27 were monoxenous (i.e., associated with a single host species), and 4 were stenoxenous (i.e., associated with a group of phylogenetically related hosts). The number of streblid species is greatly reduced in the Chaco region west of the Paraguay River, largely because of the lack of phyllostomid host bats.

Streblid flies are obligate, blood-feeding ectoparasites of bats. In temperate North America, they primarily infest vespertilionid bats (Wenzel, 1970; Guerrero, 1994), and a few species overwinter on hibernating bats (Zeve, 1958; Reisen et al., 1976). However, in Central and South America, the species richness of these flies is increased, primarily in association with phyllostomid bats (Wenzel, 1970). The most important previous studies regarding the taxonomy and distribution of neotropical Streblidae were based on faunal surveys in Panama (Wenzel et al., 1966) and Venezuela (Wenzel, 1976). During those studies, 10 new genera and 94 new species were described, and the taxonomic foundation of New World Streblidae was established. However, very little is known about the distribution and host associations of streblid flies infesting bats in the subtropical and temperate regions of South America. From 1991 to 1997, bats of the Yungas Forests in Argentina were surveyed for ectoparasites (Autino et al., 1999). Although 37 bat species are known from this region, which includes sites in the Argentine provinces of Jujuy, Salta, Tucuman, and Catamarca, only 7 species of streblids were reported (Autino et al., 1999). In southern Brazil, 23 species are known from the state of Paraná (Graciolli and de Carvalho, 2001) and 11 species from the state of Rio Grande do Sul (Graciolli and Rui, 2001). An extensive, 5-yr survey of ectoparasites infesting bats in Paraguay provided the opportunity to increase our understanding about the distribution of streblid bat flies across hosts and habitats at the interface of subtropical and temperate zones.

Paraguay is a land-locked country at the northern edge of South America's "Southern Cone." Not only do subtropical and temperate climate zones interdigitate across the Paraguayan landscape, elements of the Interior Atlantic Forest, Cerrado, Pantanal, and Chaco regions have faunal and floral connections within the country (Gorham, 1973). Eastern and western portions of Paraguay represent ecogeographic extremes. The east is dominated by hilly, subtropical deciduous forest and forms the western edge of Atlantic rainforest, whereas western Paraguay is Gran Chaco, which is dry and relatively flat, gradually gaining elevation in the west toward the border of Bolivia. Major rivers include the Paraguay, with its slow, southward-flowing channel bisecting the country into east and west; the Paraná, which is a fast-flowing river forming Paraguay's eastern border with Brazil and its southeastern border with Argentina; and the Pilcomayo, a slow-flowing river that separates southwestern Paraguay from Argentina (Fig. 1). Floristically and geographically (Hayes, 1995), the country is divided into 7 phytogeographic regions. Willig et al. (2000) provided detailed information regarding Paraguay's phytogeographic regions.

The climatic and biotic complexity of landscapes within Paraguay are ideal for surveying bats and their associated streblid bat flies. The Paraguayan bat fauna is moderately diverse, with 6 families, 28 genera, and 54 species known (López-González, 1998), and a number of the tropical bat species reach their range limits within the country (Koopman, 1982; Willig et al., 2003; Stevens et al., 2004). Few published records exist, however, for Paraguayan Streblidae; only 9 species are known from the country. García and Casal (1965) described *Euctenodes* (= *Strebla guarani*) based on 3 specimens from Paraguay, later to be identified as *S. mirabilis* (Waterhouse) (Wenzel, 1976). Wenzel et al. (1966) reported 2 species from insect collections housed at the Field Museum of Natural History (FMNH), Chicago, Illinois: *Megistopoda proxima* Séguy, and *Trichobius furmani* Wenzel. Whitaker and Abrell (1987) added 4 more species: *Aspidoptera falcata* Wenzel, *Megistopoda aranea* Coquillett, *Trichobius joblingi* Wenzel, and *T. parasiticus* Gervais. Additionally, Guerrero (1997) listed *Aspidoptera phyllostomatis* Perty and *Metelasmus pseudopterus* Coquillett. Except for *S. mirabilis*, all these species are associated exclusively with phyllostomid bats that are common and widespread in Paraguay.

The purpose of the present paper is to report the results of a faunal survey of streblid bat flies infesting bats in Paraguay and to establish a foundation for understanding the distribution and host associations of these ectoparasites in a temperate region of South America near the geographic limits of many of the bats known to host streblids in the neotropics. These faunal surveys and the host–parasite collections that they produce are fundamental to the development of future research in coevolution and biogeography.

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FIGURE 1. Map of Paraguay and the 24 localities from which bat flies were sampled. Localities are numbered 0–28 and correspond with bat locality information reported by Willig et al. (2000). Numbered localities on the map correspond with the information provided in Table 1.

MATERIALS AND METHODS

Field methods

During 1994–1999, an extensive collection of small mammals and ectoparasites was made in Paraguay during a survey entitled "Mammals of Paraguay and their ectoparasites: a tropical–subtropical interface." Bats hosting bat flies were collected from 24 localities across Paraguay (Fig. 1), and locality codes were standardized to those used by Willig et al. (2000). Site selection ensured representation of all major biomes, moisture, and temperature gradients in Paraguay. Bats were collected with nylon mist nets or by hand and were kept individually in either cloth bags or polyvinyl chloride tubes with the ends covered by cotton cloth. Details regarding the collection of bats have been reported previously by Willig et al. (2000). Bats were anesthetized and brushed for ectoparasites, which were stored in 70% ethanol. Details regarding ectoparasite collection have been described previously by Gettinger (1992). At all times, great care was taken to avoid cross-host contamination of ectoparasites.

TABLE I. Locality information for 24 sites in Paraguay at which bat flies were collected from 1995 to 1999. Site numbers are as described in Figure 1 and Willig et al. (2000).

Site	Department	Locality	Latitude (S)	Longitude (W)	Elevation (m)
0	Central	Asunción, Universidad Católica	25°19.49′	57°38.29′	120
1	Presidente Hayes	Estancia La Victoria	23°39.03′	58°34.79′	120
4	Cordillera	Estancia Sombrero	25°04.26′	56°36.08′	100
5	Paraguari	Lago Ypoá	25°56.71′	57°26.80′	120
6	Concepción	Estancia Cerrito	23°15.14′	57°29.57′	120
7	Alto Paraguay	Fuerte Olimpo	21°02.37′	57°52.29′	120
8	Misiones	Ayolas	27°23.42′	56°50.15′	70
9	Itapúa	Parque Nacional San Rafael	26°45.46′	55°51.67′	170
10	Alto Paraguay	Bahía Negra	20°10.98′	58°09.42′	90
11	San Pedro	Yaguareté Forest	23°48.50′	56°07.68′	250
12	Amambay	Parque Nacional Cerro Corá	22°37.90′	56°01.43′	280
13	Concepción	Parque Nacional Serranía de San Luis	22°37.91′	57°21.35′	270
14	Neembucú	Estancia Yacaré	26°37.94′	58°07.46′	60
15	Canindeyú	Reserva Natural del Bosque Mbaracayú	24°07.69′	55°30.34′	250
16	Presidente Hayes	Estancia Loma Porá	23°29.92′	57°32.92′	80
17	Alto Paraguay	Estancia Tres Marias	21°16.72′	59°33.13′	70
18	Presidente Hayes	Estancia Samaklay	23°28.81′	59°48.43′	120
19	Boquerón	Dr. Pedro P. Peña	22°27.16′	62°20.65′	240
21	Canindeyú	Estancia Rivas	24°30.43′	54°38.25′	300
22	Caazapá	Estancia Golondrina	25°32.30′	55°29.02′	300
23	Paraguari	Parque Nacional Ybycuí	26°04.64′	56°50.98′	150
24	Boquerón	Parque Nacional Teniente Enciso	21°11.40′	61°41.81′	250
25	Alto Paraguay	Palmar de Las Islas	19°32.91′	60°31.64′	150
28	Itapúa	Estancia Parabel	26°21.80′	55°31.45′	400

Laboratory methods

Most specimens were studied in alcohol under a dissection microscope, whereas some were slide-mounted in Canada balsam (cf. Wenzel et al. 1966) for examination under a compound microscope. Identifications were confirmed by comparison of the Paraguayan specimens to type specimens and other reference collections housed at the FMNH. The specimen information presented here extends the classic taxonomic catalogs documenting streblids in Panama (Wenzel et al., 1966) and Venezuela (Wenzel, 1976). The specimens from Paraguay have been deposited in the research collection of the FMNH as well as in other institutions that have substantial holdings of neotropical Streblidae. Each streblid specimen can be traced to a voucher host specimen that has been deposited in either the Museum of Texas Tech University or the Museo Nacional de Historia Natural del Paraguay.

RESULTS

From 2,467 fly specimens collected during the present study, we identified 11 genera and 31 nominal species of Streblidae; of these, 6 genera and 24 species are new records for Paraguay. New generic records include *Mastoptera* Wenzel, *Noctiliostrebla* Wenzel, *Paradyschiria* Speiser, *Paratrichobius* Costa Lima, *Speiseria* Kessel, and *Xenotrichobius* Wenzel. New species records include *Mastoptera guimaraesi* Wenzel, *M. minuta* Costa Lima, *Metelasmus wenzeli* Graciolli and Dick, *Noctiliostrebla aitkeni* Wenzel, *N. dubia* Rudow, *N. maai* Wenzel, *Paradyschiria fusca* Speiser, *P. parvula* Falcoz, *Paratrichobius longicrus* Miranda Ribeiro, *P. salvini* Wenzel, *Speiseria ambigua* Kessel, *Strebla chrotopteri* Wenzel, *S. curvata* Wenzel, *S. diaemi* Wenzel, *S. guajiro* Garcia and Casal, *S. wiedemanni* Kolenati, *Trichobius angulatus* Wenzel, *T. diaemi* Wenzel, *T. dugesii* Townsend, *T. galei* Wenzel, *T. jubatus* Wenzel, *T. longipes* Rudow, *T. uniformis* Curran, and *Xenotrichobius noctilionis* Wenzel. Thus, 11 genera and 33 species of streblid bat flies have been reported to occur in Paraguay.

In total, 2,893 individuals representing 45 species of bats were sampled for ectoparasites in Paraguay; streblids were collected from 19 host species (42.2%). Of 5 bat families surveyed, 3 were highly infested; Phyllostomidae (11 of 15 bat species, hosting 23 species of streblids), Noctilionidae (2 of 2 bat species, hosting 6 species of streblids), and Natalidae (1 of 1 bat species, hosting 1 species of streblid). Bats of the Molossidae also were infested, but at lower levels (5 of 15 bat species, hosting 1 streblid species). Although 52 specimens of *Pygoderma bilabiatum* Wagner (Phyllostomidae) were sampled, none yielded bat flies. No streblid flies were collected from vespertilionid bats.

Streblid bat flies were highly host specific, and their geographic distributions closely followed those of their host bats. No fly species were collected outside the range of the primary host. Species richness is much higher in eastern than in western Paraguay; of 31 species of streblids collected, 28 occur in the east (and 19 of these only in the east). In contrast, 12 species occur in the west (and 3 of these only in the west). Twenty-seven of the 31 species were monoxenous (i.e., associated with a single host species). Four species were stenoxenous (= pleioxenous; i.e., associated with ≥2 phylogenetically related host species). One of the monoxenous fly species is based on a questionable record (see *Speiseria ambigua* species account).

For each fly species, the following accounts list the author and year of description, distribution within Paraguay by site number(s) (Fig. 1, Table I), and commentary where applicable. The streblid bat fly species collected in Paraguay during the

TABLE II. List of streblid bat fly species collected in Paraguay during the present study. Host association and ecological information are presented as follows: Species = bat fly species; Primary host(s) = host species defined as primary host; SI = specificity index, percentage of total bat flies of a single species found on the primary host(s); Prevalence(s) = percentage of primary host individuals sampled that yielded bat flies (no. of positive host individuals, no. of host individuals sampled); Other host(s) = host species defined as nonprimary hosts (no. of parasites found on host).

Species	Primary host(s)	SI (%)	Prevalence(s) (%)	Other host(s)
Aspidoptera falcata	*Sturnira lilium* (230)	98.7	29.6 (120, 406)	*Artibeus fimbriatus* (1)
				A. lituratus (1)
				Platyrrhinus lineatus (1)
A. phyllostomatis	*Artibeus fimbriatus* (19)	65.5	18.5 (15, 81)	*A. lituratus* (2)
	A. jamaicensis Leach (8)	27.6	15.8 (6, 38)	
Mastoptera guimarãesi	*Phyllostomus hastatus* (1)	100.0	100.0 (1, 1)	
M. minuta	*Lophostoma brasiliense* (11)	100.0	100.0 (1, 1)	
Megistopoda aranea	*A. fimbriatus* (66)	63.5	55.6 (45, 81)	*A. lituratus* (2)
	A. jamaicensis (36)	34.6	36.8 (14, 38)	
M. proxima	*Sturnira lilium* (360)	98.1	48.3 (196, 406)	*A. fimbriatus* (2)
				A. lituratus (2)
				Carollia perspicillata (2)
				P. lineatus (1)
Metelasmus pseudopterus	*A. fimibriatus* (17)	81.0	18.5 (15, 81)	*A. lituratus* (1)
	A. jamaicensis (3)	14.3	5.3 (2, 38)	
M. wenzeli	*S. lilium* (5)	100.0	1.0 (4, 406)	
Noctiliostrebla aitkeni	*Noctilio leporinus* (79)	100.0	46.4 (13, 28)	
N. dubia	*N. leporinus* (16)	100.0	25.0 (7, 28)	
N. maai	*N. albiventris* (213)	100.0	67.2 (45, 67)	
Paradyschiria fusca	*N. leporinus* (227)	100.0	75.0 (21, 28)	
P. parvula	*N. albiventris* (434)	100.0	91.0 (61, 67)	
P. longicrus	*A. lituratus* (156)	100.0	24.4 (85, 348)	
P. salvini	*Platyrrhinus lineatus* (3)	100.0	3.4 (3, 89)	
Speiseria ambigua				*Glossophaga soricina* (1)
Stebla chrotopteri	*Chrotopterus auritus* (15)	100.0	50.0 (2, 4)	
S. curvata	*G. soricina* (5)	100.0	5.5 (3, 55)	
S. diaemi	*Diaemus youngi* (37)	97.4	80.0 (8, 10)	*Eumops patagonicus* (1)
S. guajiro	*Carollia perspicillata* (25)	96.2	23.6 (17, 72)	*A. fimbriatus* (1)
S. wiedemanni	*Desmodus rotundus* (76)	100.0	23.5 (12, 51)	
Trichobius angulatus	*P. lineatus* (10)	100.0	6.7 (6, 89)	
T. diaemi	*Diaemus youngi* (5)	100.0	30.0 (3, 10)	
T. dugesii	*G. soricina* (8)	100.0	9.1 (5, 55)	
T. galei	*Natalus stramineus* (6)	100.0	100.0 (1, 1)	
T. joblingi	*C. perspicillata* (64)	100.0	45.8 (33, 72)	
T. jubatus	*Eumops patagonicus* (29)	36.3	4.4 (23, 521)	*E. glaucinus* (1)
	Molossus rufus (27)	33.8	15.9 (17, 107)	*Molossops temminckii* (2)
	M. molossus (21)	26.3	7.4 (17, 231)	
T. longipes	*Phyllostomus hastatus* (1)	100.0	100.0 (1, 1)	
T. parasiticus	*Desmodus rotundus* (219)	100.0	31.4 (16, 51)	
T. uniformis	*G. soricina* (8)	100.0	10.9 (6, 55)	
Xenotrichobius noctilionis	*Noctilio albiventris* (6)	100.0	9.0 (6, 67)	

present study are listed in Table II. Table II also presents data relevant to the species accounts, such as the primary host(s), specificity index, prevalence, and other hosts.

Aspidoptera falcata Wenzel, 1976

Distribution: Amambay (12); Canindeyú (15, 21); Concepción (13); Cordillera (4); Itapúa (9, 28); Ñeembucú (14); Paraguari (5, 23); San Pedro (11).

Commentary: The primary host in Paraguay is *Sturnira lilium*. Because nonprimary hosts are infested only by single specimens and the primary host also was collected on the same day, the records from other host bats are considered to be contaminants. In Venezuela, 98.9% of the 755 *Aspidoptera falcata* specimens were collected from *Sturnira* spp. (Wenzel, 1976).

Aspidoptera phyllostomatis Perty, 1833

Distribution: Canindeyú (21); Concepción (13); Cordillera (4); Itapúa (28).

Commentary: The primary hosts are *Artibeus fimbriatus* and *A. jamaicensis* (together hosting 93.1% of the specimens collected). The remaining 2 specimens were collected from 2 individuals of *A. lituratus* on 2 separate days when individuals of the primary host were collected. In Venezuela, 95.5% of *A. phyllostomatis* were associated with *A. jamaicensis*, and Wenzel

(1976) also did not consider *A. lituratus* to be a true host of this fly species.

Mastoptera guimaraesi Wenzel, 1966

Distribution: Concepción (13).

Commentary: This host represents the second record of *P. hastatus* in Paraguay. The pregnant female was collected in Cerrado habitat at the extreme northeast of Paraguay.

Mastoptera minuta Costa Lima, 1921

Distribution: Presidente Hayes (1).

Commentary: In Venezuela, the characteristic host of *M. minuta* was *Lophostoma silvicolum* d'Orbigny (Wenzel, 1976). The 11 specimens from Paraguay were collected from 1 individual of *Lophostoma brasiliense*. The taxonomy of *Mastoptera* is complex and poorly understood, and Wenzel (1976) noted that undescribed species exist within *M. minuta*. We assign the Paraguayan specimens to *M. minuta*, but a revision of *Mastoptera* may establish these specimens as distinct.

Megistopoda aranea Coquillett, 1899

Distribution: Amambay (12); Caazapá (22); Canindeyú (15, 21); Concepción (6, 13); Cordillera (4); Itapúa (9, 28); Ñeembucú (14); Paraguari (5).

Commentary: The primary hosts are *Artibeus fimbriatus* and *A. jamaicensis* (together hosting 98.1% of the specimens collected). The remaining 2 flies were collected from 1 individual of *A. lituratus* on the same day that several primary hosts also were collected; we consider the records from *A. lituratus* to be contaminants. Most large *Artibeus* bats typically are infested by a species of *Aspidoptera*, a species of *Megistopoda*, and occasionally, a species of *Metelasmus*. However, *A. lituratus* is unique in that it is infested only by *Paratrichobius longicrus*.

Megistopoda proxima Séguy, 1926

Distribution: Amambay (12); Caazapá (22); Canindeyú (15, 21); Concepción (13); Cordillera (4); Itapúa (9, 28); Ñeembucú (14); Paraguari (5, 23); San Pedro (11).

Commentary: The characteristic host is *Sturnira lilium*. The remaining 7 flies were collected from 7 individuals of 4 bat species; all of these dubious records were collected on days that the primary host was collected. Thus, we consider records of *M. proxima* from hosts other than *S. lilium* to be contaminants. Wenzel (1976) suggested that *Megistopoda proxima*, as currently described, represents a complex of species; specimens infesting other species of *Sturnira* (e.g., *S. ludovici* Anthony, *S. tildae* de la Torre, *S. erythromos* Tschudi) and that have been referred to *M. proxima* almost certainly represent other species of *Megistopoda*. The morphological differences among *M. proxima sensu lato* are distinct in terms of thorax shape, degree of transverse thoracic suture, and chaetotaxy of the dorsal thoracic surface. Moreover, nomenclatural problems exist regarding *M. proxima* and *M. theodori* Wenzel (Wenzel, 1976). *Megistopoda* spp. have not been studied in detail and are in need of revision. In Venezuela, 98.7% of specimens referred to the *M. proxima* complex were collected from *Sturnira* spp. (Wenzel, 1976). In Panama, *S. lilium parvidens* was the characteristic host of *M. proxima*, and Paraguayan specimens from *S. lilium*, when compared to the Panamanian material, were referred to *M. proxima* (Wenzel et al., 1966).

Metelasmus pseudopterus Coquillett, 1907

Distribution: Canindeyú (15, 21); Concepción (13); Cordillera (4); Itapúa (28); San Pedro (11).

Other Paraguayan records (Coquillett, 1907): Paraguari: 1 (sex not given) from *Artibeus lituratus* Sapucái (no specific locality or date given).

Commentary: Coquillett (1907) briefly described *M. pseudopterus* and included the following information for the type specimen: "Sapucay, Paraguay, South America. A single specimen collected on a bat, *Artibius (sic) lituratus*." Coquillett did not identify the sex, although his illustrated specimen appears to be female. Graciolli and Dick (2004) discussed host relationships of *Metelasmus* spp. and concluded that across the range of *M. pseudopterus*, the true hosts were *A. fimbriatus, A. jamaicensis*, and *A. planirostris* (Spix). More comparative study is needed on this genus.

Metelasmus wenzeli Graciolli and Dick, 2004

Distribution: These are type localities. Canindeyú (21).

Commentary: A new form of *Metelasmus* was first reported as a result of the Smithsonian Venezuelan Project (Wenzel, 1976) from 2 flies infesting *Sturnira ludovici* in Barinas, Venezuela. Wenzel did not describe the new form, however, because the 2 specimens were damaged. The form from *S. ludovici* is almost certainly not *M. wenzeli*, but we lack specimens to confirm this (G. Graciolli, pers. comm.). *Metelasmus wenzeli* also is known from Paraná and São Paulo states in Brazil. *Metelasmus wenzeli* was described recently by Graciolli and Dick (2004), and the characteristic host in both Paraguay and Brazil was *Sturnira lilium*. *Metelasmus wenzeli* is a rarely sampled species given the prevalence of $<1\%$ in >400 bats sampled in Paraguay.

Noctiliostrebla aitkeni Wenzel, 1966

Distribution: Boquerón (19); Concepción (6); Presidente Hayes (1, 18).

Commentary: This species is known to coexist on *Noctilio leporinus* with a congener, *N. dubia* (see species account).

Noctiliostrebla dubia Rudow, 1871

Distribution: Concepción (6); Presidente Hayes (1, 18).

Commentary: It is a remarkable exception among streblid flies when congeners coexist on host individuals. Of the 7 bats hosting *N. dubia*, 6 were simultaneously infested with *N. aitkeni*; 1 bat was parasitized by 15 *N. aitkeni* and 4 *N. dubia*. These species are very similar in overall size and morphology, but they possess distinctly different second sternites. *Noctiliostrebla aitkeni* possesses the generalized sternum 2, which is slightly convex and without any heavy setae. However, *N. dubia* possesses a strongly tumid sternum 2, which is covered posteroventrally with very heavy, spinelike setae. Observational and experimental studies are needed for confirmation, but the differences in sternum 2 morphology of these coexisting congeners possibly adapt them to inhabit different microhabitats on the host's body.

Noctiliostrebla maai Wenzel, 1966

Distribution: Alto Paraguay (10); Concepción (6); Misiones (8); Paraguari (5); Presidente Hayes (1).

Paradyschiria fusca Speiser, 1900

Distribution: Boquerón (19); Concepción (6); Presidente Hayes (1, 18).

Paradyschiria parvula Falcoz, 1931

Distribution: Alto Paraguay (7, 10); Concepción (6); Misiones (8); Paraguari (5); Presidente Hayes (1).

Paratrichobius longicrus Miranda Ribeiro, 1907

Distribution: Caazapá (22); Canindeyú (15, 21); Central (0); Cordillera (4); Itapúa (28); Paraguari (23); San Pedro (11).

Commentary: As in Venezuela (Wenzel, 1976), the characteristic host in Paraguay is *Artibeus lituratus*, which is not known to host parasites of *Megistopoda* spp. and *Aspidoptera* spp., characteristic parasites of other species of *Artibeus* in Paraguay (*A. jamaicensis* and *A. fimbriatus*) and elsewhere in the New World. *Paratrichobius* and *Megistopoda* may be ecological equivalents, because they are fairly similar in gross morphology, possess long hind legs, and appear to be adapted to move over the fur of their hosts. They can be distinguished easily, however, in that *Paratrichobius* spp. have fully functional wings but *Megistopoda* spp. have nonfunctional, straplike wings.

Paratrichobius salvini Wenzel

Distribution: Amambay (12).

Commentary: Chiroderma salvini Dobson is the type host of *Paratrichobius salvini*, but this species has been reported in stenoxenous association with several related host species. Wenzel et al. (1966) in Panama, and Wenzel (1976) in Venezuela, noted a wide range of morphological variation among *P. salvini* infesting different host species. It is probable that *P. salvini* is a complex of species infesting bats of certain species in the genera of Stenodermatinae, including *Chiroderma* Peters, *Platyrrhinus* Saussure, *Vampyressa* Thomas, and *Vampyrodes* Thomas. The specimens collected from Paraguay certainly fall into this complex, and pending revisionary studies, we have assigned the Paraguayan specimens infesting *P. lineatus* to *Paratrichobius salvini*.

Speiseria ambigua Kessel, 1925

Distribution: Amambay (12).

Commentary: In Venezuela and most of the New World tropics, *Speiseria ambigua* is a characteristic parasite of *Carollia perspicillata*. Fully 96% of the *S. ambigua* collected in Venezuela were from 220 specimens of *C. perspicillata* (Wenzel, 1976). *Carollia perspicillata* also was commonly captured in Paraguay. Four individuals of *C. perspicillata* were collected at Cerro Corá the same night as this particular *Glossophaga soricina*, and one of the *Carollia* specimens possibly hosted this species of *Speiseria*. This streblid is known to be an unusually excitable species that readily abandons the host when disturbed (pers. obs.). However, it is puzzling that of the 72 *C. perspicillata* searched for parasites, none was host to *S. ambigua* (although other characteristic streblids, *Trichobius joblingi* and *Strebla guajiro*, were prevalent in Paraguay).

Strebla chrotopteri Wenzel, 1976

Distribution: Canindeyú (15); San Pedro (11).

Strebla curvata Wenzel, 1976

Distribution: Amambay (12).

Strebla diaemi Wenzel, 1966

Distribution: Alto Paraguay (7); Presidente Hayes (1, 16).

Commentary: This bat fly species is a typical parasite of the vampire bat (*Diaemus youngi*). The single specimen recorded from the molossid bat (*Eumops patagonicus*) is almost certainly a contaminant, because a specimen of *D. youngi* was sampled on the same day before the specimen of *E. patagonicus*. Moreover, Wenzel et al. (1966) and Wenzel (1976) concur that *D. youngi* is the true host of *S. diaemi*.

Strebla guajiro Garcia and Casal, 1965

Distribution: Amambay (12); Canindeyú (15, 21).

Commentary: The characteristic host in Paraguay is *Carollia perspicillata* (hosting 25 of 26 specimens [96.2%]). The single specimen from *A. fimbriatus* probably represents a contaminant, because the host bat sampled immediately before was *C. perspicillata*. In Venezuela, *S. guajiro* also was known from other species of *Carollia* (Wenzel, 1976). Of the 586 specimens of *S. guajiro* sampled during the Venezuelan survey, 577 (98.5%) were collected from *Carollia* spp. The 9 remaining specimens were sampled individually from 9 bats representing 9 different species (Wenzel, 1976).

Strebla wiedemanni Kolenati, 1856

Distribution: Alto Paraguay (7); Amambay (12); Concepción (13).

Trichobius angulatus Wenzel, 1976

Distribution: Amambay (12).

Commentary: Although *Trichobius angulatus* was recorded from *Platyrrhinus aurarius* Handley and Ferris in Venezuela, the congener *P. lineatus* appears to be the characteristic host in Paraguay.

Trichobius diaemi Wenzel, 1976

Distribution: Presidente Hayes (16).

Trichobius dugesii Townsend, 1891

Distribution: Amambay (12); Concepción (13).

Commentary: Trichobius dugesii is a characteristic parasite of *Glossophaga soricina* in Paraguay. It was known to occur commonly on *Glossophaga longirostris* Miller in Venezuela (Wenzel, 1976). This species co-occurs on *G. soricina* with another congener, *T. uniformis*.

Trichobius galei Wenzel, 1966

Distribution: Concepción (13).

Trichobius joblingi Wenzel, 1966

Distribution: Amambay (12); Caazapá (22); Canindeyú (15, 21); Concepción (13); Itapúa (9); San Pedro (11).

Trichobius jubatus Wenzel, 1976

Distribution: Alto Paraguay (17, 25); Boquerón (24); Cordillera (4); Ñeembucú (14); Paraguari (5); Presidente Hayes (1, 16, 18).

Commentary: Trichobius jubatus is exceptional among Paraguayan bat flies in that it is the only species regularly collected from more than 1 genus of host bat. However, it was collected exclusively from molossid bats. Wenzel (1976) reported *T. jubatus* from both *M. rufus* and *M. molossus*, as does the present study. However, our specimens from *E. patagonicus* represent a new host record for *T. jubatus*. The molossid genera *Molossus* É. Geoffroyi and *Promops* Gervais are closely related sister taxa, with *Eumops* Miller as the sister group to the *Molossus–Promops* clade (Jones et al., 2002; L. K. Ammerman, pers. comm.). Both *Promops centralis* Thomas (4 specimens) and *P. nasutus* Spix (8 specimens) were sampled for parasites during the present study, but both species failed to yield bat fly specimens. Given the relationships of these molossid genera, either vertical or horizontal transmission may explain the presence of *T. jubatus* on *E. patagonicus*. However, whether *T. jubatus* represents 2 or more species is unknown at this time and warrants further study. The records from *E. glaucinus* and *Molossops temminckii* could represent contamination, because primary host bats were captured on the same day.

Trichobius longipes Rudow, 1871

Distribution: Concepción (13).

Commentary: Trichobius longipes was a characteristic parasite of *P. hastatus* in Venezuela (Wenzel, 1976), but this bat species is rare in Paraguay. The pregnant female host was collected in Cerrado habitat in the extreme northeast of Paraguay, and it represents the second record of *P. hastatus* in Paraguay.

Trichobius parasiticus Gervais, 1844

Distribution: Alto Paraguay (7, 17); Amambay (12); Concepción (13); Cordillera (4).

Commentary: Wenzel et al. (1966) reported that *T. furmani* may replace *T. parasiticus* on *D. rotundus* in some parts of South America. This does not appear to be the case in Paraguay (see *Discussion*).

Trichobius uniformis Curran, 1935

Distribution: Amambay (12).

Commentary: The holotype of *T. uniformis* was collected in Panama from *Glossophaga soricina* (Curran, 1935). The strong association of *T. uniformis* with *G. soricina* has been verified by survey work in Panama (Wenzel et al., 1966) and in Venezuela (Wenzel, 1976). This bat fly co-occurs on *G. soricina* with a congener, *T. dugesii*.

Xenotrichobius noctilionis Wenzel, 1976

Distribution: Misiones (8); Presidente Hayes (1).

Commentary: To our knowledge, this is the first report of *Xenotrichobius* sp. for Paraguay. Guerrero (1998) provided a review, including the description of *X. linaresi* from Venezuelan *N. leporinus*. Two other forms (both occurring on Peruvian *N. albiventris*) were described by Guerrero (1998) but not named at the time, because only a single specimen represented each form. It remains unclear whether these 2 forms represent 1 or 2 species (Guerrero, 1998). The Paraguayan specimens compare with *Xenotrichobius* sp. (sensu Guerrero, 1998) in that the females possess long, fine, dorsolateral connexivial setae and long setae on the epiproct and the male postgonites are long, fine, and acuminate. However, they differ from *Xenotrichobius* sp. (sensu Guerrero 1998) in that the termini of the postgonites of the male Paraguayan specimens are more curved ventrally. Also, 1 of the forms reported by Guerrero (1998) had a complete longitudinal thoracic suture, whereas this suture extended only half the distance to the transverse suture in the other form. All the Paraguayan specimens possess an incomplete longitudinal suture; however, they vary in length from one-half to three-fourths of the distance to the transverse suture. We have had the opportunity to study 28 specimens (13 male and 15 female) of *Xenotrichobius* sp. collected from *N. albiventris* in the Manu Biosphere Reserve in Peru (pers. obs.). All the Manu specimens possessed a complete longitudinal suture; however, they also all possessed a short gap in the suture, approximately two-thirds of the distance to the transverse suture. The specimen reported by Guerrero (1998) possessed a truly complete longitudinal suture. Given that the character variation within *Xenotrichobius* sp. is in need of further study, and that the specimens from Manu will be treated elsewhere, we shall defer a taxonomic decision regarding the Paraguayan specimens pending a complete generic revision of *Xenotrichobius*.

DISCUSSION

This specimen-based survey provides the first extensive documentation of the taxonomy, geography, and host distribution of streblid flies infesting bats in Paraguay. Until now, only 9 species were known from the country, but the occurrence of *Strebla mirabilis* in Paraguay is controversial. García and Casal (1965) described *Euctenodes guarani* from "Paraguay, sobre murciélago." Wenzel (1976) studied those illustrations and determined that their new taxon was in synonymy with *Strebla mirabilis*, which in Venezuela is a stenoxenous parasite of *Trachops cirrhosus* Spix, *Phyllostomus elongatus* É. Geoffroy, and *P. hastatus*. To our knoweldge, the first 2 host species have never been collected in Paraguay (López-González, 1998; Willig et al. 2000), and only 2 Paraguayan specimens of *P. hastatus* are known (the second of which hosted specimens in the present study), making it improbable that *S. mirabilis* has been collected in Paraguay. However, while studying Brazilian *Strebla*, Graciolli (2004) determined that *S. guarani* was, indeed, a true species and validated the taxon in association with 2 phyllostomine bats, *Mimon bennettii* Gray and *Tonatia bidens* Spix, in Brazil. Graciolli has been unable to examine the type specimens of *S. guarani*, which are in Buenos Aires, Argentina (G. Graciolli, pers. comm.), to confirm that the Paraguayan specimens are, indeed, *S. guarani*. Nonetheless, it is plausible that *S. gua-*

rani occurs in Paraguay in association with *T. bidens*, and if so, the type specimens of García and Casal (1965) likely came from the same host.

The report by Wenzel et al. (1966) of Paraguayan *T. furmani* requires comment. One specimen is known from "Rückenau, Friesland Colony near Itacurubi del Rosario, [Department San Pedro] Paraguay, 14 June 1960, S. L. Loewen," collected from *Glossophaga soricina soricina*. *Trichobius furmani* is a characteristic parasite of the vampire bats (Wenzel et al., 1966). It is unlikely that *G. soricina* was the true host to this specimen. However, the association may represent a transitory one, because *G. soricina* and *Desmodus rotundus* have been observed roosting in close proximity (B. D. Patterson, pers. comm.; unpubl. data). In Paraguay, 58 and 11 *D. rotundus* and *Diaemus youngi*, respectively, were collected, but none was host to *T. furmani*. It has been suggested that the species may replace *Trichobius parasiticus* in some parts of South America (Wenzel et al., 1966). Indeed, 22 of 139 *Desmodus rotundus* searched for parasites in Rio de Janeiro State, Brazil, hosted 97 individuals of *T. furmani*, yet none hosted *T. parasiticus* (C. E. Esbérard, pers. comm.). Given the faunal affinities of eastern Paraguay with the Atlantic Forest region of Brazil, it is noteworthy to encounter complete species replacement in a short geographic distance.

Bat flies were recovered from only 58% of the total number of sampled bat species, but 8 of 11 genera and 23 of 31 species of flies (74%) infested phyllostmid bats. Of 10 species of phyllostomid bats with >5 specimens sampled in the survey, 9 were infested with streblids; only *Pygoderma bilabiatum* (n = 52) remained free of bat flies. *Pygoderma* is a member of the phyllostomid subtribe Stenodermatina, a highly supported monophyletic clade that includes species of *Ametrida* Gray, *Ardops* Miller, *Ariteus* Gray, *Centurio* Gray, *Pygoderma*, *Sphaeronycteris* Peters, and *Stenoderma* É. Geoffroy (Baker et al., 2003). To date, we are aware of no substantiated records of bat flies associated with any hosts in this clade. In his summary of host associations for New World Streblidae, Guerrero (1998) listed 2 species associated with *Ametrida centurio* Gray and 5 species associated with *Sphaeronycteris toxophyllum* Peters. However, Guerrero (1998) did not discriminate between primary-host associations and those that may have been transitory or the result of sample contamination. Because each of the 7 streblid species listed for these 2 hosts is strongly associated with other host species, we regard the records for species of *Ametrida* and *Sphaeronycteris* to be transitory or to represent contamination. Moreover, these bat genera, considered together, represent the most derived clade within the Phyllostomidae (Baker et al., 2003). If members of the host clade were true hosts to bat flies, we would expect the flies to form a unique fauna; to our knowledge, there exist no such flies. Three explanations are possible (Paterson et al., 1999) for the lack of streblids on the tribe Stenodermatina: (1) Streblids may have gone extinct on this lineage following the host speciation event, (2) streblids may have been absent on the ancestral population that gave rise to the host lineage, or (3) streblids occur in such low numbers on these hosts that they have not yet been detected.

Although 403 bats representing 4 genera and 12 species were sampled, streblids were not collected from any vespertilionid bats in Paraguay. In North America, Central America, and the Antilles, vespertilionid bats are infested with species of the *Trichobius major* species group (Wenzel, 1970; Peterson and Hůrka, 1974). However, species of this group reach their southern distributional limits in northern South America, and no species of the *T. major* group are known from south of Peru (Guerrero, 1994). No equivalent group of species parasitize vespertilionid bats in the southern temperate zone. Wenzel et al. (1966) provided morphological evidence suggesting that the *Trichobius major* group, along with *Anatrichobius* Wenzel and *Joblingia schmidti* Dybas and Wenzel, form a phylogenetically related group. *Anatrichobius* spp. and *J. schmidti* are relatively rare species that parasitize species of *Myotis* in Central and South America. *Joblingia schmidti* appears to be restricted to Guatemala and Panama (Guerrero, 1995), and *Anatrichobius* spp. are distributed as far south as northern Argentina and southern Brazil (Graciolli, 2003). Wenzel and Tipton (1966) stated that *A. scorzai* Wenzel and *J. schmidti* were, in Panama, restricted to the "Lower Montane Zone" of 1,500–2,600 m. In southern Brazil, *Anatrichobius* spp. are restricted to elevations >600 m (Graciolli, 2003). The highest altitude sampled in Paraguay was 400 m. Results of the present survey concur with those of Graciolli (2003), and it is probable that a lack sampling at elevations >600 m precluded the collection of bat flies from vespertilionid bats in Paraguay.

Two other families of insectan ectoparasites share many ecological and morphological characteristics with the Streblidae and infest Paraguayan bats. Nycteribiid flies (Diptera: Nycteribiidae) (Guimarães, 1972) and polyctenid bugs (Hemiptera: Polyctenidae) (Ueshima, 1972) are obligate blood-feeding associates of vespertilionid and molossid bats, respectively. In Paraguay, we collected nycteribiids from vespertilionid bats and polyctenids from molossid bats. Streblid flies were not collected from vespertilionids, and a single species, *T. jubatus*, was collected from molossids in low numbers (prevalence < 16%). These complementary faunal distributions have been proposed as evidence of competitive displacement (Wenzel and Tipton, 1966; Marshall, 1982).

Life-cycle studies with streblid bat flies show that they are not completely host limited but pupiposit on substrates near roosting bats; newly emerged adult flies must find and choose their hosts (Overal, 1980; Fritz, 1983). Given this dynamic of their life cycle, the observed level of host specificity is truly remarkable. Noctilionid bats often roost with other species of bats and usually are heavily infested with streblids. In Paraguay, we collected 6 species of streblids from both species of noctilionid bats. Eighty-eight percent of sampled noctilionids were infested with streblids; 63 of 67 *Noctilio albiventris* and 21 of 28 *N. leporinus* were infested with 653 and 322 streblids, respectively. However, the host specificity of these fly species was 100%. Moreover, of 2,467 streblid flies collected in the present study, only 21 (0.85%) were collected from nonprimary host species. Whereas this level of host specificity is remarkable alone, in all but 1 case of a nonprimary host association, the primary host species was captured and sampled the very same day. In major mammal–ectoparasite surveys conducted over the years in Panama (Wenzel et al., 1966), Venezuela (Wenzel, 1976), and Paraguay (present study), increasing emphasis has been placed, via sampling protocols, on controlling for cross-host contamination of ectoparasites. The remarkable host specificity of streblid bat flies becomes evident when such measures are in place while sampling the hosts and parasites.

Not surprisingly, the distribution of host-specific parasites, such as streblid bat flies, tends to follow the distribution of their hosts and little else. Biogeographically, the streblid fauna of Paraguay can be broken down into a rich eastern fauna, a depauperate western fauna, and a widespread fauna. For example, 19 species were collected only from localities east of the Paraguay River, whereas 3 species are known only from west of the river. Nine species were collected on both sides of the river. Of the 33 streblid species known from Paraguay, only 16 have been collected in numbers >20 individuals. Eight species (*Aspidoptera falcata, A. phyllostomatis, Megistopoda aranea, M. proxima, Paratrichobius longicrus, Metelasmus pseudopterus, Strebla guajiro*, and *Trichobius joblingi*) are parasites of frugivorous phyllostomid bats and are restricted completely to eastern Paraguay. Seven species are widespread in their distribution (*Noctiliostrebla aitkeni, N. maai, Paradyschiria fusca, P. parvula, Strebla diaemi, S. wiedemanni*, and *Trichobius parasiticus*), infesting either *Desmodus rotundus* (widespread because of the influence of domestic livestock) or noctilionid fishing bats (found along riverine habitats, especially those of the Paraguay and Pilcomayo rivers) (Fig. 1). Finally, a mostly western fauna is constituted by only 1 species, *Trichobius jubatus*, exclusively a parasite of molossid bats. Of 80 individuals of this species, 75% (60) were collected west of the Paraguay River, and only 1.25% (1 specimen) was collected in an eastern department not bordering the Paraguay River. The strong east–west distributional pattern of streblid flies mirrors the conclusions of Willig et al. (2000). Although eastern and western Paraguay are comparable in bat species richness (34 vs. 30 species, respectively), the western molossid bat assemblage supports only 1 streblid species, whereas the eastern phyllostomid bat assemblage supports 19 species.

Streblid species richness is lower in southern South America than in more tropical regions (Wenzel et al., 1966; Wenzel, 1976). Although the disparity may, in part, reflect the high level of sampling effort undertaken in the latter 2 countries, the differences are clearly explained by the species richness of host bats. For example, considering the results of these 3 large, extensive surveys, 100 bat species were sampled in Panama (Handley, 1966), 132 species in Venezuela (Handley, 1976), and 54 species in Paraguay (López-González, 1998), and bat fly species numbered 66 for Panama (Wenzel et al., 1966), 115 for Venezuela (Wenzel, 1976), and 31 for Paraguay (this study). The number of bat fly species is clearly correlated with the number of host species ($r = 0.9805$, 95% confidence interval $= 0.994$–0.947, not significant because of sample size). The most influential characteristic for lower bat fly richness in southern South America is probably the lowered species richness of phyllostomid bats.

Given the lack of previous collection in Paraguay, it is remarkable that even more new species of Streblidae were not found in this survey. Recent collections in the Manu Biosphere reserve of Peru, for example, yielded <2,000 specimens of streblid bat flies, yet these collections contain 9 undescribed species of Streblidae (unpubl. data). One explanation for the lack of new streblid species in Paraguay may relate to the bat species there. Not only does Paraguay have fewer bat species compared to most South American countries (particularly those that straddle the eastern versant of the Andes), Paraguay lacks endemic bat species, and most species occurring in Paraguay are distributed widely (López-González, 2004). We predict that the number of streblid species reported in the present paper underestimates the true number occurring in Paraguay. Given the host species known from Paraguay, and assuming that each of these species is, in Paraguay, host to fly species known from those hosts at other locations, then by following the host–parasite associations listed in Wenzel (1976), we estimate that the number of species in Paraguay may be as high as 67—more than double the number of species reported here.

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